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Role of alternative oxidase pathway in protection against drought-induced photoinhibition in pepper leaves

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Abstract

The aim of this study was to assess the impact of the mitochondrial alternative oxidase (AOX) pathway on energy metabolism in chloroplasts, and evaluate the importance of the AOX in alleviating drought-induced photoinhibition in pepper (*Capsicum annuum* L.). Inhibition of AOX pathway decreased photosynthesis and increased thermal energy dissipation in plants under normal conditions. It indicated that AOX pathway could influence chloroplast energy metabolism. Drought reduced carbon assimilation. Photoinhibition was caused by excess of absorbed light energy in spite of the increase of thermal energy dissipation and cyclic electron flow around PSI (CEF-PSI). Upregulation of AOX pathway in leaves experiencing drought would play a critical role in protection against photoinhibition by optimization of carbon assimilation and PSII function, which would avoid over-reduction of photosynthetic electron transport chain. However, inhibition of AOX pathway could be compensated by increasing the thermal energy dissipation and CEF-PSI under drought stress, and the compensation of CEF-PSI was especially significant.

Additional key words: alternative oxidase pathway; *Capsicum annuum* L; chlorophyll fluorescence; drought; photoinhibition; photosynthesis.

Introduction

Photosynthesis includes photochemical reactions and carbon assimilation (Raghavendra and Padmasree 2003). Photosynthesis captures light energy to produce ATP and NADPH, which is provided to the Calvin cycle as reducing power (Allakhverdiev 2011). The production and nocsumption of ATP and NADPH must be balanced to prevent photoinhibition or photodamage (Walker *et al*. 2014). However, excess light energy would result in the accumulation of reducing equivalents in the form of NADPH generated by photochemical reactions and be assumed to produce reactive oxygen species (Foyer *et al*. 2002, Ort and Baker 2002, Mohanty *et al.* 2007, Zhang *et al*. 2011). Accumulation of reducing equivalents in the chloroplasts causes the over-reduction of the photosynthetic electron transport chain and may result in generation of reactive oxygen species, leading to photoinhibition (Yoshida *et al*. 2007). To counteract photoinhibition, plants have evolved photoprotective mechanisms in chloroplast including thermal energy dissipation (Demmig-Adams and Adams 1996, Song *et al*. 2011), cyclic electron flow around PSII/PSI (Allakhverdiev *et al*. 1997, Walker *et al*. 2014), and water-water cycle (Asada 1999). While such intra-chloroplastic defense systems have been studied extensively, little is known about the extra-chloroplastic defense systems (Yoshida *et al.* 2007).

As the center of energy metabolism, mitochondrial respiration is thought to play roles in optimizing photosynthesis, especial under stress conditions (Raghavendra and Padmasree 2003, Yoshida *et al*. 2006, Feng *et al*. 2015). Reducing equivalents generated in the chloroplasts

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Abbreviations: AOX – alternative oxidase; AQY – apparent quantum yield; CEF-PSI – cyclic electron flow around PSI; DM – dry mass; ETR – photosynthetic electron transport rate; F_0 – minimal fluorescence yield of the dark-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; FM – fresh mass; F_v/F_m – maximal quantum yield of PSII photochemistry; LSP – photosynthetic light-saturation points; NPQ – nonphotochemical quenching coefficient; P_m – maximal P700 changes; P_{max} - maximum net photosynthetic rate; P_N – net photosynthetic rate; PEG – polyethylene glycol; q_P – photochemical quenching coefficient; RLCs – rapid light curves; RWC – relative water content; SHAM – salicylhydroxamic acid; TM – turgid mass; V_{KCN} – AOX pathway capacity; V_t – total respiration rate; Φ_{PSI} – photochemical quantum yield of PSI; Φ_{PSII} – effective quantum yield of PSII photochemistry.
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may be transported to the cytosol *via* malate/oxaloacetate shuttle and used in other cell compartments such as mitochondria (Nunes-Nesi *et al*. 2008, Hu *et al.* 2017). Alternative oxidase (AOX), the unique terminal oxidase in plant mitochondria, accepts electrons directly from ubiquinol and reduces O_2 to H_2O without proton translocation across inner membrane of mitochondria (Dahal *et al.* 2014). Therefore, mitochondrial alternative oxidase electron transport pathway (AOX pathway) is engaged in the dissipation of excess reducing equivalents from chloroplasts *via* malate/oxaloacetate shuttle, and may play a particular role in protecting plants from photoinhibition (Yoshida *et al.* 2007, Dahal *et al.* 2014). Zhang *et al.* (2012) observed that inhibition of the AOX pathway by AOX inhibitors (salicylhydroxamic acid, SHAM) decreased the initial activities of NADP-MDH (NADP-malate dehydrogenase) in *Rumex* K-1 leaves under intense light, which resulted in the rapid accumulation of NADPH in chloroplasts and the restriction of the photosynthetic linear electron flow. Compared to a wild type, *aox*1a mutant exhibited a lower net CO_2 assimilation rate and NADP-MDH activity, which was accompanied by a lower maximum electron transport rate and quantum yield of PSII, and higher excitation pressure on PSII and nonphotochemical quenching in chloroplasts (Gandin *et al.* 2012). The amounts of AOX protein and AOX pathway activities in *pgr*5 and *crr*2-2, *Arabidopsis thaliana* mutants defective in cyclic electron flow around PSI (CEF-PSI), were higher than those in the wild type (Yoshida *et al*. 2007). These results suggest that mitochondrial AOX pathway and intrachloroplastic defense systems interact with each other and protect against photoinhibition together.

Drought is a major abiotic stress and adversely restricts crop growth, development, and productivity (Boyer 1982). Drought inhibits leaf net photosynthetic rate because of stomatal limitation or/and nonstomatal limitation (Yin *et al*. 2005, Jia *et al*. 2008, Erice *et al*. 2011), which leads to reduced utilization of absorbed light energy in chloroplasts (Ort and Baker 2002, Hu *et al.* 2017). This results in imbalance between the light absorption and energy utilization in chloroplasts (Ivanov *et al.* 2008). Drought increased the amount of leaf AOX protein and also enhanced the rate of AOX pathway capacity in pea leaves (Taylor *et al*. 2002). Dahal *et al.* (2014, 2015) observed that knockdown of AOX increased the susceptibility of tobacco to a drought-induced biochemical limitation of photosynthesis, while AOX overexpression reduced this susceptibility. Upregulation of the AOX pathway protects the photosynthetic electron transport chain from harmful effects of excess light during drought in wheat leaves (Bartoli *et al*. 2005). These results indicate that AOX pathway would have influence on defense systems and maintain the energy balance in chloroplasts *via* malate/oxaloacetate shuttle under drought, however, the interactions of mitochondrial AOX pathway with chloroplast energy metabolism have not been fully elucidated.

In the present work, we examined the effects of the inhibition of AOX pathway by SHAM on the gas exchange and chlorophyll (Chl) fluorescence in pepper leaves under drought conditions. The aim of this study was to evaluate the impact of the AOX pathway on energy metabolism in chloroplasts. Photoprotection mechanisms of the AOX pathway were discussed.

Materials and methods

Plant materials: Pepper (*Capsicum annuum* L. cv. Caola No. 9) was used for this experiment. The seeds were sown in a medium containing a mixture of grass peat and perlite (8:2, v/v) in pots (30 × 30 cm) placed in a greenhouse. Plants at the 20-leaf stage were transferred into a container filled with 500 ml of Enshi nutrient solution (Yu and Matsui 1997). The environmental condition were as follows: the temperature range approximately 18–28°C, the maximum PAR was approximately 800 μmol(photon) m^{-2} s^{-1}.

Experimental design: SHAM pretreatment and water-restriction treatment started when plants were cultured in the nutrient solution for one week. Plants were sprayed with 0 or 1 mM SHAM solutions, respectively, for 4 h in a dark room. Then, half of 0 and 1 mM SHAM-pretreated plants was transferred into 15% polyethylene glycol (PEG 6000) solution with Enshi nutrient under the greenhouse conditions. The four treatments employed were:

Treatment	Solution
Control	Enshi nutrient solution/ 0 mM SHAM pretreatment
SHAM	Enshi nutrient solution/ 1 mM SHAM pretreatment
PEG	15% PEG6000 solution with Enshi/ 0 mM SHAM-pretreatment
PEG + SHAM	15% PEG6000 solution with Enshi/ 1 mM SHAM-pretreatment

The leaf relative water content, alternative pathway respiration, net photosynthetic rate (P_N) light-response curves, and Chl fluorescence in pepper leaves were measured 4 d after treatments.

Leaf water status: Leaf relative water content (RWC) was determined as described by Zandalinas *et al.* (2016).

Leaves were weighed to obtain fresh mass (FM). Then, leaves were placed in a beaker with water and kept overnight in the dark, allowing leaves to become fully hydrated. Leaves were reweighed to obtain turgid mass (TM) and dried at 80°C for 48 h to obtain dry mass (DM). Finally, RWC was calculated as:
RWC = [(FM – DM)/(TM – DM)]× 100.

Respiration rate was measured using a Clark-type oxygen electrode (*Oxygraph-lab*, *Hansatech*, UK) at 25°C according to Hu *et al.* (2017). The samples (0.1 g fresh mass) were kept in the dark for 30 min before respiration measurements were carried out. To assess the maximum capacity of the AOX pathway, the cytochrome *c* pathway was inhibited with 1 mM KCN. The AOX pathway capacity (V_{KCN}) was defined as O_2 uptake rate in the presence of KCN.

Net photosynthetic rate in response to light (P_N-PAR curve): P_N-PAR curve was measured using an *LI-6400XT* (*LI-COR Biosciences*, Lincoln, NE, USA). During the measurements, the air temperature, relative humidity, and CO_2 concentration inside the IRGA chamber were maintained at 30°C, 60%, and 380 μmol mol^{-1}. P_N was determined at 14 levels of PAR [1,600; 1,400; 1,000; 800, 600, 400, 200, 150, 120, 100, 50, 20, 0 μmol(photon) m^{-2} s^{-1}]. The leaf was exposed to 1,600 μmol(photon) m^{-2} s^{-1} for 1,200 s before P_N was determined, thereafter, the leaf was exposed to series of decreasing light intensities for 600 s at each light level. The apparent quantum yield (AQY), maximum net photosynthetic rate (P_{max}), photosynthetic light-saturation points (LSP) were analyzed with P_N-PAR response curve according to Ye (2007).

Simultaneous measurements of Chl fluorescence and P700: Chl fluorescence and P700 were synchronously measured with the *Fluo + P700* Measuring Mode of the *Dual-PAM-100/F* (*Walz*, Effeltrich, Germany) according to instruction manual for *DUAL-PAM-100*. After 30 min of adaptation in complete darkness, the minimal fluorescence yield of the dark-adapted state (F_0) and maximal fluorescence yield of the dark-adapted state (F_m) were measured. An actinic light [190 μmol(photon) m^{-2} s^{-1}] was then switched on and a saturation pulse [12,000 μmol(photon) m^{-2} s^{-1}] was applied at regular intervals (20 s) during actinic light illumination period for induction curves of Chl fluorescence and P700 parameters. RLCs (rapid light curves) was also determined after induction curves. Sample was illuminated stepwise at increasing light intensities [from 11 to 1,450 μmol(photon) m^{-2} s^{-1}]. Saturation pulse was applied at the end of each light step (illumination time was 10 s) for determination of Chl fluorescence and P700 parameters. The determined parameters included: the maximal P700 changes (P_m), maximal quantum yield of PSII photochemistry (F_v/F_m), photochemical quantum yield of PSI ($Y_{(I)}$), effective quantum yield of PSII photochemistry (Φ_{PSII}), photochemical quenching coefficient (q_P), nonphotochemical quenching coefficient (NPQ), and photosynthetic electron transport rate (ETR). The CEF-PSI were estimated by the $ETR_{(I)}/ETR_{(II)}$ (Yamori *et al.* 2011).

Statistical analysis: The results were reported as means with standard error. The significance of results was checked by using the least-significant difference (LSD) test at $P<0.05$ with *SPSS 11.5* for *Windows* (*SPSS Inc. Chicago*, IL, USA) *via* one-way analysis of variance (*ANOVA*).

Results

RWC, V_{KCN}, F_v/F_m and P_m: Plants under normal condition (control) showed RWC of 92.2 ± 1.0%, while drought (15% PEG treatment) significantly decreased RWC to values of 55.1 ± 2.9%. The total respiration rates (V_t) in the leaves under normal and drought condition were similar, but the AOX pathway capacity (V_{KCN}) increased by 34.6% in leaves under drought condition. SHAM (1 mM) inhibited V_{KCN} by about 44.8% in leaves from both normal and drought conditions. Drought induced the decrease of F_v/F_m, which was aggravated by SHAM treatment. However, there was little change in F_v/F_m when the AOX pathway was inhibited by SHAM at normal conditions. There was also little change in P_m in leaves under four treatment conditions (Table 1).

Table 1. Effects of PEG and SHAM on the relative water content (RWC), total respiration rate (V_t), AOX pathway capacity (V_{KCN}), maximal quantum yield of PSII photochemistry (F_v/F_m) and maximal P700 changes (P_m) of pepper leaves after four days of treatment. Data are the means of independent measurements of five replicates with standard errors. Values followed by *different letters* are significant at 0.05% level.

	Control	SHAM	PEG	PEG + SHAM
RWC [%]	92.02 ± 0.54^a	92.45 ± 0.41^a	55.05 ± 1.64^b	55.17 ± 1.11^b
V_t [μmol(O_2) g^{-1}(FM) h^{-1}]	26.7 ± 0.4^a	19.3 ± 0.3^c	27.2 ± 0.4^a	22.8 ± 0.2^b
V_{KCN} [μmol(O_2) g^{-1}(FM) h^{-1}]	10.7 ± 0.4^b	5.8 ± 0.2^d	14.4 ± 0.7^a	8.1 ± 0.3^c
F_v/F_m	0.840 ± 0.007^a	0.831 ± 0.009^a	0.806 ± 0.004^b	0.764 ± 0.006^c
P_m	0.452 ± 0.003^a	0.454 ± 0.002^a	0.456 ± 0.003^a	0.454 ± 0.001^a

Gas-exchange characteristics: Drought significantly decreased P_N, P_{max}, LSP, and AQY. SHAM treatment aggravated the decrease of P_N, P_{max}, LSP, and AQY in leaves under normal and drought conditions (Fig. 3, Table 2).

RLCs of Chl fluorescence parameters: Following increases of light intensity, values of Φ_{PSII} and q_P decreased, however, NPQ and $ETR_{(I)}/ETR_{(II)}$ increased. Drought induced the decreases of Φ_{PSII} and the increases of NPQ and $ETR_{(I)}/ETR_{(II)}$, however, there was no obvious change in q_P. SHAM treatment aggravated the decreases of Φ_{PSII} and q_P, but induced the increase of NPQ in leaves under normal and drought conditions. There was a slight increase of $ETR_{(I)}/ETR_{(II)}$ in leaves under drought, however, SHAM treatment significantly increased $ETR_{(I)}/ETR_{(II)}$ in drought-treated leaves (Fig. 1).

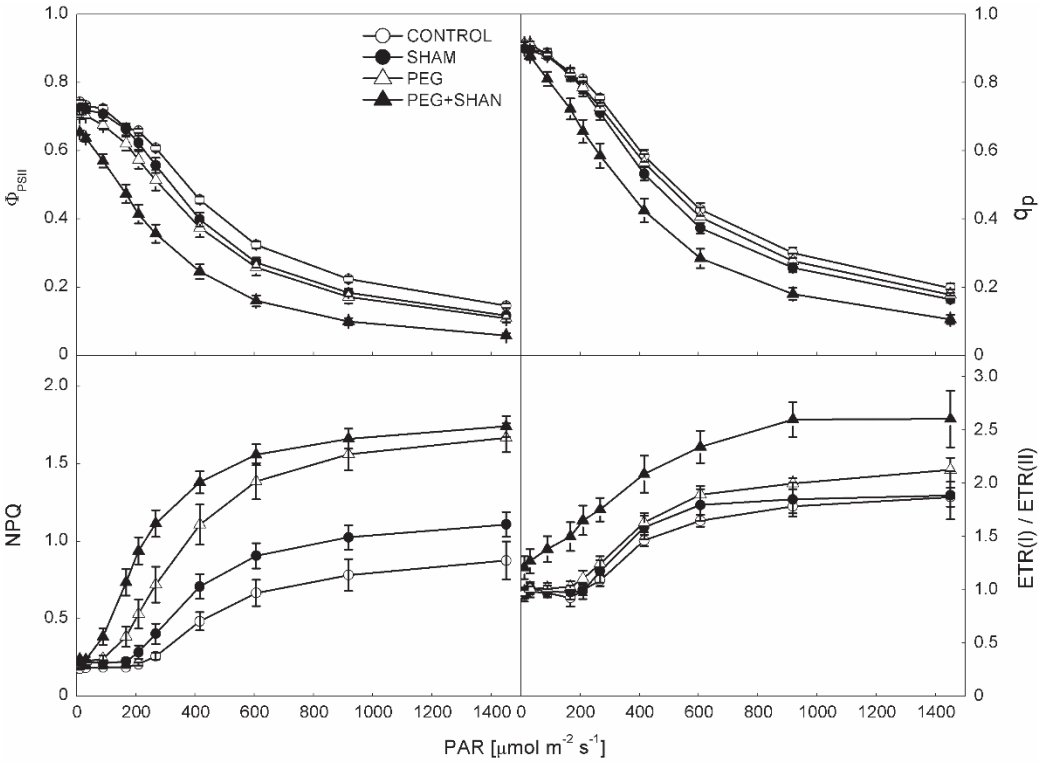

Fig. 1. Effects of PEG and SHAM on RLCs of chlorophyll fluorescence parameters of pepper leaves after four days of treatment. Data represent the means of independent measurements of five replicates with standard errors shown by vertical error bars.

Table 2. Effects of PEG and SHAM on the gas exchange characteristics of pepper leaves after four days of treatment according P_N–PAR response curve. Data are the means of independent measurements of three replicates with standard errors. Values followed by *different letters* are significant at 0.05% level.

	Control	SHAM	PEG	PEG + SHAM
P_{max} [μmol(CO_2) m^{-2} s^{-1}]	15.5 ± 0.4^a	8.8 ± 0.9^b	5.5 ± 0.7^c	2.9 ± 0.3^d
AQY	0.041 ± 0.001^a	0.034 ± 0.003^b	0.020 ± 0.002^c	0.013 ± 0.002^d
LSP [μmol(photon) m^{-2} s^{-1}]	$1{,}830.2 \pm 54.3^a$	956.6 ± 25.8^b	745.8 ± 49.0^c	598.2 ± 56.06^d

Induction curves of Chl fluorescence parameters: Values of Φ_{PSII} and q_P increased with a delay of approximate 40 s, whereas the increases of NPQ and $ETR_{(I)}/ETR_{(II)}$ occurred without a delay. During prolonged illumination, $ETR_{(I)}/ETR_{(II)}$ decreased after about 80 s. NPQ also decreased after about 100 s under normal and drought conditions, however, though it was maintained stable under SHAM and PEG + SHAM treatments. Drought caused decreases of Φ_{PSII} and q_P, but induced the increase of NPQ. SHAM treatment aggravated the decreases of PSII and q_P and promoted the increase of NPQ in leaves under normal and drought conditions. PEG + SHAM treatment induced the increase of $ETR_{(I)}/ETR_{(II)}$, however, drought only induced the increase of $ETR_{(I)}/ETR_{(II)}$ during the first illumination time (Fig. 2).

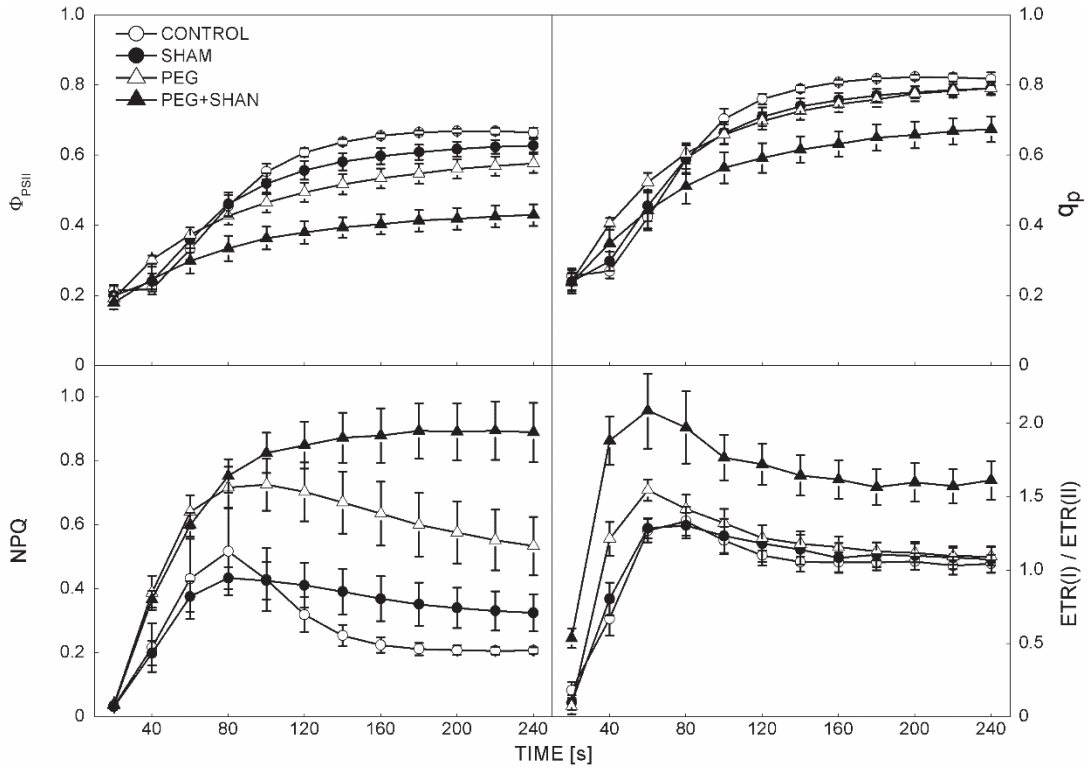

Fig. 2. Effects of PEG and SHAM on induction curves of chlorophyll fluorescence parameters of pepper leaves after 4 d of treatment. Data represent the means of independent measurements of five replicates with standard errors shown by vertical error bars.

Discussion

There are reports showing that the AOX pathway is upregulated in plants by a wide range of abiotic stresses (Wagner and Krab 1995, Clifton *et al.* 2005). The level of AOX proteins and AOX pathway capacity increased in plants subjected to drought (Taylor *et al.* 2002, Bartoli *et al*. 2005, Hu *et al*. 2010). In the present study, we also observed AOX capacity upregulated by drought (Table 1). AOX pathway is a non-phosphorylating pathway and can efficiently oxidize the excess of reducing equivalents generated in chloroplasts (Gandin *et al*. 2012, Zhang *et al*. 2012). In this way, AOX pathway is believed to benefit photosynthesis and protect against photoinhibition by balancing the cellular energy under a variety of environmental conditions (McKenzie and McIntosh 1999, Padmasree *et al.* 2002, Bartoli *et al*. 2005, Yoshida *et al.* 2007). In the present study, that decrease of F_v/F_m in pepper leaves under drought stress was accompanied by significant decreases of P_N, P_{max}, AQY, and LSP (Fig. 3; Table 1, 2) suggested that drought-induced photoinhibition was partly due to decrease of CO_2 assimilaiton. Drought-induced photoinhibition was aggravated by inhibition of the AOX pathway (Table 1). The decreases in P_N, P_{max}, AQY, and LSP were observed in leaves treated by SHAM under drought stress (Fig. 3; Table 2). These results suggested that upregulation of AOX pathway in pepper leaves could protect against drought-induced photoinhibition, which

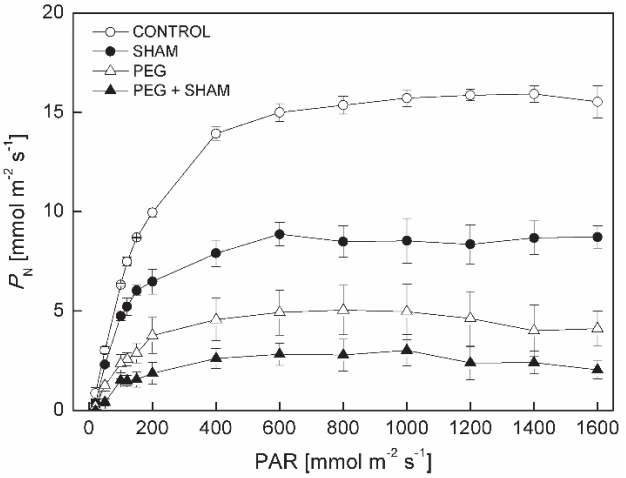

Fig. 3. Effects of PEG and SHAM on P_N-PAR response curve of pepper leaves after four days of treatment. Data represent the means of independent measurements of three replicates with standard errors shown by vertical error bars.

was partly due to the optimization of carbon assimilation. Calvin cycle is the main sink of the reducing equivalents produced by photochemical reactions (Tikkanen *et al.* 2014). We also observed that decreases of P_N, P_{max}, AQY, and LSP in SHAM-treated leaves under normal conditions

(Fig. 3; Table 2), indicating that AOX pathway is essential for the maintenance of photosynthetic carbon assimilation (Raghavendra and Padmasree 2003).

The photochemical reactions in photosynthesis are among the fastest events, taking place on time scale ranging from tens of femtoseconds to several hundred nanoseconds (Mamedov *et al.* 2015). However, activation of photosynthetic enzymes requires several minutes (Govindjee and Wasielewski 1989, Eichelmann *et al*. 2009). Chl fluorescence measurement is rapid, therefore RLCs are able to detect rapid changes in photosynthetic activity, in particular PSII function. In order to probe the effects of carbon assimilation on PSII function and energy dissipation mechanism in chloroplasts, we also measured the induction curves of Chl fluorescence.

Φ_{PSII} is an estimate of the proportion of photons used in photochemistry, and q_P is an estimate of the proportion of oxidized PSII centers (Maxwell and Johnson 2000, Bartoli *et al*. 2005). According to RLCs, there was little change in the q_P and slight decrease of Φ_{PSII} in SHAM-treated leaves under normal conditions (Fig. 1), which indicated that AOX pathway was not crucial for photochemical reaction under normal conditions. However, the inhibition of AOX activity caused significant decreases in q_P and Φ_{PSII} in leaves experiencing drought (Fig. 1). We also observed a decline of q_P and Φ_{PSII} in SHAM-treated leaves under drought conditions compared to that under normal conditions according to induction curves (Fig. 2). These results indicate that AOX activity is important in optimizing PSII function and avoiding over-reduction of PSII of plants experiencing drought, which could contribute to the protection against photoinhibition.

Thermal energy dissipation and CEF-PSI mechanisms seem to be operating in leaves exposed to drought (Golding and Johnson 2003, Živčák *et al*. 2013). If CEF-PSI is functioning, $ETR_{(I)}$ is larger than $ETR_{(II)}$ (Yamori *et al.* 2011). We observed that NPQ and $ETR_{(I)}/ETR_{(II)}$ just rapidly increased during the first illumination during induction curves (Fig. 2). This result indicated that thermal energy dissipation and CEF-PSI were the rapid forms of energy dissipation in chloroplasts. This conclusion was supported by the results that NPQ and $ETR_{(I)}/ETR_{(II)}$ rapidly increased upon increases in light intensity (Fig. 1). Drought induced higher increase of NPQ than that of $ETR_{(I)}/ETR_{(II)}$, however, there was more marked increase of $ETR_{(I)}/ETR_{(II)}$ than that of NPQ in SHAM-treated leaves under drought conditions (Fig. 1,2). These results suggested that the decrease in AOX activity could be compensated by increases in thermal energy dissipation and CEF-PSI under drought stress, especially CEF-PSI. Although CEF-PSI can serve to protect PSII, the stability of PSI is essential for the stimulation of CEF-PSI (Lei *et al*. 2014). We observed that P_m remained stable in leaves under drought with/without the SHAM treatment (Table 1). There were no changes in F_v/F_m and $ETR_{(I)}/ETR_{(II)}$, however, the significant increase of NPQ in SHAM treatment under normal conditions (Table 1; Fig. 1, 2), which suggested that AOX pathway could influence chloroplast energy metabolism under normal conditions.

In conclusion, AOX pathway could influence chloroplast energy metabolism and is essential for the maintenance of photosynthetic carbon assimilation in pepper leaves under normal conditions. Drought induced upregulation of the AOX pathway, which plays an important role in protection against drought-induced photoinhibition. AOX pathway could optimize carbon assimilation and PSII function in plants experiencing drought, which could help avoid overreduction of PSII. However, inhibition of AOX pathway could be compensated by increasing the thermal energy dissipation and CEF-PSI under drought stress, and the compensation of CEF-PSI was especially significant.

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