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ORIGINAL PAPER

Leaf movement and photosynthetic plasticity of black locust (*Robinia pseudoacacia*) alleviate stress under different light and water conditions

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Abstract Leaf morphological, physiological and biochemical characteristics of *Robinia pseudoacacia* L. seedlings were studied under different stress conditions. The plants were subjected to drought and shade stress for one month. Leaf inclination, chlorophyll fluorescence and chlorophyll content were measured at the first day (short-term stress) and at the end of the stress period (long-term stress) and in the recovery period. Leaf inclination was affected mainly by light; a low level of irradiance caused leaves to be arranged horizontally. Diurnal rhythmicity was lost after the long-term stress, but resumed, in part, in the recovery period. Drought stress caused leaves to tilt more obviously and decreased damage to the photosystem. Sun avoiding movement in a single leaf and sun tracking movement in the whole plant coexisted. Significant physiological changes occurred under different conditions of light. Increased energy dissipation and light capture were the main responses to high and low level of irradiance, respectively, and these were reflected by changes of chlorophyll fluorescence and chlorophyll content. Phenotypic plasticity in the leaflet enhanced the protective response to stress. These adaptive mechanisms may explain better survival of *R. pseudoacacia* seedlings in the understory, especially during the drought periods, and made it to be the preponderant reforestation species in Shandong Province of China.

Keywords Black locust · Chlorophyll fluorescence · Drought · Leaf inclination · Light acclimation · Photosynthetic plasticity

Abbreviations

Chl	Chlorophyll
ETR	Electron transport rate
F_0 and Fm	Initial and maximal fluorescence in the dark
Fs and Fm′	Steady-state and maximal fluorescence in the light
Fv/Fm	Maximal quantum yield
FC	Field capacity
LAI	Leaf area index
NPQ	Non-photochemical quenching
PAR	Photosynthetically active radiation
PFD	Photon flux density
PS II	Photosystem II
qP	Photochemical quenching
RLCs	Rapid light curves
SLA	Specific leaf area
Yield or Φ_{PSII}	Effective quantum yield

Introduction

Light is essential for photosynthesis, but strong irradiance can damage the photosystem II (PS II) reaction center, and weak irradiance may not be enough for photosynthesis. The amount of sunlight reaching the forest floor under the canopy and in gaps varies acutely, and it is a great challenge for seedlings to utilize the changing irradiance and to adapt to a long-term low level of sunlight, which is disadvantageous for forest regeneration (Leakey et al. 2003).

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Water is another important factor that influences the growth of plants and the spatial distribution of species in their appropriate habitats (Lemoine et al. 2001). Water is the primary factor limiting the growth of vegetation, and plant growth varies widely according to the amount of water available (Fernández et al. 2000; Thomas and Gausling 2000). When water is limited, drought tolerance is a prerequisite mechanism for the survival and growth of seedlings.

Unlike most animals, plants are sessile and cannot flee in response to acute stress. Many plants have developed defensive responses to stress conditions, including the mechanical movement of leaves, frequent in leguminous species (Kato et al. 2003; Liu et al. 2007). Diaheliotrophic (i.e., sun tracking) and parahelitrophic (i.e., sun avoiding) movements are two movement types allowing adaptation (Gamon and Pearcy 1989; Smith and Ullberg 1989). As well as the mechanical response, plants have developed physiological mechanisms that decrease the effects of stress. Stomatal closure that minimizes transpiration in drought, enhancement of light-harvesting pigments in shade and increased size of the xanthophyll cycle pool in high light are the main mechanisms induced to resist the stress (Guo et al. 2003; Niinemets et al. 2003). Phenotypic plasticity in the whole plant is another adaptive mechanism that aids drought tolerance and light acclimation (Wang et al. 2006; Guo et al. 2007). Alteration of foliar physiognomy is an important part of plasticity, as the leaf is a vital organ in photosynthesis (Mediavilla and Escudero 2003; Galmés et al. 2007).

The black locust tree *Robinia pseudoacacia* L. is a nitrogen-fixing, leguminous deciduous species. It was introduced to Shandong Province of China at the end of nineteenth century (Wang and Zhou 2000) and was widely planted for its adaptability and aggressive growth. It has an important role in vegetation restoration and ecosystem regeneration. Limestone, which is easy to dissolve and penetrate, is the representative mountain component in Shandong Province. Anthropization have perturbed the vegetation in this area and drought occurs frequently (Wang and Zhou 2000). In addition, the stand is simplex due to artificial planting and allelopathy. It is easy to beget diseases to mature trees and lead to forest gaps. Fluctuating light conditions have effects on the growth of seedlings.

Seedlings development is the most critical periods in the life-cycle of trees, and the morphological and physiological leaf attributes during these periods are key factors in tree species adaptation. It is very important to reveal the adaptive mechanisms used by *R. pseudoacacia* in response to diverse light and water conditions, which may provide useful information for plant biologists and may be important in guiding the maintenance and restoration of vegetation.

The objective of this study was to investigate (1) how leaves move under different conditions of light and water and (2) whether adaptive mechanisms can protect the leaves of *R. pseudoacacia* against shade and water stress.

Materials and methods

Study site

The study was conducted at the Fanggan Research Station of Shandong University, Shandong Province, China (36°26′N, 117°27′E). The site is characterized by a warm temperate monsoon climate, with a mean annual temperature of 13 ± 1°C, and an average annual precipitation of ca. 600–850 mm, most of which falls during summer. The soil type is a yellow cinnamon soil, and the parent material is limestone (Zhang et al. 2006). Mixed forests of the warm temperature zone are the predominant vegetation in this area. The tree species are dominated by three evergreen coniferous species, *Pinus densiflora* Sieb. et Zucc., *Pinus thunbergii* Parl. and *Platycladus orientalis* (L.) Franco, and two deciduous broadleaf species, *Robinia pseudoacacia* L. and *Quercus acutissima* Carr. The canopy had a dominant layer 14 m height. The leaf area index (LAI) was 5.12 when the trees were flourishing in August. *Vitex negundo* L. var. *heterophylla* (Franch.) Rehd. and *Zizyphus jujuba* Mill. var. *spinosa* (Bge.) Hu ex H. F. Chow are abundant in the shrub layer of the understory.

Plant materials

Seeds of *R. pseudoacacia* were collected on a hill 2 km away from the research station in March 2007 in a stand of *R. pseudoacacia*. Seeds were collected from mature trees and transported to the laboratory. They were sterilized by soaking in 3% H_2O_2 for 30 min and then soaked in distilled water for 24 h to stimulate germination. Germination occurred after about 3 days in the growth chamber with cycles of 12 h light at 28°C/12 h dark at 23°C. The relative humidity was about 70% and the photon flux density (PFD) was about 300 μmol m^{-2} s^{-1}. After the radicles reached 20 mm in length, the seedlings were transplanted to plastic pots (9 l volume, 32 × 29 cm, height × diameter), containing a 64:22:14 (v/v/v) mixture of humic soil, sand and loam. Its saturated water content was 36% by mass, the largest volumetric water content was 28% and the porosity was 72%. The pH was 4.4, and the major chemical components included 88.4 g organic matter, 3.7 g total nitrogen and 42.3 mg available phosphorus per kilogram. All of the pots were irrigated regularly and subjected to weed control before the beginning of the experiment.

Experimental design

The experiment was carried out during July and August 2007. The seedlings grown for 4 months were submitted to water and shade stress (ten plants per stress type). Water was withheld from the drought groups until the soil moisture reached 30–40% of the field capacity (FC), whilst the well-watered groups received daily irrigation to maintain the soil water content between 70 and 80% of the FC. All of the pots were moved into the rainout shelter in order to avoid the disturbance of precipitations when it was rainy. The soil water content was controlled by gravimetric probe and the pots were weighed daily to keep the two different water levels. Supplement of lost water via transpiration and evaporation was added evenly by top watering.

The shade–stress treatment was conducted in shade shelters covered by woven black nylon nets. The frame of the shelter was 5.0 × 2.5 × 3.0 m (length × width × height) and built replicated to avoid pseudoreplication. The microclimate was measured hourly using micro-quantum-sensor and temperature-sensor of Mini-PAM (Walz GmbH, Effeltrich, Germany) during the leaf inclination measurements. The average photosynthetically active radiation (PAR) measured from 07:00 to 16:00 (local time) was 544 ± 71 and 56 ± 6.7 μmol m^{-2} s^{-1} in the open field and in the shade shelter, respectively. The light transmission ratio was 10% under the stress condition compared to the control. There was no significant difference in the air temperature between the sunlit (31.1 ± 0.50°C) and shade (31.8 ± 0.53°C) conditions as determined by Student's *t* test ($P = 0.344$).

Pots were divided into four groups: (1) well-watered and sunlight; (2) well-watered and shade; (3) drought and sunlight; and (4) drought and shade. When the fixed soil moisture level was attained in the drought treatments, the shade-stressed pots were moved into the shade shelters in an evening. Leaf inclination was measured the next day and this was considered the short-term stress. The treatments were then maintained for a month (long-term stress) and measurements included leaf inclination, chlorophyll fluorescence and chlorophyll content were taken on the last day of the stress. Then the seedlings were re-watered and taken to the open field in that evening. Leaf inclination and chlorophyll fluorescence were determined on the next day (the recovery period). The orientations of each pot were fixed throughout the experiment.

Leaf inclination measurements

Forty mature leaves from eight petioles of each treatment were taken to determine leaf inclination according to Jiang et al. (2006). The uppermost mature leaves were chosen because they were able to orientate freely and were not subject to self-shading. The midrib angle and petiole angle were measured with a vertical clinometer (Haerbin Optical Instrument Co., Haerbin, China). The leaf angle was defined as 90° when the lamina or petiole was held horizontally, <90° when the leaflet or petiole was tilted upwards, and >90° when the leaf or petiole was drooping. The leaf azimuth was measured with a magnetic compass (Saura Keiki Seisakusho Co., Tokyo, Japan). Measurements of diurnal changes were carried out at 07:00 a.m., 10:00 a.m., 1:00 p.m. and 4:00 p.m.

Chlorophyll fluorescence measurements

Chlorophyll fluorescence measurements were performed using a pulse-modulated fluorimeter (Mini-PAM, Walz GmbH, Effeltrich, Germany). For each treatment, eight measurements were made on four seedlings. Leaves were dark adapted for 30 min before measurements. The background fluorescence signal (F_0) was excitated by a short burst of measuring light. Then, a saturating flash (about 8,000 μmol m^{-2} s^{-1} for 0.8 s duration) was applied to estimate the maximal fluorescence (Fm). The maximal quantum yield of PSII (Fv/Fm) was calculated as $(Fm - F_0)/Fm$ (Schreiber et al. 1994). Rapid light curves (RLCs) were generated using an automatic RLC program. Eight steps of active light from ca. 80 to 1,800 μmol m^{-2} s^{-1} were applied and each irradiation step lasted for 10 s, and ended with a saturating pulse (White and Critchley 1999). The electron transport rate (ETR) was determined as $\Phi_{PSII} \times PAR \times 0.5 \times 0.84$, where Φ_{PSII} $[(Fm'-Fs)/Fm']$ was the effective quantum yield in the light, 0.5 was a factor assuming an equal distribution of absorbed photons between PS II and PS I, and 0.84 was the assumed leaf absorption coefficient (Genty et al. 1989). The photochemical quenching $[qP = (Fm'-Fs)/(Fm'-F_0)]$ and non-photochemical quenching $[NPQ = (Fm-Fm')/Fm']$ were calculated according to Schreiber et al. (1986). After the RLCs measurements, the leaves were kept in the leaf clips for nearly 20 min dark adaptation. The light–dark relaxation kinetics (RLCs + recovery routine) was analyzed at the duration of 10, 30 s, 1, 2, 5 and 10 min to estimate the recovery of leaves after light exposure (Ralph and Gademann 2005).

Chlorophyll analysis

Four seedlings per treatment were chosen to determine leaf chlorophyll content. Ten leaf disks of each plant were removed with a cork-borer 1 cm in diameter and 20 ml ethanol (95%, v/v) in a labeled vial was used to abstract chlorophyll. The samples were kept in the dark for 24 h before chlorophyll analysis when the leaf surfaces were completely white. The absorption of the supernatant liquid was measured spectrophotometrically at the wavelengths of 665 and 649 nm for calculating the concentrations of

Table 1 The data of four-way ANOVA of the interactive effects of time (*T*), light (*L*), water (*W*) and leaf azimuth angle (*A*) on leaf midrib angle during stress and recovery periods

Factor	*df*	Short-term stress		Long-term stress		Recovery	
		F	*P*	*F*	*P*	*F*	*P*
Time (*T*)	3	72.79	<0.001	42.94	<0.001	165.95	<0.001
Light (*L*)	1	1816.19	<0.001	1708.25	<0.001	233.68	<0.001
Water (*W*)	1	65.46	<0.001	219.94	<0.001	140.92	<0.001
Azimuth (*A*)	3	1.76	0.153	16.37	<0.001	30.87	<0.001
$T \times L$	3	14.83	<0.001	18.72	<0.001	47.74	<0.001
$T \times W$	3	7.63	<0.001	2.5	0.059	13.63	<0.001
$L \times W$	1	0.38	0.539	54.55	<0.001	233.93	<0.001
$T \times A$	9	5.21	<0.001	9.8	<0.001	8.57	<0.001
$L \times A$	3	4.48	0.004	3.19	0.023	10.4	<0.001
$W \times A$	3	4.16	0.006	5.76	0.001	1.89	0.131
$T \times L \times W$	3	2.89	0.035	0.73	0.533	1.49	0.217
$T \times L \times A$	9	1.29	0.24	2.93	0.002	3.2	0.001
$T \times W \times A$	9	0.42	0.924	0.96	0.469	1.12	0.344
$L \times W \times A$	3	0.47	0.703	2.79	0.04	3.76	0.011
$T \times L \times W \times A$	9	1.08	0.376	0.75	0.663	1.4	0.183

$T \times L$ indicates the interactive effect between time and light. The rest of the abbreviations are the similar meanings. The effects are significant at the level of $P < 0.05$

chlorophyll *a* (Chl*a*) and chlorophyll *b* (Chl*b*) as described by Lichtenthaler and Wellburn (1983). Another ten leaves per plant were used to determine the specific leaf area (SLA). Leaf areas were measured with CI-203 laser area meter (CID Inc., Washington, USA). Leaf dry mass was measured after oven drying at 80°C for 48 h.

Statistical analysis

The measurement data were submitted to analysis of variance (ANOVA) and the means were compared by Duncan's multiple range test. The data at the end of the light steps were used for fluorescence measurements. The interactive effects of time, light, water and leaf orientation on leaf inclination were tested by four-way ANOVA. Leaf orientation was divided into four directions, according to the leaf azimuth angles, as follows: angles of 45°–135° were defined as facing the East; and South, West and North were defined by adding 90° in that order. All statistical analysis was done with the SPSS 13.0 software package (SPSS Inc., Chicago, USA). Plots were drawn using the Origin 7.5 software (OriginLab Co., Massachusetts, USA).

Results

Leaf movement in response to stress factors

A summary of the four-way ANOVA is given in Table 1 for the interactive effects of time, light, water and leaf orientations on leaf midrib angle. The main effect of each factor, excluding the azimuth angle during the short-term stress period, was significant ($P < 0.05$). The interactive effect of light and water treatments was also significant following the long-term stress, whereas time × water × azimuth and time × light × water × azimuth had no significant interactive effect ($P > 0.05$) on the leaf movement during the whole experimental period.

There was no significant leaf petiole inclination changing during the daily course (data not shown). By contrast, leaf midrib angle significantly changed (Fig. 1). Leaf midrib angle was inclined upwards at noon and flattened or drooped in the morning and afternoon for all the treatments during the short-term stress period (Fig. 1a), and the midrib angle changing was larger in sunlight (55%) than in shade (15%). After the long-term stress, the leaf midrib angle diurnal trend did not significantly changed in sunlight, and there was no significant change in shade and drought ($P = 0.05$) or shade and well-watered treatment ($P = 0.14$) (Fig. 1b). The midrib angle changing reappeared in the shade treatments after the recovery period, especially for the drought-stressed plants (32%) compared to the well-watered plants (18%) (Fig. 1c). The midrib and petiole angles were larger in shade stress. Drought stress caused leaves to be inclined more vertically compared to those of the well-watered plants under the same light conditions (Fig. 2). The leaf orientation affected the leaf inclination after stress, although there was no significant difference during the short-term stress period. The

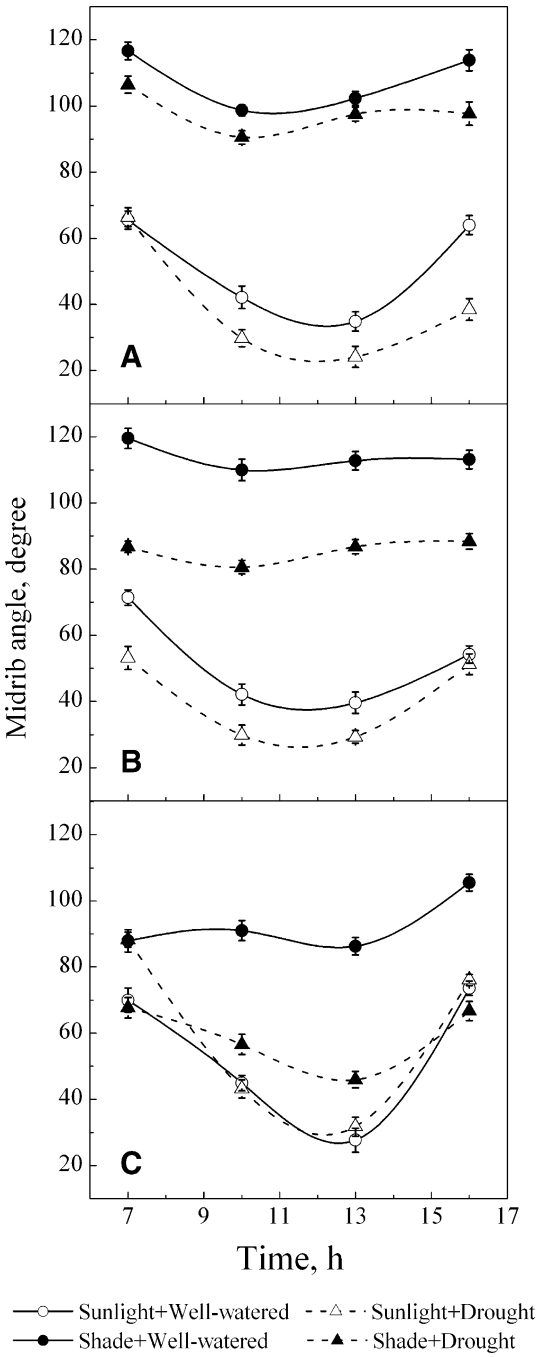

Fig. 1 Diurnal changes of leaf midrib angle in short-term stress (**a**), long-term stress (**b**) and recovery (**c**) period. Means (±SE) of 40 leaves were measured on different water (*circles* and *solid lines* for well-watered; *triangles* and *dotted lines* for drought) and light (*open symbols* for sunlight and *filled* for shade) treatments. The time scale gives the local time of the day

midrib angle of south-facing and west-facing leaves, as well as the petiole angle of east-facing and south-facing leaves, was larger because the locations of the pots were fixed after the experiment was carried out (Fig. 3).

Changes of chlorophyll fluorescence in different stress conditions

Fv/Fm of seedlings after each considered treatment was not significantly different ($P = 0.304$) (Fig. 4a). After the stress, Fv/Fm of the drought treatment was even higher than that of the well-watered groups, especially significant in shade (Fig. 4b). The seedlings grown in shade showed overt photoinhibition after transferred to the open field.

Fs increased to a steady state while Fm declined as the irradiance increased (Fig. 5a, b). The values of Fs and Fm for leaves in shade were higher than those in sunlight, and the drought-stressed plants had lower values than the well-watered plants. The trends of Yield, ETR and qP were the reverse of those of Fs and Fm (Fig. 5c–e). The leaves in sunlight had higher NPQ, but the difference between water treatments was not significant (Fig. 5f).

Dark relaxation kinetics after RLCs indicated different levels of recovery between the treatments, especially between light treatments. A large fraction of Yield (more than 80%) relaxed within the first 40 s in darkness and only 2% remained at the end of the recovery for all the treatments. The difference was not significant, although the relaxations of shade treatments were less (Fig. 6a). The relaxed proportion of NPQ in sunlight was 84 and 81% for the well-watered and drought treatment during the first 40 s recovery period, respectively, and mostly relaxed in the end. The NPQ in the shade condition recovered only 51% and 48% for the well-watered and drought treatment during the first 40 s recovery period, respectively, and approximately 5% remained after nearly 20 min in darkness (Fig. 6b).

Changes of Chl content and SLA after long-term stress

Chl *a*, Chl *b* and total Chl were significantly higher in the shade condition than in sunlight, but the Chl *a*/*b* ratio was a little lower in shade. The water treatment did not affect total Chl and the Chl *a*/*b* ratio (Fig. 7). SLA was significantly higher in shade (567 ± 2.3 and 482 ± 9.7 $cm^2\ g^{-1}$ of well-watered and drought stress, respectively) than in sunlight (289 ± 2.6 and 273 ± 8.7 $cm^2\ g^{-1}$ of well-watered and drought stress, respectively).

Discussion

The results showed that leaf inclination and orientation were affected by the duration of the shade stress. The midrib angle changing was time-lagged in the light-to-dark period but was resumed rapidly in the dark-to-light period (Fig. 1), suggesting that this leaf trait can decrease the

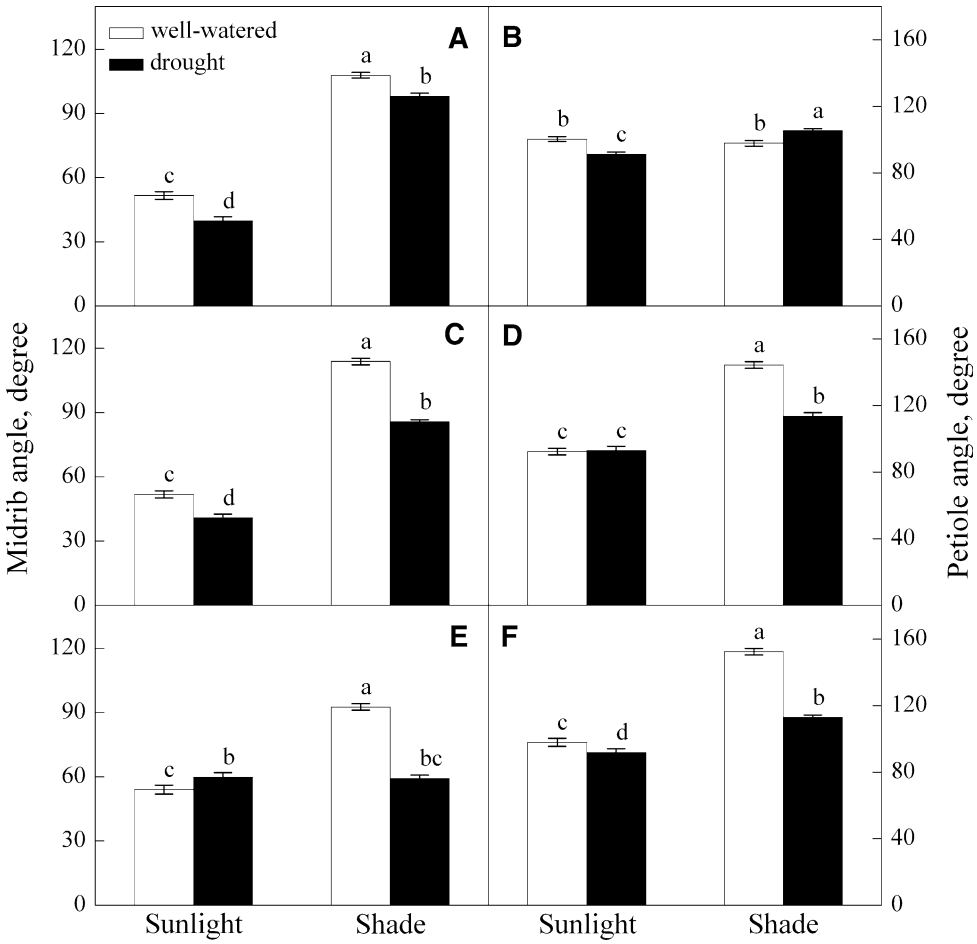

Fig. 2 Mean values of leaf midrib angle and petiole angle in short-term stress (**a**, **b**), long-term stress (**c**, **d**) and recovery (**e**, **f**) period. *Boxes* represent means and *error bars* represent ± SE of the means ($n = 160$ for midrib angle and $n = 40$ for petiole angle). Values with different letters are significantly different at $P < 0.05$ by Duncan's multiple range test

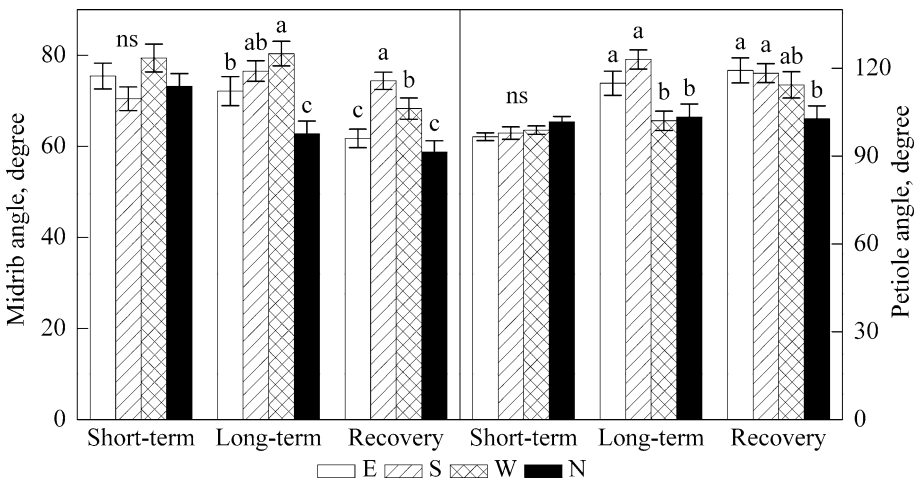

Fig. 3 Mean values of midrib angle and petiole angle in different orientations during the whole period. The orientations defined by leaf azimuth angles were divided into east- (*E*), south- (*S*), west- (*W*) and north- (*N*) facing. *Boxes* represent means and *error bars* represent ± SE of the means ($n = 120$–190 for midrib angle and $n = 35$–47 for petiole angle). Values with different letters are significantly different at $P < 0.05$ by Duncan's multiple range test. *NS* means not significant

over-loaded light damage when plants are suddenly stressed. Light had greater impact on leaf inclination, because the leaflet was flat in shade than in sunlight (Fig. 2a). Leaf movements are phytochrome-regulated events, as well as circadian regulated by potassium channels (Moshelion et al. 2002; Sharma et al. 2003). Light-dependent leaf movement is the morphological adjustment of maintaining optimal physiological status, while the endogenous rhythm is an ecological countermeasure for adapting to periodically changed circumstances (Zhang et al. 2002). Drought stress led to different extents of leaf inclination in our experiment: leaves were inclined more vertically in both sunlight and shade. The light received by the laminae of plants in the shade was never in excess, suggesting that the leaf inclination may be regulated also by air temperature to decrease leaf temperature and reduce transpiration-induced

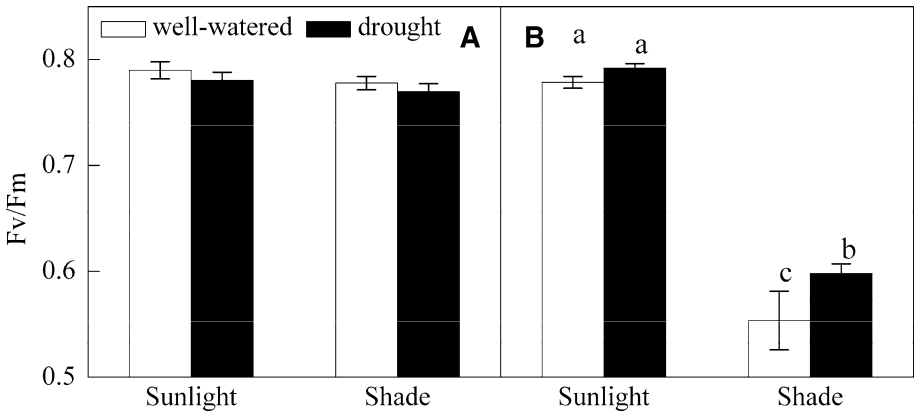

Fig. 4 Change of maximal quantum yield of PS II (Fv/Fm) following long-term stress (**a**) and during recovery (**b**) period. *Bars* represent the mean ± SE of 8 measurements from four seedlings. Values with different letters are significantly different at $P < 0.05$ by Duncan's multiple range test

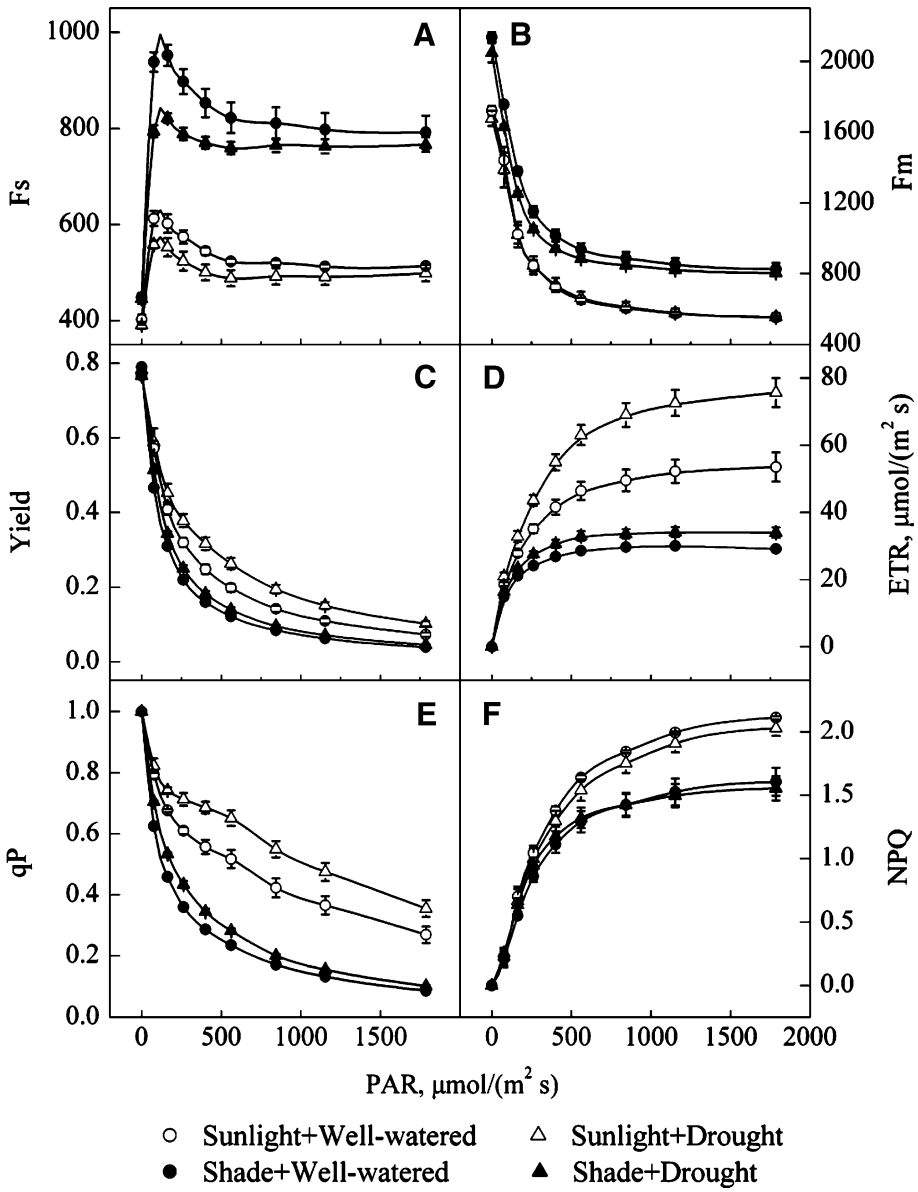

Fig. 5 Rapid light curves (*RLCs*) were measured for different water treatments (*circles* for well-watered and *triangles* for drought) and light treatments (*open symbols* for sunlight and *filled* for shade). **a** steady-state fluorescence yield (*Fs*), **b** maximal fluorescence yield (*Fm*), **c** effective quantum yield (Yield), **d** electron transport rate (*ETR*), **e** photochemical quenching (*qP*) and **f** non-photochemical quenching (*NPQ*) are plotted against PAR. Values are means ± SE. $n = 4$

water loss. Even a small decrease in leaf temperature can allow plants to survive for a long time (Richards et al. 1986). The leaf inclination in sunlight is important in preventing excessive absorption of light by the leaflet (Smith and Ullberg 1989). Photoinhibition did not occur following the long-term stress period (Fig. 4a), indicating

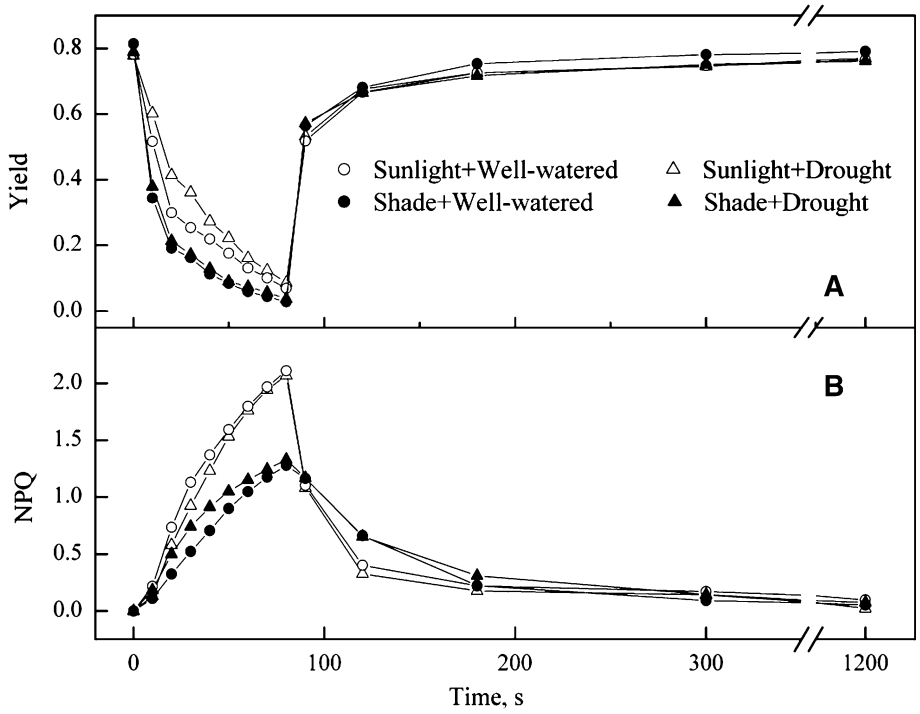

Fig. 6 Rapid light curves (*RLCs*) and recovery of yield and NPQ were measured for different water treatments (*circles* for well-watered and *triangles* for drought) and light treatments (*open symbols* for sunlight and *filled* for shade). Curves are fitted with means of 4 replications against time

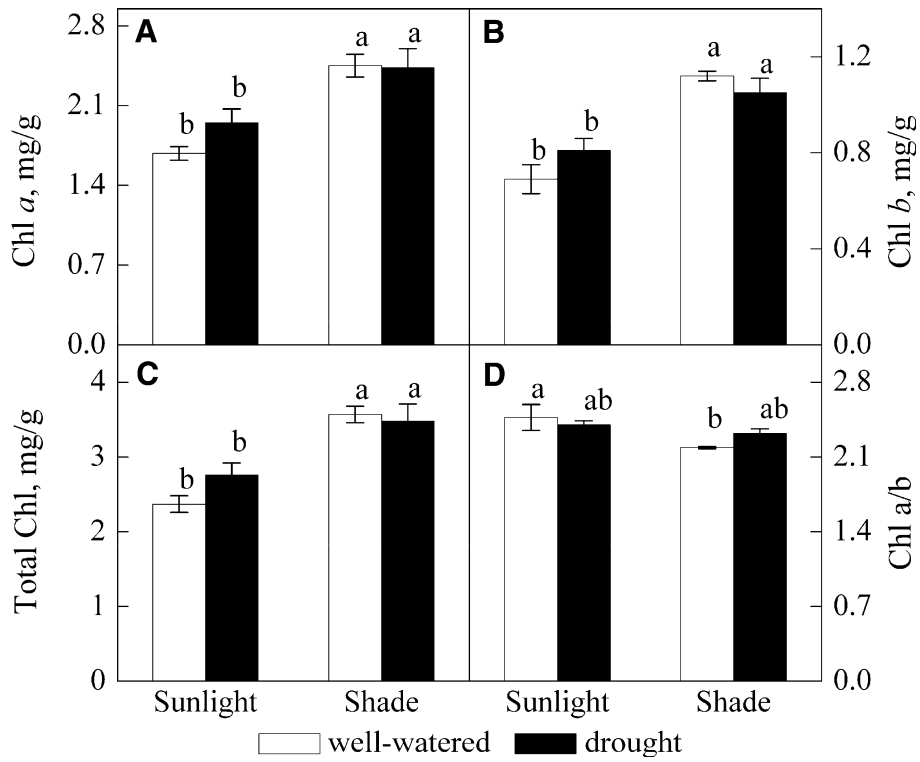

Fig. 7 Changes of chlorophyll *a*, chlorophyll *b*, total chlorophyll content and chlorophyll *a*/*b* for different treatments at the end of the long-term stress. *Boxes* represent means and *error bars* represent ± SE of the means ($n = 4$). Values with different letters are significantly different at $P < 0.05$ by Duncan's multiple range test

that the seedlings had adapted to the conditions after a certain period.

We found that morphological plasticity took place not only in the leaflet but also in the petiole. The petiole angle did not show a rapid response when the conditions were changed; the adaptation is chronic and shows significant difference at the end of stress. The inclination of the petiole in shade was stable, and was drooping compared to the seedlings in the open field (Fig. 2d). The architecture facilitates light capture by leaves, for the photosynthetic ability of the adaxial surfaces is higher than that of the abaxial surfaces (Proietti and Palliotti 1997; Sun and

Nishio 2001; Liu et al. 2007). Both the midrib and the petioles were vertical in the drought treatments. The protective mechanism is accomplished by the cooperation of lamina and petiole. The effect of lamina inclination is more significant than the petiole movement during the recovery period, which could be reflected by the Fv/Fm (Fig. 4b). The measurement of Fv/Fm is used for evaluating photoinhibition (Krause and Weis 1991). Thirty minutes is an adequate time to allow complete re-oxidation of PS II reaction centers and to ensure that all energy-dependent quenching is relaxed (Werner et al. 1999). Hence, any decrease in Fv/Fm after 30 min darkness was considered indicative of chronic photoinhibition (Osmond and Grace 1995). The shade-adapted groups showed photoinhibition for excessive light interception and the lower damage that occurred in the drought groups was associated with erect leaflets. This suggests a relationship between leaf inclination and photoinhibition, and it has been tested in other species (Muraoka et al. 1998; Ikeda and Matsuda 2002; Lin and Hsu 2004; Cui et al. 2006).

Moreover, although there was parahelitrophical movement of the leaflet during the day and of the petiole at the end of the stress period, the leaf and petiole from different orientations showed diaheliotrophical movement (Figs. 2, 3). We suggested that parahelitrophical movement was induced mainly by light for avoiding stress in the short period, and diaheliotrophical movement following the long-term period allowing plant growth. The coordinated acclimation strategy developed in a single leaf and in the whole canopy ensured a better adaptation of the seedlings to stress (Ishida et al. 1999).

A greater proportion of the largest PS II reaction center inactivation at the RLCs in the shade stress condition could be ascribed to the low xanthopyhll cycle pool for energy dissipation as reflected by NPQ (Fig. 5), according to the results of Barker and Adams (1997). The components of non-photochemical quenching could be distinguished on the basis of the dark relaxation kinetics (Quick and Stitt 1989; Johnson et al. 1993). Energy-dependent quenching was the major component in the sunlit leaves, whereas the shaded leaves showed a slow recovery, induced mainly by inactive turnover of the reaction center (Fig. 6). Evidence for a reversible dissociation of light-harvesting complex from the PS II reaction center complex in soybean leaves (Hong and Xu 1999; Liao and Xu 2007) indicated the damage mechanism of saturating light to shade-adapted plants. A vertically tilted leaf in drought stress could minimize xanthophyll cycle activity and reduced the cost of xanthophyll biosynthesis (Figs. 5, 6). Therefore, photosynthetic activity could be enhanced helping seedlings to survive under stress (Liu et al. 2003).

Leaves under the shade stress increased the content of Chl, which maximized the light capture ability (Fig. 7). Meanwhile, the larger SLA was accommodated to decrease self-shading of chloroplasts in the lower part of leaves (Parker and Mohammed 2000; Quero et al. 2006). This is an adaptive strategy for plants to deal with conditions of low levels of irradiance. Drought stress restricted the SLA but did not decrease the Chl content. It might be that the smaller leaflet made it easier to tilt vertically and the Chl components were then less injured in the open field.

As a preponderant species in vegetation restoration, *R. pseudoacacia* must rely on certain adaptive mechanisms for recruitment and survival of tree populations. Physiological and biochemical alterations can acclimatize seedlings to long-term stress, but these protective strategies are established at the expense of losing the ability to respond rapidly to fluctuations of the environment, which could be detrimental in future. The leaf tropism and rhythmic movements are the optimum combination of growth and defense. A rapid response of *R. pseudoacacia* at leaf level to stress factors might justify its adaptability to perturbation thus making this species more suitable for reforestation. In conclusion, both physiological and morphological characteristics of leaves contribute to the survival of *R. pseudoacacia* seedlings in the understory and during drought. However, the maladaptation after exposure to large amount of light may be a problem for forest regeneration. The length of time needed to establish a response system and the degree of damage caused by photoinhibition at different ages of seedlings warrants further study.

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