



Comparison of the activities of photosystem II of four table grapevine cultivars during high-temperature stress

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Abstract

High-temperature stress influences the growth and development of grapevines, and plant responses to this stress vary between laboratory and natural conditions. In the present study, the responses to high-temperature stress in four grapevine cultivars ('Summer Black', 'Zuijinxiang', 'Hupei1#', and 'Shenfeng') were studied by comparing chlorophyll *a* fluorescence and the levels of heat-shock protein 21 (HSP21) after exposure to control (35 °C in controlled laboratory conditions or at 37 °C in a greenhouse with naturally fluctuating temperatures) and high-temperature stress treatments (45 °C in laboratory conditions or 42 °C in the field conditions). Leaf water loss in 'Summer Black' was less than that in the three other cultivars after treatment at 45 °C. Some parameters (Ψ_{E_0} , W_k , RC_{QA} , and M_o) of photosystem II (PSII) activity were altered in 'Shenfeng', 'Zuijinxiang', and 'Hupei1#', but were unaltered in 'Summer Black' after treatment at 45 °C. Other parameters (maximum photochemical efficiency (F_v/F_m), performance index on absorption basis (PI_{ABS}), Φ_{P_0} , Φ_{E_0} , and HSP21 levels) were altered in 'Summer Black', but to a lesser extent than in the three other cultivars under high-temperature stress. Unlike 'Summer Black', extreme injury owing to leaf water loss to 'Shenfeng', 'Zuijinxiang', and 'Hupei1#' could be explained by disruption of PSII activity. Furthermore, there were the observed differences in PSII activity between in laboratory and field conditions, which could be considered as the mechanisms for high-temperature acclimation and other environment factors.

Keywords Chlorophyll *a* fluorescence · Heat-shock protein · Heat tolerance · 'Summer Black'

Abbreviations

PIABS	Performance index on absorption basis
PQ	Plastoquinone
PS	Photosystem
RC	Reaction centers
QA	Quinone electron acceptor
HSP	Heat shock protein

1 Introduction

Temperature is a key parameter that controls plant growth and development, and rising temperatures are expected in the future (Karl et al. 2015). When grapevines are exposed to heat shock at 45 °C for 3 h, severe injury may occur. Grapevine leaves exposed to such high temperature exhibit chlorophyll photooxidation mediated by reactive oxygen species and severe alterations in the photosynthetic apparatus (Zha et al. 2016). In order to breed grapevine crops for better heat tolerance, we need to better understand the physiological damage that occurs during heat shock.

The photosynthetic apparatus is sensitive to high temperatures and is an ideal system for evaluating the degree of damage from high-temperature stress (Rachmilevitch et al. 2006). These evaluations are based on changes in chlorophyll *a* fluorescence and the OJIP transient, defined by the steps of the O, J, I, and P phases corresponding to the redox states of photosystem (PS) II and PSI and the efficiencies of electron transfer to the final electron acceptors of PSI (Strasser et al. 2000, 2004). The steps of O, J, I, and P

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reflect energy absorption, trapping, and electron transport (Schansker et al. 2005). The O step reflects the minimum fluorescence when the primary quinone electron acceptor (Q_A) is fully oxidized. The P step corresponds to the state in which Q_A is fully reduced. The rise from phase O to phase J reflects a reduction in Q_A and is associated with the primary photochemical reactions of PSII. Therefore, the intermediate step, I, and the final step, P, reflect the existence of reducing plastoquinone (PQ) centers as well as different redox states of the reaction center (RC) complex in PSII (Strasser and Srivastava 1995; Strasser et al. 2000, 2004). The OJIP transient is an ideal signal and a reliable method exists for detecting and quantifying high-temperature-induced changes in the activity of PSII in plant leaves (Tóth et al. 2005; Wen et al. 2005; Strauss et al. 2006).

As a molecular chaperone, it is mainly involved in the folding, assembly and transfer of protein.

Small heat-shock proteins (sHSPs, ranging from 15 to 42 kDa), act as molecular chaperones, are mainly involved in the folding, assembling and transferring proteins (Basha et al. 2012). In plants, sHSPs are abundant and are highly expressed under high-temperature stress to protect cells against damage (Sun et al. 2002; Sun and MacRae 2005). Heat-shock protein 21 (HSP21) protects PSII against environmental stresses including high-temperature stress (Wang and Luthe 2003; Neta-Sharir et al. 2005; Kim et al. 2012).

Most studies focusing on the changes in PSII under high-temperature stress have been conducted in grapevines cultivated under laboratory conditions. Studies on the response of different grapevine cultivars to high-temperature stress in both laboratory and field conditions are needed. Accordingly, our study evaluated the activity of PSII and levels of HSP21 in four table grapevine cultivars under high-temperature stress induced in controlled laboratory conditions and in a field with naturally fluctuating temperatures in order to compare their performance and to identify heat-tolerant grapevine cultivars.

2 Materials and methods

2.1 Plant materials and treatments under field conditions

Six-year-old plants of the four table grapevine cultivars (*Vitis vinifera* × *V. labrusca* L.), ‘Summer Black’, ‘Zuijinxiang’, ‘Hupei1#’, and ‘Shenfeng’, were grown in an 8 m × 20 m greenhouse in Shanghai, China (30°89 N, 121°39 E). They received standard horticultural practices including disease and pest control. Air temperatures were measured using a HOBO U23-002 (Onset Computer Corporation, Cape Cod, MA, USA). In 2015, the average daily temperature before July 24 was below 30 °C and the highest temperature was

below 40 °C (Fig. 1, Table S1). After July 24, the average daily temperature was above 30 °C until July 31st, and the highest temperature during the day was above 40 °C. On July 23, 2015, the highest daily temperature in the greenhouse was recorded at 37 °C, and on July 31, 2015, the recorded highest daily temperature was 42 °C; these were the days chosen as the control and high temperature, respectively, to measure chlorophyll *a* fluorescence and levels of HSP21. Fully expanded mature leaves were collected at 13:00 h for the measurements, which was the time at which the temperature reached the highest point each day. Three biological replicates with five technical replicates were used for each measurement.

2.2 Plant materials and treatments under laboratory conditions

Stem cuttings were taken from grapevine cultivars of the same growth stage grown in a greenhouse in Shanghai, China (31°96 N, 121°48 E) and were rooted in a plastic container (radius: height = 15 cm: 40 cm) containing a mixture of peat moss and perlite (1:1, v/v). The stem cuttings were acclimated in a laboratory environment using a 1000-L artificial culture light box (Qianjiang Instrument and Equipment Co. Ltd., Hanzhou, China) for about 2 weeks at 25 °C, 65–70% relative humidity, and a light intensity of 200 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Thereafter, one group was maintained at 35 °C and the other group was exposed to a 45 °C treatment for 3 h. Fully expanded mature leaves were used for the measurements of chlorophyll *a* fluorescence and HSP21 levels at 0 and 3 h after the treatments. These experiments were performed on three biological replicates with five technical replicates.

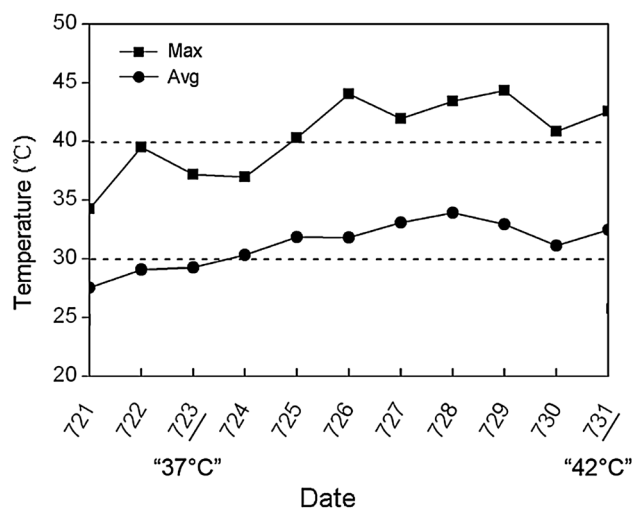


Fig. 1 Temperatures from July 21 to July 31 in 2015. July 21 is denoted by 721; all other dates are indicated in the same format. Max: highest daily temperature; Avg: average daily temperature

2.3 Measurements of chlorophyll *a* fluorescence

Chlorophyll *a* fluorescence was measured according to the method of Strasser and Srivastava (1995) with a Plant Efficiency Analyzer (Hansatech Instruments Ltd., King's Lynn, Norfolk, UK), which provides information on the photochemical activity of PSII and the status of the PQ pool (Strauss et al. 2006). Before measurement, the leaves were dark-acclimated for 20 min. The indicators and their descriptions are presented in Table 1.

2.4 Protein immunoblot assay

Total protein was extracted with the trichloroacetic acid/acetone method (Shultz et al. 2005). The anti-HSP21 polyclonal antibody (Abcam, Bristol, UK) was provided by Wang et al. (2010). The protein immunoblot was analyzed according to the methods of Zha et al. (2016).

2.5 Statistical analysis

Data were processed with Microsoft Excel 2007. Differences were evaluated using two-sample *t*-tests assuming equal variances at $p < 0.05$ or $p < 0.01$.

3 Results

In the field, daily temperatures reached 40 °C from July 25 to July 31 for 1–7 h each day, and the highest temperature was recorded on July 31 at 44.3 °C (Table S1). The temperature treatments in the laboratory conditions (35 and 45 °C)

were set for further verification of the results of the field treatments. In the laboratory treatment, the 'Zuijinxiang', 'Hupei1#', and 'Shenfeng' plants were dehydrated more significantly at 45 °C for 3 h than those at 35 °C. However, only young leaves and stems of 'Summer Black' were dehydrated under the 45 °C treatment (Fig. 2).

The maximum photochemical efficiency (F_v/F_m) and performance index on absorption basis (PI_{ABS}) were significantly decreased under the high temperature treatments (45 °C/42 °C) compared with the control temperatures (35 °C/37 °C) for 'Zuijinxiang', 'Hupei1#', and 'Shenfeng' (Fig. 3). The values of F_v/F_m and PI_{ABS} for 'Summer Black' decreased after treatment at 45 °C, but not at 42 °C compared with the controls (Fig. 3).

PI_{ABS} is a combination of the indices of three parameters: (1) Ψ_{Eo} : the probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A^- , (2) Φ_{Po} : the maximum quantum yield of primary photochemistry, and (3) Φ_{Eo} : the efficiency with which a trapped exciton can move an electron into the electron transport chain. PI_{ABS} decreased following the 45 °C treatment in 'Zuijinxiang', 'Hupei1#', and 'Shenfeng'. The Ψ_{Eo} of 'Summer Black' did not differ significantly between the laboratory treatment at 45 °C and the field treatment at 42 °C (Fig. 4). Electron transport decreased as the temperature increased. Additionally, the values of Ψ_{Eo} , Φ_{Po} , and Φ_{Eo} decreased after treatment at 42 °C for the 'Zuijinxiang' cultivar throughout the experiment (Fig. 4).

No changes were found in the amplitude of phase K (W_k) in 'Summer Black' and 'Zuijinxiang' (Fig. 5); however, the W_k was significantly increased after treatment at 45 or 42 °C in 'Hupei 1#' and 'Shenfeng'. These data indicated that the oxygen-evolving complexes of 'Summer Black' and 'Zuijinxiang' were not damaged under the high-temperature

Table 1 Polyphasic chlorophyll *a* fluorescence transient (OJIP) test: summary of indicators and their description

Indicators	Description
F_o	The fluorescence intensity at 0 μ s
$F_j = F_{2ms}$	The fluorescence intensity at 2 ms
$F_i = F_{30ms}$	The fluorescence intensity at 30 ms
$F_p = F_m$	The fluorescence intensity at maximum
$F_v = F_m - F_o$	The variable fluorescence intensity
F_v/F_m	The maximum photochemical efficiency
PI_{ABS}	Performance index (PI) on absorption basis
$W_k = (F_{300\mu s} - F_o)/(F_j - F_o)$	Represents the damage to the oxygen evolving complex (OEC)
$M_o = 4(F_{300\mu s} - F_o)/(F_m - F_o)$	Approximated initial slope of the fluorescence transient $V = f(t)$
$\Phi_{Po} = 1 - (F_o/F_m)$	Maximum quantum yield of primary photochemistry at $t=0$
$\Psi_{Eo} = 1 - (F_j - F_o)/(F_m - F_o)$	Quantum yield for electron transport at $t=0$
$\Phi_{Po} = (F_v/F_m) * \Psi_{Eo}$	Probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A^-
$\delta_{Ro} = [1 - (F_i - F_o)/(F_m - F_o)]/\Psi_{Eo}$	Efficiency with which an electron can move from PQ through PSI to the PSI end electron acceptors
$RC_{QA} = \Phi_{Po} * (ABS/CS_m) * [(1 - \Psi_{Eo})/M_o]$	Amount of active PSII RCs (Q_A^- -reducing PSII reaction centers) per CS at $t=m$

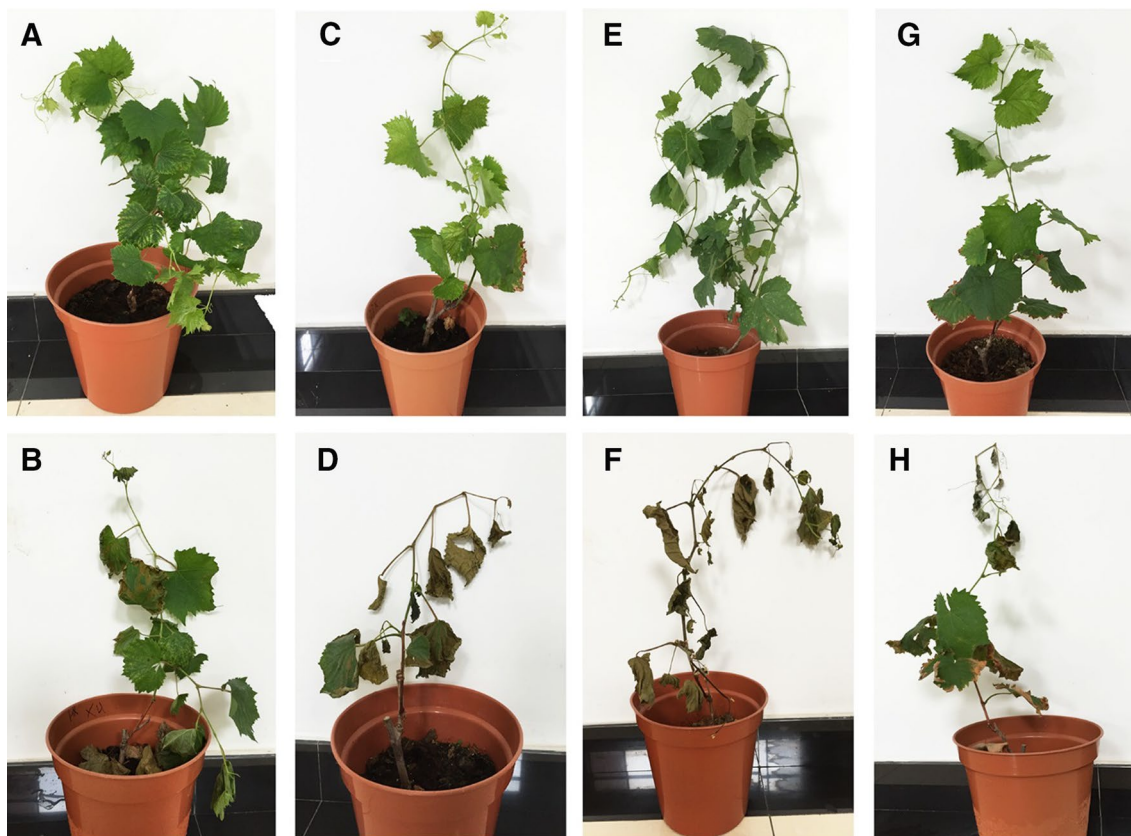


Fig. 2 Phenotypes of the four grapevine cultivars during the different laboratory heat treatments at 6 h. ‘Summer Black’ at the 35 °C treatment (a); ‘Summer Black’ at the 45 °C treatment (b); ‘Zuijinxiang’ at the 35 °C treatment (c); ‘Zuijinxiang’ at the 45 °C treatment (d);

‘Hupei1#’ at the 35 °C treatment (e); ‘Hupei1#’ at the 45 °C treatment (f); ‘Shenfeng’ at the 35 °C treatment (g); ‘Shenfeng’ at the 45 °C treatment (h)

treatments. However, these high-temperature treatments altered the density of the Q_A^- reducing reaction centers of PSII (RC_{QA}) in the three other grapevine cultivars, but did not influence the RC_{QA} of ‘Summer Black’.

‘Summer Black’ did not show significant alteration of the approximate initial slope of the fluorescence transient (M_o) after treatment at 45 or 42 °C, but changes in M_o were observed in ‘Shenfeng’, ‘Zuijinxiang’, and ‘Hupei1#’ (Fig. 6). The redox state of PSI (δ_{R_o}) for the four grapevine cultivars significantly increased after the laboratory treatment at 45 °C; however, there were no changes in δ_{R_o} after the field treatment at 42 °C compared with δ_{R_o} after treatment at 37 °C (Fig. 6).

As shown in Fig. 7, HSP21 levels, representing the immune signal, increased in ‘Summer Black’, but decreased in ‘Shenfeng’, ‘Zuijinxiang’, and ‘Hupei1#’ after treatment for 3 h at 45 °C. In the field treatment, this signal increased in ‘Summer Black’ and ‘Hupei1#’, but decreased in ‘Shenfeng’ and ‘Zuijinxiang’ after treatment at 42 °C as compared with that after treatment at 37 °C.

4 Discussion

In the present study, all four cultivars suffered various degrees of leaf blade dehydration under the 45 °C treatment for 3 h. ‘Summer Black’ showed slight dehydration, whereas ‘Shenfeng’, ‘Zuijinxiang’, and ‘Hupei1#’ showed marked dehydration. Thus, ‘Summer Black’ may be more tolerant to high-temperature stress than the other cultivars.

The OJIP transients were used to evaluate several biophysical reactions that allow us to quantify the function of PSII. Changes in OJIP transients caused by high temperature stress have been used to study heat tolerance in apples and beans (Chen and Cheng 2009; Stefanov et al. 2011). F_v/F_m , the maximum quantum yield of primary PSII photochemistry, has been used to determine the health of plants in many studies (Stirbet and Govindjee 2011; Chen et al. 2013; Murchie and Lawson 2013). Our results of the F_v/F_m (ranging from 0.78 to 0.84 for the four grapevine cultivars) showed that the PSII activity were at the normal levels. High-temperature stress decreased the F_v/F_m in previous studies (Bjorkman and Demmig 1987; Murchie and Lawson

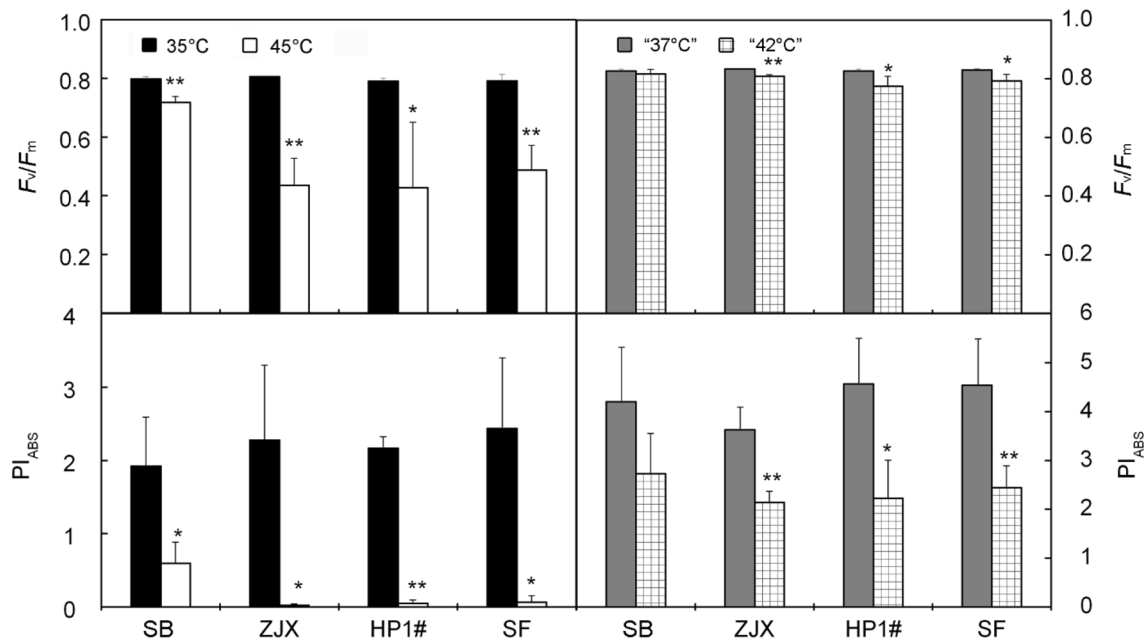


Fig. 3 F_v/F_m and PI_{ABS} of PSII in the leaves of grapevines. The field conditions on July 23 and July 31, 2015 are denoted by “37” and “42 °C”, respectively. SB: ‘Summer Black’; ZJX: ‘Zuijinxiang’; HP1#: ‘Hupei1#’; SF: ‘Shenfeng’. Significant differences among the

different temperature treatments at the same time point are indicated by * ($p < 0.05$) or ** ($p < 0.01$). Vertical bars represent standard errors of the means from three replications

2013), and in our study, the F_v/F_m decreased markedly after treatment at 45 °C in all four grapevine cultivars, with ‘Summer Black’ showing the smallest changes. Moreover, only ‘Summer Black’ had no obvious changes in the F_v/F_m after treatment at 42 °C, whereas the F_v/F_m of the other cultivars decreased significantly, indicating that ‘Summer Black’ was more tolerant to high temperatures and ‘Zuijinxiang’, ‘Hupei 1#’, and ‘Shenfeng’ were heat-sensitive.

PI_{ABS} , which is associated with Ψ_{E_0} , Φ_{P_0} , and Φ_{E_0} , provides useful information regarding plant health (Perboni et al. 2012; Singh and Sarkar 2014). In an earlier study, the ratios of Ψ_{E_0} , Φ_{P_0} , Φ_{E_0} , F_v/F_m , and PI_{ABS} of the co-dominant species *Quercus ilex* and *Phillyrea latifolia* were decreased under the combined effect of heat and drought stresses (Ogaya et al. 2011). In our study, the reductions in some of these parameters were more dramatic in the high temperature-sensitive cultivars (‘Zuijinxiang’, ‘Hupei 1#’, and ‘Shenfeng’) than in the heat-tolerant grapevine cultivar (‘Summer Black’) under high-temperature stress.

In our study, W_k (donor side parameter of PSII), RC_{QA} (reaction center parameter of PSII), and M_o and δ_{Ro} (acceptor side parameters of PSII) of the grapevine cultivars were altered under the high-temperature treatments, consistent

with the findings of a previous study (Wang et al. 2010). Notably, the degree of those changes was smallest for ‘Summer Black’, further supporting that ‘Summer Black’ is more heat tolerant with regard to the stability of PSII activity.

HSP21 stabilizes proteins and prevents protein aggregation, thereby functioning in the protection of PSII (Neta-Sharir et al. 2005). In the present study, HSP21 levels increased in ‘Summer Black’ and decreased in the three other cultivars at 45 °C, indicating that the leaves of ‘Shenfeng’, ‘Zuijinxiang’, and ‘Hupei1#’ were heavily damaged due to high temperature stress, and that they were unable to effectively synthesize proteins to maintain normal physiological processes.

The patterns of variation in the chlorophyll *a* fluorescence parameters and HSP21 levels between the laboratory and field conditions were similar, which suggested that the major driver of the response of PSII in grapevines is temperature. The differences among the four grapevine cultivars might be due to differences in their genetic backgrounds. Additionally, the extreme injury to ‘Shenfeng’, ‘Zuijinxiang’, and ‘Hupei1#’ cultivars could be explained by disruption of the activity of PSII during high-temperature stress.

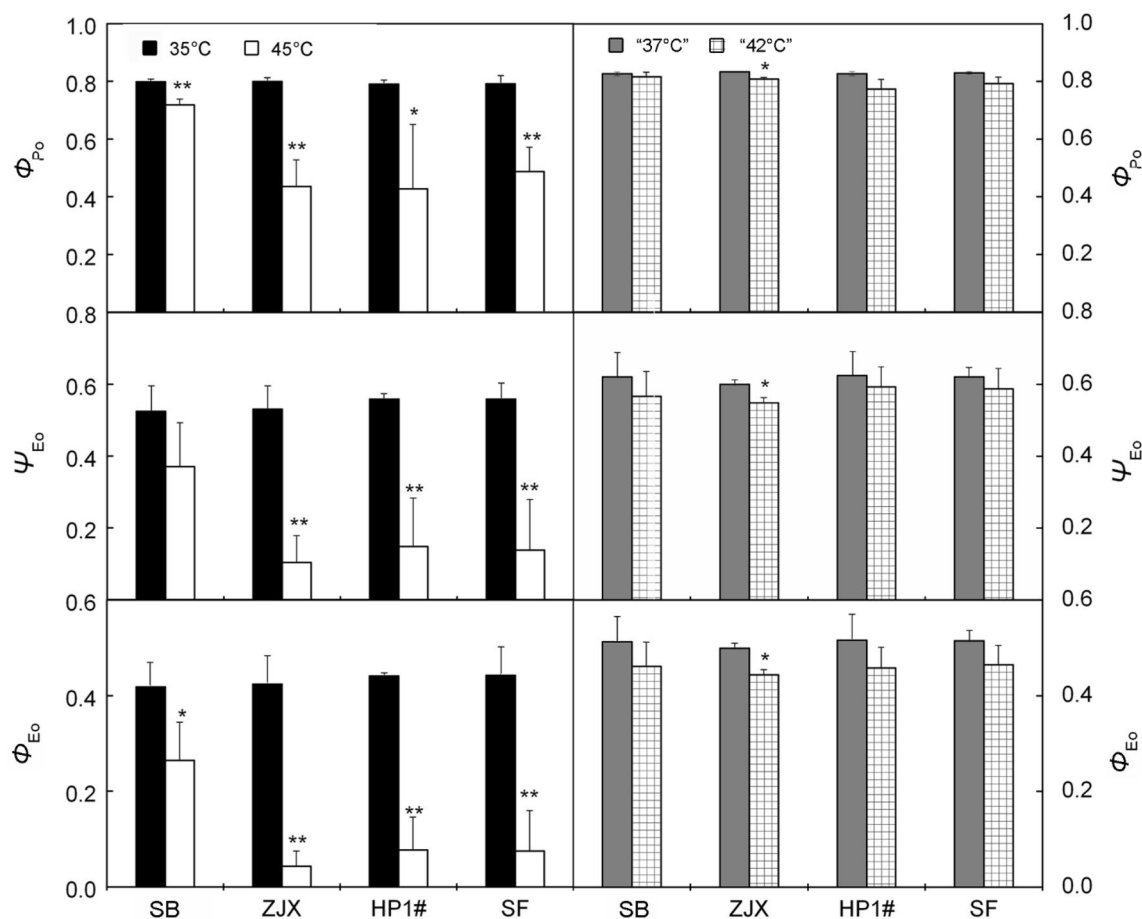


Fig. 4 Φ_{Po} and electron acceptor parameters (Ψ_{Eo} and Φ_{Eo}) of PSII in the leaves of grapevines. The field conditions on July 23 and July 31, 2015 are denoted by “37” and “42 °C”, respectively. SB: ‘Summer Black’; ZJX: ‘Zuijinxiang’; HP1#: ‘Hupei1#’; SF: ‘Shenfeng’. Sig-

nificant differences among the different temperature treatments at the same time point are indicated by * ($p < 0.05$) or ** ($p < 0.01$). Vertical bars represent standard errors of the means from three replications

Different behaviors of PSII and HSP21 levels in the four grapevine cultivars were seen in the laboratory and field conditions. Accordingly, the lower Φ_{Po} value occurring at 45 °C was considered as a positive adaptation for the down-regulation of photosynthetic excitation pressure (Raven 2011). However, these changes did not occur after the field treatment at 42 °C, suggesting the involvement of other factors. In the field, temperatures gradually increased, which may have enhanced the ability of the plants to adapt to the higher temperatures (42 °C), thereby, improving the resistance to heat stress. This high-temperature acclimation theory

was consistent with that of previous reports (Havaux 1993; Horowitz 2002; Larkindale and Vierling 2008; Hasanuz-zaman et al. 2013). Additionally, the differences in performance between the different cultivars may be attributed to their inherent vigor. Other environmental factors may have attributed to the differences in some parameters, including HSP21 levels, between the laboratory and field conditions. Although it is difficult to simulate natural high-temperature stress, our findings provide experimental and theoretical guidance for the production of heat-tolerant cultivars.

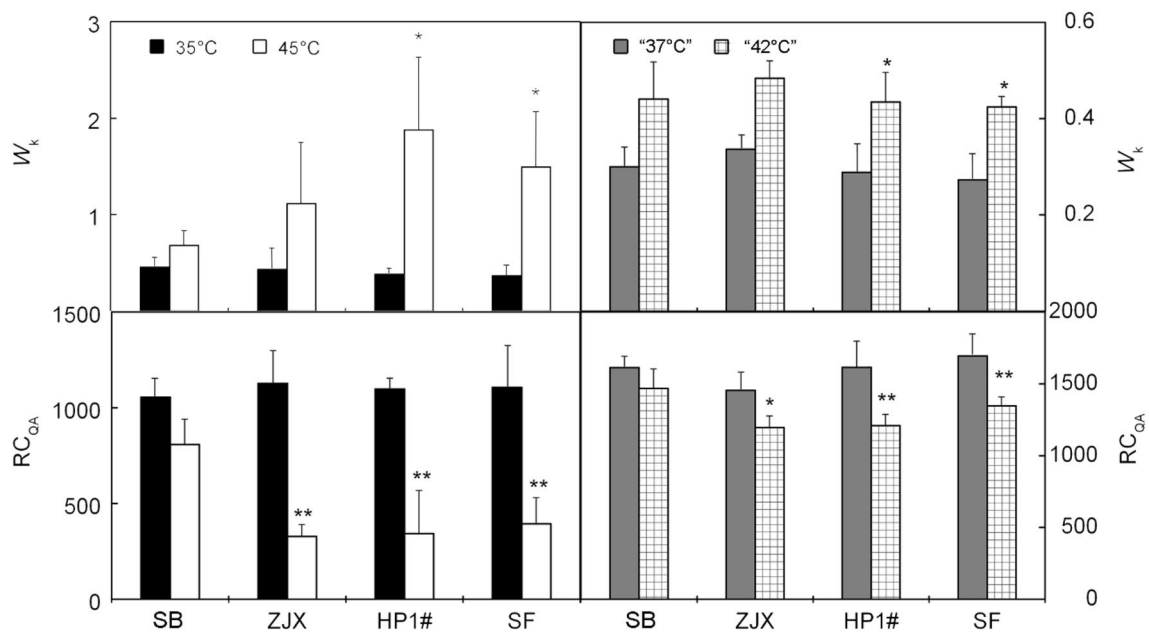


Fig. 5 Donor side indicator (W_k) and reaction center indicator (RC_{QA}) of PSII in the leaves of grapevines. The field conditions on July 23 and July 31, 2015 are denoted by “37” and “42 °C”, respectively. SB: ‘Summer Black’; ZJX: ‘Zuijinxiang’; HP1#: ‘Hupei1#’; SF:

‘Shenfeng’. Significant differences among the different temperature treatments at the same time point are indicated by * ($p < 0.05$) or ** ($p < 0.01$). Vertical bars represent standard errors of the means from three replications

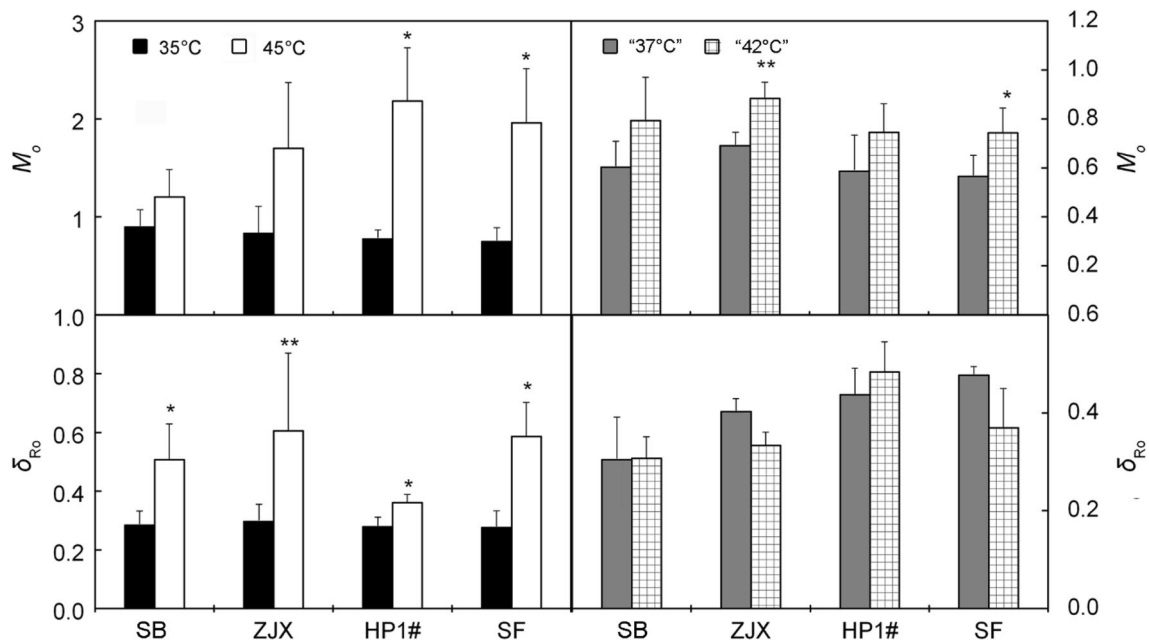


Fig. 6 Acceptor side parameters M_o and δ_{Ro} in the leaves of grapevines. The field conditions on July 23 and July 31, 2015 are denoted by “37” and “42 °C”, respectively. SB: ‘Summer Black’; ZJX: ‘Zuijinxiang’; HP1#: ‘Hupei1#’; SF: ‘Shenfeng’. Significant differences

among the different temperature treatments at the same time point are indicated by * ($p < 0.05$) or ** ($p < 0.01$). Vertical bars represent standard errors of the means from three replications

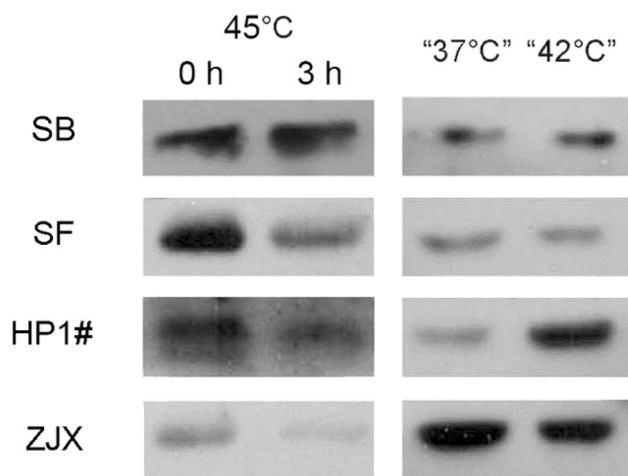


Fig. 7 HSP21 expression levels in the leaves of grapevine. The field conditions on July 23 and July 31, 2015 are denoted by “37” and “42 °C”, respectively

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