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# Photorespiration and photoinhibition in the bracts of cotton under water stress

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## Abstract

Gas exchange and chlorophyll fluorescence parameters of PSII were analyzed in the bracts and leaves of cotton plants after anthesis. Photosynthetic activity and photorespiration were measured in the leaves and bracts of cotton grown under either normal or reduced water-saving drip irrigation. The photosynthetic performance, amount of chlorophyll and Rubisco, and net photosynthesis were greater in the bracts than that in the leaves under water stress. The actual photochemical efficiency of PSII decreased in both the bracts and leaves after anthesis under reduced irrigation. However, the decrease was smaller in the bracts than in the leaves, indicating that the bracts experienced less severe photoinhibition compared to the leaves. The greater drought tolerance of bracts could be related to differences in relative water content, instantaneous water-use efficiency, and photorespiration rate. The ratio of photorespiration to net photosynthesis was much higher in the bracts than in leaves. Furthermore, water deficiency (due to the water-saving drip irrigation) had no significant effect on that ratio in the bracts. We hypothesized that photorespiration in the bracts alleviated photoinhibition and maintained photosynthetic activity.

*Additional key words*: electron flow; *Gossypium hirsutum*; photoprotection; PSII.

## Introduction

Cotton (*Gossypium hirsutum* L.) is one of the most widely cultivated crops in the Xinjiang Uyghur Autonomous Region, China. Drought is the main abiotic stress limiting cotton production in this region (Bai *et al.* 2008). The arid continental climate is characterized by high temperatures, high radiation levels, and a progressive increase in water stress during the cotton growing season (Yi *et al.* 2011). An excess of photon energy causes photoinhibition of PSII in thylakoid membranes (Asada *et al.* 1999, Kato *et al.* 2003, Miyake *et al.* 2005). The degradation of thylakoid membranes in chloroplasts is characterized by loss of photosynthetic electron transport activity and leaf photosynthetic activity (Guiamét 1996, Noodén 1997, Murata *et al.* 2007).

Photoinhibition and photorespiration are both considered inevitable in photosynthetic organisms under field conditions (Osmond *et al.* 1995). However, photosynthetic organisms are able to overcome the harmful effects of light *via* rapid and efficient repair of PSII. The essential inefficiencies of photosynthetic organisms can help preserve their competence (Osmond and Björkman *et al.* 1994). For example, photorespiration can stimulate photon utilization in photosynthetic organisms (Russell *et al.* 1995). Photorespiration is believed to protect the photosynthetic apparatus against photoinhibition (Osmond *et al.* 1994, Wingler *et al.* 1999); the photoprotective function of photorespiration is particularly important under the conditions of high irradiance and high temperature occurring during moderate drought (Bai *et al.* 2008, Guan *et al.* 2009).

Photosynthesis in non-foliar green organs (the main-stem, bracts, and capsule walls) of cotton has been under discussion for years; however, most scientists previously believed that leaves were the main source of photosynthetic assimilates in cotton (Wullschleger *et al.* 1991,

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*Abbreviations*: $g_s$ – stomatal conductance; $J_C$ – electron flow to carboxylation; $J_O$ – electron flow to oxygenation; $J_T$ – electron transport rate; NDI – normal drip irrigation; $P_N$ – net photosynthetic rate; $P_R$ – photorespiration rate; $R_D$ – respiration rate; RWC – relative water content; WSDI – water-saving drip irrigation; WUE – instantaneous water-use efficiency; $\Phi_{PSII}$ – actual photochemical efficiency of PSII.

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Bondada *et al.* 2003). It is now accepted that the bracts of cotton are also the important source of assimilated carbon (Du *et al.* 2009, Zhang *et al.* 2010, Hu *et al.* 2012, 2013), especially during late-season drought stress (Hu *et al.* 2013). Xeromorphic anatomy (Bondada *et al.* 2003) and osmotic adjustment (Serraj and Sinclair 2002) in cotton bracts may help the bracts to maintain a water status under conditions of high temperature, high irradiance, and water stress. Bracts are closer to cotton fruits than the leaves and may be a better source of assimilates because their photosynthetic activity is greater than that of leaves under drought conditions (Kumar *et al.* 2001, Redondo-Gómez *et al.* 2010). As it is not clear how bracts can maintain relatively high photosynthetic activity under drought conditions, the objective of this field study was to compare the photosynthetic and photorespiration activity of cotton bracts and leaves.

## Materials and methods

**Experimental design**: The experiment was conducted in field plots near the Shihezi University, Xinjiang Province, China (45.32°N, 86.05°E). Cotton (cv. Xinluzao 33) was sown on April 25, 2012, and April 23, 2013. The plots were 5.4 m × 8 m. The row spacing was 12 cm and the plant density was 27 plants m$^{-2}$. Pest and weed control was carried out according to local practices.

The plots were irrigated regularly until the plants achieved anthesis (*i.e.*, 11 weeks after planting). At this time, two irrigation treatments were initiated: normal drip irrigation (NDI; 5,230 m$^3$ ha$^{-1}$) and water-saving drip irrigation (WSDI; 3,870 m$^3$ ha$^{-1}$, a rate that was 60% of normal drip irrigation). The plots were irrigated once each week, and each treatment was replicated three times. The relative soil water content was measured using *Watermark* soil moisture sensors (*200SS, Irrometer Co.,* Riverside, Calif., USA) every evening after anthesis (Fig. 1S, *supplementary material available online*). Maximum temperatures, minimum temperatures, and rainfall amounts were measured at a nearby weather station (Fig. 2S, *supplementary material available online*)

The cotton plants were tip-pruned on July 7, 2012 (67 days after sowing, DAS) and July 12, 2013 (72 DAS). Gas exchange, Chl fluorescence, and relative water content were measured using the penultimate main leaves and their associated bracts under the main-stem leaves. The measurements were made using the leaves and bracts of three plants after 85, 95, 105, 115, and 125 DAS. To minimize age-related variability in the parameters, approximately 400 cotton leaves and bracts were labeled on July 19, 2012, and July 21, 2013, for use in the study.

**Gas exchange and chlorophyll (Chl) fluorescence**: Gas exchange (*LI6400*; *6400–02B LED*, *LI-COR*, Lincoln, NE, USA) and Chl fluorescence (*PAM–2100* Chl fluorometer, *WALZ*, Effeltrich, Germany) were monitored on leaves and bracts, the penultimate main leaves, and their associated bracts under the main-stem leaves between 11:00 and 14:00 h. Response curves of the net photosynthetic rate ($P_N$) in relation to PAR were measured at 2,000; 1,800; 1,200; 600, 200, 50, and 0 µmol(photon) m$^{-2}$ s$^{-1}$. Leaf temperature (33–38°C) and chamber CO$_2$ concentration (380–390 µmol m$^{-2}$ s$^{-1}$ CO$_2$) were kept under atmospheric conditions. For measurements of $P_N$–$C_i$ curves, leaves and bracts were measured at 0 µmol mol$^{-1}$ of chamber CO$_2$, and then CO$_2$ was increased stepwise up to 2,000 µmol mol$^{-1}$. Light intensity was kept at 2,000 µmol(photon) m$^{-2}$ s$^{-1}$, and leaf temperature (33–38°C) was kept under atmospheric conditions. $P_N$ at 5:00–6:00 h were used as mitochondrial respiration during the night ($R_n$). The actual photochemical efficiency ($\Phi_{PSII}$) was measured at 1,800 µmol m$^{-2}$ s$^{-1}$ PAR between 11:00 and 14:00 h, and the maximal photochemical efficiency ($F_v/F_m$) was measured at 5:00–6:00 h.

**Relative water content (RWC) and Chl content**: RWC was measured on discs (5 mm in diameter) from paired leaves and bracts. The samples were weighed ($w_i$), floated on distilled water at 4ºC overnight, weighed again ($w_f$), dried at 80ºC for 48 h, and then weighed a third time ($w_d$). RWC was calculated as:

$$\text{RWC [\%]} = 100\,(w_i - w_d)/(w_f - w_d).$$

The Chl content was determined by extracting leaf and bract samples with 80% (v/v) acetone for 3 d at room temperature in the dark. The absorbance of each extract was measured with a spectrophotometer at 663 and 645 nm (*U-3900, Hitachi,* Tokyo, Japan). The Chl content was calculated according to Lichtenthaler (1987).

**Calculations**: Mitochondrial respiration during the day ($R_D$) was extrapolated at different temperatures using a $Q_{10}$ relation as follows:

$$R_D = R_n\,Q_{10}{}^{(T_d - T_n)/10}\ (Q_{10} = 2.2)\ \text{(Bai \textit{et al.} 2008)}\quad (1)$$

where $R_D$ and $R_n$ are the respiration in dark and before dawn, respectively, and $T_n$ and $T_d$ are leaf temperatures during the day and during the night, respectively.

$$J_T = \Phi_{PSII}\ \text{PAR}\ \alpha f\ \text{(Galmés \textit{et al.} 2007)}\quad (2)$$

where $J_T$ is the total electron flow; α is the ratio of radiation absorbed by the leaf as compared to incidence radiation (generally 84%), and *f* is 0.5 in C$_3$ plants.

$$J_c = 1/3[J_T + 8(P_N + R_D)]\ \text{(Valentini \textit{et al.} 1995)}\quad (3)$$
$$J_o = 2/3[J_T - 4(P_N + R_D)]\ \text{(Valentini \textit{et al.} 1995)}\quad (4)$$
$$P_R = 1/12[J_T - 4(P_N + R_D)]\ \text{(Valentini \textit{et al.} 1995)}\quad (5)$$

where $J_C$ is electron flow to carboxylation, $J_O$ is electron flow to oxygenation, and $P_R$ is photorespiration.

$V_{cmax} = C_i \times [A_c + R_D - K_c(1 + O/K_o)]/(C_i - \Gamma^*)$
(Farquhar *et al.* 1980) (6)

where $V_{cmax}$ is the maximum velocity of ribulose-1,5-bisphosphate (RuBP) carboxylation; $A_c$ is the $CO_2$ assimilation rate limited by Rubisco activity; $C_i$ and $O$ are the partial pressures of $CO_2$ and $O_2$ in the intracellular space, $K_c$ and $K_o$ are the Michaelis constants of Rubisco activity for $CO_2$ and $O_2$, respectively; and $\Gamma^*$ is the $CO_2$ compensation point in the absence of mitochondrial respiration.

Rubisco [$mol \cdot m^{-2}$] = $(V_{cmax}/10^6)/8\ k_{cat}$
(Hymus *et al.* 2002) ($k_{cat} = 3.3$) (7)

Instantaneous water-use efficiency (WUE) was calculated as: WUE = $P_N/E$ (8)

**Statistical analysis**: Analysis of variance was performed with *SPSS* version *11.5* software. Differences between treatments were considered significant at $P<0.05$ according to least significant difference (LSD) tests. The figures were plotted using *SigmaPlot* version *10.0* software. The data are presented as the mean ± SD.

## Results

**Plant water status**: The RWC of both leaves and bracts decreased as the cotton plants matured, regardless of the irrigation system (Fig. 1*A*,*B*). The RWC decreased more in the leaves (29–40%) than in the bracts (17–19%) between 85 and 125 DAS. There were significant differences in RWC of the leaves between the NDI and WSDI treatments. In contrast, there were no significant differences in RWC of the bracts between the two treatments.

The bracts showed significantly greater WUE than the leaves between 85 and 125 DAS (Fig. 2). The WSDI treatment had no significant effect on WUE of the bracts.

**Photochemical efficiency of leaves and bracts**: Chl fluorescence measurements showed a sharp decay in the photochemical efficiency ($\Phi_{PSII}$) of the cotton leaves between 85 and 125 DAS (Fig. 3*A*). In contrast, the $\Phi_{PSII}$ of the bracts peaked around 95 DAS and then decreased for the rest of the period (Fig. 3*B*). The $\Phi_{PSII}$ of the bracts showed lower values than that in the leaves between 95 and 125 DAS. Overall, $\Phi_{PSII}$ decreased by 59–69% in the leaves and by 33–38% in the bracts. The $\Phi_{PSII}$ of the leaves was significantly lower under the WSDI treatment than that of NDI treatment.

We found no significant effects on the $\Phi_{PSII}$ in the cotton bracts under the two irrigation treatments. The irrigation treatments had no significant effects on the $F_v/F_m$ ratio in either leaves or bracts (Fig. 3S).

**Photosynthetic performance**: On a surface area basis, the amount of Chl was significantly lower in the bracts than that in the leaves (Fig. 4*A*,*B*). Leaf Chl steadily declined between 85 and 125 DAS. It decreased faster in the plants that received the WSDI treatment than in those under NDI, especially between 110 and 125 DAS. By comparison, the amount of Chl in the bracts peaked around 95 DAS and then declined. There was no significant difference in the amount of Chl in the bracts between the two irrigation treatments.

The $P_N$ of the leaves decreased sharply between 85 and 125 DAS (Fig. 5*A*). The leaf $P_N$ decreased faster in the plants under WSDI treatment than in those under NDI. The $P_N$ of the bracts peaked around 95 DAS and then

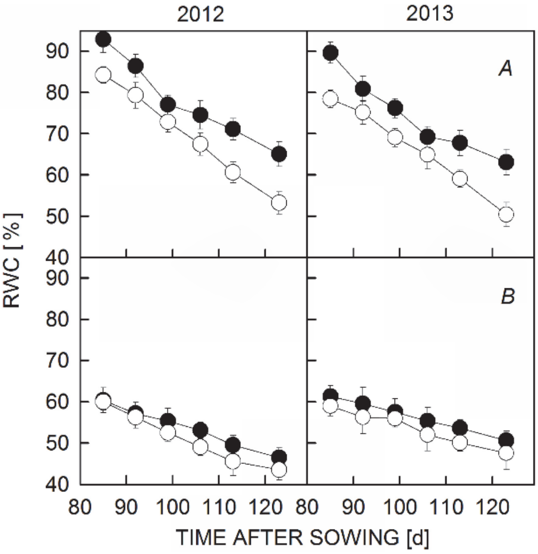

Fig. 1. Relative water content (RWC) of leaves (*A*) and bracts (*B*) of cotton plants grown with normal drip irrigation (*black circles*) or water-saving drip irrigation (*white circles*) during 2012 and 2013. Values are means ± SD.

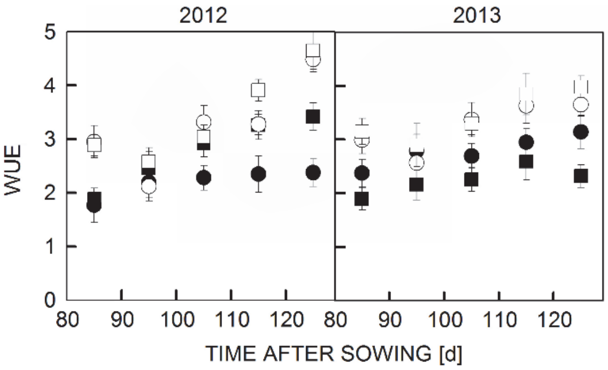

Fig. 2. The instantaneous water-use efficiency (WUE) of leaves (*black symbols*) and bracts (*white symbols*) of cotton plants during 2012 and 2013. Values are means ± SD. *Circles* assign normal drip irrigation and *squares* water-saving drip irrigation.

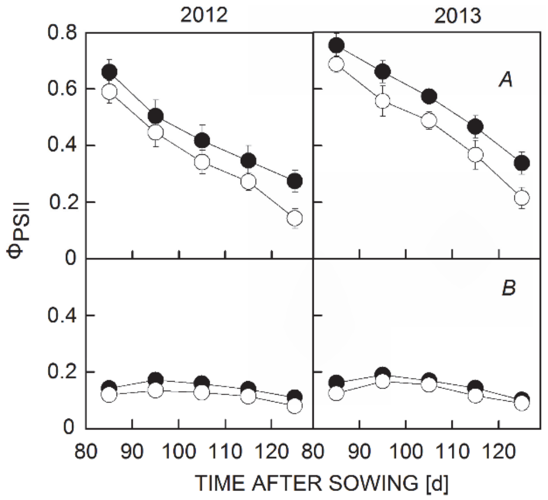

Fig. 3. The actual photochemical efficiency ($\Phi_{PSII}$) of leaves (*A*) and bracts (*B*) of cotton plants grown under normal drip irrigation (*black circles*) or water-saving drip irrigation (*white circles*) during 2012 and 2013. PAR = 1,800 μmol $m^{-2}$ $s^{-1}$. Values are means ± SD.

decreased (Fig. 5*B*). The $P_N$ of the bracts was nearly the same at 85 d as at 125 DAS. There was no significant difference in the $P_N$ of bracts under both irrigation treatments.

The Rubisco content of the leaves decreased significantly by 69–75% between 85 and 125 DAS (Fig. 6*A*). In comparison, the Rubisco content of the bracts reached a peak at about 95 DAS and then decreased during the rest of the growing season (Fig. 6*B*). The Rubisco content of the bracts was 45–48% lower at 125 DAS than that at 85 DAS. The WSDI treatment significantly reduced the Rubisco content of the leaves but not of the bracts.

**Photorespiration**: The $P_R$ of some shrub vegetation in dry environments can be estimated by combining measurements of gas exchange and Chl fluorescence (Galmés *et al.* 2007).The $P_R$ of the leaves decreased significantly by 46–64% between 85 and 125 DAS (Fig. 7*A*) (PAR = 1,800 μmol $m^{-2}$ $s^{-1}$ ). In comparison, $P_R$ in the bracts rose by 21–27% between 85 and 95 DAS and then decreased during the rest of the growing season. The $P_R$ of the bracts was 28–35% lower at 125 DAS than that at 85 DAS (Fig. 7*B*). There was no significant difference in the $P_R$ of the bracts under both two irrigation treatments.

***$P_R$/$P_N$* and $J_C$/$J_O$**: The combined measurements of gas exchange and Chl fluorescence may be used to measure $J_C$ and $J_O$, as well as $P_N$. We used both the $P_R$/$P_N$ and $J_C$/$J_O$ ratios to express the partitioning of electron flow.

The $P_R$/$P_N$ ratio was much lower in the leaves than that in the bracts (Fig. 8*A*). Furthermore, water stress had no effect on the $P_R$/$P_N$ ratio of the bracts. The $J_C$/$J_O$ ratio in the bracts, but not in the leaves, remained stable between 85 and 125 DAS (Fig. 8*B*).

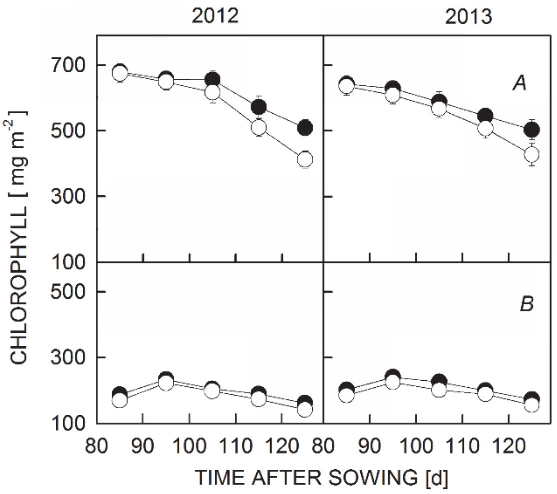

Fig. 4. Total amount of chlorophyll (expressed on a surface area basis) of leaves (*A*) and bracts (*B*) of cotton plants grown with normal drip irrigation (*black circles*) or water-saving drip irrigation (*white circles*) during 2012 and 2013. Values are means ± SD.

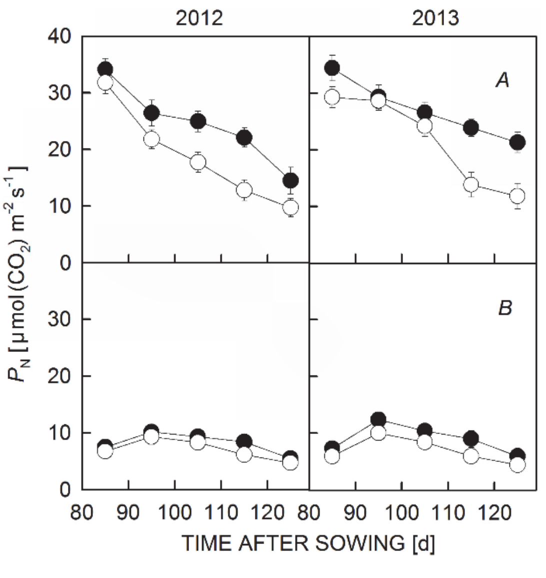

Fig. 5. Net $CO_2$ assimilation rates in leaves (*A*) and bracts (*B*) of cotton plants grown with normal drip irrigation (*black circles*) or water-saving drip irrigation (*white circles*) during 2012 and 2013. PAR = 1,800 μmol $m^{-2}$ $s^{-1}$. Values are means ± SD.

## Discussion

**Drought tolerance of bracts *vs.* leaves**: Some previous studies have examined the photosynthetic performance of non-foliar green organs, compared to leaves, under water-saving drip irrigation conditions (Kumar *et al.* 2001, Redondo *et al.* 2010). Several studies indicated that the photosynthetic performance of cotton bracts was better than that of leaves when cotton was under water stress late in the growing season (Zhang *et al.* 2008, Du *et al.* 2009, Zhang *et al.* 2010, Hu *et al.* 2012, 2013).

In our study, we observed that the amounts of Chl and Rubisco and the $P_N$ were significantly less affected by water stress in the bracts than in the leaves (Figs. 4-6). The decline in the $P_N$ was much smaller in the bracts than that in the leaves under WSDI conditions between 85 and 125 DAS (Figs. 4-6). The WUE of the bracts was significantly higher than that of the leaves in both the NDI and WSDI treatments (Fig. 2). Therefore, the accompanying increase of WUE may be considered to be an indicator of better photosynthetic performance of the bract.

The greater drought tolerance of non-foliar green organs could be associated either with their xerophytic structure (Hu *et al.* 2013) or with $C_4$ or CAM metabolism (Sage *et al.* 2002). The RWC was less affected in the bracts than in the leaves under WSDI conditions during the late growth stages (Fig. 1). Xu and Ishii (1990) reported that under water stress, non-foliar green organs of wheat maintained more stable RWC than that in leaves; they concluded that the drought resistance of non-foliar green organs is greater than that of leaves. Serraj and Sinclair (2002) reported that greater capacity for osmotic adjustment in non-foliar green organs than that in leaves might contribute to the more stable RWC and the better photosynthetic performance of non-foliar green organs. Several studies have discussed $C_4$ or CAM metabolism in non-foliar green organs, including wheat bracts and awns (Xu *et al.* 1990, Araus *et al.* 1993b, Chollet *et al.* 1996), cotton bracts

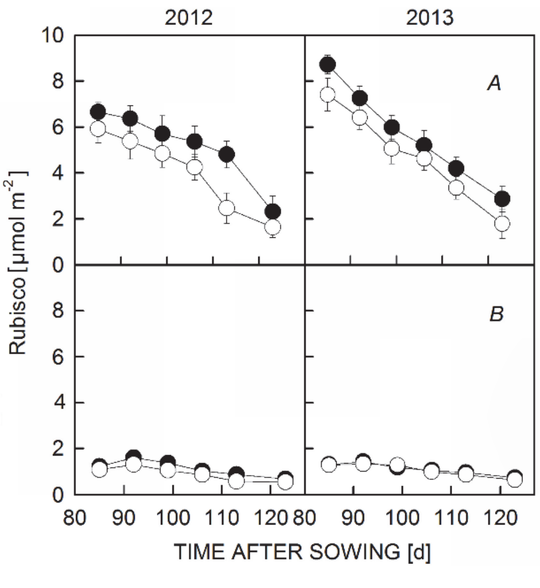

Fig. 6. Rubisco content in leaves (*A*) and bracts (*B*) of cotton plants grown with normal drip irrigation (*black circles*) or water-saving drip irrigation (*white circles*) during 2012 and 2013. PAR = 1,800 μmol m$^{-2}$ s$^{-1}$. Values are means ± SD.

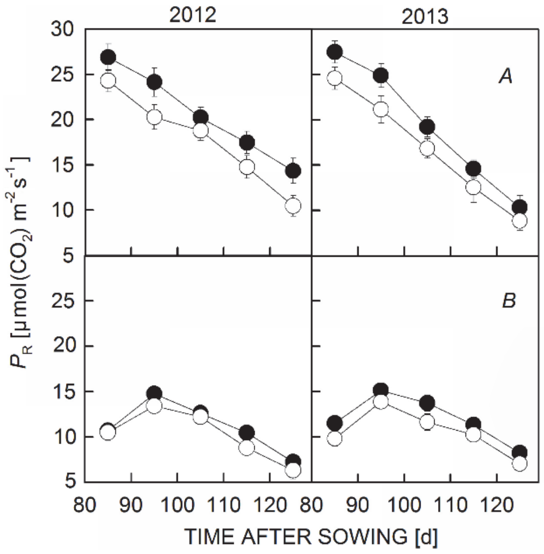

Fig. 7. Photorespiration rates in leaves (*A*) and bracts (*B*) of cotton plants grown with normal drip irrigation (*black circles*) or water-saving drip irrigation (*white circles*) during 2012 and 2013. PAR = 1,800 μmol m$^{-2}$ s$^{-1}$. Values are means ± SD.

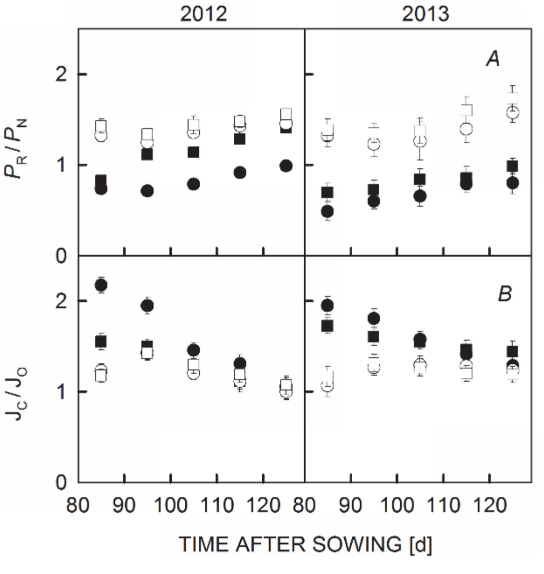

Fig. 8. The $P_R/P_N$ (*A*) and $J_C/J_O$ (*B*) ratios in leaves (*black symbols*) and bracts (*white symbols*) of cotton plants grown with normal drip irrigation (*circles*) or water-saving drip irrigation (*squares*) during 2012 and 2013. PAR = 1,800 μmol m$^{-2}$ s$^{-1}$. Values are means ± SD. $J_O$ – electron flow to oxygenation; $J_C$ – electron flow to carboxylation; $P_N$ – net photosynthetic rate; $P_R$ – photorespiration rate.

(Li *et al.* 2002), and rice spikelets (Imaizumi *et al.* 1990). The greater tolerance of non-foliar green organs may be supported by measurements of $C_4$ or CAM photosynthesis under water-saving conditions (Eduardo *et al.* 2005).

**The relationship between photorespiration and photosynthesis of PSII under water stress**: Photoinhibition, which occurs when photon energy exceeds the amount of energy used by photosynthesis, is characterized by a decline in $\Phi_{PSII}$ (Schreiber 2004, Bai *et al.* 2008, Takahashi and Murata 2008). The extent of photoinhibition depends on the amount of excessive photon energy. High irradiance and high temperature often occur simultaneously with water stress, potentially increasing the amount of excess photon energy.

The decline of $\Phi_{PSII}$ in our study implies that drought led to photoinhibition of the photosynthetic apparatus. In the WSDI treatment, $\Phi_{PSII}$ decreased by 59 to 69% in the leaves and by 33 to 38% in the bracts between 85 and 125 DAS. These results indicated that photoinhibition affected less the photosynthetic performance of the bracts than that of the leaves under both irrigation treatments (Fig. 3). However, the decrease in $\Phi_{PSII}$ was lesser in the bracts than that in the leaves.

The Mehler reaction is ignored when photorespiration is estimated by the combined measurement of gas exchange and Chl fluorescence. Bondada *et al.* (2003) reported that cotton leaves contain both palisade and spongy tissues. In contrast, cotton bracts are composed of loosely arranged spongy tissue. Moreover, bracts contain less Chl than leaves and are physically thinner than the leaves (Hu *et al.* 2013). As a result, the photoprotective function of photorespiration in cotton bracts is overestimated by using the value of energy absorption rate (0.84). However, the degree of thylakoid grana stacking in bracts is significantly higher than that in leaves and the bracts can increase the PSII capacity to capture more light (Bondada *et al.* 2003). Therefore, the estimated values of photorespiration in bracts and leaves are reasonable. At the same time, there is the usual problem of comparing whole-tissue photosynthetic performance as measured by gas exchange and Chl fluorescence with that (*e.g.*, $J_T$ from which, among other parameters, $P_R$ is calculated) of chloroplasts localized at a particular tissue depth from which the Chl fluorescence signal is detected. There is no convenient solution to this problem at present, thus the estimated values are errors within the permissible range.

$P_R$ is closely related to $P_N$, $\Phi_{PSII}$, and $R_D$. We observed that the change in $P_R$ after anthesis was similar to the changes in $P_N$ and $\Phi_{PSII}$. The $P_R$ of the bracts appeared to be less affected than that of the leaves under WSDI conditions (Fig. 7). The $J_C/J_O$ ratio, which is a good indicator of the relative rates of carboxylation *vs.* oxygenation, may be directly controlled by the kinetic properties of Rubisco (Valentini *et al.* 1995). The decline of $J_C/J_O$ after sowing suggests that photorespiration may consume excessive electrons and stimulate photon utilization in photosynthetic organisms. The $P_R/P_N$ ratio indicates the relative rates of photorespiration and photosynthesis (Ogren 1984, Valentini *et al.* 1995, Bai *et al.* 2008). The average $P_R/P_N$ ratios in leaves were 0.94 under the NDI treatment and 1.07 in the WSDI treatment. By comparison, the average $P_R/P_N$ ratios in the bracts were much higher, 1.31 in the NDI treatment and 1.38 in the WSDI treatment (Fig. 8). The low $J_C/J_O$ ratio and the higher $P_R/P_N$ ratio in cotton bracts emphasize the importance of photorespiration under WSDI conditions.

**Conclusion**: Our experiment indicated that under water stress, the photosynthetic performance of bracts was superior to that of leaves, due to the higher drought tolerance of the bracts. Our measurements of $\Phi_{PSII}$, $P_R$, and electron partitioning indicated that photorespiration played an important role in protecting the photosynthetic apparatus in bracts against photoinhibition.

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