



Heat acclimation of photosynthesis in wheat genotypes of different origin

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ABSTRACT

Heat acclimation at non-lethal elevated temperatures may provide protection against a subsequent high temperature stress. The aim of the present work was to evaluate the effects of heat acclimation in young wheat plants with different origins. Various photosynthetic parameters were used to characterise the physiological responses of plants to high temperature stress with or without heat acclimation at 30 °C. The elevated acclimating temperature did not induce either stomatal closure or photoinhibition. Certain genotypes were able to induce transpiration at acclimating temperature and did not reduce net assimilation. Heat tolerant genotypes could also close stomata faster when they were exposed to severe high temperatures. Heat acclimation could also be detected in various chlorophyll-*a* fluorescence induction parameters; however, these were less genotype-dependent, and less reflected the differences between varieties. Heat sensitivity and heat acclimation indexes provided useful tool to differentiate the heat responses of the different wheat genotypes. Further studies are needed to establish whether the heat acclimation processes and the differences between the genotypes can also be manifested in adult plants.

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1. Introduction

Heat stress is one of the most important abiotic stressors that may limit the growth of crop plants in many regions of the world, and it may lead to dramatic reduction in the economic yield. Furthermore, recent climate trends have had a discernible negative impact on global production of several major crops (Lobell and Field, 2007). Climate change, in parallel with global warming, may also exacerbate the frequency and severity of many stress factors, including high temperature extremities.

Heat stress alters various physiological, biochemical, and molecular responses of plants, including photosynthetic activity. Photosynthesis has been known as one of the most heat-sensitive processes for a very long time (Berry and Björkman, 1980). The effects of warmer temperatures on photosynthesis will be one of the most important determinants of the impact of global warming on crop yield (Ainsworth and Ort, 2010). Decreased crop productivity under high temperature conditions tend to be primarily caused by limited photosynthetic carbon assimilation and persisting mitochondrial respiration. Increased temperature often results in increased vapour pressure deficit, which may exacerbate the diffusion limitations (Perez-Martin et al., 2009). High temperature

may irreversibly damage the photosystems and the activity of Rubisco (Hawaux, 1993; Hawaux and Tardy, 1996; Law and Crafts-Brandner, 1999; Zhang et al., 2005). A recent proteomic study demonstrated that chlorophyll synthesis, carbon fixation, protein turnover, and redox regulation were the most remarkable heat-responsive processes in the flag leaves of wheat plants (Lu et al., 2017).

Subjecting plants even with low basal thermotolerance to mild, non-lethal elevated temperatures (heat-acclimation) may provide protection against a subsequent high temperature stress (acquired thermotolerance). Heat acclimation also involves several molecular mechanisms including the alteration of signalling cascades and transcriptional control (Sairam et al., 2000; Almeselmani et al., 2006), synthesis of osmoprotectants, heat shock proteins (Hasanuzzaman et al., 2013), and the induction of antioxidative systems to prevent the over-accumulation of reactive oxidant species and membrane lipid peroxidation during severe heat stress (Xu et al., 2006). The mechanisms of heat acclimation of the photosynthetic processes have also been extensively studied in various crop species, including wheat. Earlier results indicated that Rubisco activase sensitivity to high temperature varies among plant species: for example the Rubisco activase from cotton is more heat tolerant than that of wheat; but it can acclimate during a relatively short period (Law and Crafts-Brandner, 1999).

Among the three major commercially important crops, such as rice, maize and wheat, the later one is usually grown in cooler regions; therefore it is the less adapted to warmer temperatures. Worldwide, heat stress can reduce the yield of wheat by as much as 15% (Qin et al., 2008). Based on recent data originating from the US, autumn freezing temperatures and extreme heat in the spring are the biggest drivers of

Abbreviations: HIS, heat sensitivity index; HAI, heat acclimation index; WUE, water use efficiency; NA, non-acclimated; HA, heat-acclimated; SWC%, soil water content; PS II, Photosystem II.

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yield loss in wheat (Tack et al., 2015). Since enabling heat adaptation of photosynthetic process can be a potential option for improving wheat thermotolerance, better understanding of the molecular mechanisms of heat acclimation may also have important practical aspects. Extending the heat tolerance period may be a potential target of wheat breeding. The aim of the present work was to evaluate of the effects of heat acclimation in wheat plants with different origins. We focused on various photosynthetic parameters in order to further characterise the physiological responses of these plants to high temperature stress with or without heat acclimation. Since little is still known about the genotypic differences in the heat acclimation processes in wheat, particular question was that which processes were general in these genotypes, and which were different among them.

2. Materials and methods

2.1. Plant materials and growth conditions

Different wheat (*Triticum aestivum* L.) genotypes, including var. Ellvis originated from Germany, a French genotype Soissons, and 3 Croatian breeding materials, var. Zitarka, Srpanjka and Antonija were used in the experiments. Twelve seeds were germinated in a pot (11 cm Ø) filled with 3:1 (v:v) mixture of loamy soil and sand. Plants were grown in a Conviron PGV-36 growth chamber (Controlled Environments Ltd., Winnipeg Canada) at 20/18 °C day/night temperature with 16/8 h photoperiod at 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) at the canopy level, and 75% relative humidity. After 10 days a part of the plants (10 pots of each genotype) were heat-acclimated at 30/27 °C day/night temperature, while others (10 pots) were grown at 22/20 °C (controls) in Conviron PGR-15 growth chamber for 14 days. Then, heat stress was applied in a greenhouse under natural light conditions for 3 days when the air temperature was above 40 °C between 10 and 15 h. In order to avoid drastic photodamage, the greenhouse was shadowed, so the maximum daily PPFD did not exceed 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The average daily T curve is presented in Fig. 1. During the experiment, the soil humidity was checked twice a day (at 8 h and 16 h) and the plants were well-watered to avoid the differences between the responses of drought stress often accompanying heat stress. Samples were taken and measurements were carried out at different days indicated at the different measurements.

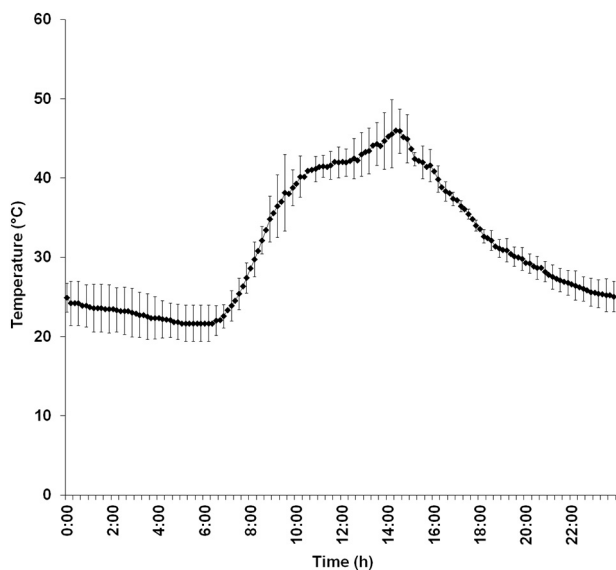


Fig. 1. Changes in the temperature during the heat stress treatment in the greenhouse. The average temperature of the 3 days, when the plants were subjected to heat stress.

2.2. Gas exchange measurements

Two types of gas exchange analysis were carried out with a Ciras 3 Portable Photosynthetic System (PP Systems Amesbury, MA, USA) using a narrow leaf area (2.5 cm²) chamber. First, the CO₂ assimilation rate (P_n), stomatal conductance (g_s), and transpiration rate (E) were measured on 3rd attached leaves of plants grown at 22/20 °C or 30/27 °C and these parameters were determined at the steady-state level of photosynthesis. In a second type of experiment, the gas exchange parameters were recorded at different leaf chamber temperatures (at 22, 30, 35 and 40 °C) after reaching the steady state conditions at the given temperature, respectively. In both cases, the reference level of CO₂ was 390 $\mu\text{L L}^{-1}$ and the light intensity was 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

2.3. Determination of soil water content

The soil moisture content was checked regularly with a Soil Moisture Meter HH2 connected with a SM200 sensor (Delta-T Devices, Cambridge, UK).

2.4. Estimation of chlorophyll content

Chlorophyll contents were estimated in the 3rd fully developed leaves using a SPAD-502 chlorophyll meter (Konica-Minolta, Osaka, Japan).

2.5. Chlorophyll-a fluorescence induction measurements

The effect of heat priming on the chlorophyll-a fluorescence was measured with a pulse amplitude modulated fluorometer (Imaging-PAM M-series, Walz, Effeltrich, Germany). Detached leaves were dark-adapted for 20 min after which the Fv/Fm parameter was determined using a 1.0 s saturated pulse (PPFD = 3000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) provided by a LED-Array Illumination Unit IMAG-MAX/L ($\lambda = 450 \text{ nm}$). Photosynthesis was then activated using 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ actinic light intensity for 15 min and the quenching analyses was performed using a 40 s saturation pulse frequency. The quenching parameters were determined under steady state conditions according to the nomenclature described by Klughammer and Schreiber (2008). Two types of measurements were performed. The quenching analyses were performed at ambient (25 °C) and at elevated (42 °C) temperatures, which were controlled by a thermoelectric module equipped with a thermocouple thermometer. The heat-induced changes of chlorophyll-a fluorescence parameters were also determined at increasing temperature from 25 and to 55 °C as described by Dulai et al. (1998). The measurements were started at 25 °C and after the photosynthesis was steady (15 min) it was followed by heating the leaves from 25 to 55 °C at a rate of 1.5 °C min⁻¹. During the measurements saturated flashes were applied at each °C. After recording the F_s vs T curves, the critical points (T_c and T_p) of Y(II), Y(NPQ) and Y(NO) vs T were determined as described by Schreiber and Berry (1977).

The effective quantum yield Y(II) of non-acclimated and heat-acclimated plants were also determined in attached leaves under growth (22 or 30 °C) and heat stress conditions using a PAM-2001 instrument (PAM-2001, Walz, Effeltrich, Germany) at 14 h pm in the last day of the heat treatment. In this case, the actinic light intensity was fixed at 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

2.6. Determination of temperature sensitivity and acclimation capacity of genotypes

The heat stress response and the impact of heat acclimation was determined by the calculation of heat sensitivity index (HSI) and heat acclimation index (HAI), as described by Perdomo et al. (2016). The HSI compares the given parameters in control and heat stressed plants

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