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Leaf diaheliotropic movement can improve carbon gain and water use efficiency and not intensify photoinhibition in upland cotton (*Gossypium hirsutum* L.)

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Abstract

Upland cotton (*Gossypium hirsutum* L.) can move leaves to track the sun throughout the day, so-called leaf diaheliotropic movement. This paper reports an experimental test of the hypothesis that leaf diaheliotropic movement in upland cotton can enhance carbon assimilation and not increase the risk of stress from high energy load. In this experiment, cotton leaves were divided into two groups: one was that leaves could track the sun freely; another was that leaves were retained to the horizontal position. The diaheliotropic leaves recorded higher incident irradiance than the restrained ones, especially in the morning and late afternoon. Compared with restrained leaves, diaheliotropic leaves were generally warmer throughout the day. As expected, diaheliotropic leaves had significantly higher diurnal time courses of net photosynthetic rate (P_N) than restrained leaves, except during 14:00–18:00 of the local time. Higher instantaneous water-use efficiency (WUE) was observed in diaheliotropic leaves in the early morning and late afternoon than in the restrained leaves. During the given day, diaheliotropic and restrained leaves had similar diurnal time courses of recovery of maximal quantum yield of PSII photochemistry (F_v/F_m). Diaheliotropic leaves recorded lower or similar photochemical quenching coefficient (q_p) than restrained leaves did throughout the day. These results suggest that cotton leaf diaheliotropic movement can improve carbon gain and water use efficiency and not intensify photoinhibition.

Additional key words: carbon assimilation; chlorophyll fluorescence; leaf movement; photoinhibition; water use efficiency.

Introduction

Many higher plant species, such as ephemerals or annuals, as well as cultivated crops, can move their leaves to track the sun throughout the day, so-called leaf diaheliotropic movement. Thus incident sunlight on their leaves can be substantially higher than on the leaves with a static position (Ehleringer and Forseth 1980, Smith 1984). Clearly, this property has the immediate advantage of maximum interception of sunlight, thereby making more light energy available for photosynthesis. Previous studies reported that diaheliotropic leaves have the physiological ability, especially a high light-saturation point, to use high sunlight and therefore increase the daily rate of carbon assimilation (Mooney and Ehleringer 1978, Ehleringer and Forseth 1980 1989, Jurik and Akey 1994). Another important advantage is high instantaneous water use efficiency (WUE) resulting from diaheliotropic leaves (Mooney and Ehleringer 1978, Forseth and Teramura 1986, Jurik and Akey 1994). However, there are disadvantages of diaheliotropism. At the leaf level, diaheliotropic movement, one form of solar tracking, has tremendous impacts on energy load because of increased water loss from leaves and their heat load (Ehleringer and

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Abbreviations: F_m – maximal chlorophyll fluorescence of dark-adapted state; F_m' – maximal chlorophyll fluorescence of light-adapted state; F_o – minimal chlorophyll fluorescence of dark-adapted state; F_o' – minimal chlorophyll fluorescence of light-adapted state; F_P – fluorescence intensity at the peak of the OJIP at the dark-adapted state; F_t – steady-state fluorescence during illumination; F_v, F_v' – variable fluorescence in the dark- and light-adapted state, respectively; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PSII – photosystem II; q_p – photochemical quenching coefficient; WUE – water use efficiency.

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Forseth 1980). At the canopy level, diaheliotropic movement will reduce light available for photosynthesis of leaves at the bottom of canopy by increasing light interception of leaves at the top (Ehleringer and Forseth 1980, Thanisawanyangkura *et al.* 1997).

Cotton (*Gossypium* spp.) is a plant of tropical origin, the most important textile-fibre crops, and the second most important oil-seed crops after soybean worldwide. Upland cotton (*Gossypium hirsutum*) has diaheliotropism but Pima cotton (*G. barbadense*) has not (Lang 1973, Ehleringer and Hammond 1987). Ehleringer and Hammond (1987) reported that in upland cotton, diaheliotropic leaves have a similar diurnal rate of carbon assimilation compared to leaves fixed in a horizontal position, except at the low sunlight of early morning and late afternoon. As discussed by Ehleringer and Hammond (1987), it may be that photosynthesis was saturated by approximately 1200 μmol m^{-2} s^{-1}, 60% of midday light levels in their experiment. Thus, some researchers (Fukai and Loomis 1976, Ehleringer and Forseth 1989, Gutschick 1991) wondered that at midday diaheliotropic movement of upland cotton does not increase carbon assimilation as leaves are light-saturated but increased risks of water-, temperature- and light stress. However, many studies (*e.g.* Sassenrath-Cole *et al.* 1996, Wise *et al.* 2000, Pettigrew 2004) reported that young leaves of upland cotton do not exhibit light saturation of photosynthesis up to levels of incident light >2000 μmol m^{-2} s^{-1}. Similar observations were made in our preliminary experiment on many upland cotton cultivars, including *cvs.* Xinluzao 6, Xinluzao 10 and Xinluzao 13. In addition, Sailaja and Ramadas (1996) demonstrated in many solar tracking plants that diaheliotropic leaf movements were associated with higher quantum efficiency of photosystem II that prevent damage to photosynthesis induced by high light and temperature; thus, lack of photoinhibition in the field was observed on diaheliotropic leaves. As reviewed by Long *et al.* (1994), plants can alleviate photoinhibition stress through many photoprotective mechanisms. Cotton leaves have a strong capacity to dissipate excessive irradiance that can damage photosynthetic apparatus *e.g.* by photorespiration and thermal energy dissipation (Perry *et al.* 1983, Björkman and Demming-Adams 1994, Kornyeyev *et al.* 2005). The principal aim of this study was to test the hypothesis that leaf diaheliotropic movement in upland cotton can enhance carbon assimilation and not increase the risk of stress from high energy load.

Materials and methods

The experiment was conducted in a field of Shihezi Agricultural College, Shihezi University, Xinjiang, China (45°19′N, 86°03′E) in 2008. Cotton (*Gossypium hirsutum* L. cv. Xinluzao 13) was grown under field conditions with under-mulch drip irrigation. Seeds were sown on 24 April 2008 at a plant density of 1.8×10^5 ha^{-1}. N and P_2O_5 were applied at 240 and 172.5 kg ha^{-1}, respectively. The plots were drip-irrigated and maintained well watered throughout the growing season. Pest (aphid and cotton bollworm) was controlled using pesticide and no pesticide applied during the measurement period. Weeds were hand-pulled periodically.

In mid-July, cotton was about 80 cm high at the peak of the bloom growth stage. Plants were selected at random and from each selected plant, the topmost west-facing full-expanded leaf on the main stem was chosen and chlorophyll (Chl) content was 6.5±0.33 mg dm^{-2}. On the day of measurement, some leaves were brought to the horizontal position and retained in that position by nylon strips tied to a metal frame. From now on, the retained leaves are termed ‘restrained leaves’; and leaves allowed free diaheliotropic movement are ‘diaheliotropic leaves’. Measurements were conducted three times under clear-sky conditions with natural sunlight, temperature and relative humidity and only one-day (16th July) data was present here due to similarity of the results of these three days.

Chl fluorescence was measured in diurnal time courses using a portable saturation-pulse fluorometer *PAM-2100* equipped with a *2030-B* leaf clip holder (*PAM-2100*, *Walz*, Effeltrich, Germany) every two hours from 8:00 to 20:00 of the local solar time. PPFD incident on the leaf surface was measured with a micro-quantum sensor on the leaf clip. Leaf temperatures were recorded simultaneously with a Ni/NiCr-thermocouple of the leaf clip holder appressed to the abaxial leaf surface. For each treatment, 10 individual leaves were sampled and labelled. Care was taken to not disturb the position of the leaf being measured and its exposure to light. Three measurements were made at different points on each adaxial leaf surface.

Maximal (F_m) and minimal (F_o) fluorescence of dark-adapted leaves were measured at predawn. F_o was obtained with a measuring light of 0.5 μmol m^{-2} s^{-1} at a frequency of 0.6 kHz, while F_m was measured with a 0.8-s saturating pulse at >8000 μmol m^{-2} s^{-1}. Maximal quantum yield of photosystem II (PSII) photochemistry (F_v/F_m) was calculated, where F_v is variable fluorescence ($F_v = F_m - F_o$) (Genty *et al.* 1989). During the diurnal time courses, F_t (steady-state fluorescence during illumination) and F_m' (maximal chlorophyll fluorescence of light-adapted state) were measured under natural sunlight (actinic light). F_t was obtained by setting the measuring light to frequency of 20 kHz; F_m' was measured with a 0.8-s saturating pulse at >8000 μmol m^{-2} s^{-1}. Photochemical quenching coefficient (q_p) was calculated as $(F_m' - F_t)/(F_m' - F_o')$ (Krause and Weis 1991), although F_o' was not measured and F_o used instead (Jones *et al.* 1999, McMinn *et al.* 2003). Nonphotochemical quenching (NPQ) was calculated as $(F_m - F_m')/F_m'$, where F_m is the value of the predawn measurements (Bilger and Björkman 1990).

F_v/F_m after 30 min of dark adaptation using leaf clips was determined using a nonmodulated fluorimeter *PEA* (*Hansatech*, King´s Lynn, UK). All fluorescence transients were recorded during a 2-s pulse of red radiation of 3000 μmol m^{-2} s^{-1} provided by an array of six light-emitting diodes and F_P value was supposed to be equal to F_m. During the day, measurement was done at 6:00, 10:00, 14:00, 18:00 and 22:00 on the attached diaheliotropic and restrained leaves. The leaves were the same as those used for the measurements. Different leaves were used for the fluorescence quenching parameters and gas exchange parameters. For each treatment, at least five leaves were measured.

Gas exchange: Immediately after Chl fluorescence measurement (*i.e.* within the next 20 s), P_N, g_s, and WUE, calculated from the ratio of P_N to transpiration rate, were determined with a *Li-6400 IRGA* equipped with a *6400-02B* LED light source (*LI-6400, LI-COR Inc.*, Lincoln, NE, USA) on the same portion of the previously labelled leaves used for the fluorescence quenching, taking care not to disturb the leaf position. The air flow in the chamber was 500 μmol s^{-1}. Red-blue light was used for tracking natural incident PPFD on leaves measured by the *2010-B* leaf holder of the *PAM 2100*.

Photosynthetic light-response curves were obtained with the automatic device of *LI-6400 IRGA*. Illumination was provided by a *6400-02B* LED light source. P_N of each leaf was measured after equilibration (about 2 min) at each of the twelve irradiances applied. Four leaves were measured using different plants.

Leaf movement was measured as a change in the midrib angle using an inclinometer and a protractor according to Zhang *et al.* (2002). The leaf position and orientation can be determined quantitatively by measuring three separate angles: (*1*) azimuth angle, the angle of the leaf relative to North; (*2*) lamina (directional) angle, an index of directional tilt of the leaf lamina; and (*3*) midrib angle, an index of leaf hang (Fig. 1). For each treatment, 10 leaves were chosen at random for measurement.

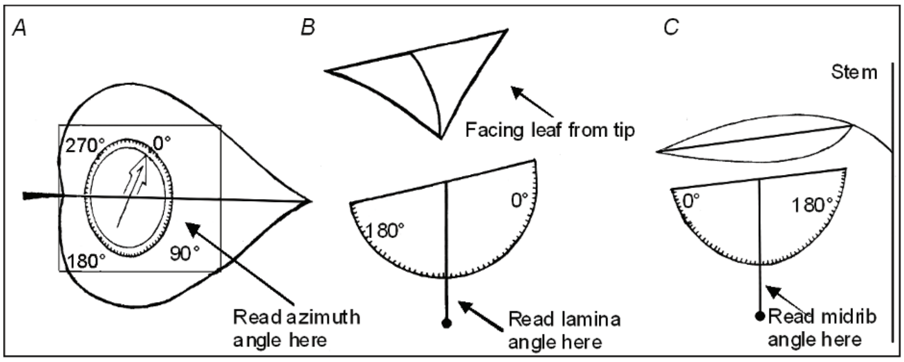

Fig. 1. Diagram for measurement of leaf orientation. *A*: azimuth angle; *B*: lamina (directional) angle; *C*: midrib angle.

Environmental conditions: Ambient photosynthetic photon flux density (PPFD) was measured with an external quantum sensor of a *Li-6400 IRGA* by positioning the sensor perpendicular to the sunlight or horizontal to the ground. Air temperature and relative humidity were measured with a *HOBO* hygro-thermometer (*Onset*, Bourne, MA, USA) 1 m above the ground at the top of canopy.

Data analyses: The statistical analysis of the data was performed by one-way *ANOVA* and least significant differences (LSD) test at the 5% level of significance using *SPSS 13.0* for *Windows*, Chicago, IL, USA.

Results

Climate: As typical for summer in Xinjiang, the growing season was characterised by high irradiance and air temperatures. At 8:00 h, PPFD was approximately 900 μmol m^{-2} s^{-1} when perpendicular to the sun, and only 250 μmol m^{-2} s^{-1} when measured horizontally, with both reaching about 2000 μmol m^{-2} s^{-1} at midday (Fig. 2*A*). Air temperature corresponded to irradiance, increasing from 20 to 35°C, and then decreasing to 24°C in the evening (22:00 h) (Fig. 2*B*). As air temperature gradually increased during the day, the relative humidity dropped from about 78% in the early morning (8:00 h), to < 30% at midday (Fig. 2*B*).

Leaf movement, leaf incident PPFD and leaf temperature: As expected, there was diaheliotropic movement of leaves in the field-grown cotton. With the changes of solar angle during the day, leaves midrib angle changed correspondingly, thereby increasing capture of incident light (Fig. 3*A*). However, azimuth angle (270°) and lamina angle (90°) remained more or less constant. In the morning the west-facing leaves all faced an easterly direction through upward movement,

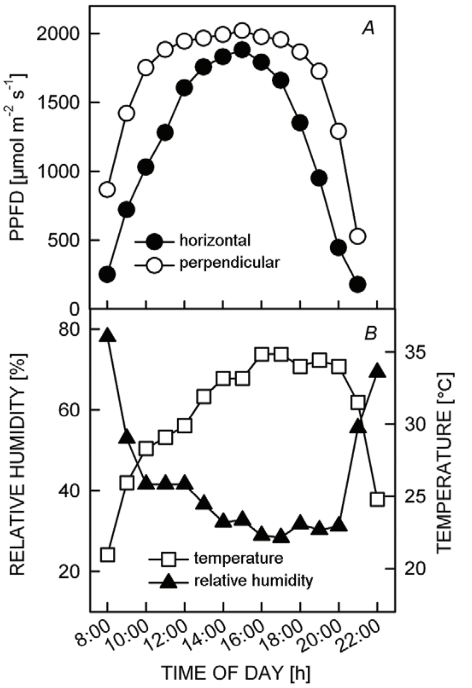

Fig. 2. Diurnal time course of *A*: PPFD on a surface horizontal to the ground or perpendicular to the sun, *B*: air temperature and relative humidity.

and in the afternoon moved to face westerly through downward movement. Moreover, there was a greater extent of leaf diaheliotropic movement in the morning than in the afternoon (Fig. 3*A*); the leaf midrib angles were means of 124° (34° from horizontal) and 82° (8° from horizontal), in the morning and afternoon, respectively. As a result, when leaves were restrained to be horizontal (azimuth angle = 270°; lamina angle = 90°; midrib angle = 90°), there was a difference in leaf incident PPFD between diaheliotropic and restrained leaves. Consequently, the diaheliotropic leaves recorded higher incident PPFD than restrained leaves, especially in the morning and late afternoon (Fig. 3*B*). Furthermore, diaheliotropic leaves recorded higher incident PPFD in the morning than the afternoon, in that unrestrained leaves had greater diaheliotropic movement in the morning. As a consequence of diaheliotropic movement, diaheliotropic leaves were generally warmer than restrained leaves throughout the day (Fig. 3*C*).

Gas exchange: To evaluate the impact of leaf diaheliotropic movement on carbon gain, the diurnal gas exchanges of diaheliotropic and restrained leaves were measured. In cotton leaves, the diurnal pattern of P_N followed that of PPFD in the morning, and after midday the P_N began to decline (Fig. 4*A*). However, the diurnal time-courses of P_N differed between diaheliotropic and restrained leaves. In the morning (8:00–12:00 h), diaheliotropic leaves had significantly higher P_N than the restrained ones. During 14:00–18:00 h, both diaheliotropic and restrained leaves had similar P_N. In the late afternoon, there were again higher P_N in diaheliotropic leaves. Clearly, the diurnal time course of P_N observations suggested that cotton leaves were not light-saturated during the day, as further demonstrated by photosynthetic light response curves (Fig. 5). Even though PPFD reached 2000 μmol m^{-2} s^{-1}, the daily maximum PPFD during the growing season (Fig. 1*A*), P_N had no distinct light-saturation point. As expected, the diurnal time courses of g_s also showed marked differences between treatments (Fig. 4*B*). The patterns were similar to those shown for P_N.

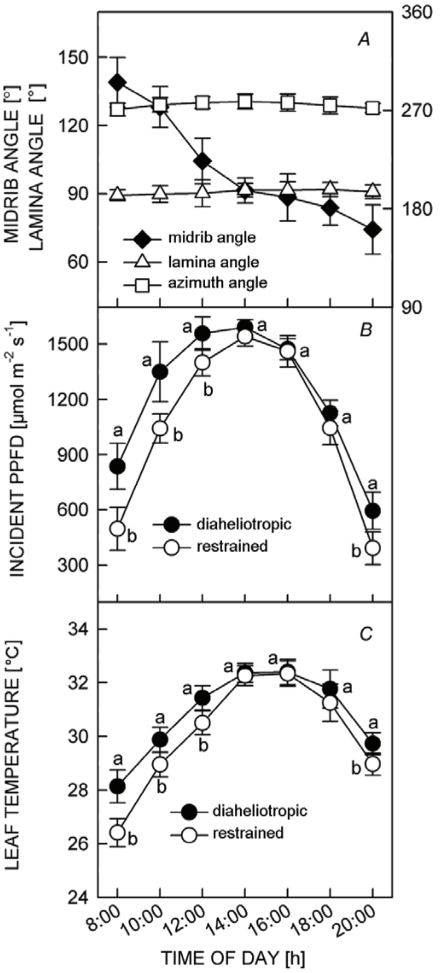

Fig. 3. Diurnal time course of *A*: leaf angle in diaheliotropic leaves and *B*: leaf incident PPFD and *C*: leaf temperature in diaheliotropic and restrained leaves. Different letters indicate differences between treatments at the same time of day at $P<0.05$. Bars represent SE ($n = 10$).

Diaheliotropic leaves had higher instantaneous WUE in the early morning and late afternoon than the restrained ones (Fig. 4*C*). For the rest of the given day, there was similar WUE in diaheliotropic and restrained leaves.

Chl fluorescence: The diurnal time courses of recovery of F_v/F_m after 30 min of dark adaption had similar

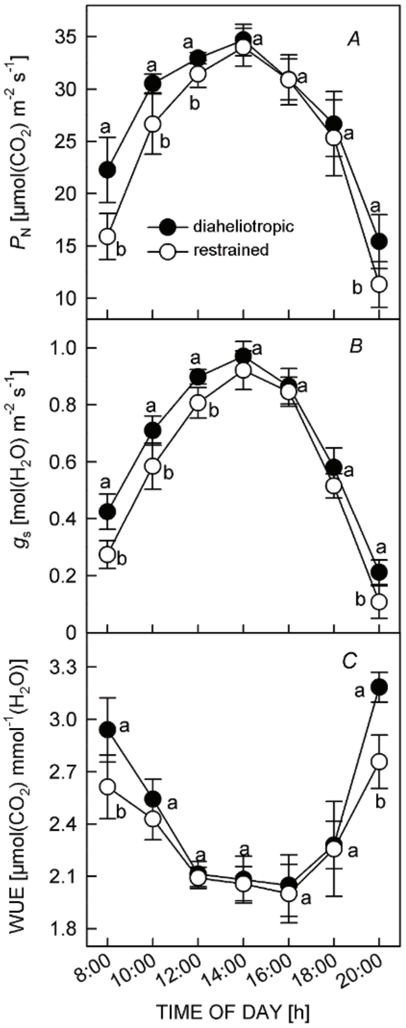

Fig. 4. Diurnal time course of *A*: net photosynthetic rate (P_N), *B*: stomatal conductance (g_s) and *C*: water use efficiency (WUE) in diaheliotropic and restrained leaves. Different letters indicate differences between treatments at the same time of day at $P<0.05$. Bars represent SE ($n = 10$).

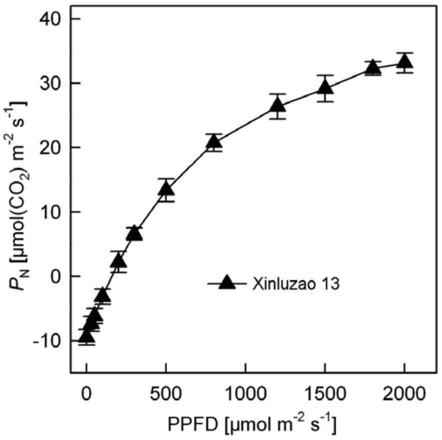

Fig. 5. Photosynthetic light response curve of *G. hirsutum* (cv. Xinluzao 13) cotton leaves (leaf temperature of 31–33°C). Bars represent SE ($n = 4$).

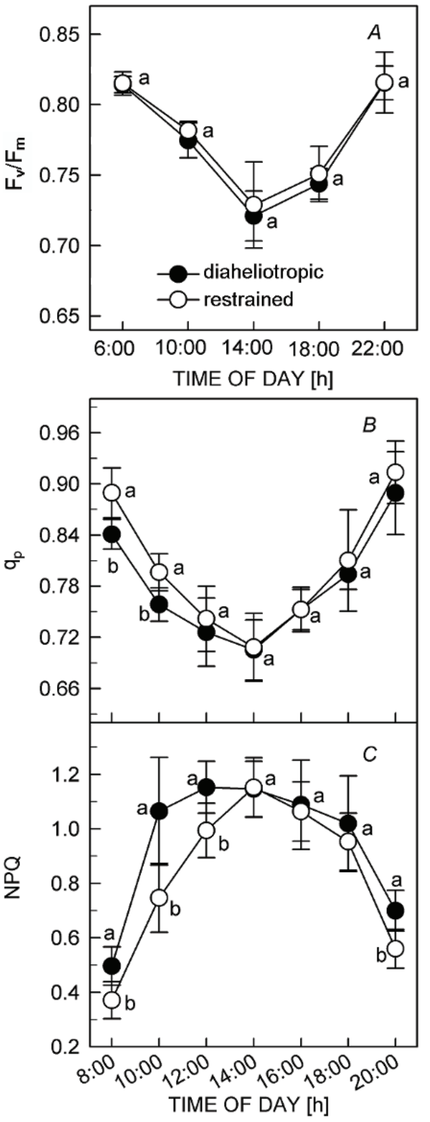

Fig. 6. Diurnal time course of *A*: recovery of maximal quantum yield of PSII photochemistry (F_v/F_m), *B*: photochemical quenching coefficient (q_p) and *C*: nonphotochemical quenching (*NPQ*) in diaheliotropic and restrained leaves. Different letters indicate differences between treatments at the same time of day at $P<0.05$. Bars represent SE [$n = 10$, except F_v/F_m ($n = 5$)].

patterns for diaheliotropic and restrained leaves (Fig. 6*A*). During the given day, diaheliotropic and restrained leaves had similar F_v/F_m. As expected, at 22:00 h, there were no differences in F_v/F_m between diaheliotropic and restrained leaves. Diaheliotropic leaves recorded lower or similar q_p than restrained leaves did throughout the day (Fig. 6*B*). At midday, both diaheliotropic and restrained leaves had similar minimum values of about 0.7. On the other hand, NPQ resulted in higher values for diaheliotropic compared to restrained leaves, particularly in the morning and afternoon, with no significant differences at midday (Fig. 6*C*).

Discussion

Leaf diaheliotropic movement regulated the light incident on leaves and their heat load: The present data clearly showed diaheliotropism in cotton leaves (Fig. 3*A*), as reported by Lang (1973) and Ehleringer and Hammond (1987). As expected, diaheliotropic movement increased the light incident on leaves (Fig. 3*B*). Thus, cotton plants had the benefit of diaheliotropic movement to increase the potential photosynthetic carbon gain because of more light energy available for photosynthesis (discussed below). However, there are also drawbacks to diaheliotropic movement. The increased light-energy load increased leaf temperature (Fig. 3*C*). This may help to activate enzymes of the Calvin-Benson cycle and increased photosynthetic carbon gain during the early morning, when air temperature was low (21°C at 8:00 h). However, this may be detrimental during midday and early afternoon, when air temperature was high (35°C at 16:00 h). The extents of leaf diaheliotropic movement differed between morning and afternoon (Fig. 3*A*), showing that the extent of diaheliotropism was less in the early afternoon. Thus, during 14:00–18:00 h, there was no significant difference in light incident on diaheliotropic and restrained leaves (Fig. 3*B*). As a result, there was a similar trend in leaf temperature (Fig. 3*C*). On the given day, soil water stress did not occur and generally the air temperature in the afternoon was higher than that in the morning; this phenomenon may indicate that leaf diaheliotropic movement was controlled by air temperature, as reported by Fu and Ehleringer (1989) for common beans (*Phaseolus vulgaris*). Clearly, in the afternoon, when air temperature was not favourable, diaheliotropic movement could modify the light incident on leaves, as well as leaf temperature, to maintain the optimum energy for photosynthesis.

Leaf diaheliotropic movement improves carbon gain and WUE: Diaheliotropic movement has been studied most extensively in desert species. In previous studies, *Malvastrum rotundifolium* (Mooney and Ehleringer 1978) and velvetleaf (*Abutilon theophrasti*, Jurik and Akey 1994), the diaheliotropic leaves had benefits of carbon gain. However, Ehleringer and Hammond (1987) reported that in contrast to some other annual plant species, diaheliotropic movement of the cotton leaves did not enhance carbon assimilation of fully exposed sunlit leaves, because light saturation of leaf photosynthesis occurred in approximately 60% of midday full sunlight. In the present experiment, however, P_N was not saturated at full sunlight (about 2000 μmol m^{-2} s^{-1}; Fig. 5). Similar results were reported in cotton by Sassenrath-Cole *et al.* (1996), Wise *et al.* (2000), Pettigrew (2004) and also in our preliminary experiment. These reports indicate that cotton plants have high photosynthetic capacity, enough to utilize the high light, even at full sunlight. As expected, like many other plants with diaheliotropic movements, cotton leaves also had higher P_N than the restrained leaves in the morning and late afternoon (Fig. 4*A*). Nevertheless, during 14:00–18:00 h there was no difference between diaheliotropic and restrained leaves (Fig. 4*A*); however, it was not because diaheliotropic leaves were saturated by light but because diaheliotropic and restrained leaves had similar incident light through regulation of the extent of diaheliotropic movement (discussed above). In addition, high P_N in diaheliotropic leaves resulted from not only high incident light, but also high g_s, indicating that P_N is of low value because of potential stomatal limitation of photosynthesis as well.

Increased instantaneous WUE due to diaheliotropism has been found in several species, *e.g. Malvastrum rotundifolium* (Mooney and Ehleringer 1978), kudzu (*Pueraria lobata*, Forseth and Teramura 1986) and velvetleaf (Jurik and Akey 1994). However, in cotton plants, Ehleringer and Hammond (1987) speculated that diaheliotropism typically increased leaf transpiration but often decreased WUE, because P_N did not increase. In contrast to their speculation, in the present experiment diaheliotropic movements consistently increased transpiration rate (data not shown) and ameliorated leaf heat-load, while P_N also increased correspondingly. Thus, diaheliotropic leaves in upland cotton had higher instantaneous WUE, especially in the early morning and late afternoon (Fig. 4*C*).

Leaf diaheliotropic movement does not intensify photoinhibition: Recovery of F_v/F_m 30 min after dark adaptation has been widely used as an indication of photoinhibition (Björkman and Demmig 1987). There was no significant difference in recovery of F_v/F_m between diaheliotropic and restrained leaves (Fig. 6*A*). Thus, although diaheliotropic movement increased the energy load on leaves (discussed above), diaheliotropic movement did not result in reduction of the photochemical efficiency of PSII. This contention is further supported by q_p (Fig. 6*B*). Even though there was higher q_p on restrained leaves in the early morning and late afternoon, there was similar q_p for diaheliotropic and restrained leaves near midday (Fig. 6*B*). Therefore, it is concluded that leaf diaheliotropic movement did not intensify photoinhibition and maintained a comparable proportion of open to total PSII centres.

NPQ can protect photosynthetic apparatus in environments in which light energy absorption exceeds the capacity for light utilization (Bilger and Björkman 1990). There was higher NPQ in diaheliotropic leaves (Fig. 6*C*), indicating that the dissipation of thermal energy of PSII was also enhanced in diaheliotropic leaves as a protection against photodamage.

In conclusion, diaheliotropic movement of upland cotton could regulate light incident on leaves, as well as leaf temperature. Furthermore, upland cotton leaves have the physiological capacity to use high light and to protect them against energy load stress. Therefore, cotton leaf diaheliotropic movement can improve carbon gain and WUE and not intensify photoinhibition in upland cotton.

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