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Research article

Multiple heat priming enhances thermo-tolerance to a later high temperature stress *via* improving subcellular antioxidant activities in wheat seedlings

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Seedlings of winter wheat (*Triticum aestivum* L.) were firstly twice heat-primed at 32/24 °C, and subsequently subjected to a more severe high temperature stress at 35/27 °C. The later high temperature stress significantly decreased plant biomass and leaf total soluble sugars concentration. However, plants experienced priming (PH) up-regulated the Rubisco activase B encoding gene *RcaB*, which was in accordance with the higher photosynthesis rate in relation to the non-primed plants (NH) under the later high temperature stress. In relation to NH, the major chlorophyll a/b-binding protein gene *Cab* was down-regulated in PH plants, implying a reduction of the light absorption to protect the photosystem II from excitation energy under high temperature stress. At the same time, under the later high temperature stress PH plants showed significantly higher actual photochemical efficiency, indicating an improvement of light use efficiency due to the priming pre-treatment. Under the later high temperature stress, PH could be maintained a better redox homeostasis than NH, as exemplified by the higher activities of superoxide dismutase (SOD) in chloroplasts and glutathione reductase (GR), and of peroxidase (POD) in mitochondria, which contributed to the lower superoxide radical production rate and malondialdehyde concentration in both chloroplasts and mitochondria. The improved antioxidant capacity in chloroplasts and mitochondria was related to the up-regulated expressions of *Cu/Zn-SOD*, *Mn-SOD* and *GR* in PH. Collectively, heat priming effectively improved thermo-tolerance of wheat seedlings subjected to a later high temperature stress, which could be largely ascribed to the enhanced anti-oxidation at the subcellular level.

1. Introduction

Extreme heat events have been world-widely categorized as one dominant adversity limiting growth and causing losses of both grain yield and quality in field crops including wheat (Berry and Bjorkman, 1980; Boyer, 1982). High temperature is reported to cause low carbon- and light- use-efficiency, consequently affect carbon and nitrogen accumulation and allocation, and finally impair crop growth and development (Bohnert and Sheveleva, 1998; Ingram and Bartels, 1996).

Pre-treatment at a moderate temperature (heat priming) could improve tolerance to a subsequent high temperature stress in plants (Larkindale and Huang, 2004). The heat tolerance has been linked to increased thermo-tolerance of the photosynthetic apparatus (Berry and Bjorkman, 1980). In addition, it is well established that high temperature stress causes the malfunction of photosystem II (PSII), reduces the efficiency of electron transport and consequently leading to increased production of reactive oxygen species (ROS) in plant cells (Melis, 1999). Plants under abiotic stresses usually accumulate more ROS in both chloroplasts and mitochondria, which can severely damage DNA and cause cell

Abbreviations: GR, glutathione reductase (EC 1.6.4.2); g_s, stomatal conductance; H_2O_2, hydrogen peroxide; MDA, malondialdehyde; MII, membrane injury index; ΦNPQ, the quantum yield of quenching due to light-induced processes; $O_2^{\cdot-}$, superoxide radical; Pn, photosynthetic rate; POD, peroxidase (EC 1.11.1.7); ΦPSII, actual photochemical efficiency; ROS, reactive oxygen species; RuBP, ribulose-1,5-bisphosphate; SOD, superoxide dismutase (EC 1.15.1.1); TSS, total soluble sugars.

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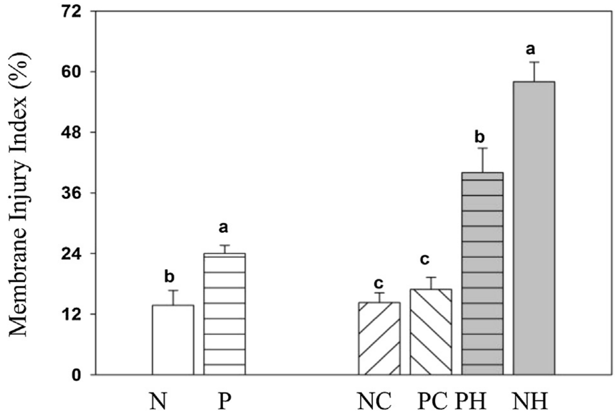

Fig. 1. Change in membrane injury index (MII) in leaf due to heat priming and/or a later high temperature stress event. Note: N and P indicate without and with heat priming pretreatment, respectively. NC and NH indicate no heat priming pre-treatment without and with a later high temperature stress, respectively; whist PC and PH indicate early heat priming pre-treatment without and with a later high temperature stress, respectively. Data are means ± SE of three replicates. Within the priming or stress group, different lowercase letters indicate significant difference at $P < 0.05$.

membrane lipid peroxidation (Kukavica and Jovanovic, 2004; Bowler et al., 1992). A number of studies have demonstrated that the ROS detoxification mechanisms play an important role in protecting plants against high temperature stress (Larkindale and Knight, 2002; Suzuki and Mittler, 2006). Thus, plant tolerance to environmental stresses is also closely correlated to increased capacity of scavenging and detoxifying the ROS (Foyer et al., 1994). It has also been shown that the induction of thermo-tolerance in heat primed plants under high temperature may be ascribed to maintenance of better membrane thermo-stability, and low level of ROS accumulation (Xu et al., 2006) due to improved antioxidant capacity (Shi et al., 2001), as compared with the non-primed plants.

We have previously reported that heat priming before anthesis resulted in higher grain yield under a subsequent high temperature stress during grain filling, which mainly attribute to the effectively alleviated photosynthetic and oxidative damage (Wang et al., 2011), and enhanced carbohydrate remobilization from stems to grains in the primed plants (Wang et al., 2012). It is known that chloroplasts (Foyer et al., 1994) and mitochondria (Møller, 2001) are the major sites for ROS production. However, limited information is available on performances of ROS generation and antioxidative systems in chloroplasts and mitochondria in heat primed *vs.* non-primed plants under the subsequent high temperature stress.

Our hypothesis is that mitochondria and chloroplast of primed plants might suffer from less severe oxidative damage than the non-primed plants under a later high temperature stress in wheat plants. In the present study, wheat seedlings were firstly heat-primed and then subjected to a more severe high temperature stress. The variations in accumulation of superoxide radicals and activities of the antioxidant enzymes in chloroplasts and mitochondria were compared between the primed and non-primed seedlings under a later high temperature stress. The results might contribute to better understanding of the heat priming effects on thermal tolerance formation in plants.

2. Results

2.1. Membrane injury index (MII) in leaves, $O_2^{-\cdot}$ production rate and MDA concentration in chloroplasts and mitochondria

After twice heat priming pre-treatment, leaf MII increased 52% in primed plants (P) in relation to the non-primed plants (N). Under high temperature stress, however, MII increased 378% in the non-primed plants (NH) while only increased 189% in the primed plants (PH), as compared with the non-stress treatment (NC) (Fig. 1).

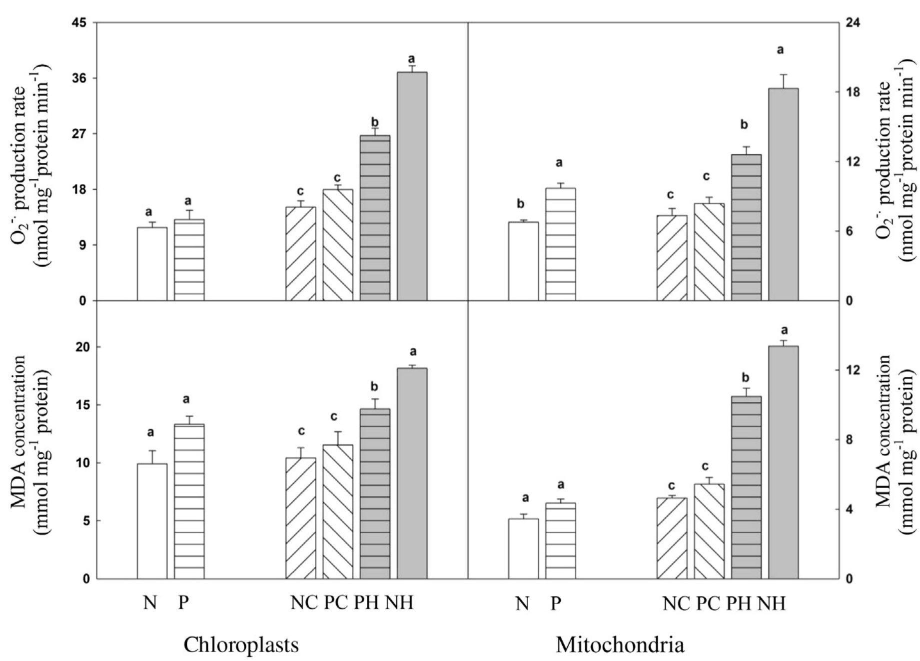

Fig. 2. Changes in $O_2^{-\cdot}$ production rate and concentration of malondialdehyde (MDA) in chloroplasts (left) and mitochondria (right) in wheat seedlings due to heat priming and/or a later high temperature stress event. Note: N and P indicate without and with heat priming pre-treatment, respectively. NC and NH indicate no heat priming pre-treatment without and with a later high temperature stress, respectively; whist PC and PH indicate early heat priming pre-treatment without and with a later high temperature stress, respectively. Data are means ± SE of three replicates. Within the priming or stress group, different lowercase letters indicate significant difference at $P < 0.05$.