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Research article

Improved tolerance to post-anthesis drought stress by pre-drought priming at vegetative stages in drought-tolerant and -sensitive wheat cultivars

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Wheat crop endures a considerable penalty of yield reduction to escape the drought events during post-anthesis period. Drought priming under a pre-drought stress can enhance the crop potential to tolerate the subsequent drought stress by triggering a faster and stronger defense mechanism. Towards these understandings, a set of controlled moderate drought stress at 55–60% field capacity (FC) was developed to prime the plants of two wheat cultivars namely Luhan-7 (drought tolerant) and Yangmai-16 (drought sensitive) during tillering (Feekes 2 stage) and jointing (Feekes 6 stage), respectively. The comparative response of primed and non-primed plants, cultivars and priming stages was evaluated by applying a subsequent severe drought stress at 7 days after anthesis. The results showed that primed plants of both cultivars showed higher potential to tolerate the post-anthesis drought stress through improved leaf water potential, more chlorophyll, and ribulose-1, 5-bisphosphate carboxylase/oxygenase contents, enhanced photosynthesis, better photoprotection and efficient enzymatic antioxidant system leading to less yield reductions. The primed plants of Luhan-7 showed higher capability to adapt the drought stress events than Yangmai-16. The positive effects of drought priming to sustain higher grain yield were pronounced in plants primed at tillering than those primed at jointing. In consequence, upregulated functioning of photosynthetic apparatus and efficient enzymatic antioxidant activities in primed plants indicated their superior potential to alleviate a subsequently occurring drought stress, which contributed to lower yield reductions than non-primed plants. However, genotypic and priming stages differences in response to drought stress also contributed to affect the capability of primed plants to tolerate the post-anthesis drought stress conditions in wheat.

1. Introduction

Drought stress has become the most devastating constraint to crop productivity due to aridifying and warming climatic trends, and its prevalence is expected to diversify in future at regional and global scales (Backhaus et al., 2014). Wheat is one of the foremost staple food crops and is reported to be highly susceptible to drought stress which often occurs at post-anthesis phase consequencing considerable yield penalties (Wang et al., 2014a).

Grain yield is the ultimate product of photosynthesis and closely interrelated physiological processes. Fluctuations around the normal values of photosynthesis and its interlinked processes are the key indicators of plant fitness and extent of environmental stress (Zlatev and Lidon, 2012). Mild drought stress declines the rate of photosynthesis due to limited stomatal conductance, meanwhile the photosynthetic apparatus is not significantly affected (Cornic, 2000). In contrast, under severe drought stress, stomatal limitation, the poor efficiency of photosystemII (PSII) as well as declined activities of CO_2 assimilating enzymes such as ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) have been reported as the primary constraints to lower photosynthetic rates (Bota et al., 2004).

In addition to direct drought-induced damages to the photosynthetic process, it also leads to the light-induced oxidative stress by the generation of reactive oxygen species (ROS) in the plant cells (Reddy et al., 2004). If the drought stress proceeds and ROS

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accumulation is not quenched by antioxidants, it results in protein oxidation, membrane lipid peroxidation, inhibition of DNA, RNAs and hormonal activities, eventually turning the cell into a state called as "oxidative stress", which adversities the normal growth or even causes the death of plants (Liu et al., 2015). The limited wheat yield under environmental stresses is mostly attributed to the downregulation of key yield influential photosynthesis and other interdependent physiological processes functioning in the flag leaf during grain filling (Bruce et al., 2007; Zlatev and Lidon, 2012). Therefore, improving the tolerance to drought stress, especially at post-anthesis phase is of great significance in yield production of wheat. Previous research efforts provide promising evidence that priming "the pre-exposure of plants to a stimulus stress enabling them to mobilize their rapid and intense defense mechanism" can induce improved tolerance in plants to later-occurring stress events (Bruce et al., 2007).

To date, various priming techniques have been used in different crop species against a range of environmental disasters. So far, mainly attention has been focused to exogenously applied chemical-induced priming such as nitric oxide for drought priming in rice (Farooq et al., 2010), hydrogen sulphide for drought priming in wheat (Shan et al., 2011), hydrogen peroxide for salt stress priming in wheat (Li et al., 2011a,b) and β-aminobutyric acid for pathogens attack priming in Arabidopsis (Zimmerli et al., 2000). Similarly, the priming state has also been achieved by biotic-induced colonization of plants with beneficial micro-organisms (Abdel Latef and Chaoxing, 2011) and by the epigenetic changes in plants for the initiation and regulation of their potential defense metabolism (Beckers et al., 2009).

Some recent studies in various crop species have revealed that the plants pre-exposed to environmental stress can also attain the potential to display a faster and stronger activation of their defense system in response to the subsequent challenge stress events (Backhaus et al., 2014; Vu et al., 2015). For example, the plants of *Arrhenatherum elatius* experiencing an early drought episode showed an improved photo-protection and higher biomass under a second drought event than non pre-exposed plants (Walter et al., 2011). Similarly, pre- exposure of vegetative stage rice plants to sub-lethal heat stress improved the thermo-tolerance to heat stress during grain filling (Shi et al., 2015). Likewise, these beneficial pre-stress imprints have also been reported in tobacco (Choi and Sano, 2007), radish (Vu et al., 2015) and some grass species (Meisner et al., 2013).

A few current studies addressing these legacy effects of pre-stress priming are also available in wheat. For example, wheat plants exposed to early stage heat stress, displayed an improved antioxidative capacity and higher grain yields against terminal high-temperature stress (Wang et al., 2014b). Another study on wheat investigated that waterlogging pre-treatment during vegetative growth stage enhanced dry matter accumulation and its distribution to grain formation resulting in a noticeably improved grain yield (Li et al., 2011a,b).

The studies exploring the response of pre-drought stress-induced drought priming to post-anthesis drought events in wheat are rare (Wang et al., 2014a). Moreover, the response of primed plants to succeeding drought stress may vary due to the interval between priming and the reoccurring stress (Backhaus et al., 2014), due to response difference of growth stages to drought stress (Wang et al., 2015) as well as due to genotypic differences in tolerance to drought stress (Rampino et al., 2006; Khanna-Chopra and Selote, 2007). So, we suggest that drought priming study should be extended to gain insights into the resilience response difference of wheat cultivars and priming growth stages to the subsequent drought stress. This study was aimed to investigate that (1) whether drought priming during vegetative growth stages in wheat plants develops a memory to adapt the subsequent drought occurrence, and (2) whether the drought priming effect varies under varying cultivars and vegetative growth stages selected for priming. Hopefully, the projected results of the study would be supportive for research programs seeking to develop anti-drought stress practices for wheat.

2. Materials and methods

2.1. Plant culture and growth conditions

A greenhouse experiment was carried out at Pailou Experimental Station of Nanjing Agricultural University, China (32°04′ N, 118°76′ E), during the growing season of 2014–2015. Two winter wheat cultivars with contrasting attitude towards drought stress namely Luhan-7 (drought resistant) and Yuangmai-16 (drought sensitive) (Wang et al., 2007), were used as experimental material in the present study. Fifteen surface sterilized uniform seeds were planted in the free-draining plastic pots having 22 cm and 25 cm height and diameter, respectively. Each pot was filled with 8 kg air-dried, sieved (0.5 mm) and uniformly mixed clay loam soil having 13% soil moisture. At the time of soil filling, 0.8 g N, 0.5 g P_2O_5 and 1.1 g K_2O/pot were applied for each treatment. Further, 0.4 g/pot N was applied at jointing and booting, respectively. Thinning was carried out 10 days after germination at 10 seedlings per pot. Then a week later, second thinning was carried out and seven uniform seedlings per pot were selected for the subsequent studies. Each pot was irrigated to 80% field capacity (FC) with tap water characterized with 7.5 pH, 2.8 dsm^{-1}electrical conductivity (EC) and 1200 mg L^{-1} total soluble salts (TSS) until start of the treatments. Soil water status was measured before the application of water to the pots. The amount of water required for irrigation was calculated by using the following equation:

$$W = Y \times H \times A \times (FC1 - FC0) \quad (1)$$

where, W is amount of irrigation water, Y is soil bulk density, H is soil depth, A is the area of the pot, FC1 is the desired soil FC, and FC0 is the actual soil FC before irrigation.

Each treatment had 20 replicates (pots). The pots with different treatments were rotated on every alternate day to ensure that all the pots received equal radiation and other environmental exposures till maturity.

2.2. Treatments application and management

2.2.1. Drought priming treatments

The drought priming treatments were carried out at tillering (40 days after planting, Feekes 2.0, beginning of tillering, 4 leaf stage) and at jointing (125 days after planting, Feekes 6.0, when first node was visible, 6 leaf stage), as described in experimental description under Fig. 1. At each priming stage, the irrigation to pots was withheld until a moderate drought stress stage at 55–60% FC reached. This moderate drought stress level as priming treatment at tillering and jointing respectively was maintained for 10 days by compensating the lost water. Meanwhile, the control pots kept on irrigating at 80% FC. After priming at both stages, the pots were re-watered to the level of control pots until the application of the subsequent drought stress. Thus, four priming treatments for each cultivar were designated as PT and PJ for priming at tillering and jointing, meanwhile non-primed plants were designated as **N**T and **N**J during tillering and jointing, respectively. The overall non-primed plants were designated as NN.