Responses of young wheat plants to moderate heat stress

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Abstract
Moderate heat stress may provide protection against a subsequent severe high temperature stress in plants. However, the exact mechanisms of heat acclimation of wheat are still poorly understood. In the present work, two wheat varieties Ellvis and Soissons were exposed to a moderate elevated temperature at 30 °C, and the changes of certain protective mechanisms were investigated. Although the differences in the proline level between the genotypes were not substantial, it was approx. 2–3 times higher in the heat-treated plants than in the controls. After exposure to moderate elevated temperature, the activities of ascorbate peroxidase and catalase were also induced. Similarly, the amount of the free salicylic acid also increased after moderate heat stress, independently on the genotypes. The amount of the main polyamines, namely, putrescine, spermidine, and spermine either did not change or decreased after the same period. However, heat acclimation increased the level of 1,3-diaminopropane, in parallel with a polyamine oxidase gene, TaPAO. While the expression level of the peroxisomal polyamine oxidase gene TaperPAO hardly changed, TaPAO showed a substantial increase after 1 day, especially in Soissons, and at the end of the heat treatment was still significantly higher than in the controls. These suggest that signalling processes related to polyamine metabolisms or salicylic acid-related processes might also contribute to the higher heat tolerance induced by moderate heat stress. The variations in recorded measurements were mainly temperature dependent, and the effect of genotype was less pronounced than the effect of moderate heat treatment itself.

Keywords Abiotic stress · Antioxidant activity · Heat acclimation · Moderate heat stress · Polyamine cycle · Triticum aestivum l.

Abbreviations
APX Ascorbate peroxidase
CAT Catalase
DAP 1,3-Diaminopropane
G-POD Guaiacol peroxidase
GR Glutathione reductase
GST Glutathione-S-transferase
oHCA Ortho-hydroxy-cinnamic acid
PAO Polyamine oxidase
PUT Putrescine
qRT-PCR Quantitative real-time PCR
SA Salicylic acid

SPD Spermidine
SPDS Spermidine synthase
SPM Spermine
TaPAO Putative apoplastic polyamine oxidase gene
TaperPAO Peroxisomal polyamine oxidase gene

Introduction
Heat stress is one of the most important abiotic stress factors limiting growth of crop plants in many regions of the world leading to dramatic reduction in the economic yield (Battisti and Naylor 2009). Wheat plants, especially winter varieties are usually less adapted to warmer temperatures than other main crops, such as maize or rice. Worldwide, heat stress can reduce the yield of wheat by as much as 15% (Qin et al. 2008). Global climate change has also exacerbated the severity of many abiotic stresses, including temperature extremes, with significant yield reductions in several crop plants (Huang et al. 2018). Plants have evolved effective mechanisms to acclimate to the variable environment.
However, when these changes are rapid and extreme, they are often unable to avoid or significantly mitigate stress. This is especially true for crop plants, which often originate from far regions with different climate and have relatively narrow genetic diversity to cope with the fluctuating environment. Better understanding of stress adaptation mechanisms may also provide useful information for breeders for developing new crops with better stress tolerance.

In general, responses to high temperatures may involve, among others, alteration of transcriptional control, synthesis of osmoprotectants, heat shock proteins (Hasanuzzaman et al. 2013), modifying carbohydrate metabolism (Wang et al. 2012) or the induction of various signalling processes (Proveniers and van Zanten 2013), and antioxidative systems to reduce the harmful effects of oxidative damage (Zhou et al. 2019). Exposure of plants to non-lethal, slightly elevated temperatures may provide protection against a subsequent severe high temperature stress (heat acclimation). The mechanisms of heat acclimation of the photosynthetic machinery have been extensively studied in various crop species, including wheat. The effectiveness of heat acclimation depends on various factors. For example, it also shows a season dependence, as it was recently demonstrated in winter wheat plants (Zhou et al. 2018).

Polyamines (PAs), such as putrescine (PUT), spermidine (SPD), and spermine (SPM), can be found in relatively high amounts in all living cells, and their protective role has been demonstrated under various stress conditions (Pál et al. 2015, 2018a, b). Besides their direct protective role, they also regulate fundamental cellular processes as signalling molecules. Recent results suggest that stress tolerance induced by the different PAs is mainly related to their signalling role rather than to their accumulation (Alcázar et al. 2010; Pál et al. 2015, 2019; Szalai et al. 2017). However, the involvement of the PA cycle in the heat-acclimation processes has not been characterised yet.

It has been shown that the differences in heat tolerance in different wheat genotypes may be associated with multiple mechanisms regulated by various transcription factors and involving several stress-related genes (Qin et al. 2008). However, in spite of the extensive research on this field, the molecular mechanisms of the heat-acclimation processes, especially in cereals, are still poorly understood. We have recently demonstrated that wheat varieties of different origins could be efficiently heat-acclimated when plants were exposed to 30 °C for a certain period (Végh et al. 2018). Growing at this acclimating temperature did not induce either substantial stomatal closure or photoinhibition. Certain genotypes were able to induce transpiration at this temperature and did not reduce net assimilation. Using different heat sensitivity and heat-acclimation indexes, it was possible to differentiate the heat responses of the different wheat genotypes (Perdomo et al. 2015; Végh et al. 2018).

Using our previously described heat-acclimation system in wheat (Végh et al. 2018), the next goal was to further evaluate the effects of moderate heat stress in these plants. The present work aimed at identifying processes with substantial changes after heat treatment, and those with variation between the genotypes with different levels of heat tolerance. In the present study, we focused on certain stress acclimation mechanisms, which may play decisive role in various stress responses. These included the accumulation of proline or salicylic acid and induction of antioxidant enzymes. Special attention has been focused on PA signalling and metabolisms both at metabolite and gene expression levels.

Materials and methods

Plant materials and growth conditions

Wheat (Triticum aestivum L.) genotypes var. Ellvis and Soissons were grown in pots filled with 3:1 (v:v) mixture of loamy soil and sand in a Conviron PGV-15 growth chamber (Controlled Environments Ltd., Winnipeg Canada) at 20/18 °C day/night temperature with 16/8 h photoperiod at 250 µmol m−2 s−1 photosynthetic photon flux density (PPFD) at the canopy level, and 75% relative humidity. 10 days after sowing (young plants with 2–3 leaves) part of the plants were heat-treated at 30/27 °C day/night temperature, while others were grown at 22/20 °C (controls) for 14 days. Samples were taken and measurements were carried out at different days indicated at the measurements.

Determination of proline content

The determination of proline content was based on its reaction with ninhydrin according to the methods of Bates et al. (1973). In the experiments, 0.5 g of leaf sample was extracted with 5 ml 3% sulfosalicylic acid (w/v). After centrifugation, 1 ml supernatant was reacted with 1 ml ninhydrin and 1 ml of glacial acetic acid for 1 h at 100 °C. The chromophore was extracted with 4 ml toluene from the cooled reaction mixture, and the absorbance of chromophore was read at 520 nm, using toluene as a blank. The proline concentration was determined from a standard curve and calculated as mg proline/FW.

Measurements of antioxidant enzymes

For the analysis of antioxidant enzyme activity, 0.5 g leaf tissue was homogenized in 2.5 ml ice-cold Tris buffer (0.5 M, pH 7.5) containing 3 mM MgCl₂ and 1 mM EDTA. The enzyme activities were determined photometrically with a UV–visible recording spectrophotometer (UV–Vis 160A,
Shimadzu Corp. Kyoto, Japan), and expressed in nkat g⁻¹ fresh weight (FW). The ascorbate peroxidase (APX; EC 1.11.1.11.) and the catalase (EC 1.11.1.6.) activities were measured as described earlier (Janda et al. 1999). The guaiacol peroxidase (G-POD; EC 1.11.1.7.), the glutathione reductase (GR; EC 1.6.4.2.), and the glutathione-S-transferase (GST; EC 2.5.1.18.) activities were determined according to Ádám et al. (1995), Smith et al. (1988), and Mannervik and Guthenberg (1981), respectively.

**Determination of salicylic acid and ortho-hydroxy-cinnamic acid**

Salicylic acid (SA) extractions were performed according to Pál et al. (2005) by grinding 0.5 g of plant tissue in liquid nitrogen in a mortar and pestle, in the presence of 0.5 g quartz sand. After separation on a reverse phase column (Synergi Fusion-RP, 80A, 150 × 4.6 mm; 4 μm, Phenomenex, Inc. California, USA) SA and ortho-hydroxy-cinnamic acid (oHCA) were quantified fluorimetrically (W474 scanning fluorescence detector, Waters, Milford, USA), with excitation at 317 nm and emission at 436 nm for oHCA, followed by excitation at 305 nm and emission at 407 nm for SA.

**PA and 1,3-diaminopropane analyses**

The analyses were carried out as described earlier (Németh et al. 2002) with slight modifications. 200 mg of leaves were homogenized with 1 ml 0.2 M ice-cold perchloric acid and were left to stand for 20 min on ice. The extract was centrifuged at 10,000 g for 20 min and the supernatant was used. PUT, SPD, and SPM, together with the catabol of the latter two ones, 1,3-diaminopropane (DAP) were analysed as dansylated derivatives via HPLC using a W2690 separation module and a W474 scanning fluorescence detector for excitation at 340 nm and emission at 515 nm (Waters, Milford, MA, USA).

**Real-time PCR**

Total RNA was extracted from fully developed leaf and root samples using TRI Reagent®. The samples were treated with DNase I and cleaned with a Direct-zol™ RNA MiniPrep Kit (Zymo Research, Irvine, CA, USA) according to the manufacturer’s instructions. cDNA synthesis was carried out using M-MLV Reverse Transcriptase (Promega Corporation, Madison, WI, USA). The candidate genes encoding for PAO were identified with RNAseq analysis according to Xiong et al. (2017). The presence of peroxisomal target signal of the candidate gene Q4 was analyzed via P Pero PTS1 Type Peroxisomal Protein Prediction Model (Wang et al. 2017). Gene-specific primers and housekeeping primers (Table 1), PCRBIO SyGreen Mix (PCR Biosystems, London, UK), and CFX96 Touch™ Real-Time PCR Detection System (Bio-Rad, Hercules, CA, USA) were used for quantitative real-time PCR (qRT-PCR) reaction. The relative gene expression values were determined with the ∆∆Ct method (Livak and Schmittgen 2001). Ct values were normalized by the Ct values of housekeeping gene Ta2291 encoding for an ADP-ribosylation factor. All reactions were performed in triplicate.

**Statistical analyses**

Usually, five parallel samples were collected for each measurements. Significant differences between the treatments and the genotypes were probed using the t test method.

**Results**

**Effects of moderate heat stress in young wheat plants**

Under control conditions, slightly, higher proline level could be detected in the leaves of young Ellvis than in Soissons (Fig. 1). Exposure to acclimating temperature at 30 °C for 14 days significantly increased, approx.

### Table 1 Reference gene and target genes investigated in wheat plants using qRT-PCR

| Gene name | Primer sequences (5′ → 3′) | Reference |
|-----------|---------------------------|-----------|
| Ta2291 (ADP-ribosylation factor) | F: GCTCTCCAACAACTTGCCAAC<br>R: GCTCTGCTGTCACATAGCG | Paolacci et al. (2009) |
| Traes_7AL_425787F27 (Q2;TaPAO) (putative apoplastic PAO) | F: CCAGCCTCCAGCTCGCAAC<br>R: GCCGACGCTTCCACCTCGTC | Xiong et al. (2017) |
| Traes_2BL_DA615F345 (Q4;TaperPAO) (putative peroxisomal PAO) | F: GCTCATAAATCGCAATTCCT<br>R: TCGGCCATTTGTGGCCTG | |

F forward, R reversed primers
doubled the proline level in both genotypes. In the heat-treated plants, the difference between the varieties was not significant.

To better understand the effects of moderate heat stress on the antioxidant capacity, five antioxidant enzymes, namely, APX, GR, CAT, G-POD, and GST, were measured. Among these neither the genotype nor the elevated temperature significantly affected the activities of GR and G-POD enzymes (data not shown). The most pronounced changes occurred in the activities of APX. Its activity was significantly (ca. 50%) higher in the heat-treated plants than in the controls, but there was no significant difference between the genotypes (Fig. 2a). Catalase activity was higher in the Soissons than in Ellvis at control temperature. The moderate heat stress increased the catalase activity in Ellvis resulting in similar values, as was obtained in Soissons (Fig. 2b). The GST activities only showed a slight, but statistically significant increase after heat priming in Soissons (Fig. 2c).

The level of both free and bound (conjugated) forms of endogenous SA was also measured together with one of its putative precursors, oHCA. SA was mainly present in the leaves in bound form, either in the control or in the heat-treated plants (Fig. 3). Exposure to 30 °C for 14 days almost doubled the level of free and bound SA forms in both genotypes. Ellvis usually could be characterised with higher amount of free SA as compared to Soissons both under control and heat-acclimated conditions. However, these differences were not observed in the bound form. The free oHCA level did not differ between either the treatments or the genotypes, but the bound oHCA was slightly (but statistically significantly) higher in the heat-treated Soissons than in the heat-acclimated Ellvis.
Effects of moderate heat stress on PA metabolism in wheat plants

Under control conditions, SPM was the most abundant PA in both genotypes, and its level was slightly higher in Soissons than in Ellvis. The amount of SPM significantly decreased in the heat-treated samples and the original difference between the genotypes could not be detected. Similarly, the amount of SPD significantly decreased during the moderate heat stress, but it was statistically significant only in case of Soissons. The level of PUT did not differ significantly either between the genotypes or between the treatments. In contrast to the PUT, SPD, and SPM, the moderate heat stress resulted in a doubled accumulation of DAP, the catabolic product of SPM and SPD, in both genotypes (Fig. 4).

Since the conversion of SPD or SPM depends on the activity of PA oxidases (PAOs), the expression levels of two genes encoding two different types of PAOs, namely, Tauper-PAO (peroxisomal localised PAO, mainly responsible for the back-conversion of SPM/SPD to PUT) and TapaPAO (putative apoplastic localised PAO, responsible for the production of DAP), have been determined not only at the end of the heat-treatment period (2 weeks), but also after 1 day at 30 °C. While the expression level of TauperPAO hardly changed during the experiment (Fig. 5a), TapaPAO showed a substantial increase (> 25-times higher) after 1 day, especially in Soissons. At the end of the heat treatment, the expression level of TapaPAO was lower, but still significantly higher than in the control plants (Fig. 5b).

Discussion

We have previously described a heat-acclimation system, where wheat plants could be efficiently acclimated to elevated temperatures (Végh et al. 2018). In that work, a moderate heat stress at 30 °C was applied, which could be considered as heat acclimation showing positive effects during the subsequent heat stress responses of the photosynthetic processes. In this way, wheat Soissons was characterised with a relatively high heat-acclimating index, which indicated that this variety was a relatively heat tolerant genotype at young age. In contrast to this, Ellvis showed a high heat sensitivity (Végh et al. 2018). To better understand the acclimation mechanisms of these plants, in the present study, we used these genotypes with different heat tolerance, and a moderate heat stress was applied under the same experimental conditions as before (Végh et al. 2018).

Proline accumulation has been described in various plants exposed to different types of stressors, including unfavourable temperature conditions, either at low or high temperatures (Hayat et al. 2012; Majláth et al. 2012). Proline may act as a signalling molecule to regulate mitochondrial functions, and it also modulates redox balance and energy status (Szabados and Savouré 2010). Accumulation of proline or other osmolytes may also alleviate osmotic stress induced by heat stress (Li et al. 2018). Under the present experimental conditions, although the difference in the proline level between the wheat genotypes were not substantial, it was approx. 2–3 times higher in plants exposed to moderate heat stress at 30 °C than in the controls. This is in consistancy
with other studies, where even much higher increase was reported in heat-exposed wheat plants (Khan et al. 2015a). In contrast to this, decrease in the proline levels has also been reported above a threshold temperature region, or after exposure of wheat plants to short-term heat shock (Song et al. 2005; Kumar et al. 2012). Our results supported that the present applied heat-treatment caused only a mild, stimulating stress. Furthermore, proline accumulation was much more affected by the environmental conditions and the physiological stage of the plants than by the genotype; therefore, proline can hardly be claimed as an indicator of heat tolerance.

Due to enhanced production of reactive oxygen species, abiotic stresses are often accompanied with oxidative stress, which further damages several cell functions. Earlier studies have shown that heat stress acclimation processes also include antioxidant defence mechanisms, which are also associated with the acquisition of thermotolerance (Camejo et al. 2007; Zhao et al. 2014). Furthermore, in some cases, higher abiotic stress tolerance was assumed at least partially due to the higher constitutive antioxidant enzyme activities in the tolerant than in the sensitive plant genotypes (Zhao et al. 2011). Our results, based on the measurements of various antioxidant enzymes in control and heat-treated wheat plants, partly support that moderate heat stress can induce antioxidant defence mechanisms. After exposure to elevated, but non-lethal, acclimating temperature, the activities of certain antioxidant enzymes, such as APX and CAT, were induced. These enzymes play decisive role in the elimination of excess hydrogen peroxide accumulating under various stress conditions. However, although there were some differences between the wheat varieties investigated in our present work, the effects of moderate heat stress were more significant than the differences between the genotypes.

The activity of the antioxidant enzymes has also been regulated by several factors. SA is a phenolic compound, and it functions as a plant growth regulator. The role of SA in the regulation of various physiological processes, including stress responses has been widely reported (Pancheva and Popova 1998; Uzunova and Popova 2000; Janda et al. 2012). Studies have also shown that SA may alleviate the damaging effects of abiotic stressors, including low (Janda et al. 1999) or high temperatures (Dat et al. 1998; Larkindale and Knight 2002). The mode of action of SA in the induction of stress tolerance is complex. It may include induction of osmolites or antioxidant capacity, it may interact with other hormones (Khan et al. 2015b). In wheat plants exogenous SA also alleviated the adverse effects of heat stress on photosynthesis by mechanism of induced proline accumulation and interaction with ethylene (Khan et al. 2013). Similar to proline, free and bound SA also increased after exposure to moderate heat stress under the present experimental conditions, independently on the genotypes. However, the putative precursor, O\textsubscript{HCA}, did not show substantial differences, in contrast to what was found during cold hardening period in wheat, where substantial increase in its bound form was reported (Janda et al. 2007). Besides its role in SA synthesis, O\textsubscript{HCA} has also been characterised as a potential antioxidant compound (Foley et al. 1999). Since neither the majority of the antioxidant enzymes nor the O\textsubscript{HCA} level were substantially higher at the end of the heat-acclimation period, these results suggest that, under the present experimental conditions, the protection against oxidative damage could not be the main mechanism of the acquired thermotolerance in these genotypes.

PAs are essential compounds playing role in various cell functions including responses to environmental stresses. Recent findings suggest that they are not only direct protective materials, but also function as signal triggering certain acclimation mechanisms. The interaction between PA metabolism and proline synthesis, SA signalling, or other stress-related processes has also been described (Pál et al. 2015, 2018b; Szalai et al. 2017). Some PAOs catalyse the
production of metabolic end-products of PAs, while some may catalyse the reverse reaction of PA synthesis in the PA cycle, the back-conversion of PAs (Pál et al. 2015; Chen et al. 2019). The conversion of PAs (PUT–SPD–SPM) is often described under stress conditions (Pál et al. 2015). To date, much less studies have focused on the molecular functions of PAs in plants under high temperature stress than under other stress conditions (Chen et al. 2019). Exogenous SPD could improve carbohydrate and nitrogen status of tomato seedlings at high temperatures through regulating the gene expression and activity of key enzymes for nitrogen metabolism (Shan et al. 2016). The present results showed that moderate heat stress in young wheat plants did not increase the levels of the major PAs, as PUT did not change, while the SPD and SPM decreased during the heat-treatment period. These results, in accordance with the slight changes of other metabolites and antioxidants, also supported that moderate heat stress under the present environmental conditions did not result in serious stress symptoms in the plants. Degradation of SPD by apoplastic localised PAO produces 1-pyrroline and DAP, whereas breakdown of SPM yields 1,3-aminopropylpyrroline and with DAP and hydrogen peroxide (Smith 1985; Bagni and Tassoni 2001). DAP can be further converted into alanine, while 1-pyrroline via γ-aminobutyric acid to succinate. Thus, PA catabolism is not simply a degradative process, but may also serves as a signal playing role in stress acclimation processes (Pál et al. 2015). In our experiments, the accumulation of DAP was mainly mediated by the TaPAO gene rather than TaperPAO, as induced expression was found only in the case of the former one. A substantial increase in the gene expression level was found after 1 day of the heat-acclimation period, then it was less pronounced after two weeks. This is in agreement with earlier findings, that heat acclimation has less effects on gene expression under prolonged treatments than at short-term heat stress in wheat (Qin et al. 2008). These results suggest that heat acclimation in young wheat plants does not involve the stress-induced accumulation of main PAs, rather though the terminal catabolism of PAs, and DAP might be important via inducing other stress-related protective mechanisms (Pál et al. 2015).

In conclusion, the present results showed that various mechanisms, including higher proline level, or probably with less importance, increased antioxidant activity could contribute to the elevated heat tolerance of young wheat plants exposed to moderate heat stress. PA levels did not increase after this moderate heat treatment; however, signalling processes related to PA metabolisms or SA-related processes might also contribute to the higher heat tolerance. Most of these processes were mainly temperature dependent, and the differences between these genotypes were less pronounced than the effects of moderate heat stress itself.

**Author contribution statement** TJ: project supervisor, responsible for experimental design, data collection, interpretation of results, and writer of the manuscript, RK: cultivation of plants, performing proline, and antioxidant analyses, JT: performing gene expression analyses, MP: performing analytical (HPLC) measurements, including salicylic acid and PA determinations, and ÉD: edited the manuscript and provided guidance during experimentation.

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