Increasing cyclic electron flow mediated by NDH is related to heat tolerance under low light in grape leaves

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Examination of the effects of high temperature (42 ℃) on the photoinhibition of photosystem II (PSII) in grape leaves revealed that the extent of photoinhibition of PSII was lower in the light (200 μmol m^{-2} s^{-1}) than in the dark. Heat stress in the dark induced severe injury in the grapevines, as determined by the critical temperature (Tc). The maximal efficiency of PSII photochemistry (Fv/Fm) decreased significantly in the dark, but it decreased much less in the light. In addition, there was a lower level of degradation of the D1 protein in the light than in the dark. Furthermore, the NAD(P)H dehydrogenase (NDH)-dependent cyclic electron flow (CEF) was remarkably enhanced in the light, but it was suppressed in the dark. The half-time of $P700^+$ re-reduction (t1/2) was reduced moer in in the light than in the dark during heat stress. Compared to the control leaves, the antimycin A (AA)-treated leaves showed much less of a decrease in Fv/Fm in the light than in the dark during heat stress; however, this increase seemed to disappear in methyl viologen (MV)-treated leaves. Based on these results, we propose a significant physiological function of the NDH-dependent CEF pathway under low light is the protection of PSII against heat-induced photoinhibition.

Increasing Cyclic Electron Flow Mediated by NDH is Related to Heat Tolerance under Low Light in Grape Leaves

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Abstract: Examination of the effects of high temperature (42 ℃) on the photoinhibition of photosystem II (PSII) in grape leaves revealed that the extent of photoinhibition of PSII was lower in the light (200 μmol m^{-2} s^{-1}) than in the dark. Heat stress in the dark induced severe injury in the grapevines, as determined by the critical temperature (Tc). The maximal efficiency of PSII photochemistry (Fv/Fm) decreased significantly in the dark, but it decreased much less in the light. In addition, there was a lower level of degradation of the D1 protein in the light than in the dark. Furthermore, the NAD(P)H dehydrogenase (NDH)-dependent cyclic electron flow (CEF) was remarkably enhanced in the light, but it was suppressed in the dark. The half-time of $P700^+$ re-reduction (t1/2) was reduced moer in in the light than in the dark during heat stress. Compared to the control leaves, the antimycin A (AA)-treated leaves showed much less of a decrease in Fv/Fm in the light than in the dark during heat stress; however, this increase seemed to disappear in methyl viologen (MV)-treated leaves. Based on these results, we propose a significant physiological function of the NDH-dependent CEF pathway under low light is the protection of PSII against heat-induced photoinhibition.

Keywords: heat stress; low light; photoinhibition; NAD(P)H dehydrogenase; cyclic electron transport; grapevine

1. Introduction

There is general agreement that photosynthesis in higher plants is one of the most heat-sensitive processes that we know of (Berry & Bjorkman 1980; Salvucci 2008; Sharkey 2005). Photosystem II (PSII), with its oxygen-evolving complex and carbon assimilation, is believed to be the major heat stress-sensitive site in photosynthetic machinery (Murata et al. 2007; Nishiyama et al. 2006). Some authors have also suggested that high temperature suppresses the synthesis of D1 proteins de novo through the accumulation of reactive oxygen species (ROS), which inhibit the repair process of PSII (Murata et al. 2007; Takahashi & Badger 2011).

The damage to PSII caused by high temperatures in the absence of light has been widely observed among plant species (Essemine et al. 2016; Li et al. 2009; Xu et al. 2006). Interestingly, a protective effect of light on the photosynthetic performance of plants that are subjected to high temperature was reported (Buchner et al. 2015; Havaux et al. 1991; Marutani et al. 2012). However, the mechanisms underlying the relationship between light and temperature in determining the damage to photosystems are still unclear.

It has been determined that the cyclic electron flow (CEF) around photosystem I is essential for photoprotection in higher plants (Brestic et al. 2016; Essemine et al. 2017; Munekage et al. 2004; Sun et al. 2016). Recently, it was suggested that the CEF also plays an important role in the stabilization of the oxygen evolving complex (OEC) (Huang et al. 2016). Two possible CEF pathways exist in higher plants; the major pathway depends on two additional proteins, PGR5 and PGR5-LIKE1 (PGRL1) (DalCorso et al. 2008; Munekage et al. 2002), and the activity of the minor pathway is mediated by a chloroplast NADH dehydrogenase-like (NDH) complex (Yamori et al. 2011). It is generally accepted that the NDH-dependent CEF functions to alleviate oxidative stress through preventing over-reduction of the stroma (Shikanai 2007). Most studies have focused on the role of the NDH-dependent CEF in alleviating oxidative damage under high light (Chen et al. 2016; Herbert et al. 1995; Quiles & López 2004). However, recent work has indicated that enhancing the NDH-dependent CEF contributed to improvements in photosynthesis at low

light (Yamori et al. 2015). Since NDH could be activated by low light (Teicher & Scheller 1998) and NDH-dependent CEF was important for ATP (Yamanaka et al. 2011), we speculated that NDH-dependent CEF plays a role in protecting PSII against heat-induced photoinhibition under low light.

In this study, we carried out a detailed analysis of the alleviation of heat-derived damage of PSII by focusing on the NDH-dependent cyclic electron flow that was enhanced in the presence of light. We propose that the cyclic electron transport around PS I mediated by NDH functions in alleviating the heat-induced photoinhibition at low light in grape leaves.

2. Materials and methods

2.1 Plant material and growth conditions

One-year-old grapevines (*Vitis vinifera* L. cv. 'Cabernet Sauvignon') were grown in 25 cm diameter plastic pots containing a mixture of garden earth, sand, and matrix soil (2:1:1) at 26/22 ℃ day/night temperatures in a growth chamber with a photon flux density (PFD) of 600±100 μmol m^{-2} s^{-1}, a relative humidity of 60±10%, and a photoperiod of 14/10 h light/dark. Sufficient water was supplied to avoid drought stress.

2.2 Heat treatment

The middle-node (4/5) leaves from the grape seedlings were used in the experiment when the shoots had ten leaves. To study the effects of heat stress on photosystem activities, the chosen leaves were exposed to a high temperature (42 ℃) for 4 h in the dark (HT/Dark). In addition, to examine the role of low light on the response of the photosystem to heat stress, the chosen leaves were also subjected to heat treatments at a photosynthetic photon flux density of 200 μmol m^{-2} s^{-1} (HT/LL). The leaves of the controls were exposed to normal temperature (25 ℃) in the dark (NT/Dark) or in the light of 200 μmol m^{-2} s^{-1} (NT/LL) for 4 h.

The critical temperature (Tc) was determined according to the methods of Weng and Lai (Weng & Lai 2005). Leaf discs (2 cm in diameter) were cut from the detached leaves, and leaf blades were placed abaxially in contact with moist filter paper and then placed in a small vessel made of aluminum foil. The vessels were then floated on water in a temperature-controlled water bath. Leaf discs from each treatment were heated from 22 ℃ to 55 ℃ at a rate of approximately 1 ℃ min^{-1}. The chlorophyll fluorescence was measured every 1-2 min with a Handy Plant Efficiency Analyzer (Hansatech, UK). All the discs from each treatment that had been dark-adapted for 15 min were measured.

2.3 Measurement of chlorophyll a fluorescence

A Handy Plant Efficiency Analyzer was used to measure the chlorophyll a fluorescence transients (OJIP) at 25 ℃. Measurements were taken on leaves that had been dark-adapted for 30 min. The chlorophyll a fluorescence intensity rose rapidly from an initial minimal level, Fo (the O step), to the maximal level, Fm (P step). Two intermediate steps, designated K (Fk) and J (Fj), appeared at 0.3 and 2 ms, respectively. The fluorescence parameters were calculated as follows, according to the JIP test (Strasser 1997): the maximum quantum yield of photosystem II (Fv/Fm), Fv/Fm = (Fm-Fo)/Fm; and the normalized relative variable fluorescence at the K band (Wk), which represents the damage to OEC, Wk = (Fk-Fo)/(Fj-Fo).

The PSI photosynthetic parameters were evaluated with a Dual PAM-100 system (Heinz Walz, Effeltrich, Germany) connected to a computer and based on the P700 oxidation signal (Klughammer & Schreiber 2008). The maximum level (Pm) was determined by applying a saturation pulse after pre-illumination with a far-red light after 20 min of dark adaptation. The reduction kinetics of P700 were monitored in dark-adapted leaves as the light-induced absorbance changed at 830 nm. P700 was oxidized by the far-red light for 10 s, and the subsequent re-reduction of $P700^{+}$ in darkness was monitored. Leaves were dark-adapted for 30 min before being illuminated by the far-red light (Järvi et al. 2016; Li et al. 2016). The mature leaves were dark-adapted at for 20 min, the initial fluorescence (Fo) was obtained after the

measuring light was turned on, and the leaves were then exposed to actinic light (AL, 384 μmol photons m^{-2} s^{-1}). A transient post-illumination increase in chlorophyll fluorescence was recorded after termination of the 2 min illumination as an indicator of NDH activity (Mi et al. 1995; Wang et al. 2006).

2.4 Detection of D1 protein

The protein was detected in the thylakoid membranes of the treated leaves using Western blot analysis. For thylakoid membrane preparation, the leaf fragments were homogenized in an ice-cold isolation buffer (100 mM sucrose, 50 mM Hepes, pH 7.8, 20 mM NaCl, 2 mM EDTA, and 2 mM $MgCl_2$) and were then filtered through three layers of pledget. The filtrate was centrifuged at 3000 *g* for 10 min. The sediments were washed with isolation buffer, re-centrifuged, and then finally suspended in an isolation buffer. The thylakoid membrane proteins were then denatured and separated using a 12% polyacrylamide gradient gel. The denatured protein complexes in the gel were then electroblotted onto polyvinylidene fluoride (PVDF) membranes (Millipore, Billerica, MA, USA), probed with D1 antibody, and then visualized using an enhanced chemi-luminescence method. The quantitative image analysis of the protein levels was performed using the Gel-Pro Analyzer 4.0 software.

2.5 Photo-inhibitory treatments

Chloramphenicol (CM, 1 mM) was used to inhibit the D1 protein synthesis (Nishiyama et al. 2011; Ueno et al. 2016). Methyl viologen (MV, 300 μM) was used to promote electron flow from photosystem I to O_2 and to abolish the CEF (Huang et al. 2016; Munekage et al. 2002), and 10 μM antimycin A (AA) was used to inhibit the PGR5-dependent CEF (Munekage et al. 2004). The fully expanded leaves were excised from the plants at the end of the petiole. The petioles of the excised leaves were quickly dipped into treatment solutions with a second excision in the solution under weak irradiance (50 μmol photons m^{-2} s^{-1}) for 4 h, and they were then placed on wet tissues and treated at 42 °C in the dark or under low light (200 μmol photons m^{-2} s^{-1}) for 4 h.

2.6 Statistical analyses

All the experiments were repeated at least three times. Data are reported as the mean ± standard error (SE). The data were analyzed by performing one-way analysis of variance (ANOVA) and Duncan's multiple range tests for the independent samples using SPSS version 13.0 (IBM Corporation). The confidence coefficient was set at 95%.

3. Results

3.1 The critical temperature (Tc) for the investigation of heat tolerance

The critical temperature (Tc) was used to estimate the grape leaves' resistance to high temperature (Xu et al. 2014; Weng and Lai 2005). As shown in Figure 1, the minimal fluorescence level (Fo) and the maximal efficiency of the PSII photochemistry (Fv/Fm) responded differently to a gradual increase in temperature of the leaves. With an increase in leaf temperature from 22 ℃ to 55 ℃, the Tc was approximately 42 ℃ based on Fo (43.3 ℃) and Fv/Fm (42.4 ℃) values in the dark. However, the Tc increased to approximately 47 ℃ based on Fo (47.1 ℃) and Fv/Fm (47.2 ℃) values in the light. The Tc was approximately 4 ℃ higher in the light than in the dark. These results indicate that the grape leaves were more tolerant to the elevated temperatures in the presence of light.

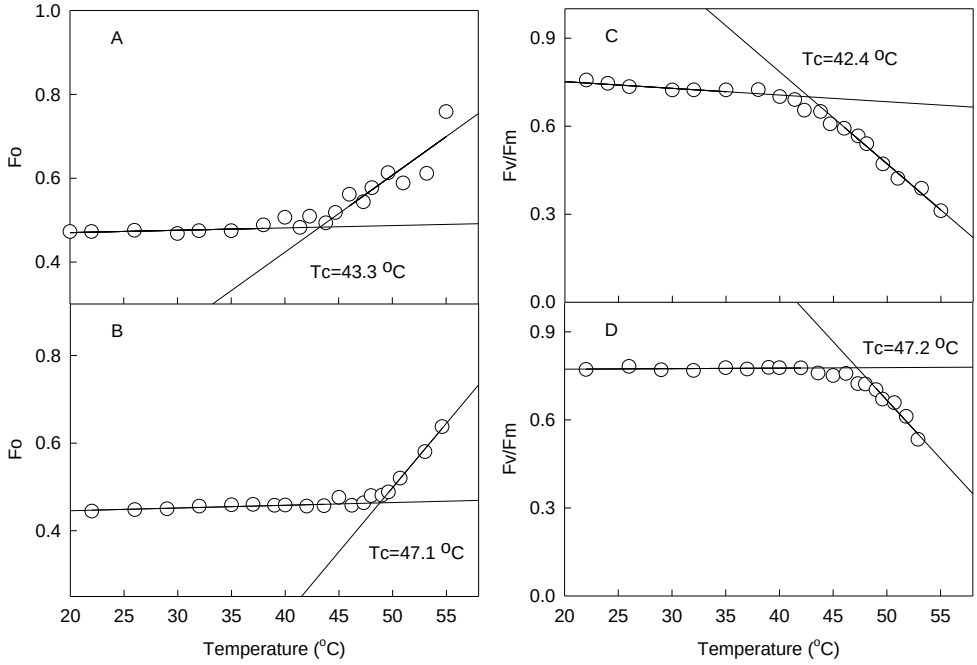

Fig. 1 Changes in Fo (A, B) and Fv/Fm (C, D) upon increases in temperature over time in the presence or absence of light. Tc was determined from the intersection of the two regression lines extrapolated from the slow- and fast-rising portions of the temperature-dependent Fv/Fm and Fo response.

3.2 Effect of high temperature on PSI and PSII photochemical activities

To understand how the light interacts with the change in PS I and PS II photochemical activities after adaption at a high temperature, we compared the maximum photooxidizable P700 (Pm) and Fv/Fm levels in the presence or absence of low light in heated leaves. There was no difference in the Fv/Fm level between conditions of darkness and low light before the heat treatment. After approximately 1 h, heat stress in the dark caused a significant decrease in Fv/Fm. In contrast, when the leaves were exposed to a high temperature in the light, no significant decrease of Fv/Fm was detected. After incubation at 42 ℃ for 4 h, Fv/Fm decreased by approximately 13.8% in the dark and by only 1.8% under low light (Figure 2A). Meanwhile, the Pm value remained stable during this process (Figure 2B). Figure 2C shows the changes in the amplitude of the K step expressed as the ratio W_K. Compared with the unstressed leaves, W_K progressively increased during the high-temperature treatment. After a heat treatment of 42 ℃ for 4 h, W_K of the grape leaves increased by approximately 22% in the heated leaves in the dark and by only 7% in the heated leaves under low light.

PSII activity depends on the balance between the rate of PSII photodamage and the rate of PSII repair under stress conditions (Murata et al. 2007). We monitored the effects of high temperature on the D1 protein level in the presence or absence of light (Figure 2D). The results showed that high temperature in the dark significantly decreased the D1 levels. In contrast, the presence of light alleviated the degradation of the D1 protein. In the presence of chloramphenicol (CM), an inhibitor of de novo D1 protein synthesis (Nishiyama et al. 2011), Fv/Fm progressively decreased during the high-temperature treatment, but no significant difference was observed in Fv/Fm between the dark and light treatments (Figure 2E). This result further implies that the D1 degradation was involved in determining photoinhibition in heated leaves in the dark.

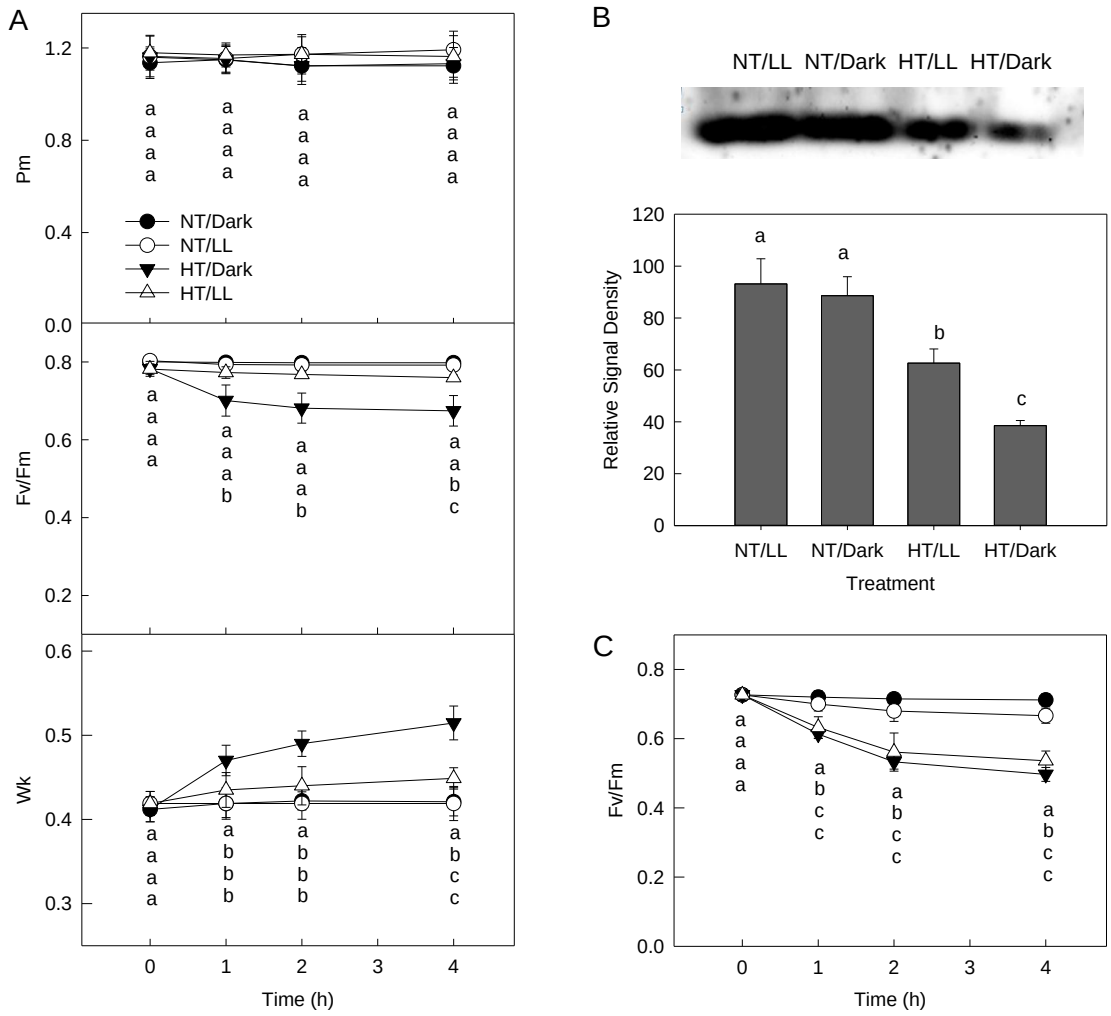

Fig. 2 Effects of high temperature in the presence or absence of light on photosystem photochemical activity and D1 protein levels. A, Changes in Pm, Fv/Fm and Wk. D, Changes in D1 protein levels and quantitative image analysis of protein levels. E, Effects of chloramphenicol (CM) on the decrease in Fv/Fm. Means ± SE were calculated from 6–8 plants. Different letters indicate significant differences between the treatments, $P<0.05$.

3.3 The contribution of CEF to the difference in heat tolerance

A transient increase in chlorophyll fluorescence after illumination was used to measure the NDH-dependent CEF activity (Burrows et al. 1998; Mi et al. 1995). Figure 3A shows that there was a visible transient postillumination increase in chlorophyll fluorescence in the unstressed leaves, and this increase was greater in the light than in the dark. When the leaves were treated at 42 ℃, the initial rate of the increasing phase in chlorophyll fluorescence was enhanced in the light, with only a trace increase in the dark. The results suggest that light treatment could activate the NDH, which was consistent with a previous study on barley (Teicher and Scheller 1998). The electrons transferred from the reduced plastoquinone pool though the operation of the NDH-dependent CEF can accelerate the re-reduction of $P700^+$ (Mi et al. 1995). The half-time of $P700^+$ re-reduction (t1/2) was calculated after treatment with 42 ℃ (Figure 3B). Under heat stress, there was a greater decrease in the t1/2 of $P700^+$ re-reduction both in the dark and in the light, and a further decrease was found in heated leaves under low light, which can be explained by the contribution of the NDH-dependent CEF (Li et al. 2016).

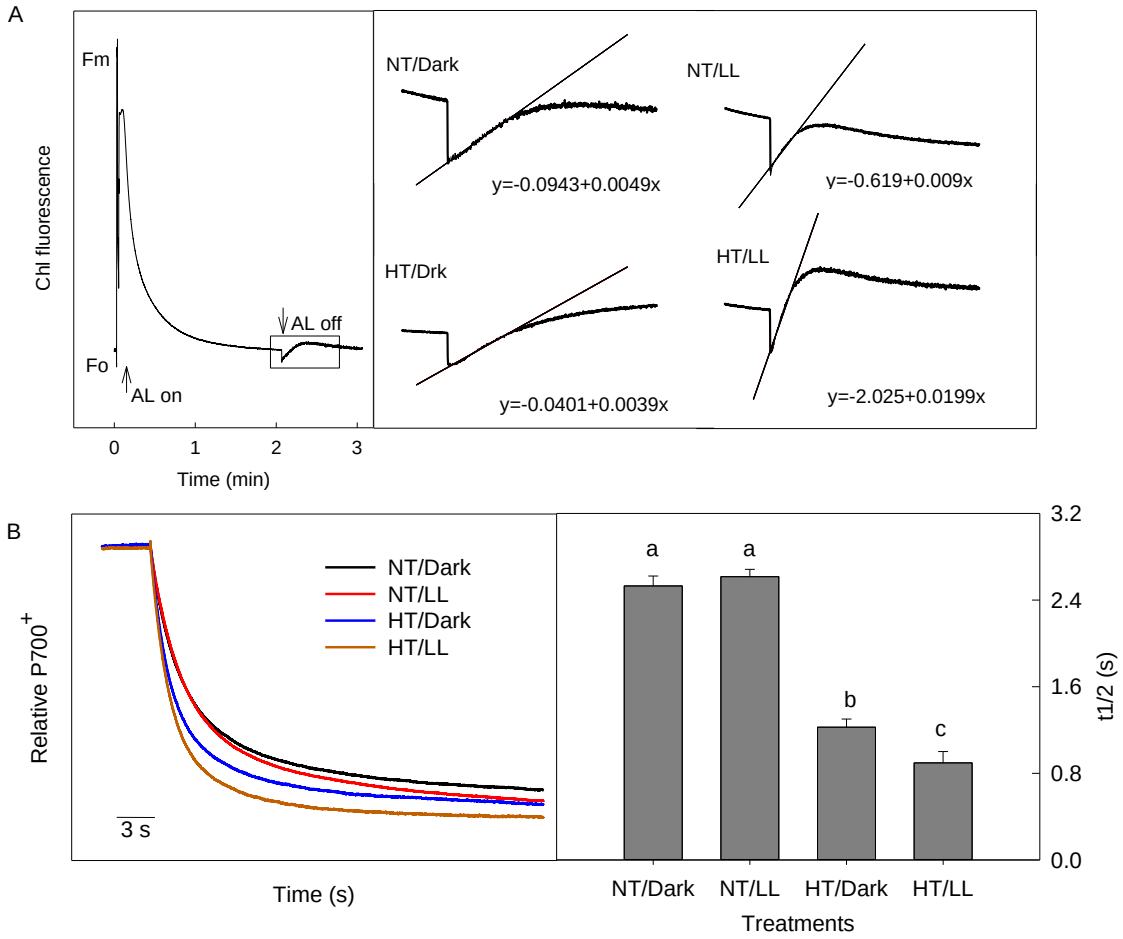

Fig. 3 Effects of high temperature in the presence or absence of light on the NDH-dependent CEF activity. A, Monitoring of the NDH-1 activity using chlorophyll fluorescence analysis. The left curve shows a typical trace chlorophyll fluorescence in grape leaves. Leaves were exposed to actinic light (384 μmol photons m^{-2} s^{-1}) for 2 min after the measuring light was turned on. The white actinic light was turned off and the subsequent changes in chlorophyll fluorescence were monitored as an indicator of NDH activity. B, Kinetics of $P700^+$ re-reduction in darkness after turning off the far-red light. The typical trace of the dark re-reduction of $P700^+$ was measured following illumination by the far-red light (>705 nm, 4 μmol m^{-2} s^{-1}). Curves are normalized to the maximal signal. The half-time (t1/2) of the re-reduction of the $P700^+$ was determined after turning off the FR. Leaves were dark-adapted in a temperature-controlled chamber at the indicated temperatures for 20 min, and fluorescence was measured at the same temperature. Each transient represents the average of eight samples. Means ± SE were calculated using 6–8 plants. Different letters indicate significant differences between the treatments, $P<0.05$.

To further examine the role of the CEF in protecting PSII from photoinhibition under heat stress in the presence or absence of light, the grape discs were incubated at 25 ℃ and 42 °C at designated light intensities, and the activity of PSII was measured in the presence of antimycin A (AA, to inhibit PGR-dependent CEF) and methyl viologen (MV, to abolish any CEF) solutions (Figure 4). The presence of light did not change the PSII activity significantly at 25 ℃ in the AA-fed leaves compared with the leaves in the dark. Fv/Fm progressively decreased during the high-temperature treatment, but the decreases of Fv/Fm in the dark were more significant than the decreases in the light (Figure 4A). Fv/Fm decreased by approximately 12% and 60% after a 4-h, high-temperature treatment in the light and in the dark, respectively. These results suggest that the extent of PSII photoinhibition caused by the inhibition of the

PGR5-dependent CEF was much lower when the heated leaves had been exposed to light. In the MV-fed leaves, compared with the unstressed leaves, Fv/Fm decreased by approximately 43% and 65% after high-temperature treatment in the light and in the dark, respectively (Figure 4B). The significant difference in Fv/Fm between the AA-treated and MV-treated samples further indicated that the NDH-dependent CEF, which was activated by light could depress the level of PSII photodamage in heated leaves.

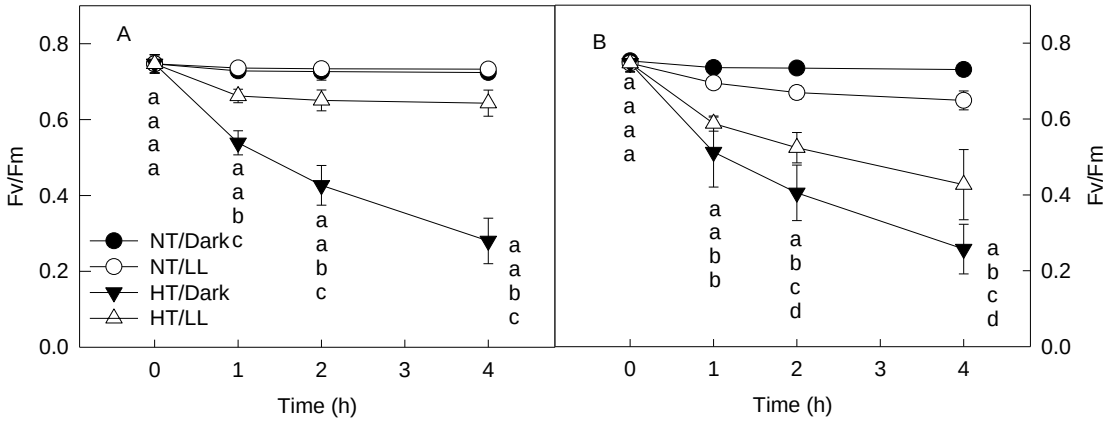

Fig. 4 Effects of antimycin A (AA, A) and methyl viologen (MV, B) on the decrease in Fv/Fm induced by high temperature in the presence or absence of light. Means ± SE of three replicates are presented. Different letters indicate significant differences between the treatments, $P<0.05$.

4. Discussion

Although the inhibition of photosynthesis by high temperatures has been widely studied, little attention has been paid to the effect of light on the response of plants to heat stress. In this study, the heat tolerance of plants in both the dark and the light was determined by exposing leaf sections to a range of temperatures, followed by measuring chlorophyll a fluorescence (Fv/Fm and Fo). In leaf discs that were exposed to elevated temperatures, the critical temperature (Tc) was remarkably lower in the dark than in the light, suggesting that grape leaves tolerate heat better in the light.

PSII is generally considered to be sensitive to heat stress (Havaux 1993; Havaux et al. 1991; Li et al. 2009). Our results indicate that heat stress in the dark led to a greater decrease of Fv/Fm compared with heat stress in the presence of light. Furthermore, high temperatures in the dark significantly damaged the OEC, which was indicated by a significant increase of relative variable fluorescence at the K step (Wk), the indicator of injury to the OEC (Li et al. 2009; Strasser 1997). These results suggest that heat stress induced more PSII photodamage in the dark. The PSII activity depends on the balance between the rates of photodamage and repair (Murata et al. 2007; Takahashi & Badger 2011). Photosynthetic organisms are able to overcome the PSII photodamage through the process of repairing the synthesis of the D1 proteins de novo (Aro et al. 1993). As observed in the study, the D1 protein was degraded more effectively by high temperatures in the dark (Figure 2D). When the leaves were exposed to high temperatures at the same intensity in the presence of chloramphenicol, which blocks the repair of PSII, the light-mediated change of Fv/Fm was eliminated (Figure 2E). This finding confirmed that the enhancement of the PSII heat tolerance in the presence of light was partly caused by alleviation of the inhibition of D1 protein synthesis (Marutani et al. 2012).

The D1 protein synthesis and repair process of damaged PSII requires a large amount of ATP in a short time (Allakhverdiev et al. 2005). The NDH-dependent CEF was thought to supply ATP through additional proton transport across the thylakoid membrane (Yamori et al. 2015). The impairment of NDH-dependent

CEF rescued the proton motive force (*pmf*) in Arabidopsis at low- to moderate-light intensities (Wang et al. 2015). In our study, heat induced a higher initial rate of the transient postillumination increase in chlorophyll fluorescence when exposed to light. In contrast, when treated in the dark, a decreased level of fluorescence with slower kinetics was observed (Figure 3A), suggesting that the activity of NDH-dependent CEF can be activated significantly by light treatment. Compared with the unstressed leaves, there was a decrease in the half-time of $P700^+$ re-reduction (t1/2), and this decrease was greater in the light than in the dark (Figure 3B), suggesting that the operation of the NDH-dependent CEF accelerates the re-reduction of $P700^+$ (Mi et al. 1995).

Antimycin A specifically inhibits PGR5-dependent CEF (Munekage et al. 2004; Shikanai 2007). The AA-treated leaves showed much less of a decrease in Fv/Fm in the light than in the dark during heat stress; however, this increase seemed to disappear in leaves in the presence of methyl viologen, an inhibitor that blocks the cyclic electron transport. The difference in the level of PSII photoinhibition between the AA and MV-treated leaves suggests that the activation of NDH-dependent CEF in the presence of light played a role in protecting PSII against photodamage under high temperatures.

Heat stress inhibits Rubisco activase (Crafts-Brandner & Salvucci 2000). Research has suggested that Rubisco activase was activated by electron transport through PSI (Campbell & Ogren 1990). The function of the NDH-dependent CEF contributed to the lower level of suppression of Rubisco activase by providing extra ATP under heat stress (Wang et al. 2006). Whether NDH-dependent CEF activity under heat stress in the light could alleviate the inhibition of Rubisco activase activity merits further study.

5. Conclusions

The heat tolerance of PSII in grape leaves differs under different light conditions. Heat stress in the dark resulted in substantial PSII photoinhibition, accompanied with a lower level of degradation of the D1 protein. The activity of NDH-dependent CEF can be activated significantly by light treatment, contributing to the re-reduction of $P700^+$ in heated leaves. When the PGR-dependent CEF was inhibited, the extent of PSII photoinhibition caused by heat stress was much lower in the light than in the dark, further implying NDH-dependent CEF played a role in protecting PSII against photodamage under high temperatures. Therefore, low light acts as an efficient protector of the photochemical activity against heat stress by alleviating the degradation of the D1 protein through stimulating the NDH-dependent CEF pathway.

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References

Allakhverdiev SI, Nishiyama Y, Takahashi S, Miyairi S, Suzuki I, and Murata N. 2005. Systematic analysis of the relation of electron transport and ATP synthesis to the photodamage and repair of photosystem II in Synechocystis. *Plant Physiol* 137:263-273.

Aro EM, Virgin I, and Andersson B. 1993. Photoinhibition of photosystem II. Inactivation, protein damage and turnover. *Biochim Biophys Acta* 1143:113-134.

Berry J, and Bjorkman O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Ann Rev Plant Physiol* 31:491-543.

Brestic M, Zivcak M, Kunderlikova K, and Allakhverdiev SI. 2016. High temperature specifically affects the photoprotective responses of chlorophyll b-deficient wheat mutant lines. *Photosynth Res* 130:1-16.

Buchner O, Stoll M, Karadar M, Kranner I, and Neuner G. 2015. Application of heat stress in situ demonstrates a protective role of irradiation on photosynthetic performance in alpine plants. *Plant Cell Environ* 38:812-826.

Burrows PA, Sazanov LA, Svab Z, Maliga P, and Nixon PJ. 1998. Identification of a functional respiratory complex in chloroplasts through analysis of tobacco mutants containing disrupted plastid ndh genes. *EMBO J* 17:868-876.

Campbell WJ, and Ogren WL. 1990. Electron transport through photosystem I stimulates light activation of ribulose bisphosphate carboxylase/oxygenase (Rubisco) by Rubisco activase. *Plant Physiol* 94:479-484.

Chen X, He Z, Xu M, Peng L, and Mi H. 2016. NdhV subunit regulates the activity of type-1 NAD (P) H dehydrogenase under high light conditions in cyanobacterium *Synechocystis* sp. PCC 6803. *Sci Rep* 6:28361.

Crafts-Brandner SJ, and Salvucci ME. 2000. Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO_2. *Proc Nat Acad Sci* 97:13430-13435.

DalCorso G, Pesaresi P, Masiero S, Aseeva E, Schünemann D, Finazzi G, Joliot D, Barbato R, and Leister D. 2008. A complex containing PGRL1 and PGR5 is involved in the switch between linear and cyclic electron flow in Arabidopsis. *Cell* 132:273-285.

Essemine J, Qu M, Mi H, and Zhu XG. 2016. Response of chloroplast NAD(P)H dehydrogenase-mediated cyclic electron flow to a shortage or lack in ferredoxin-quinone oxidoreductase-dependent pathway in rice following short-term heat stress. *Front Plant Sci* 7:383.

Essemine J, Xiao Y, Qu M, Mi H, and Zhu XG. 2017. Cyclic electron flow may provide some protection against PSII photoinhibition in rice (*Oryza sativa* L.) leaves under heat stress. *J Plant Physiol* 211:138-146.

Havaux M. 1993. Characterization of thermal damage to the photosynthetic electron transport system in potato leaves. *Plant Sci* 94:19-33.

Havaux M, Greppin H, and Strasser RJ. 1991. Functioning of photosystems I and II in pea leaves exposed to heat stress in the presence or absence of light: Analysis using in-vivo fluorescence, absorbance, oxygen and photoacoustic measurements. *Planta* 186:88-98.

Herbert SK, Martin RE, and Fork DC. 1995. Light adaptation of cyclic electron transport through photosystem I in the cyanobacterium Synechococcus sp. PCC 7942. *Photosynth Res* 46:277-285.

Huang W, Yang YJ, Hu H, Zhang SB, and Cao KF. 2016. Evidence for the role of cyclic electron flow in photoprotection for oxygen-evolving complex. *J Plant Physiol* 194:54-60.

Järvi S, Suorsa M, Tadini L, Ivanauskaite A, Rantala S, Allahverdiyeva Y, D. L, and Aro EM. 2016. Thylakoid-bound FtsH proteins facilitate proper biosynthesis of photosystem I. *Plant Physiol* 171:1333-1343.

Klughammer C, and Schreiber U. 2008. Complementary PS II quantum yields calculated from simple fluorescence parameters measured by PAM fluorometry and the Saturation Pulse method. *PAM Appl Notes* 1:27–35.

Li P, Cheng L, Gao H, Jiang C, and Peng T. 2009. Heterogeneous behavior of PSII in soybean (*Glycine* max) leaves with identical PSII photochemistry efficiency under different high temperature treatments. *J Plant Physiol* 166:1607-1615.

Li Q, Yao ZJ, and Mi H. 2016. Alleviation of photoinhibition by co-ordination of chlororespiration and cyclic electron flow mediated by NDH under heat stressed condition in tobacco. *Front Plant Sci* 7:285.

Marutani Y, Yamauchi Y, Kimura Y, Mizutani M, and Sugimoto Y. 2012. Damage to photosystem II due to heat stress without light-driven electron flow: involvement of enhanced introduction of reducing power into thylakoid membranes. *Planta* 236:753-761.

Mi H, Endo T, Ogawa T, and Asada K. 1995. Thylakoid membrane-bound, NADPH-specific pyridine nucleotide dehydrogenase complex mediates cyclic electron transport in the cyanobacterium *Synechocystis* sp. PCC 6803. *Plant Cell Physiol* 36:661-668.

Munekage Y, Hashimoto M, Miyake C, Tomizawa KI, Endo T, Tasaka M, and Shikanai T. 2004. Cyclic electron flow around photosystem I is essential for photosynthesis. *Nature* 429: 579-582.

Munekage Y, Hojo M, Meurer J, Endo T, Tasaka M, and Shikanai T. 2002. PGR5 is involved in cyclic electron flow around photosystem I and is essential for photoprotection in Arabidopsis. *Cell* 110:361-371.

Murata N, Takahashi S, Nishiyama Y, and Allakhverdiev SI. 2007. Photoinhibition of photosystem II under environmental stress. *Biochim Biophys Acta* 1767:414-421.

Nishiyama Y, Allakhverdiev SI, and Murata N. 2006. A new paradigm for the action of reactive oxygen species in the photoinhibition of photosystem II. *Biochim Biophys Acta* 1757:742-749.

Nishiyama Y, Allakhverdiev SI, and Murata N. 2011. Protein synthesis is the primary target of reactive oxygen species in the photoinhibition of photosystem II. *Physiol Plant* 142:35-46.

Quiles MJ, and López NI. 2004. Photoinhibition of photosystems I and II induced by exposure to high light intensity during oat plant growth: effects on the chloroplast NADH dehydrogenase complex. *Plant Sci* 166:815-823.

Salvucci ME. 2008. Association of Rubisco activase with chaperonin-60β: a possible mechanism for protecting photosynthesis during heat stress. *J Exp Bot* 59:1923-1933.

Sharkey TD. 2005. Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. *Plant Cell Environ* 28:269-277.

Shikanai T. 2007. Cyclic electron transport around photosystem I: genetic approaches. *Annu Rev Plant Biol* 58:199-217.

Strasser BJ. 1997. Donor side capacity of photosystem II probed by chlorophyll a fluorescence transients. *Photosynth Res* 52: 147-155.

Sun Y, Geng Q, Du Y, Yang X, and Zhai H. 2016. Induction of cyclic electron flow around photosystem I during heat stress in grape leaves. *Plant Sci* 256:65-71.

Takahashi S, and Badger MR. 2011. Photoprotection in plants: a new light on photosystem II damage. *Trends Plant Sci* 16:53-60.

Teicher HB, and Scheller HV. 1998. The NAD (P) H dehydrogenase in barley thylakoids is photoactivatable and uses NADPH as well as NADH. *Plant Physiol* 117:525-532.

Ueno M, Sae-Tang P, Kusama Y, Hihara Y, Matsuda M, Hasunuma T, and Nishiyama Y. 2016. Moderate heat stress stimulates repair of photosystem II during photoinhibition in *Synechocystis* sp. PCC 6803. *Plant Cell Physiol* 57:2417-2426.

Wang C, Yamamoto H, and Shikanai T. 2015. Role of cyclic electron transport around photosystem I in regulating proton motive force. *Biochim Biophys Acta* 1847:931-938.

Wang P, Duan W, Takabayashi A, Endo T, Shikanai T, Ye JY, and Mi H. 2006. Chloroplastic NAD(P)H dehydrogenase in tobacco leaves functions in alleviation of oxidative damage caused by temperature stress. *Plant Physiol* 141:465-474.

Weng JH, and Lai MF. 2005. Estimating heat tolerance among plant species by two chlorophyll fluorescence parameters. *Photosynthetica* 43:439-444.

Xu S, Li J, Zhang X, Wei H, and Cui L. 2006. Effects of heat acclimation pretreatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultrastructure of chloroplasts in two cool-season turfgrass species under heat stress. *Environ Experim Bot* 56:274-285.

Yamanaka R, Nakamura K, and Murakami A. 2011. Reduction of exogenous ketones depends upon NADPH generated photosynthetically in cells of the cyanobacterium *Synechococcus PCC 7942*. *AMB Express* 1:1-8.

Yamori W, Sakata N, Suzuki Y, Shikanai T, and Makino A. 2011. Cyclic electron flow around photosystem I via chloroplast NAD (P) H dehydrogenase (NDH) complex performs a significant physiological role during photosynthesis and plant growth at low temperature in rice. *Plant J* 68:966-976.

Yamori W, Shikanai T, and Makino A. 2015. Photosystem I cyclic electron flow via chloroplast NADH dehydrogenase-like complex performs a physiological role for photosynthesis at low light. *Sci Rep*:5.