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Heliotropic leaf movement of *Sophora alopecuroides* L.: An efficient strategy to optimise photochemical performance

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Abstract

We studied the survival adaptation strategy of *Sophora alopecuroides* L. to habitat conditions in an arid desert riparian ecosystem. We examined the responses of heliotropic leaf movement to light conditions and their effects on plant photochemical performance. *S. alopecuroides* leaves did not show any observable nyctinastic movement but they presented sensitive diaheliotropic and paraheliotropic leaf movement in the forenoon and at midday. Solar radiation was a major factor inducing leaf movement, in addition, air temperature and vapour pressure deficit could also influence the heliotropic leaf movement in the afternoon. Both diaheliotropic leaf movement in the forenoon and paraheliotropic leaf movement at midday could help maintain higher photochemical efficiency and capability of light utilisation than fixed leaves. Paraheliotropic leaf movement at midday helped plants maintain a potentially higher photosynthetic capability and relieve a risk of photoinhibition. Our findings indicated the effective adaptation strategy of *S. alopecuroides* to high light, high temperature, and dry conditions in arid regions. This strategy can optimise the leaf energy balance and photochemical performance and ensure photosystem II function.

Additional key words: electron transport rate; energy dissipation; leaf tilt angle; nonphotochemical quenching; petiole angle; photosynthesis; quantum yield; trichome.

Introduction

Light is the most important ecological factor for plants (Ehleringer and Foreseth 1980, Müller *et al.* 2001). Solar irradiation not only provides the energy for photosynthesis but also induces some key physiological activities of plants, such as activation of enzymes and photoperiodic induction of the flowering response (Ehleringer and Foreseth 1980, Müller *et al.* 2001, Zhang *et al.* 2002). In arid regions, concomitant with seasonal water deficits, most plants experience a high irradiance load at midday and extreme diurnal variation of solar irradiance that induces plant photosynthesis to respond in different ways (Koller 1990, Bielenberg *et al.* 2003). Previous studies demonstrated that excessive incident irradiation might damage the photosynthetic apparatus and aggravate the energy balance in the leaf blade (Powles *et al.* 1983, Fu and Ehleringer 1992, Greer *et al.* 1993, Long *et al.* 1994, Proietti and Palliotti 1997). It is certainly a great challenge for plants in arid areas to utilise this changing irradiance and maintain optimal photosynthetic performance for photosynthesis, because plants cannot flee in response to acute stress.

Many plants have developed defensive responses and adaptation mechanisms to stress conditions, including the mechanical movement of leaves that is frequent in leguminous species (Kato *et al.* 2003, Liu *et al.* 2007). Phototropic movement of plant leaves is an effective mechanism for adapting to light conditions. Plants with this mechanism can optimise light interception and improve light conditions by adjusting the angle of their leaves in relation to incident light (Kao and Forseth 1992,

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Abbreviations: D – fraction of energy lost by thermal dissipation; ETR – electron transport rate; F_0 – minimum fluorescence yield of the dark-adapted state; F_0' – minimum fluorescence yield of the light-adapted state; F_m – maximum fluorescence yield of the dark-adapted state; F_m' – maximum fluorescence yield of the light-adapted state; F_s – steady-state fluorescence; NPQ – nonphotochemical quenching; P – fraction of energy allocated to PSII photochemistry; q_P – photochemical quenching; SEM – scanning electron microscopy; VPD – vapor pressure deficit; X – excess excitation energy; Φ_{PSII} – effective quantum yield of PSII in light-adapted leaves.

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Zhang and Gao 2001, Minoru *et al.* 2002, Herbert 2003, Zhang *et al.* 2003). Diaheliotropism and paraheliotropism are two types of heliotropism that have been observed in many studies (Smith 1984, Koller 1986, 1990; Rosa and Forseth 1995, Bielenberg *et al.* 2003, Pastenes *et al.* 2005, Arena *et al.* 2008). Some previous studies have demonstrated that plants can improve their photosynthetic performance, promote carbon assimilation and water-use efficiency, and prevent light overload and blade overheating by heliotropic leaf movement (Jurik and Akey 1994, Caldas *et al.* 1997, Bielenberg *et al.* 2003, Liu *et al.* 2003, Pastenes *et al.* 2005, Arena *et al.* 2008, Zhang *et al.* 2009, Habermann *et al.* 2011).

Sophora alopecuroides L. (Leguminosae) is a perennial herbaceous plant that is characterised by resistance to sand burial. It grows mainly in sandy soil in arid desert, grassland edges, and continental river ecosystems and it is used as a medicine. Adult individuals with odd-pinnate leaves and an oval leaf shape can grow up to 60–80 cm in height (Fig. 1). It is a dominant species of herbaceous synusia and major forage grass species in the continental river ecosystems of northwest China. Research focusing on its responses to biotope could help us better understand survival strategies of herbaceous plants in arid regions. However, previous studies on *S. alopecuroides* focused mainly on phytochemistry and phytopharmacology (Pu *et al.* 1987, Yu *et al.* 1993, Atta-ur-Rahman *et al.* 2000, Wang *et al.* 2013). Only few studies focused on a survival strategy and adaptation mechanism to environmental conditions, especially in the hyperarid desert.

Although there are a lot of reports about leaf movement of leguminous plants (Fu and Ehleringer 1989, 1992; Zhang *et al.* 2002, Bielenberg *et al.* 2003, Kato *et al.* 2003, Pastenes *et al.* 2005, Jiang *et al.* 2006, Liu *et al.* 2007), the characteristics and physiological processes of leaf movement often vary with local environmental conditions and species. The environmental factors affecting plant leaf movement are various, including soil moisture (Berg and Hsiao 1986, Berg and Heuchelin 1990), temperature (Fu and Ehleringer 1989, Kao and Forseth 1992, Yu and Berg 1994), and plant nutritional status (Fu and Ehleringer 1992, Kao and Forseth 1992).

Chlorophyll (Chl) fluorescence analytical technology is a great tool to assess energy transduction processes at the leaf level. Therefore we focused mainly on the leaf Chl fluorescence characteristics and photochemical performance of PSII in *S. alopecuroides* plants. The aim of this work was to find more on the adaptive mechanism of *S. alopecuroides* to light conditions by monitoring the characteristics of leaf movement and their photochemical performance responses. Our results could provide information to aid ecology and phytobiology research in an arid desert riparian forest ecosystem.

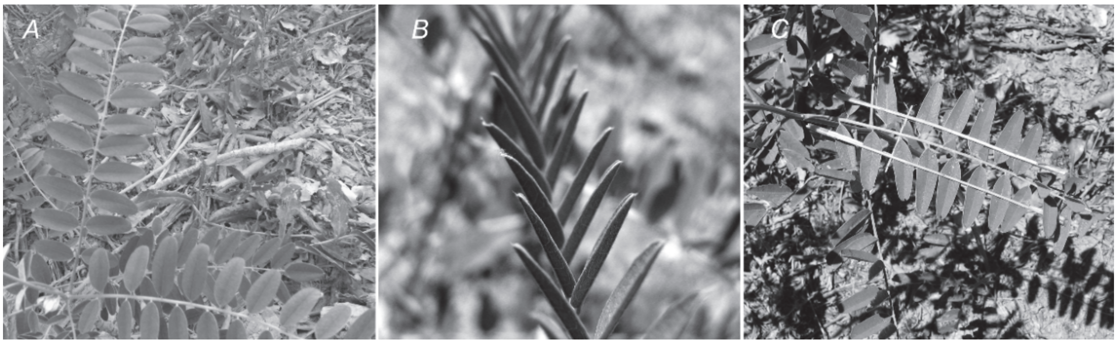

Fig. 1. Shape and position of unrestrained *Sophora alopecuroides* leaves in the forenoon (*A*), midday (*B*), and in the restrained leaves (*C*).

Materials and methods

Study area: The study area was located in the Ejina basin of Inner Mongolia, northwest China, which is the lower reaches of the second largest continental river (Heihe River) in China (between 99°30'–102°00' E and 40°20'–42°30' N). This region has an adverse natural environment characterised by scarce precipitation, high pan evaporation rate and solar irradiation, a large diurnal temperature range, and frequent dust storms. The mean annual temperature at Ejina is 8.2ºC, with a maximum daily temperature of 41ºC (July) and a minimum of –36.4ºC (January). The mean annual precipitation is only 36.6 mm (Zhang *et al.* 2011). There is a typical arid desert riparian forest ecosystem that separates the deserts of Xinjiang and Inner Mongolia and plays a barrier role in preventing dust storms from northern China. However, the natural vegetation in the region has degraded seriously due to inferior natural conditions and water shortage caused by excessive water utilisation in the middle reaches of Heihe River (Wang and Cheng 1999, Ji *et al.* 2006, Guo *et al.* 2009).

Experimental design and method: The experimental site was located in the Wulantuge ecological monitoring section that is about 18 km from Dalaihubu town, a Mongolian area in the lower reaches of Heihe River. This work randomly selected six sample plots with a 5 × 5 m area each, three under a forest canopy with shaded conditions and the others in a forest clearing with sunny conditions. Total 60 individuals were randomly selected from six plots as experimental samples that were randomly distributed in space. All of the experimental plants were adult and healthy, 50–70 cm in height. The leaf angle, Chl fluorescence, and structural characteristics of the leaf surface of randomly selected samples were surveyed from 29 July to 4 August, 2013, on clear days. In order to obtain a better understanding of the effects of leaf movement on the photochemical process of *S. alopecuroides*, we also compared leaves with heliotropic movement and restrained leaves that were fixed with sticks to prevent leaf movement (Fig. 1*C*). About 100 leaves of ten randomly selected plants were restrained on predawn. We selected the woody sticks with about 2 mm in diameter to fix a leaf in order to reduce the impact of fixture on the leaf as far as possible.

Data collection: Meteorological factors including air temperature (T), photosynthetically active radiation (PAR), relative humidity (RH), and vapour pressure deficit (VPD) during the measurements were obtained using a portable weather station (*ZCX7-JKY/WATCH DOG-2900ET*, *Spectrum Technology*, USA) that automatically measured and recorded at 10 min intervals.

Sixty healthy and fully expanded leaves from the upper canopy of 15 plants under shading and sunny conditions, respectively, were chosen to measure a leaf angle. The leaf azimuth angle, the petiole angle, and the tilt angle were measured from 06:00–20:00 h at 2-h intervals to obtain the characteristics of leaf movement. The leaf azimuth was defined as the angle of leaf apex relative to north that was measured with a magnetic compass (*DQY-1*, *Haerbin Optical Instrument Co*., China). The leaf petiole angle was defined as the angle of petiole relative to the plumb line passing the attachment region of a leaf petiole that was taken using a protractor and a fine thread with weight passing the petiole joint. The petiole angle equal to 0, 90, and 180 degrees meant that the petiole was vertically up, horizontal, and vertically down, respectively. The leaf tilt angle was defined as the angle of the leaf relative to the horizontal plane.

Chl fluorescence was measured with a portable modulated fluorometer (*Mini–PAM*, *Walz*, Germany). Red light [intensity < 0.1 μmol(photon) m^{-2} s^{-1}] was used as the measurement light, and a saturation light pulse of 0.8 s duration [intensity > 10,000 μmol(photon) m^{-2} s^{-1}] was supplied by the inner halide lamp. Chl fluorescence of 20 randomly selected unrestrained leaves and restrained leaves under sunny conditions, respectively, were measured on clear days from 08:00–14:00 h at 2-h intervals to obtain the steady state fluorescence (F_s) and maximum fluorescence yield of the light-adapted state (F_m'). The minimum fluorescence yield of the dark-adapted state (F_0) and the maximum fluorescence yield of the dark-adapted state (F_m) were measured before dawn (05:00 h) and at midday (14:00 h), and replicated 15 times. Midday values were taken after shading with a black cloth for 30 min. Rapid light curve was measured at 09:00–10:00 h and 13:00–14:00 h, and replicated six times for unrestrained and restrained leaves, respectively. The minimum fluorescence yield of the light-adapted state (F_0'), effective photochemical quantum yield of PSII in light-adapted leaves (Φ_{PSII}), electron transport rate (ETR), maximum photochemical quantum yield of PSII in dark-adapted leaves (F_v/F_m), potential activity of PSII in dark-adapted leaves (F_v/F_o), photochemical quenching coefficient (q_P), nonphotochemical quenching (NPQ), the fractions of the excitation energy absorbed by PSII allocated to PSII photochemistry (P), thermal dissipation (D), and excess excitation energy (X) were calculated using the following formulas, respectively:

$F_0' = F_0/(F_v/F_m + F_0/F_m')$ (Oxborough and Baker 1997)
$\Phi_{PSII} = (F_m' - F_s)/F_m'$ (Genty *et al.* 1989)
$ETR = \Phi_{PSII} \times PAR \times 0.5 \times 0.84$ (Schreiber 2004)
$F_v/F_m = (F_m - F_0)/F_m$
$F_v/F_o = (F_m - F_0)/F_o$ (Babani and Lichtenthaler 1996, Roháček 2002)
$q_P = (F_m' - F_s)/(F_m' - F_0')$ (Schreiber *et al.* 1986)
$NPQ = F_m/F_m' - 1$ (Bilger and Björkman 1990)
$P = F_v'/F_m' \times q_P$ (Demmig-Adams *et al.* 1996)
$D = 1 - F_v'/F_m'$
$X = F_v'/F_m' \times (1 - q_P)$

Structural characteristics of the leaf surface were assessed by scanning electron microscopy (SEM) analysis. After the fieldwork, 8–10 health and fully expanded leaves of *S. alopecuroides* from five individuals were taken and saved in formalin-acetic acid-alcohol fixative [FAA; 5 ml 38% formalin, 5 ml acetic acid , 50% alcohol (90 ml and 5 ml glycerol)]. The leaf material was washed 3 times with 0.1 M phosphoric acid cushion liquid, 10 min each time. After then, the leaves were steeped in ethanol of different concentrations and absolute tert-butyl alcohol to remove the cushion liquid and dehydration. The concentration gradients of ethanol and steeping time is 50% ethanol for 30 min, 75% for 30 min, 85% for 30 min, 95% for 30 min, then steeped with absolute alcohol and tert-butyl alcohol twice, respectively, 15 min for each.

After freeze-dried for a whole night and gold-plated, the leaf materials were used for SEM analysis (*SUPRA 55 SAPPHIRE*, *Carl Zeiss*, Germany).

Statistical analysis: Data processing, map-making, and statistical analysis were performed using *Excel 2003* (*Microsoft Corporation*, USA), *Sigmaplot 11.0* (*Systat Software Inc*., USA), and *SPSS 13.0* (*IBM SPSS* software, USA), respectively. Significant differences between randomly selected samples in various experimental groups with random design were tested with analysis of variance (*ANOVA*) and LSD multi-compare. The relationship between Φ_{PSII} and PAR was fitted by a three parameter single exponential decay function, and the relationship between NPQ, ETR, and PAR were fitted by a three parameter single exponential growth function.

Results

Environmental meteorological factors: The mean air temperature and VPD during the study reached the lowest levels before dawn, and then rapidly rose, with the increasing PAR from 06:00–12:00 h. T and VPD decreased obviously after that and maintained at a steady and high state from 12:00–18:00 h. PAR quickly rose from 06:00 h and reached the peak at 13:00 h, then quickly declined (Fig. 2). Meteorological conditions during the study were within the average ranges of this area.

Characteristics of leaf heliotropic movement: Leaf heliotropic movement in *S. alopecuroides* responded to habitat light conditions and varying PAR in different ways. The *S. alopecuroides* individuals grown under the forest canopy with shaded conditions could receive only 10–20% of the PAR compared to those grown under sunny conditions in the forest clearing, which receive mainly scattered light. The PAR reaching leaves under shaded conditions changed little from 10:00 to 18:00 h, and these leaves showed little response in the leaf angle to varying PAR (Table 1). Generally, these plants kept their leaves horizontal, with an about 90 degree petiole angle and the tilt angle changed little.

However, the leaves of the individuals under sunny conditions in the forest clearing showed sensitive heliotropic movement to daily PAR variation. When the light intensity, T, and VPD were low at dawn, the leaves of the plants in the forest clearing presented a similar horizontal angle as those individuals under the forest canopy. With the rapidly increased PAR from 08:00–11:00 h, the plants under sunny conditions showed significant diaheliotropic leaf movement, but leaves with different azimuths responded in different ways. At 08:00 h, when the incident light mainly came from the east, the leaves with an eastern, northern, and southern azimuth generally maintained a similar petiole angle, but showed a significantly increased tilt angle that made the leaves tilt to the east. The leaves with a western azimuth showed a significantly decreased petiole angle and increased tilt angle that made the leaves turn toward the east. Additionally, the two half-leaves on both sides of the midrib leaned toward one another with the midrib. With the increasing solar incident angle, at 10:00 h, the leaves with a western azimuth were close to an upright position with the continuously decreased petiole angle, and the two half-leaves leaned toward one another more than the leaves with an eastern azimuth. For the leaves with a northern and southern azimuth, the petiole angle changed little, but the tilt angle significantly increased, especially for the western half-leaf relative to the midrib. The obvious diaheliotropism of leaves was maintained until about 11:00. From 12:00–13:00 h, when the solar incident angle increased to maximum and PAR increased to more than 1,900 μmol m^{-2} s^{-1}, all of the leaves under sunny conditions presented a significantly reduced petiole angle than in the forenoon, especially the upper leaves. The opposite pinnate leaves moved toward one another, closing to an upright angle, and the two half-leaves leaned toward one another with the midrib more than ever, being close to overlapping (Fig. 1*B*). The obvious leaf paraheliotropism was maintained until about 17:00 h, and the petiole angle and tilt angle started to increase and decrease, respectively, with the declined PAR, T, and VPD. The plants started to expand their leaves, but none of the leaves moved back to a horizontal position until sunset at 20:00 h. The leaves of *S. alopecuroides* did not present obvious diaheliotropism in the afternoon and at dusk (Table 1).

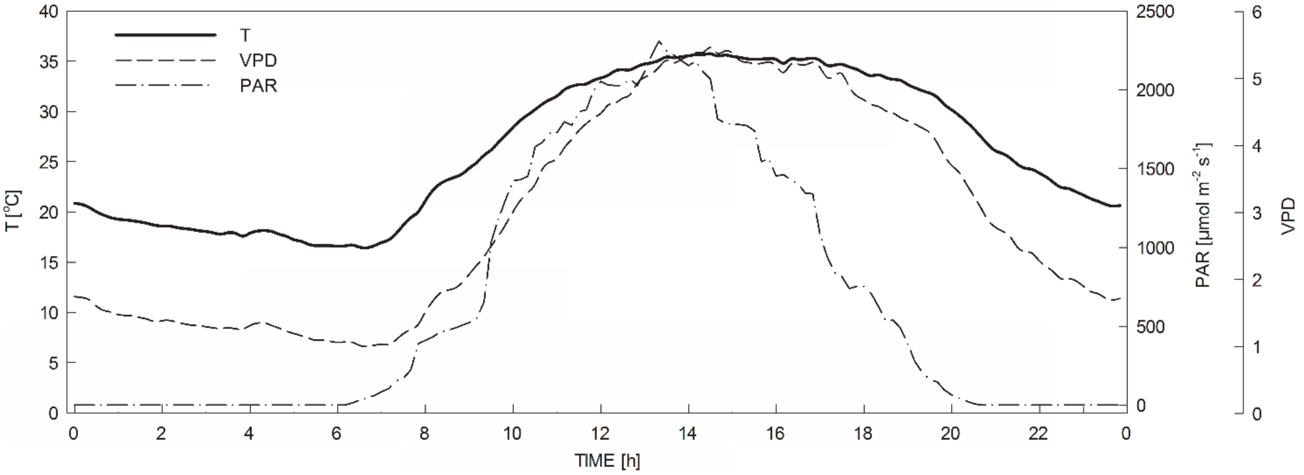

Fig. 2. Mean diurnal variation of photosynthetically active radiation (PAR), air temperature (T), and vapor pressure deficit (VPD) during the experiment.

Table 1. The diurnal variation of petiole angle, and tilt angle of *Sophora alopecuroides* L. leaves with different azimuth angle and under different light conditions. The values are mean ± standard deviation, and mean values ($n = 15$) in each column followed by a distinct *lowercase letters* are significantly different ($P<0.05$).

Measuring time [h]	Azimuth angle [°]	Shading Petiole angle [°]	Leaf tilt angle [°]	Sunny Petiole angle [°]	Leaf tilt angle [°]	PAR shaded/sunny [μmol m^{-2} s^{-1}]	T [°C]	VPD
06:00	0–20, 330–360	95.32 ± 5.40^{a}	3.26 ± 2.10^{a}	84.24 ± 5.10^{a}	3.60 ± 2.45^{a}	0.00/0.00	16.60	1.05
	70–110	98.25 ± 3.65^{a}	5.10 ± 3.20^{a}	87.21 ± 3.57^{a}	2.10 ± 1.80^{a}			
	160–200	90.56 ± 5.25^{a}	2.10 ± 2.43^{a}	91.26 ± 2.48^{a}	2.78 ± 2.23^{a}			
	250–290	92.60 ± 4.51^{a}	3.13 ± 2.25^{a}	86.46 ± 4.91^{a}	1.83 ± 1.55^{a}			
08:00	0–20, 330–360	93.25 ± 4.25^{a}	3.98 ± 2.80^{a}	82.40 ± 2.70^{a}	22.79 ± 7.65^{b}	80.50/412.00	21.14	1.51
	70–110	86.54 ± 4.20^{a}	3.28 ± 1.24^{a}	94.15 ± 3.15^{a}	15.21 ± 8.20^{b}			
	160–200	89.55 ± 2.44^{a}	2.25 ± 1.55^{a}	85.60 ± 2.84^{a}	24.63 ± 5.36^{b}			
	250–290	91.30 ± 3.12^{a}	4.69 ± 1.35^{a}	35.70 ± 12.54^{b}	20.91 ± 5.46^{b}			
10:00	0–20, 330–360	90.25 ± 2.55^{a}	3.91 ± 2.63^{a}	80.33 ± 8.25^{a}	68.25 ± 12.34^{c}	190.50/1424.75	28.45	3.01
	70–110	88.45 ± 4.12^{a}	4.83 ± 1.52^{a}	82.46 ± 6.10^{a}	25.31 ± 7.35^{c}			
	160–200	89.10 ± 3.21^{a}	4.38 ± 2.92^{a}	79.16 ± 10.45^{a}	72.18 ± 11.56^{c}			
	250–290	87.22 ± 3.26^{a}	3.52 ± 3.40^{a}	10.40 ± 8.61^{c}	22.45 ± 10.72^{b}			
12:00	0–20, 330–360	85.55 ± 4.36^{a}	3.89 ± 2.95^{a}	45.55 ± 8.25^{b}	36.15 ± 10.25^{d}	205.54/1951.75	33.33	4.47
	70–110	88.33 ± 6.21^{a}	3.77 ± 1.92^{a}	40.73 ± 6.25^{b}	37.17 ± 12.34^{d}			
	160–200	90.26 ± 2.56^{a}	3.85 ± 2.55^{a}	52.25 ± 7.20^{b}	42.43 ± 8.23^{d}			
	250–290	86.15 ± 2.15^{a}	4.56 ± 2.34^{a}	38.41 ± 12.31^{b}	37.70 ± 7.68^{d}			
14:00	0–20, 330–360	89.10 ± 3.14^{a}	3.77 ± 1.62^{a}	10.25 ± 5.23^{c}	36.96 ± 7.35^{d}	220.47/2154.13	35.53	5.32
	70–110	88.41 ± 4.11^{a}	4.71 ± 2.15^{a}	12.40 ± 4.33^{c}	31.80 ± 6.20^{d}			
	160–200	85.80 ± 2.75^{a}	1.91 ± 1.15^{a}	11.55 ± 6.21^{c}	39.57 ± 5.15^{d}			
	250–290	88.90 ± 3.65^{a}	3.72 ± 1.92^{a}	8.77 ± 6.80^{c}	35.84 ± 5.80^{d}			
16:00	0–20, 330–360	89.20 ± 2.57^{a}	3.26 ± 1.91^{a}	12.45 ± 7.80^{c}	35.12 ± 7.35^{d}	217.05/1427.88	35.23	5.20
	70–110	90.15 ± 5.16^{a}	4.56 ± 3.44^{a}	15.70 ± 8.15^{c}	40.50 ± 6.52^{d}			
	160–200	86.29 ± 4.66^{a}	2.93 ± 1.50^{a}	13.50 ± 7.23^{c}	38.80 ± 10.20^{d}			
	250–290	87.55 ± 5.41^{a}	3.47 ± 2.26^{a}	13.33 ± 8.50^{c}	40.76 ± 7.15^{d}			
18:00	0–20, 330–360	90.22 ± 2.44^{a}	3.29 ± 1.47^{a}	45.53 ± 8.53^{b}	30.20 ± 4.26^{d}	132.35/672.63	33.80	4.67
	70–110	87.33 ± 6.11^{a}	3.72 ± 1.98^{a}	55.25 ± 10.45^{b}	27.29 ± 7.35^{c}			
	160–200	85.60 ± 2.10^{a}	4.44 ± 2.^{74a}	40.12 ± 6.51^{b}	35.91 ± 6.25^{d}			
	250–290	88.45 ± 4.20^{a}	4.27 ± 1.06^{a}	60.43 ± 7.40^{d}	25.89 ± 7.24^{b}			
20:00	0–20, 330–360	90.15 ± 2.58^{a}	3.15 ± 1.77^{a}	70.23 ± 12.10^{d}	15.77 ± 5.62^{b}	10.65/63.88	30.16	3.69
	70–110	89.87 ± 6.10^{a}	2.84 ± 2.71^{a}	52.43 ± 8.22^{b}	16.49 ± 8.20^{b}			
	160–200	91.05 ± 3.80^{a}	3.87 ± 1.62^{a}	73.05 ± 9.23^{d}	14.74 ± 10.27^{e}			
	250–290	93.87 ± 2.48^{a}	2.96 ± 1.46^{a}	75.10 ± 11.20^{d}	15.29 ± 6.10^{c}			

Structural characteristics of the leaf surface: According to SEM analysis, *S. alopecuroides* presented a trichome indumentum with the same direction on both surfaces of the leaf. However, there was a significant difference in trichome density and trichome length between the adaxial and abaxial leaf surfaces. The trichome density and length on the adaxial surface were 67.06 ± 7.87 mm^{-2} and 378.11 ± 18.26 μm, respectively, which was significantly lower than those on the abaxial surface, *i.e.*, 119.21 ± 13.48 mm^{-2} and 427.25 ± 20.29 μm, respectively (Fig. 3).

Effects of heliotropic leaf movement on photochemical performance: The leaves with heliotropic movement could keep sounder predawn values of F_v/F_m (0.81) compared with the restrained leaves. With the increasing PAR, T, and VPD from predawn to midday, the F_v/F_m and F_v/F_0 of unrestrained leaves significantly declined. A similar trend was also found in restrained leaves, but the downtrend of F_v/F_m and F_v/F_0 was more significant than in unrestrained leaves. The restrained leaves had significantly lower F_v/F_m and F_v/F_0 values than the unrestrained leaves both before dawn and at midday (Table 2).

The leaves with diaheliotropic movement in the forenoon presented higher Φ_{PSII}, ETR, and NPQ that increased by 3.9, 10.7, and 6.6% on average, respectively, compared with the restrained leaves (Fig. 4). The difference was significant when the light intensities reaching the leaf were higher than 1,000 μmol m^{-2} s^{-1}. At midday, the leaves with paraheliotropic movement also showed significantly higher Φ_{PSII}, ETR, and NPQ than the restrained leaves when light intensities reaching the leaf were higher than 1,000 μmol m^{-2} s^{-1}. The differences between the unrestrained and

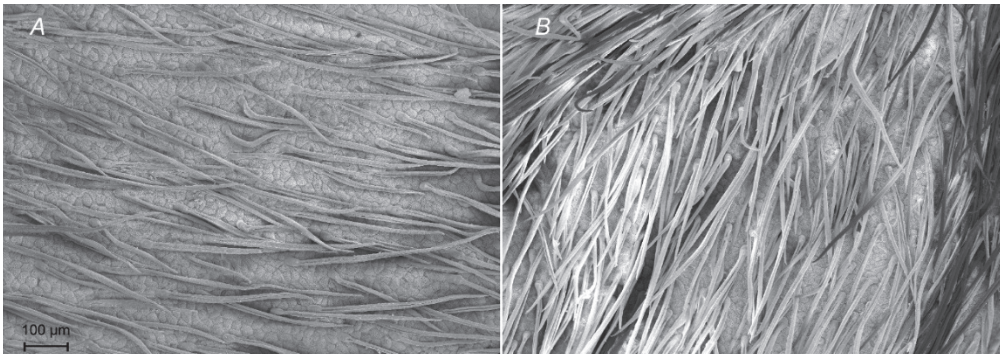

Fig. 3. The scanning electron microscopy of surface structural characteristics of *Sophora alopecuroides* leaf; adaxial (*A*) and abaxial surface (*B*).

Table 2. The predawn and midday values of maximum quantum yield of PSII in the dark-adapted leaves (F_v/F_m) and potential activity of PSII (F_v/F_o) in unrestrained and restrained leaves of *Sophora alopecuroides* L. under sunny conditions. The values are mean ± standard deviation, and mean values (n = 15) in each column followed by distinct *lowercase letters* are significantly different (P<0.05).

	Predawn values		Midday values	
	F_v/F_m	F_v/F_o	F_v/F_m	F_v/F_o
Unrestrained leaves	0.81 ± 0.01^a	4.40 ± 0.12^a	0.74 ± 0.02^b	2.91 ± 0.09^b
Restrained leaves	0.75 ± 0.03^b	3.10 ± 0.13^b	0.63 ± 0.03^c	1.82 ± 0.12^c

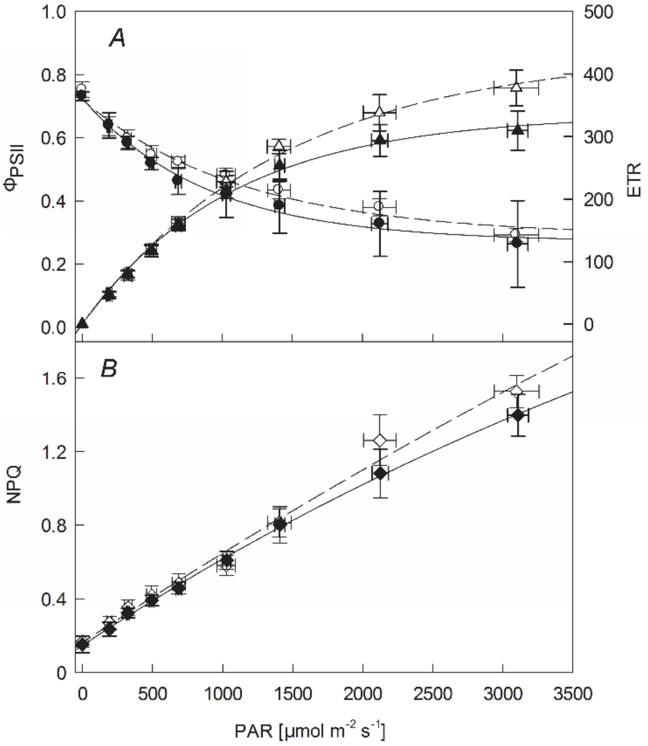

Fig. 4. The effective quantum yield of PSII in light-adapted leaves (Φ_{PSII}), electron transport rate (ETR) (*A*), and nonphotochemical quenching (NPQ) (*B*) of diaheliotropic leaves and restrained leaves under sunny conditions in the forenoon (9:00–10:00 h). The error bars in rapid light curves are SD of six replicates. (n = 6).

restrained leaves were greater in midday than in the forenoon, especially, under high light intensity (Fig. 5). Compared to the forenoon, the plants showed lower Φ_{PSII} and ETR and higher NPQ at midday. The variation trend of ETR showed that the heliotropic leaves reached higher light saturation point than the restrained leaves, both in the forenoon and midday.

When PAR and T were relatively low in the forenoon, the leaves with diaheliotropic movement could intercept more light and showed higher leaf temperature compared to the restrained leaves (Table 3). However, when PAR and T reached the maximum at midday, the leaves with paraheliotropism movement showed lower leaf temperature and significantly lower light interception compared to the restrained leaves. Whether due to diaheliotropic movement in the forenoon or paraheliotropic movement

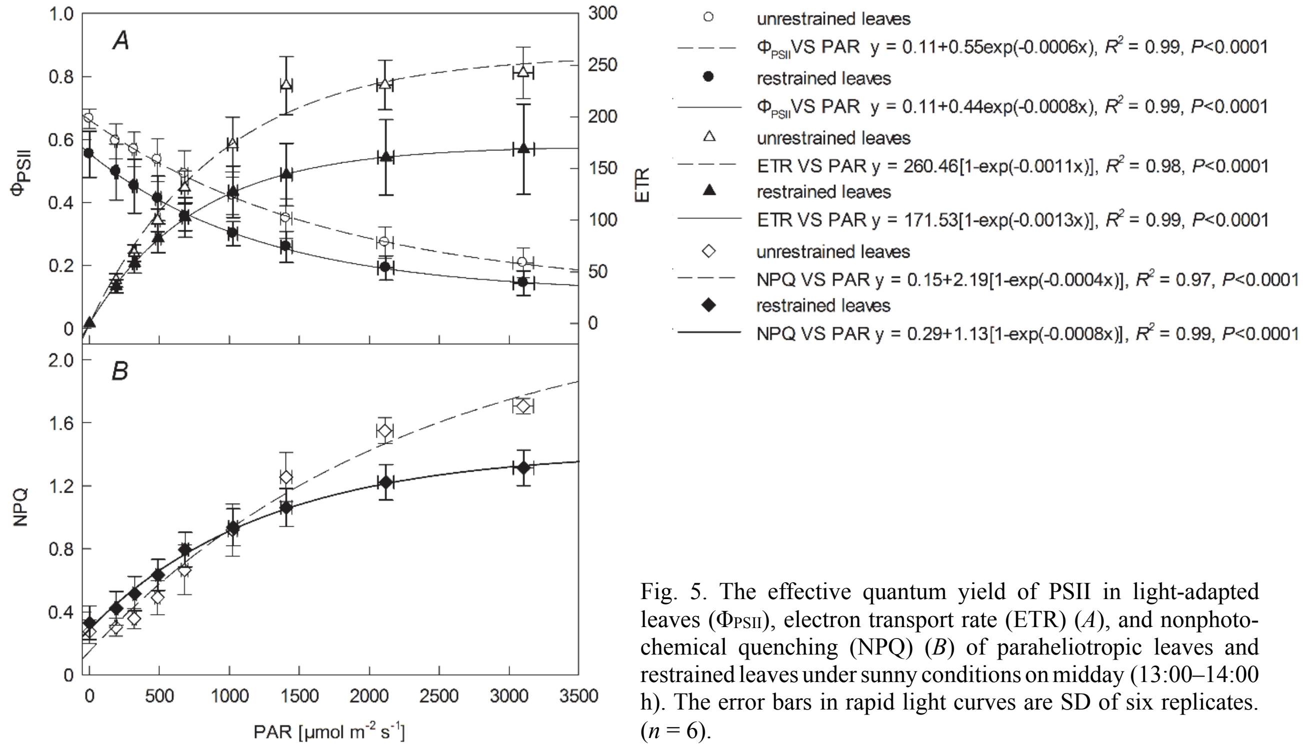

Fig. 5. The effective quantum yield of PSII in light-adapted leaves (Φ_{PSII}), electron transport rate (ETR) (*A*), and nonphotochemical quenching (NPQ) (*B*) of paraheliotropic leaves and restrained leaves under sunny conditions on midday (13:00–14:00 h). The error bars in rapid light curves are SD of six replicates. (n = 6).

Table 3. Comparisons of fractions of energy allocated to PSII photochemistry (P), fractions of energy lost by thermal dissipation (D), and excess excitation energy (X) of unrestrained and restrained leaves of *Sophora alopecuroides* L. in the forenoon and at midday. The values are mean ± standard deviation, and mean values (n = 15) in each column followed by distinct *lowercase letters* are significantly different ($P<0.05$).

Time [h]	PAR/T [μmol m^{-2} s^{-1}]/[ºC]	Treatments	P	D	X	PAR interception by leaf [μmol m^{-2} s^{-1}]	Leaf temperature [ºC]
Forenoon (9:00–10:00)	1,100–1,300/ 26.90–29.10	unrestrained	0.53 ± 0.04^a	0.28 ± 0.02^a	0.19 ± 0.03^a	1080.30 ± 107.25^a	29.06 ± 0.13^a
		restrained	0.51 ± 0.05^a	0.27 ± 0.02^a	0.21 ± 0.03^a	735.52 ± 84.24^b	27.20 ± 0.12^a
Midday (13:00–14:00)	2,200–2,500/ 35.10–39.50	unrestrained	0.45 ± 0.05^a	0.38 ± 0.02^a	0.17 ± 0.03^a	790.65 ± 72.33^a	36.80 ± 0.29^a
		restrained	0.35 ± 0.05^b	0.42 ± 0.02^b	0.23 ± 0.03^b	1859.70 ± 95.62^b	37.73 ± 0.19^a

at midday, the unrestrained leaves always showed a higher P and lower X compared with the restrained leaves. There was little difference in D in the forenoon between the unrestrained and restrained leaves, but the value was significantly higher in the restrained leaves at midday than that in the unstrained leaves (Table 3).

Discussion

We revealed that *S. alopecuroides* leaves could sensitively respond to light conditions and present amazing heliotropic movements with varying PAR from forenoon to midday. Nyctinasty is widely observed in leguminous plants (Ueda and Nakamura 2007), but *S. alopecuroides* leaves did not show evident nyctinastic movement in our study. The leaf angle of *S. alopecuroides* under different light conditions changed little at dawn. The leaf of *S. alopecuroides* under shaded condition did not move like as those under sunny conditions which demonstrated that heliotropic leaf movement of *S. alopecuroides* might be induced by solar radiation directly on the leaf. Zhang *et al.* (2002) also obtained similar results on leaf movement characteristics by using another leguminous species.

S. alopecuroides in the forest clearing did not sensitively change the leaf angle after midday when PAR significantly declined. The plants maintained leaves of paraheliotropic positions similarly as on midday until 17:00 h. After that, the plants gradually expanded their leaves with decreasing T and VPD. These variations indicated that air temperature and degree of drought may play an important role in the induction of leaf movement in the afternoon, in addition to solar radiation. Some studies based on other leguminous species also proved that T and VPD could induce and exert an influence on leaf movement (Fu and Ehleringer 1989, Kao and Forseth 1992, Yu and Berg 1994, Arena *et al.* 2008). *S. alopecuroides* preferred maintaining paraheliotropism in the afternoon when PAR significantly declined but T and VPD were relatively high. This may be related to the water utilisation strategy of plants, because paraheliotropism can contribute to reduced transpiration (Bielenberg *et al.* 2003, Pastenes *et al.* 2005, Liu *et al.* 2007). Optimising water utilisation is a major adaptive strategy to the tough environment for plants growth in arid regions.

Based on our results, diaheliotropic leaves in the forenoon maintained higher photochemical performance, higher light saturation point, and light utilisation than the restrained leaves that can be showed by higher ETR, Φ_{PSII}, F_v/F_m, rapid light curves, higher P, and lower X, respectively. The leaves with diaheliotropic movement could intercept more light (Table 3), and presented a trend of relatively higher leaf temperature than that of the restrained leaves. This could contribute to higher photochemical performance and better capability to use high-intensity light. Similar conclusions have been also reached in some previous studies (Ehleringer and Forseth 1980, Jurik and Akey 1994, Zhang *et al.* 2009). The plants benefited from diaheliotropic movement to increase the potential photosynthesis as more light energy became available. The increased light energy load tended to increase leaf temperature, which might have helped to activate enzymes of the Calvin cycle and improve photosynthesis during the early morning when air temperature was relatively low. Ehleringer and Forseth (1980) have indicated that diaheliotropic movement may impact the energy and heat load of leaves. In this work, diaheliotropic leaf movement significantly increased light interception; however, it did not impose negative effects on energy load of leaves but reduced the X in PSII and increased the light energy utilisation. This attributed to an increase of photochemical efficiency and xanthophyll cycle pool size that led diaheliotropic leaves to show higher P and NPQ and lower X than the restrained leaves. The increased transpiration and NPQ as demonstrated by Zhang *et al.* (2009) also contribute to the remission of heat load on leaves that can help maintain a suitable leaf temperature. Additionally, the trichome indumentum with the same direction on the leaf surfaces also contributes to improvement of light energy supply when leaves present diaheliotropism.

When PAR, T, and VPD were high at midday, *S. alopecuroides* presented under sunny conditions obvious paraheliotropic leaf movement and reduced photochemical performance, as demonstrated by the reduction of F_v/F_m, F_v/F_0, ETR, and Φ_{PSII}. These reductions of physiological performance are not only physiological responses of plants to an adverse environment; they also represent a survival strategy. A lot of plants growing in arid desert generally present a decreased physiological performance, such as photosynthetic midday depression in *Populus euphratica*, to respond the adverse environmental conditions. However, physiological responses alone are generally not enough to deal with the tough conditions at midday in arid regions; paraheliotropic leaf movement is the effective strategy used by many plants to cope with the adverse conditions at midday (Bielenberg *et al.* 2003, Pastenes *et al.* 2005, Arena *et al.* 2008).

The leaves with paraheliotropic movement exhibited significantly higher photochemical performance that was demonstrated as significantly higher ETR, Φ_{PSII}, NPQ, F_v/F_m, F_v/F_0, and P compared with the restrained leaves. Due to paraheliotropic movement, leaves could significantly minimise the light interception at midday than the restrained leaves (Table 3), which led to a relatively lower leaf temperature than that in the restrained leaves. This contributed to the alleviation of negative effects of high PAR, T, and VPD on the plants. The significantly higher F_v/F_m and F_v/F_0 indicated that inhibition of photochemical performance of PSII was lesser in paraheliotropic leaves than that of the restrained leaves. Moreover, the leaves with heliotropic movement could effectively restore the photochemical performance and photosystem function during the night, as demonstrated by high predawn values of F_v/F_m. This suggests the reduction of photochemical performance at midday in paraheliotropic leaves as the photoprotection (Siam *et al.* 2008). The photoinhibition damage actually occurred in the restrained leaves and the repair capability of the photosystems in those leaves was obviously affected. It was proved by significantly declined photochemical efficiency in the restrained leaves that could not fully recover through the night. The photoinhibition in the restrained leaves also impacted the energy dissipation under high light intensity. This was demonstrated by the lower NPQ than that in the leaves with paraheliotropic movement. The restrained leaves intercepted more light at midday, however, they presented significantly lower P than the leaves with paraheliotropic movement. The D in the restrained leaves on midday significantly increased, however, that was not enough to relieve the increasing excess energy. This resulted in a significantly increased excess energy (X) at noon that might impact the repair of PSII (Takahashi and Murata 2006, 2008; Murata 2007). Although lower light interception in paraheliotropic leaves may reduce the size of the xanthophyll cycle pool and the fraction of excitation energy dissipated as heat (Barker and Adams 1997), the paraheliotropic leaves at midday could minimise xanthophyll cycle activity and reduce the cost of xanthophyll biosynthesis. Therefore, more photosynthates and substances might be used in photosynthesis and other physiological regulatory processes, and photosynthetic activity could be enhanced (Liu *et al.* 2003). Additionally, due to lower light supply and the proportion of inactivated PSII reaction centres, the paraheliotropic leaves can allocate more light energy to the photochemical processes. Therefore, the leaves can maintain higher photochemical performance and a lower fraction of X.

At midday, the paraheliotropic leaves tended to exhibit slightly lower leaf temperature than the restrained leaves. Previous study indicated that even a small decrease in leaf temperature can allow leaves to survive for a long time in an adverse environment (Richards *et al.* 1986). In this study, most paraheliotropic leaves were illuminated on both sides, and even greater proportion of light energy was intercepted by the abaxial leaf surface at midday. Compared to the adaxial side, the denser and longer trichomes on the abaxial leaf surface may contribute to the lower leaf temperature and light energy load. Habermann *et al.* (2008, 2011) using *Styrax camporum* also showed that paraheliotropic leaves illuminated on both sides had a lower leaf temperature and higher stomatal conductance. It has been also demonstrated that higher photochemical performance could make heliotropic leaves maintain higher stomatal conductance and CO_2 assimilation rate compared to the restrained leaves (Arena *et al.* 2008). This indicated that both the special leaf structure and leaf paraheliotropic movement provided an effectively adaptive strategy to high light at midday for *S. alopecuroides*.

Conclusion: *S. alopecuroides* leaves did not show observable nyctinastic movement. The plants under sunny conditions showed sensitive heliotropic leaf movement with varying PAR, but those individuals under a forest canopy with shaded conditions exhibited no significant leaf movement. The leaves of *S. alopecuroides* under sunny conditions presented diaheliotropism in the forenoon and paraheliotropism at midday by changing the petiole angle and leaf tilt angle. Solar radiation reaching the leaf might be the major factor inducing leaf movement, while T and VPD played an important role, especially in the afternoon.

Both the diaheliotropic leaf movement in the forenoon and the paraheliotropic leaf movement at midday could optimise the energy balance in the leaf, and help maintain an optimal leaf temperature and photochemical performance. Paraheliotropic leaf movement at midday could maintain a potentially higher photosynthetic capability and relieve the risk of photoinhibition. The heliotropic leaf movement and the leaf structure of *S. alopecuroides* could help better adapt to the high PAR, T, and VPD conditions in arid regions, and maintain photosystem functioning.

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