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ORIGINAL PAPER

High temperature effects on D1 protein turnover in three wheat varieties with different heat susceptibility

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Abstract Heat stress is one of the main abiotic stresses that limit plant growth. The effects of high temperature on oxidative damage, PSII activity and D1 protein turnover were studied in three wheat varieties with different heat susceptibility (CS, YN949 and AK58). The results showed that heat stress induced lower lipid peroxidation in AK58 and YN949 than CS, which was related to different changes of SOD, CAT, POD and H_2O_2. Similarly, AK58 and YN949 performed better PSII photochemical efficiency (F_v/F_m, ΦPSII and ETR) under high temperature, which was attributed to rapid synthesis and degradation of D1 protein. Moreover, higher expression of D1 protein turnover-related genes (*PsbA*, *STN8*, *PBCP*, *Deg1*, *Deg2*, *Deg5*, *Deg8*, *FtsH1/5* and *FtsH2/8*) and SOD activity in AK58 and YN949 under normal conditions also established a basis for acclimatizing high temperatures, thereby alleviating PSII photoinhibition and reducing oxidative damage when exposed to heat stress.

Keywords High temperature · PSII photochemical efficiency · D1 protein · Wheat

Abbreviations

CAT	Catalase
DAB	3,3′-Diaminobenzidine tetrahydrochloride
F_v/F_m	Potential photochemical efficiency
OEC	Oxygen evolving complex
POD	Peroxidase
PSII	Photosystem II
ROS	Reactive oxygen species
SOD	Superoxide dismutase
TBARS	Thiobarbituric acid-reactive substances
ΦPSII	Actual photochemical efficiency

Introduction

Food is the basis for human survival. With the global climate changes, plants often suffer from various kinds of stresses, especially high temperature, which has become a major abiotic stress. High temperature usually induces photoinhibition (Wang et al. 2014), reduces photosynthesis, and thus limits the biomass production and productivity of plants (Yamori et al. 2006).

Photosynthesis is known to be one of the most heat-sensitive processes (Yordanov et al. 1986). Previous studies confirmed that photosynthetic apparatus damage induced by high temperature is the main reason of photosynthetic rate reduction (Berry and Bjorkman 1980; Allakhverdiev and Murata 2004), it will be more severe when the photosynthetic electron transfer blocked, the light energy increased and excessive reactive oxygen species (ROS) produced (Nath et al. 2013a, b). Photosystem II (PSII), with low thermal stability, is the most vulnerable photosynthetic apparatus to heat stress (Sonoike 2011).

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Heat stress could lead to the dissociation of the peripheral antenna complex of PSII from its core complex, decrease the activity of the oxygen evolving complex (OEC), and inhibit the process of electron transfer in PSII, but under moderate high temperature, the reduction of PSII activity was mainly due to PSII repair inhibition rather than serious PSII damage (Allakhverdiev et al. 2008). While the PSII repair is closely related to D1 protein turnover in PSII reaction center (Giardi et al. 2013).

The turnover of D1 protein consists of four processes, including synthesis, phosphorylation, dephosphorylation and degradation (Aro et al. 1993; Tikkanen and Aro 2012). Once D1 protein is damaged, it will be phosphorylated by protein kinase STN8 (Pesaresi et al. 2011; Nath et al. 2013b), and then the phosphorylated D1 protein can be used as a signal to guide the damaged PSII to stroma lamella. After the damaged PSII reaches stroma lamella, phosphorylated D1 protein will be dephosphorylated by phosphatase PBCP (Samol et al. 2012). Subsequently, D1 protein degradation occurs under the action of the protease FtsHs and Degs (Edelman and Mattoo 2008; Sun et al. 2010). Finally, a newly synthesized D1 protein, encoded by PsbA, is reassembled into PSII, thus recovering PSII activity.

In general, rapid synthesis of D1 protein is the basis of reassembly of activated PSII, reversible phosphorylation of D1 protein is a prerequisite for D1 protein degradation, and D1 protein degradation requires protease FtsHs (FtsH1, FtsH2, FtsH5, FtsH8) and Degs (Deg1, Deg2, Deg5, Deg7, Deg8). The problem is that which genes or processes play a crucial role in D1 protein turnover or PSII repair when exposed to high temperature. In this study, the effects of high-temperature on D1 protein turnover in three wheat cultivars were compared and heat response mechanism was discussed. This is very important to obtain new varieties with high tolerance to heat stress.

Materials and methods

Plant growth and treatments

The seeds of three wheat cultivars (Chinese Spring, CS, Ai Kang58, AK58 and Yu Nong949, YN949) were supplied by National Engineering Research Center for Wheat in Henan, China. After surface-sterilized, wheat seeds were germinated on the wetted filter paper for 3 days in dark, and then cultured in 1/2 Hoagland nutrient solution, in the conditions of 25/22 °C (light/dark) with 14 h photoperiod, 300 μmol m^{-2} s^{-1} light intensity and 70 % relative humidity. Two weeks later (three leaves stage), the seedlings were divided into two groups. One group was cultured under normal conditions (as the control). The other group was transferred to moderate high temperature (40 °C) for 48 h. After treatment, the second leaf was collected for analysis.

Detection of H_2O_2, TBARS content and SOD, CAT, POD activities

H_2O_2 was detected according to Christou et al. (2013). TBARS was determined by the method of Heath and Packer (1968). The activities of SOD, CAT and POD were quantified referring to the description of Giannopolitis and Ries (1977), Aebi (1984) and Upadhyaya et al. (1985) respectively.

Western blotting assay

The thylakoid membrane protein was prepared as described in Su et al. (2014). In brief, samples were ground in liquid nitrogen, transferred into extraction buffer, and then filtered with four layers of gauze. Subsequently, the filtrate was centrifuged at 4 °C, 5000*g* for 5 min, removed the supernatant and suspended the precipitate with 5 mM $MgCl_2$ and 10 mM NaF, and then centrifuged again. Finally the storage buffer was used to dissolve the precipitate. The protein concentration was quantified according to Bradford (1976). The standard curve was prepared with bovine serum albumin.

Western blotting assay was operated according to Guo et al. (2006). 15 μg proteins were separated by 15 % SDS-PAGE and then transferred onto polyvinylidene difluoride membranes. Non-specific binding protein was blocked with TBST (containing 5 % milk, pH 7.4) for 1 h at room temperature or overnight at 4 °C. Membranes were then incubated 1–2 h at room temperature with primary antibodies (anti-PsbA (anti-D1-DE) or phosphorylated anti-PsbA) in TBST plus 1 % milk, Anti-rabbit IgG as the secondary antibody. The color was developed with DAB (3, 3′-diaminobenzidine tetrahydrochloride).

Analysis of chlorophyll fluorescence

Ultra portable modulated chlorophyll fluorometer (MINI-PAM-II, walz, Germany) was used to detect Chlorophyll fluorescence (Li et al. 2015). The operating conditions of measuring instrument were 400 μmol m^{-2} s^{-1} actinic light intensity and 8000 μmol m^{-2} s^{-1} saturated flash intensity. After 20 min dark adaption, measurement was performed using the light induction curve program. According to the monitoring data (such as F_m, F_0, F_m', F_0' and F), the values of F_v/F_m, ΦPSII and ETR can be calculated using the included software ($F_v/F_m = (F_m - F_0)/F_m$; $\Phi PSII = (F_m' - F)/F_m'$; $ETR = PAR \cdot 0.84 \cdot 0.5 \cdot \Phi PSII$).

Cloning of D1 protein turnover- related genes and sequence alignment

Firstly, the full or part sequences of D1 protein turnover-related genes were assembled by the method of in silico cloning, which was described in previous (Li et al. 2015). And then the assembled sequences were applied to ORF prediction, as a result, the full-length CDS sequences of *Deg5*, *FtsH2/8* and *PBCP* were obtained according to in silico cloning, but for *Deg1*, *Deg2*, *Deg7*, *Deg8* and *FtsH1/5*, the CDS regions were incomplete (*Deg1*, *Deg7*, *FtsH1/5* missing the 5′ end and *Deg2*, *Deg8* missing the 3′ end). Secondly, these 5 genes were applied to homologous alignment, the corresponding homologous genes in barley or *Brachypodium distachyon* were found, then PCR amplification was performed using the primers designed from these homologous genes and assembled sequences. The missing end of *Deg1*, *Deg2* and *Deg8* were referred to the genes in barley, *Deg7* and *FtsH1/5* were referred to the genes in *Brachypodium distachyon* (the sequences of *Deg7* and *FtsH1/5* in barley are not full-length CDS). The specific primer information for gene clone was shown in Supplemental data S1. Finally, the amplified gene fragments were cloned into T-vector for sequencing by the method of pEASY®-Blunt Cloning Kit (TRANS). The alignments of protein sequences among *Triticum aestivum*, *Brachypodium distachyon* and *Arabidopsis thaliana* were performed with DNAMAN v6.0 software.

Real time-PCR analysis

Total RNA was isolated using Trizol (Invitrogen) and 1 μg RNA was used for cDNA synthesis according to PrimeScript™ RT reagent Kit with gDNA Eraser (Takara). Quantitative real time RT-PCR (qRT-PCR) was performed using a CFX96 Real-Time PCR Detection System (Bio-Rad) with SYBR® Premix Ex Taq™ (Takara). The values of relative expression levels were the relative to control samples of CS after normalization to *Actin*. The primers for *Actin* (AB181991.1), *PsbA* (AB042240.3) and *STN8* (AK332199.1) were from the sequences in NCBI, the primers for other genes were designed according to the obtained sequence above. The specific primer information for RT-PCR was showed in Supplemental data S2.

Statistical analysis

All the results were shown as the means of at least three independent experiments. For the statistical analysis, one-way variance (ANOVA) combined with Duncan's multiple range test were used. It was considered statistically significant, when $P < 0.05$.

Results

Effect of high temperature on the photochemical efficiency of PSII

As shown in Table 1, after high temperature (40 °C) treatment, PSII maximum quantum yield (F_v/F_m), effective quantum yield (ΦPSII) and relative electron transport rate (ETR) were significantly decreased in three wheat varieties. However, the inhibitory effect of heat stress on chlorophyll fluorescence was weaker in AK58 and YN949 compared to CS. Under heat stress, the values of F_v/F_m, ΦPSII and ETR was higher in AK58 and YN949 than that in CS.

Effect of high temperature on H_2O_2, lipid peroxidation and antioxidase activities

High temperature induced lipid peroxidation. Under heat stress, the TBARS content in CS and YN949 increased to 1.7 and 1.2 times of the control group respectively, but it was substantially unchanged in AK58 (Fig. 1a). This result suggested that high temperature induced more severe oxidative damage in CS compared to YN949 and AK58. However, the change of H_2O_2 content was reversed. Compared to CS, H_2O_2 content was at a higher level in YN949 and AK58 under both normal conditions and high temperature (Fig. 1b), which may be related to the collective effects of SOD, CAT and POD activities. Higher SOD activity (Fig. 1c) and lower CAT and POD activities were found in AK58 under heat stress (Fig. 1d, e), even under normal conditions, the activity of POD also showed lower value in AK58 than other two varieties.

Table 1 The changes of photochemical efficiency (F_v/F_m), actual photochemical efficiency (ΦPSII), and electron transfer rate (ETR) of PSII under heat stress

Treatment	F_v/F_m	ΦPSII	ETR
Control			
CS	0.809 ± 0.0075b	0.3247 ± 0.0121a	84.93 ± 3.21b
AK58	0.8378 ± 0.0124a	0.3278 ± 0.0458a	90.28 ± 9.86a
YN949	0.8382 ± 0.0141a	0.3195 ± 0.0151a	89.97 ± 4.36a
Heat			
CS	0.6496 ± 0.0018d	0.1265 ± 0.0074d	31.95 ± 1.89e
AK58	0.6812 ± 0.0053c	0.3122 ± 0.0084b	78.83 ± 2.19c
YN949	0.67 ± 0.0017c	0.2068 ± 0.0422c	55.95 ± 9.37d

Values are the mean ± standard deviation (SD) ($n = 5$). Different letters in the same column indicate statistically significant differences ($P < 0.05$)

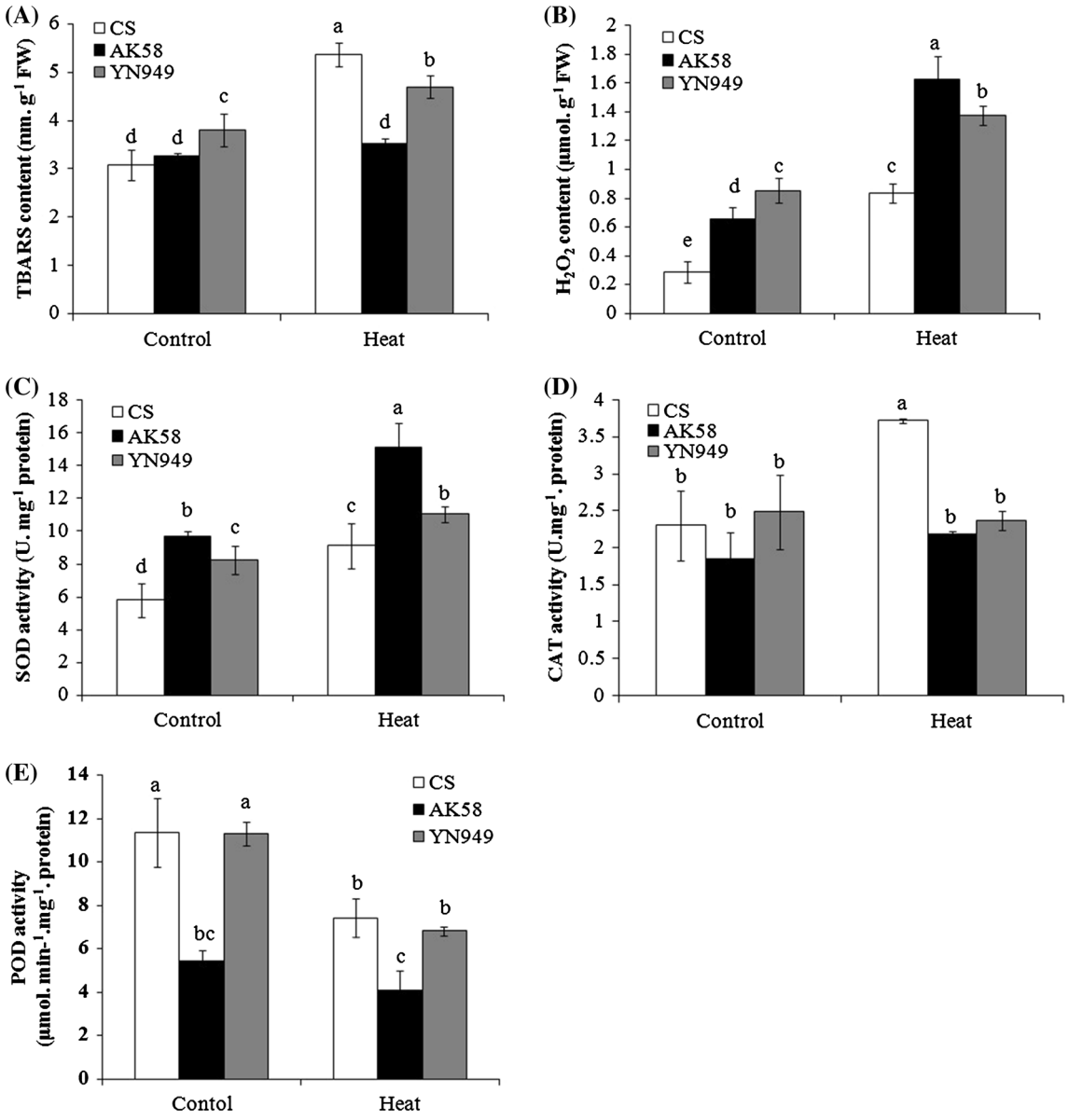

Fig. 1 The contents of TBARS (**a**) and H_2O_2 (**b**), activity of SOD (**c**), CAT (**d**) and POD (**e**) in three wheat cultivars. Seedlings were grown in 1/2 Hoagland solution for 2 weeks, and then performed heat treatment with 40 °C for 48 h, 25 °C culture conditions as the control. Values are the mean ± standard deviation (SD) ($n = 3$). The *same letter above the bars* shows no significant difference at $P < 0.05$

The effect of high temperature on D1 protein

Under heat stress, D1 protein is the most vulnerable component in PSII reaction center. Therefore, the content of D1 protein was detected in three wheat varieties. As shown in Fig. 2a, D1 protein content significantly decreased when exposed to high temperature, only 44, 62 and 76 % of the control in CS, YN949 and AK58 respectively. Furthermore, D1 protein accumulation in AK58 was more than that in other two varieties even under normal conditions. And the variation tendency of transcript expression of *PsbA* was same to D1 protein (Fig. 2b). However, the performance of phosphorated D1 protein was in contrast with D1 protein (Fig. 3a). Under heat stress, the content of phosphorated D1 protein in AK58 (28 % of the control) was far below than that in CS (51 % of the control) and YN949 (72 % of the control), which might result from the lower expression of *STN8* and *PBCP* in AK58 (Fig. 3b). Strangely, under high temperature, there were less *STN8* and *PBCP* expression but with more phosphorated D1 protein accumulation in YN949 compared to CS. This suggested that the changes

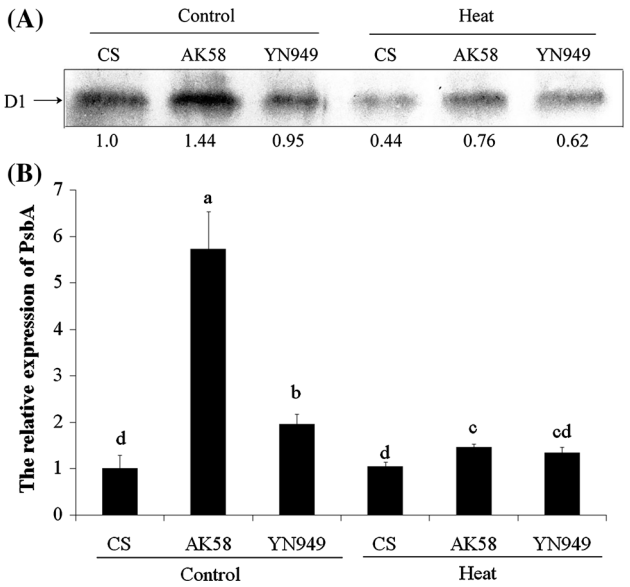

Fig. 2 The translation and transcription levels of PsbA. Seedlings were grown in 1/2 Hoagland solution for 2 weeks, and then performed heat treatment with 40 °C for 48 h, 25 °C culture conditions as the control. After that, thylakoid protein and total RNAs thylakoid protein were extracted from leaves for western blotting and qRT-PCR assays respectively. The *number below the band* indicates relative abundance of D1 protein and the *same letter above the bars* shows no significant difference at $P < 0.05$. Values are the mean ± standard deviation (SD) ($n = 3$)

of phosphorated D1 protein may be related to the follow-up process, D1 protein degradation.

Cloning and expression analysis of D1 protein degradation-related genes

Except D1 protein synthetase PsbA and phosphorylase kinase STN8, other D1 protein turnover-related genes in wheat are unknown. Therefore, this study cloned these genes by the method of in silico cloning and homology cloning. Finally, the full ORF of *PBCP*, *Deg1*, *Deg2*, *Deg5*, *Deg7*, *Deg8*, *FtsH1/5* and *FtsH2/8* were obtained, the number of amino acids was 322aa, 427aa, 607aa, 311aa, 1091aa, 445aa, 687aa and 673aa respectively, and the homology of these genes between *Arabidopsis thaliana* and wheat was 49.3, 72.4, 65.6, 51.9, 70.1, 65.9, 78.0 and 82.0 % respectively (Supplemental data S3). The homology was higher when alignment to genes in *Brachypodium distachyon*, it was 84.0, 85.6, 93.5, 86.1, 94.7, 89.0, 94.8 and 95.4 % respectively (Supplemental data S4).

The expression of D1 protein degradation-related genes in three varieties were shown in Fig. 4. Under normal conditions, the transcript level of all the genes, with the exception of *Deg7*, was highest in AK58, lowest in CS and middle in YN949. Under heat treatment, *Deg1*, *Deg7* and

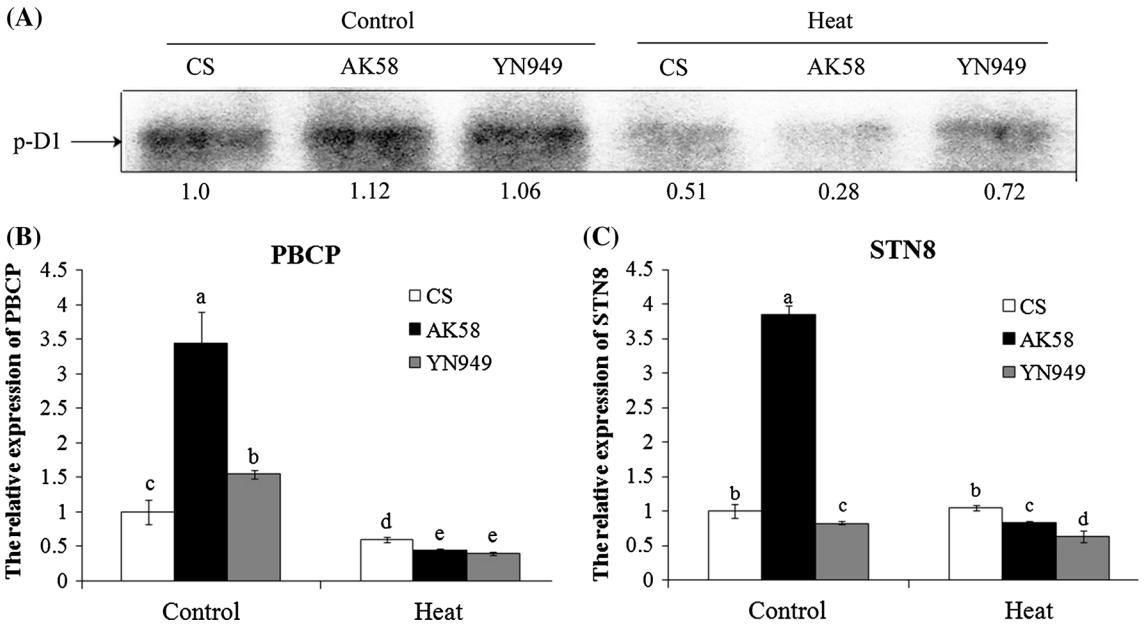

Fig. 3 The content of phosphorylated D1 protein (p-D1) (**a**) and expression analysis of PBCP (**b**) and STN8 (**c**). Seedlings were grown in 1/2 Hoagland solution for 2 weeks, and then performed heat treatment with 40 °C for 48 h, 25 °C culture conditions as the control. After that, thylakoid protein and total RNAs were extracted from leaves for western blotting and qRT-PCR assays respectively. The *number below the band* indicates relative abundance of phosphorylated D1 protein and the *same letter above the bars* shows no significant difference at $P < 0.05$. Values are the mean ± standard deviation (SD) ($n = 3$)

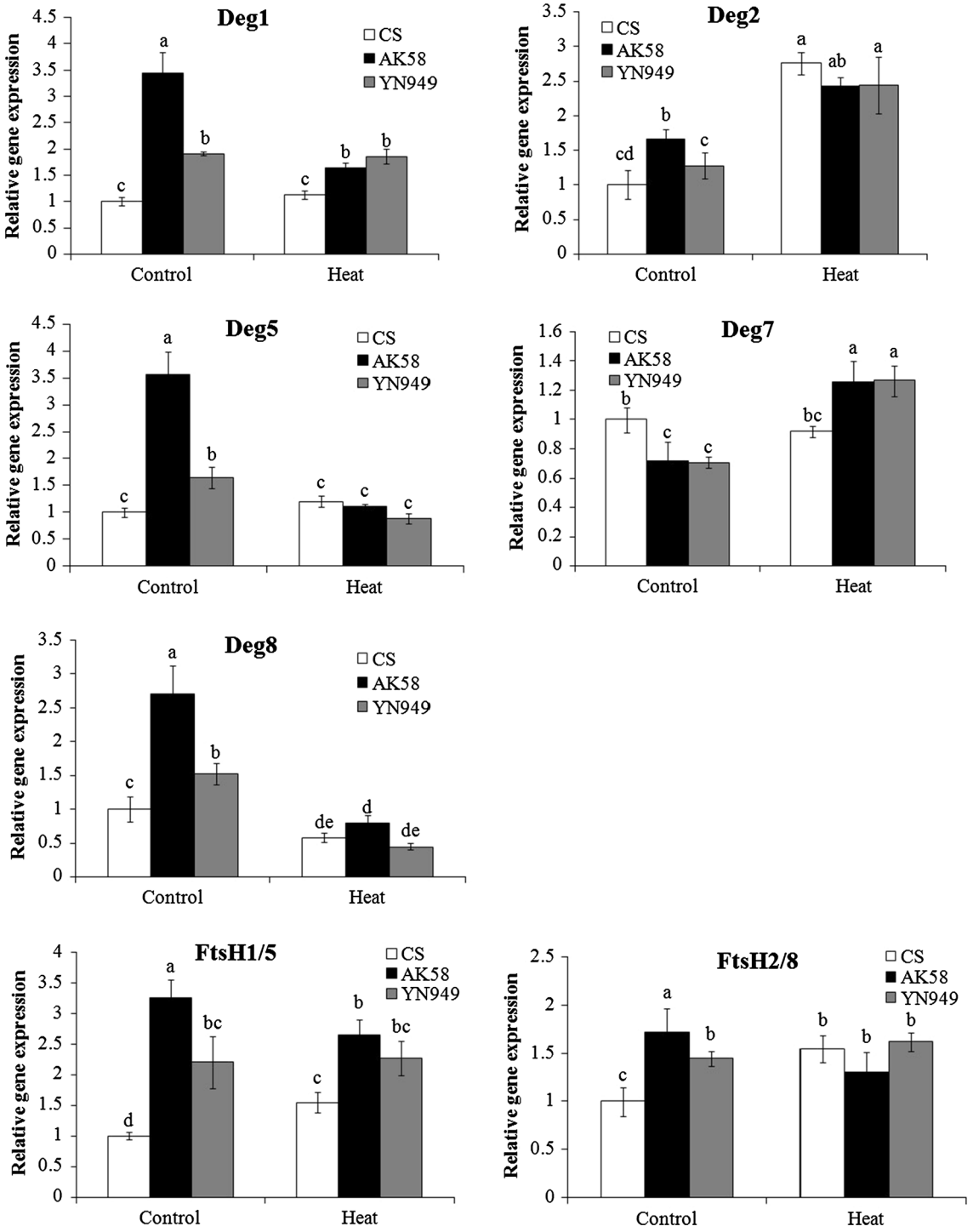

Fig. 4 The expression of D1 protein degradation-related genes in leaves. Seedlings were grown in 1/2 Hoagland solution for 2 weeks, and then performed heat treatment with 40 °C for 48 h, 25 °C culture conditions as the control. After that, total RNAs was extracted from leaves for qRT-PCR assays. The *same letter above the bars* shows no significant difference at $P < 0.05$. Values are the mean ± standard deviation (SD) ($n = 3$)

FtsH1/5 showed a higher transcription in AK58 and YN949 compared to CS, but there were no significant differences among three varieties in the expression of *Deg2*, *Deg5*, *Deg8* and F*tsH2/8*. These results suggested that *Deg1*, *Deg7* and *FtsH1/5* might be more important to high temperature tolerance of wheat.

Discussion

PSII is a critical damage site by a variety of stress factors, such as drought, salinity, low and high temperature. High temperature is easy to destroy protein structure, induce excessive ROS production and lead to photosynthetic apparatus damage. Chlorophyll fluorescence analysis is a sensitive and reliable method for quantitative measurement of stress induced changes in the photosynthetic apparatus (Brestic et al. 2012; Kautz et al. 2014). In this study, the chlorophyll fluorescence F_v/F_m, ΦPSII and ETR markedly decreased under heat stress in three wheat varieties, which proved that the PSII activity was inhibited by high temperature. However, less reduction in F_v/F_m, ΦPSII and ETR was found in AK58 in comparison to other two cultivars, particularly CS (Table 1). Sharma et al. (2012) verified chlorophyll fluorescence can be used to detect genotypic differences of wheat in response to heat stress. Therefore, the results about chlorophyll fluorescence in this study demonstrated that AK58 exhibited higher heat tolerance.

The decreased chlorophyll fluorescence under heat stress suggested that photosynthetic apparatus and the electron transfer had been damaged. These changes lead to electronic leak and transfer electrons to oxygen molecules to produce ROS, such as superoxideradicals ($O_2^{\cdot-}$) and singlet oxygen ($^1O_2$), thereby inducing oxidative damage in plants (Allakhverdiev et al. 2008). Therefore, in accordance to the variation tendency of chlorophyll fluorescence, the TBARS content was the lowest in AK58, followed by YN949 and CS under heat stress. ROS can be scavenged by a series of antioxidant enzymes, such as superoxide dismutase (SOD) and catalase (CAT) (Bukhov and Mohanty 1999). SOD reduces oxidative damage by converting hyperactive superoxide radicals to hydrogen peroxide (Krieger-Liszkay 2005; Asada 2006). So, it is not difficult to understand that higher SOD activity was found in AK58. Unexpectedly, CAT, an important enzyme for removing H_2O_2, performed lower activity in AK58 and YN949 than that in CS, which resulted in higher H_2O_2 content in AK58 and YN949 (Fig. 1b, d). Furthermore, lower peroxidase (POD) activity intensified the accumulation of H_2O_2 in AK58 (Fig. 1e). Many reports indicated that higher concentration of H_2O_2 is toxic. But there are different points, for example, exogenous H_2O_2 induced heat shock proteins (Banzet et al. 1998), which are important for protecting cells against high temperature and other stresses (Barua et al. 2003). H_2O_2 increased potato thermotolerance (Lopez-Delgado et al. 1998). An inductive pulse of hydrogen peroxide pretreatment restores redox-homeostasis and oxidative membrane damage under extremes of temperature in two rice cultivars (Bhattacharjee 2012). Wang and Li (2006) found that higher heat resistance was obtained by application of SA in grape leaves with higher H_2O_2 content. Similarly, higher H_2O_2 content was found in thermotolerance wheat (AK58) under both normal and heat stress conditions. These results suggested that H_2O_2 may play a signaling role during acclimation to high temperature (Larkindale and Huang 2005).

Plants have evolved many ways to adapt to high temperature. In vivo, the extent of damage depends on the balance between damage and repair processes when exposed to stress. The relative instability of PSII protein is: D1, D2 > Cyt b559 > CP43 > CP47 (Mattoo et al. 1999). Therefore, the D1 and D2 protein are main factors affecting PSII instability, especially the D1 protein. A newly synthesized D1 protein reassembled to PSII is regarded as the primary event of the PSII repair cycle. Thus, the higher expression of *PsbA* and D1 protein accumulation in thermotolerance wheat (AK58) (Fig. 2) laid a solid foundation for PSII repair. Previous studies reported that the phosphorylation of D1 protein is required for D1 protein turnover (Tikkanen et al. 2008; Nath et al. 2013a), but Bonardi et al. (2005) showed that *stn8* mutant plants, with much lower phosphorylated D1 protein, did not show any alteration in D1 protein turnover. These indicated that phosphorylation/dephosphorylation cycle was not crucial for D1 turnover and PSII repair, but rather might act to fine-tune the process (Pesaresi et al. 2011). In this study, under high temperature, although the reversible phosphorylation was slower, the photoinhibition and oxidative damage were weaker in AK58 and YN949, which also suggested that the reversible phosphorylation of D1 protein was not the key factor for affecting D1 turnover under heat stress.

After the damaged D1 protein being degraded, a new D1 protein could be inserted into PSII to complete PSII repair. *Deg1*, *Deg7*, *Deg8* and *FtsH1/5* performed higher expression in AK58 when exposed to high temperature, which suggested that fast D1 protein degradation favored PSII repair. It's worth noting that all the D1 protein turnover-related genes, with the exception of *Deg7*, were significantly higher expression in AK58 compared to CS under normal conditions (Figs. 2, 3, 4). It meant that AK58 had the faster D1 protein turnover under normal conditions, which maybe contribute to acclimatizing high temperatures, and thus reducing damage (Fig. 1) and alleviating PSII photoinhibition (Table 1) when exposed to heat stress.

In summary, these results showed that there were two ways to alleviate photoinhibition induced by high temperature in thermotolerance wheat: First, rapid D1 protein synthesis and degradation promoted PSII repair under heat stress; Second, high level of D1 protein turnover under normal conditions provided a basis for PSII stability when exposed to high temperature, thus balancing the damage and repair process of PSII.

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