

SHORT COMMUNICATION

Effects of Short-Term High Temperature on Photosynthesis and Photosystem II Performance in Sorghum

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Abstract

Gas exchange and chlorophyll a fluorescence transient were examined in leaves of sorghum at high temperatures. No changes were found in photosynthetic rate (Pn) and photosystem II (PS II) performance index on absorption base (PI(abs)) at 40 °C for 1 h. But transpiration rate was enhanced significantly, which served as a self-protection response for dissipating heat. The Pn decreased significantly at 40 °C for 3 h, and the decrease became greater at 45 °C. Decrease in Pn mainly resulted from stomatal limitation at 40 °C for 3 h, whereas it was due to non-stomatal limitation at 45 °C. Decline in PS II function indicated by the significant decrease in PI(abs), trapped energy flux and electron transport flux were responsible for the decrease in Pn at 45 °C. PS II reaction centre and oxygen-evolving complex in the donor side were not affected at high temperatures, but electron transport in the acceptor side was sensitive to high temperature. The PS II function recovered completely 1 day after high temperature stress even as high as 45 °C, which is favourable for sorghum to meet the challenge of global warming. However, Pn did not completely recover possibly due to heat-induced irreversible damage to CO₂ fixation process.

Introduction

Due to greenhouse effect, global surface temperature is predicted to continue to increase in the future (IPCC 2007). High temperature stress has negative effects on plant growth and then gives rise to decrease of crop yield (Ulukan 2008, Dias and Lidon 2009, Shao et al. 2009, Li et al. 2010, Ruan et al. 2010). In consequence, global warming can aggravate food crisis of feeding the world's human population, particularly in the developing countries (Battisti and Naylor 2009). Improving plant heat tolerance is a feasible way to solve the food crisis induced by global warming. Beforehand, however, we should figure out the plant responses to high temperature stress and their underlying physiological mechanisms, as it can provide insights into how plants may be modified to become more tolerant (Ni et al. 2009; Zhang et al. 2009,

Zhao et al. 2009, Ma et al. 2010, Sharkey and Zhang 2010, Wang et al. 2010, Xu et al. 2010).

Along with global warming, an increased frequency of periods with exceptionally high temperatures is one of the most important characteristics of accelerated climatic changes (Meehl et al. 2007). For example, air temperature in the summer midday often rose to 40 °C and even to 45 °C sometimes in recent years in some regions of China. Photosynthesis is closely related to plant growth and crop yields, and it seems highly sensitive to high temperature. Photosystem II (PS II) is considered as the most heat-sensitive component of the photosynthetic apparatus (Berry and Bjorkman 1980). Compared with reversible decline in photosynthesis after moderate heat stress, irreversible damage to the photosynthetic apparatus with subsequent greater inhibition of plant growth can be induced by severe heat stress for only a short period. So

this article focused on the effects of short-term high temperature on photosynthesis and PS II in the leaves of sorghum. So far, many studies have demonstrated that high temperature can decrease photosynthetic rate and PS II photochemistry efficiency in plants (e.g., Hamerlynck et al. 2000, Qiu and Lu 2003, Krause et al. 2010), however, few of them paid attention to the heat sensitivity of components in PS II. Maximal PS II photochemistry efficiency (Fv/Fm) is a classic parameter to reflect the whole PS II function, and its decrease indicates PS II damage or photo inhibition under environmental stress (Baker 2008). Nonetheless, this parameter was demonstrated to be less sensitive to high temperature stress, and cannot accurately reveal alterations of PSII behaviour (Wen et al. 2005). Recently, Li et al. (2009) reported that reaction centre and donor side of PS II in soybean leaves exhibited inconsistent changes but with the same decreased extent of Fv/Fm under different high temperature treatments. In other words, response of PS II to high temperature is a process including heterogeneous behaviours of its components, which was also proved by Mathur et al. (2011).

Chlorophyll a fluorescence transient (O-J-I-P) is the kinetics of fast fluorescence rise process, and has been accepted as a reliable and popular tool in photosynthesis research, especially to study PS II behaviour (Toth et al. 2007, Yang et al. 2007, Rapacz et al. 2008, 2010, Yan et al. 2008). The O-J-I-P transient seems very sensitive to environmental stress, and in particular to high temperature (Strasser 1997). O, J, I and P are a sequence of phases in the kinetics of fast fluorescence rise. Environmental stress often provokes the occurrence of K phase in this transient, suggesting that damage occurred in oxygen-evolving complex in the donor side of PS II (Strasser et al. 2004). A method called JIP test has been developed for quantification of OJIP transient using fluorescence intensity in these phases (Govindjee 1995). This test is a powerful tool for *in vivo* investigation of the whole PS II function including fluxes of absorption, trapping and electron transport (Strasser et al. 2000). In addition, it can show heterogeneous behaviours of the PS II components including reaction centres, donor side and acceptor side under environmental stress (Strasser et al. 2004). In this study, JIP test was adopted to investigate PS II behaviour in sorghum under high temperature stress.

Sorghum, an annual C4 crop, is commonly consumed as human food and livestock feed (Anglani 1998, Yildiz et al. 1998) and it feeds more than 500 million people in 98 countries (Pennisi 2009). High temperature studies on sorghum have been carried out for many years. It has been reported that high temperature delayed panicle emergence, decreased plant height, pollen production, pollen viability, seed set and seed yield, but had no significant effect on leaf water content in sorghum (Machado

and Paulsen 2001, Prasad et al. 2006, 2008, Jain et al. 2007, 2010). The negative effects of high temperature on photosynthesis and PS II in sorghum have been reported as well, but these studies associate with long-term effects of heat stress (Jagtap et al. 1998; Djanaguiraman et al. 2010). Jagtap et al. (1998) reported that marked decrease in Fv/Fm and chlorophyll content was observed in leaves of sorghum exposed to 40 °C even for 48 h. More recently, Djanaguiraman et al. (2010) found that long-term high temperature stress (45 days, 40/30 °C day/night) reduced photosynthetic rate, Fv/Fm and antioxidant enzymes activities in the leaves of grain sorghum. However, it is important to study the photosynthetic responses to short period of heat stress from an ecophysiological viewpoint, since exceptionally high temperature occurred mainly in the summer midday. In addition, no detailed PS II behaviour under high temperature can be found in previous studies on sorghum. Although Lu and Zhang (1998) have reported the decline of PS II function in sorghum under short-term high temperature stress, detached leaves were used in their experiment and the response of gas exchange was not elucidated.

In this study, gas exchange analysis and JIP test were carried out to dissect heat tolerance mechanism in sorghum, which may provide important information for its cultivation and management under global warming. Photosynthetic recovery after heat stress was detected as well, since it is one of the most important factors determining crop growth. We hypothesised that (i) short-term high temperature might decrease photosynthetic rate and PS II photochemistry capacity in leaves of sorghum, and heterogeneous behaviours of PS II components would occur. (ii) PS II photochemistry capacity might not completely recover 1 day after severe heat stress as high as 45 °C.

Materials and Methods

Plant material and treatment

Sorghum (*Sorghum bicolor* (L.) Moench) used in this study was a hybrid variety with cultivars L405A and 626 as its parents. Seeds were sown in plastic pots containing soil (five seeds per pot) and germinated. After 30 days, seedlings were transferred to plastic bottles (one seedling per bottle) containing 100 ml Hoagland nutrient solution (pH 5.7) and grown in artificial climatic chambers (Huier, Zheda Industrial Park, Hangzhou, China). The photon flux density was approximately 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (12 h per day from 07:00 to 19:00) in the chambers. Day/night temperature and humidity were controlled at 25/18 °C and 65 %, respectively, in the chambers. The nutrient solution was aerated for 10 min every day and refreshed every 2 days. After 30 days, seedlings with

uniform growth pattern (about 30 cm height and 0.7 cm diameter of the stem) were selected as experimental materials, and the newest fully expanded leaves were used for measuring photosynthetic and fluorescent parameters.

Artificial climatic chamber was used for high temperature treatments. The treatments were 40 °C for 1 h (H1), 40 °C for 3 h (H2), 45 °C for 1 h (H3) and 45 °C for 2 h (H4). Seedlings not exposed to high temperature were taken as control (CK). Three replicate seedlings were used for each treatment as well as CK. After high temperature treatments, seedlings were returned to room temperature (25 ± 1 °C), and then gas exchange and chlorophyll a fluorescence transient were analysed. These parameters were also measured in the seedlings 1 day after H2, H3 and H4 treatments.

Analysis of gas exchange

Measurement of gas exchange was carried out using an open photosynthetic system (TPS-1; PP Systems, Cambridge, UK). Photon flux density was set at $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ in leaf cuvette and the temperature, CO_2 concentration and relative humidity were dependent on ambient conditions. Photosynthetic rate (Pn), stomatal conductance (g_s), intercellular CO_2 concentration (Ci) and transpiration rate (E) were recorded simultaneously.

Measurement of chlorophyll a fluorescence transient

Chlorophyll a fluorescence emission was measured by a Handy PEA fluorometer (Hansatech, Cambridge, UK). Leaves were dark adapted for 30 min before they were measured. Illumination consisted of a 1 s pulse of continuous red light (650 nm peak wavelength, $3000 \text{ mol photons m}^{-2} \text{s}^{-1}$ maximum light intensity) provided by an array of three light-emitting diodes. Chlorophyll a fluorescence transients (OJIP) were quantified according to the JIP test (Strasser *et al.* 2004) by utilising the following original data: (i) fluorescence intensity at $20 \mu\text{s}$ (F_0 , when all reaction centres of PSII are open); (ii) the maximum fluorescence intensity (F_m , when all reaction centres of PSII are closed) and (iii) fluorescence intensities at $300 \mu\text{s}$ (K-step) and 2 ms (J-step). Using these original data, the following parameters can be calculated for quantifying PS II behaviour: (i) PS II performance index on absorption basis (PI(abs)); (ii) amount of active reaction centres per excited cross section (RC/CS); (iii) specific energy flux for absorption (ABS/RC), trapping (TR_0/RC), electron transport (ET_0/RC) and dissipation (DI_0/RC) per active reaction centre; (iv) relative variable fluorescence at $300 \mu\text{s}$ (V_k), the ratio of variable fluorescence $F_{300\mu\text{s}} - F_0$ to the amplitude $F_{2\text{ms}} - F_0$ (W_k), probability that a trapped exciton moves an electron into the electron transport

chain beyond Q_A (ψ_o) and quantum yield for electron transport (ψ_{Eo}). The calculation for these parameters has been illustrated by Strasser *et al.* (2004).

Statistical analysis

One-way ANOVA was carried out using SPSS computer package (SPSS Inc. 1999, Chicago, IL, USA) for all sets of data, and significant differences between means were determined through LSD test. Differences were considered statistically significant when $P < 0.05$.

Results

Effects of high temperature on gas exchange

Compared with CK, no significant change occurred in Pn, g_s and Ci after H1 treatment, but E increased significantly (Fig. 1). After H2 treatment, Pn and g_s significantly decreased ($P < 0.05$), and decrease also occurred in Ci and E (Fig. 1). After H3 and H4 treatments, Pn decreased significantly ($P < 0.05$), and the decrease was greater than that after H2 treatment (Fig. 1a). The H3 treatment had no significant effects on g_s and E, but significantly increased Ci ($P < 0.05$) (Fig. 1b–d). Significant increase in Ci was noted after H4 treatment ($P < 0.05$), and significant decrease in g_s and E occurred concomitantly ($P < 0.05$) (Fig. 1b–d).

Effects of high temperature on PS II performance and reaction centre

Insignificant decrease was observed in PI(abs) after H1 treatment (Fig. 2a). PI(abs) decreased after H2, H3 and H4 treatments significantly ($P < 0.05$), and the decrease was the greatest after H4 treatment and lowest after H2 treatment (Fig. 2a). It is shown in Figure 2b that no changes occurred in RC/CS after these treatments.

Effects of high temperature on PS II specific energy flux

It is shown in Figure 3a that no changes occurred in ABS/RC after these treatments. TR_0/RC and ET_0/RC were significantly decreased after all the treatments ($P < 0.05$) (Fig. 3b, c). Increase was observed in DI_0/RC after all the treatments, but the increase was significant only after H3 and H4 treatments ($P < 0.05$) (Fig. 3d).

Effects of high temperature on the donor and acceptor sides of PS II

It is shown in Figure 4a that no significant changes occurred in V_k after these treatments. The W_k decreased

Fig. 1 Changes in photosynthetic rate (Pn, a), stomatal conductance (g_s , b), intercellular CO₂ concentration (Ci, c) and transpiration rate (E, d) at high temperatures. CK indicates control without high temperature treatment; H1 indicates treatment at 40 °C for 1 h; H2 indicates treatment at 40 °C for 3 h; H3 indicates treatment at 45 °C for 1 h; H4 indicates treatment at 45 °C for 2 h. Data in the figure indicate mean of three replicates (\pm S.D.). Different letters on error bars indicate significant difference at $P < 0.05$. Symbols are the same in following figures.

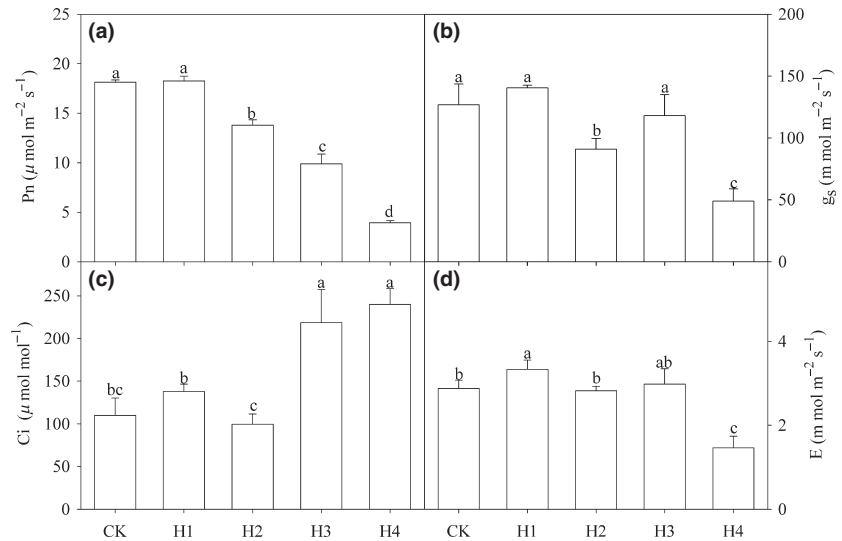
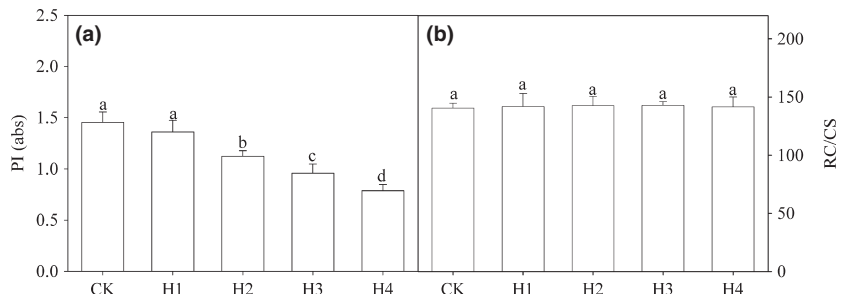


Fig. 2 Changes in PS II performance index on absorption basis (PI(abs), a) and amount of active reaction centres per excited cross section (RC/CS, b) at high temperatures.



significantly after all the treatments (Fig. 4b). Significant decrease was observed in ψ_o and ψ_{Eo} after H2, H3 and H4 treatments (Fig. 4c, d).

Effects of high temperature on chlorophyll a fluorescence transient

It is shown in Figure 5 that K-step did not appear after H4 treatment, but J-step is clearly higher than that in CK.

Photosynthetic recovery after high temperature treatments

PI(abs) and ψ_o recovered to CK level 1 day after H2, H3 and H4 treatments (Table 1). Pn recovered to CK level 1 day after H2 treatment, while it recovered to 80 % and 64 % of CK level, respectively, 1 day after H3 and H4 treatments (Table 1).

Discussion

Photosynthesis involves the parts of CO₂ fixation, photosynthetic electron transport for reducing power, and pro-

ton transport for adenosine triphosphate generation. The Pn would decrease if any part of photosynthesis was inhibited under environmental stress. PI(abs) reflects photosynthetic capability of the entire PS II similar to Fv/Fm, but is more acuter (Appenroth et al. 2001). Photosynthesis and PS II were not affected in leaves of sorghum at 40 °C for 1 h, as no significant changes were found in Pn and PI(abs) (Figs 1a & 2a). In contrast, transpiration was enhanced following increase in g_s under this treatment (Fig. 1b, d). It has been proved that reduced transpiration led to increase in leaf temperature and subsequent negative effects on photosynthesis in peach leaves (Duan et al. 2008). Thus, we propose that the enhanced transpiration served as a self-protection response in leaves of sorghum under this treatment, as it can help dissipate the harmful heat. Significant decrease in Pn was found under prolonged stress at 40 °C for 3 h, and the decrease became greater at 45 °C (Fig. 1a). It indicates that photosynthetic process was suppressed, but the reasons were not consistent under these treatments. It has been suggested that whether stomatal or non-stomatal factors are the main cause of the reduced Pn can be judged by the change patterns of g_s and Ci (Farquhar and

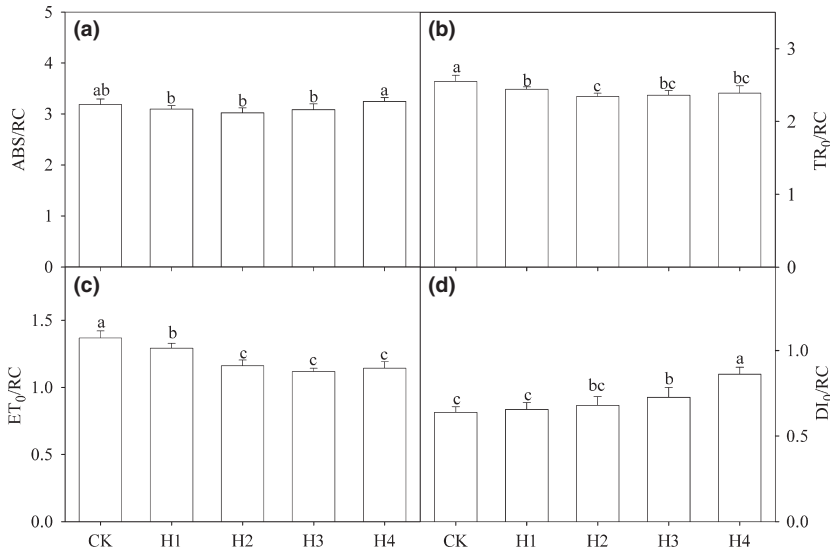


Fig. 3 Changes in specific energy flux for absorption (ABS/RC, a), trapping (TR₀/RC, b), electron transport (ET₀/RC, c) and dissipation (DI₀/RC, d) per reaction centre at high temperatures.

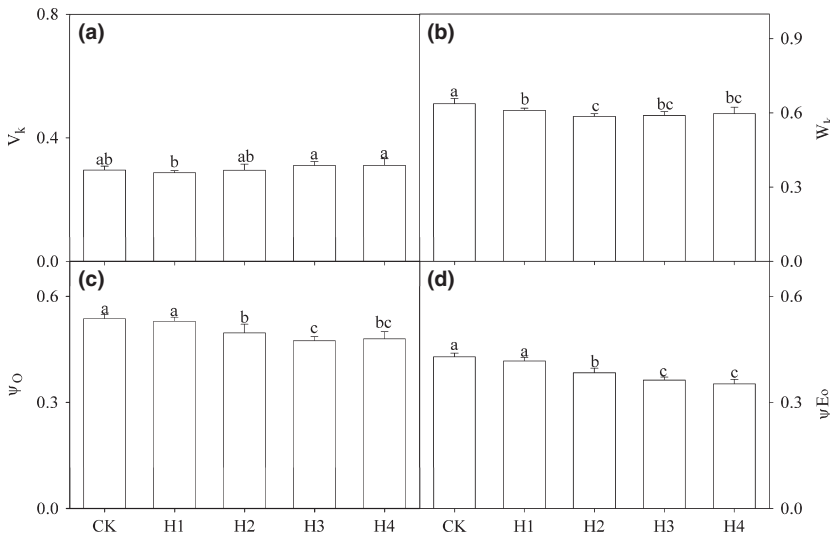


Fig. 4 Changes in relative variable fluorescence at 300 μs (V_k, a), the ratio of variable fluorescence F_{300μs}-F₀ to the amplitude F_{2ms}-F₀ (W_k, b), probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A (ψ₀, c) and quantum yield for electron transport (ψE₀, d) at high temperatures.

Sharkey 1982). If both C_i and g_s decreased simultaneously, Pn is mainly limited by stomatal conductance. If C_i increased but g_s decreased or kept constant, the decrease of Pn can be ascribed to the non-stomatal factors. At 40 °C for 3 h, decrease in Pn was mainly ascribed to stomatal limitation, as both C_i and g_s decreased simultaneously (Fig. 1b, c). Moreover, decline in PS II function indicated by the decreased PI(abs) also contributed to the decrease in Pn (Fig. 2a). By contrast, decrease in Pn did not result from stomatal limitation at 45 °C, as significant increase in C_i together with no increase in g_s was observed (Fig. 1b, c). Greater decrease in PI(abs) suggests more severe stress on PS II at 45 °C (Fig. 2a), which might be the primary cause for decrease in Pn.

The PI(abs) is a combined parameter, and changes of energy flux or density of reaction centres in PS II can

influence its value (Strasser et al. 2004). The photon flux can be absorbed by antenna pigments (called absorption flux, ABS) creating excited chlorophyll. Part of the excitation energy is dissipated mainly as heat, and the other part is transferred to the reaction centre (called trapping flux, TR). Part of the trapped energy is converted to redox energy by reducing the electron acceptor Q_A to Q_A⁻ which is then re-oxidised to Q_A by reducing the electron transport chain beyond Q_A⁻ (called electron transport flux, ET). Our results show no changes in RC/CS and ABS/RC at high temperatures (Figs 2b & 3a), indicating that PS II reaction centres and antenna pigments in leaves of sorghum possess a certain heat tolerance. However, the absorbed energy by antenna was largely dissipated as heat at high temperatures, which is showed by higher DI₀/RC (Fig. 3d). As a result, TP₀/RC

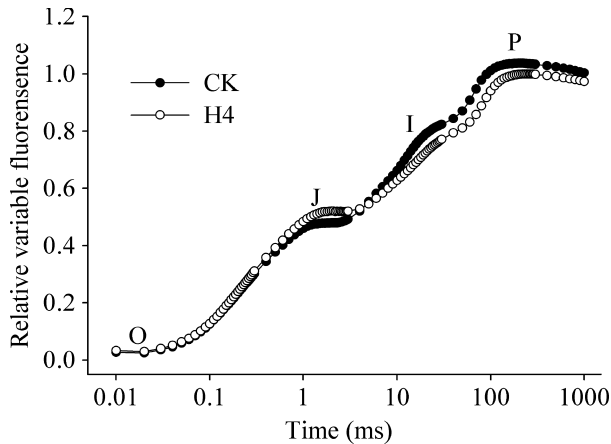


Fig. 5 Chlorophyll a fluorescence transient at 45 °C for 2 h. O, J, I and P indicates the specific steps in this transient.

Table 1 Changes in photosynthetic rate (Pn), PS II performance index on absorption basis (PI(abs)) and probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A (ψ_o) 1 day after high temperature stress

Treatments	Pn	PI(abs)	ψ_o
CK	18.5 ± 0.5	1.46 ± 0.10	0.54 ± 0.01
H2	18.2 ± 0.7	1.51 ± 0.16	0.54 ± 0.03
H3	15.2 ± 1.1	1.45 ± 0.14	0.53 ± 0.01
H4	11.3 ± 0.3	1.49 ± 0.19	0.53 ± 0.01

Data in the table indicate means of three replicates (\pm S.D.).

CK indicates control without high temperature treatment; H2 indicates treatment at 40 °C for 3 h; H3 indicates treatment at 45 °C for 1 h; H4 indicates treatment at 45 °C for 2 h.

and ET_0/RC declined (Fig. 3b, c), which might result in the decrease of PI(abs). Contrary to our results, Wen et al. (2005) demonstrated that TP_0/RC and ET_0/RC increased markedly in the leaves of *Artemisia anethifolia* under high temperature stress, and this change could be explained by heat-induced decrease in RC/CS. Since no changes in RC/CS and ABS/RC were noted in this study, decline of TP_0/RC and ET_0/RC should be due to changes in the donor side and/or acceptor side of PS II at high temperatures.

It has been widely reported that an early step labelled 'K' occurred around 300 μ s during the rise of O-J-I-P transient in heat-treated leaves, and then O-J-I-P transient becomes O-K-J-I-P transient (Wen et al. 2005, Yang et al. 2007). K-step occurred due to the damage in donor side of PS II, especially the oxygen-evolving complex (Strasser et al. 2004). However, K-step was not found during the rise of O-J-I-P transient in leaves of sorghum even after 45 °C treatment for 2 h (Fig. 5). Consistently, no signifi-

cant increase in V_k was recorded after all the treatments (Fig. 4a). It implies that donor side in leaves of sorghum is resistant to high temperature stress. Increase in W_k is also commonly used to indicate the heat-induced damage of oxygen-evolving complex in donor side of PS II (Wen et al. 2005, Li et al. 2009). Nonetheless, significant decrease in W_k unlike the constant V_k was found in leaves of sorghum at high temperatures (Fig. 4b). The W_k equals to V_k divided by V_j (Strasser et al. 2004), so changes in W_k associate with the increase of V_j at high temperatures in this study. J-step appears because accumulation of Q_A^- reaches the maximal level (Govindjee 1995, Strasser et al. 1995). An obvious higher J-step could be found in the O-J-I-P transient at 45 °C for 2 h (Fig. 5), indicating the increased accumulation of Q_A^- due to the inhibited electron transport beyond Q_A . It has been reported that donor side of PS II was more sensitive to high temperature than the acceptor side in leaves of soybean and wheat (Lu and Zhang 2000, Li et al. 2009, Hamid et al. 2010). In contrary, the electron transport in acceptor side was proved to be more susceptible to high temperature in leaves of sorghum, since significant decrease in ψ_o as well as ψ_{Eo} already occurred at 40 °C for 3 h and became greater at 45 °C (Fig. 4c, d).

To further investigate the heat tolerance of photosynthesis and PS II in sorghum, photosynthetic recovery after high temperature stress was examined. The PS II performance and electron transport in the acceptor side completely recovered 1 day after high temperature stress even as high as 45 °C, which was shown by the parameters of PI(abs) and ψ_o in Table 1. The timely recovery of PS II performance after high temperature stress reflects the high self-remediation capacity of photosynthetic apparatus, which is favourable for sorghum to meet the challenge of global warming. Salvucci and Crafts-Brandner (2004) demonstrated that CO_2 fixation process was also greatly sensitive to heat stress due to inhibited Rubisco activation via a direct effect on Rubisco activase. In this study, Pn did not recover in parallel with PI(abs) after 45 °C stress (Table 1), and we infer that it resulted from the heat-induced irreversible damage to CO_2 fixation process. Thus, to enhance the heat stability of CO_2 fixation may be crucial for improving growth of sorghum under global warming, considering the timely recovery of photosynthetic apparatus function after high temperature stress.

To summarise, in agreement with the first hypothesis, photosynthesis and PS II performance in leaves of sorghum were negatively affected by high temperature, and acceptor side of PS II was more sensitive to high temperature stress than donor side and reaction centre. The PS II performance completely recovered 1 day after high temperature stress even at 45 °C, which is in disagreement with the last hypothesis.

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