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Waterlogging pretreatment during vegetative growth improves tolerance to waterlogging after anthesis in wheat

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ABSTRACT

The interaction of multiple waterlogging events during vegetative growth (at the seven- and nine-leaf stage, and at heading) to a waterlogging event during the generative growth stage was studied in wheat (*Triticum aestivum* L. cv. Yangmai 9). Waterlogging before anthesis was found to effectively enhance tolerance to a waterlogging event after anthesis, as indicated by: (1) increasing net photosynthetsis (P_N), stomatal conductance (g_s) and transpiration (Tr) and maintaining high SPAD (soil plant analysis development) values; (2) enhancing use-efficiency of absorbed light energy in the stressed plants due to high maximum and actual quantum yield (F_v/F_m, Φ_{PSII}); (3) increasing activities of superoxide dismutase (SOD), ascorbate peroxidase (APX) and catalase (CAT); (4) enhancing dry matter accumulation after anthesis and its contribution to grain mass, which further resulting in significantly improved grain yields. The results indicate that hardening by waterlogging applied before anthesis can effectively improve the tolerance of wheat to waterlogging events occurring during the generative growth stage.

1. Introduction

When water stands on the soil surface for a prolonged period of time or when the available water fraction in the soil surface layer is at least 20% higher than the field water capacity, the soil is defined as waterlogged soil [1]. Tolerance to waterlogging by plants is defined as the capability to maintain high rates of growth, biomass accumulation and grain yield under these conditions [2]. Due to the increased frequency of extreme climate events [3], waterlogging has become an important constraint to crop production globally, causing significant yield reductions. For instance, waterlogging has been shown to severely reduce grain yields of wheat in the UK [4–6], North America [7,8] and Australia [9,10] by about 20–50%.

In Asia, especially in southeast China, wheat is commonly planted in paddy fields which are frequently saturated with water due to excessive rainfall during the growing season. Here, much of the rainfall occurs between anthesis and maturity [11]. Since this period is critical for grain yield formation, waterlogging during the generative growth stage has become a major constraint for wheat production in this area [12].

Waterlogging occurring at any growth stage usually causes degradation of chlorophyll in leaves [13,14] and of protein content in grains [15] and decreases the concentrations of nitrogen, phosphorous and potassium in plant shoots [16]. Reductions in shoot and root growth [17], dry matter accumulation [18] and final grain yield have been reported due to waterlogging [5,16,19,20]. In order to maintain high grain yield and grain quality under these conditions, numerous attempts have been made to improve the tolerance of crops to waterlogging by both traditional breeding programs [21] and biotechnological methods, although to date only few practical results have been obtained [2,9].

It has been shown that the process of priming (or hardening) by exposure to abiotic stresses such as drought [22,23], chilling [24], heat [25,26], anoxia [27] or salinity [28] may trigger the resistance to additional stress events by activation of various defense mechanisms. However, little is know if the waterlogging priming applied during the vegetative growth stage also trigger the resistance to the waterlogging stresss during grain filling period.

The physiological and biochemical responses of wheat to waterlogging events have been extensively investigated. Photosynthetic rate (P_N), stomatal conductance (g_s) and transpiration rate (Tr) was decreased [29] and led to restrictions in carbohydrate metabolism in both shoots [30] and roots [31]. This resulted in a decrease in both the accumulation of dry matter [18], and the amount of dry matter transfered into the grains [32]. To date, however, only limited information is available on the effects of hardening by waterlogging

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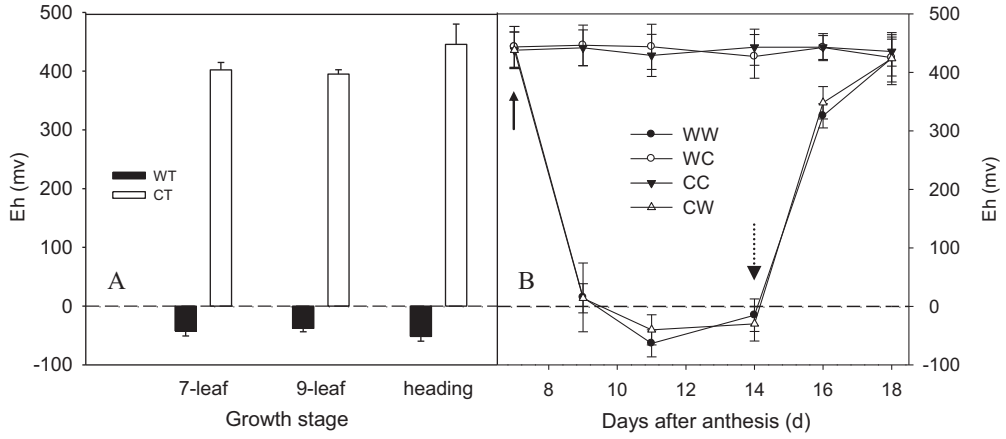

Fig. 1. Soil redox potential (Eh) of the waterlogging pre-treatment before anthesis (A) and time-course changes in Eh from the onset of post-anthesis waterlogging stresss (B). In (A): WT – waterlogging at the 7-leaf, 9-leaf and heading; CT – no-waterlogging before anthesis. In (B): CC – no waterlogging; CW – waterlogging after anthesis; WC – waterlogging before anthesis; WW – hardening by waterlogging before anthesis followed by waterlogging after anthesis. The solid arrow indicates the onset of post-anthesis waterlogging, the dot arrow indicates the removal of waterlogging. Data are means ± SD of three replicates.

before anthesis on leaf photosynthesis and dry matter redistribution during a waterlogging event after anthesis.

Under abiotic stress, reactive oxygen species (ROS) are produced, which cause severe damage to membranes, DNA and proteins in plant cells [33]. To protect cellular and subcellular organelles from damage caused by ROS, endogenous scavenging mechanisms, including both enzyme and non-enzyme approaches, are activated. Of these, superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) are considered to be the most important antioxidative enzymes [34,35]. Waterlogging is reported to induce ROS production and to inhibit activities of antioxidative enzymes [32]. Exogenous growth regulators such as the polyamines spermidine [36] and putrescine [37] effectively enhance activities of the ROS scavenging enzymes, thus effectively alleviating damages caused by waterlogging. However, little is known weather hardening to waterlogging is caused by increased activities of antioxidative enzymes and how this is related to tolerance to a later waterlogging event.

Our preliminary studies indicated that a single waterlogging treatment was not sufficient to induce tolerance to this stress at a later stage. Therefore, in this study, wheat plants were subjected to three individual waterlogging treatments at vegetative growth stages (seven- and nine-leaf stages as well as during heading), followed by a waterlogging event after anthesis. Thus the aim of this study was to test the hypothesis that multiple waterlogging events applied to wheat during the vegetative growth stage will lead to tolerance to this stress during the generative growth stage. Carbon- and light use-efficiencies as well as the activities of antioxidative enzymes were analysed in flag leaves of plants from all treatments.

2. Materials and methods

2.1. Experimental design

The experiment was conducted in the growing season of 2008–2009 at the Experimental Station of Nanjing Agricultural University, Jiangsu Province, P. R. China. Selected seeds of wheat (*Triticum aestivum* L., cv. Yangmai 9) were grown in plastic pots (22 cm in height and 25 cm in diameter), which were filled with 7.5 kg of clay soil. The soil contained 10.9 g kg^{-1} organic matter, 1.0 g kg^{-1} total N, 76.3 mg kg^{-1} available N, 28.9 mg kg^{-1} Olsen-P, 130.2 mg kg^{-1} available K, and was pre-mixed with 20.0 g organic fertilizer, 0.9 g N, 0.36 g P_2O_5, and 0.9 g K_2O per pot. Another 0.3 g N per pot was applied at jointing. Fifteen selected seeds were sown in per pot, and were thinned to 7 seedlings at the 3-leaf stage. The plants were then subjected to two water treatments before anthesis: (1) control, the soil relative water content was maintained at 70–80%, and (2) pre-waterlogging (maintenance of a 1-2 cm tap water, pH around 7.0) layer above the soil for 2 days which was then drained. This pre-waterlogging treatment was repeated three times, i.e. at the seven- and nine-leaf stage as well as the heading stage. From 7 days after anthesis (DAA), seedlings from both treatments were divided into two sub-groups and separately subjected to two water treatments, which lasted for 7 days each. Thus, four treatments were established from 7 DAA onwards: (1) control, no waterlogging stress (CC); (2) waterlogging after anthesis only (CW); (3) pre-anthesis waterlogging only (WC); (4) hardening by waterlogging before anthesis followed by waterlogging after anthesis (WW). The experiment was a completely random block design with three replicates for each treatment. Plants in one pot were treated as one replicate for each harvest or measurement.

2.2. Soil redox potential (Eh)

Soil Eh was monitored at 5 cm below the soil surface and at about 10 cm distance from the wheat plants, using a combined platinum-calomel electrode (*FJA-4*; Nanjing Zhuandi Instrument Co. Ltd., Nanjing, China). In the WC and WW treatment, Eh was logged at the end of the waterlogging period as shown in Fig. 1B.

2.3. Gas exchange

Rates pf photosynthesis (P_N), transpiration (Tr) and stomatal conductance (g_s) of the flag leaf were measured using a portable photosynthesis system (*LI-6400, LI-Cor*, USA) at a CO_2 concentration of about 385 μmol mol^{-1}, and with a photosynthetically active radiation of 1200 μmol m^{-2} s^{-1}. All measurements were conducted in sunny days from 09:30 to 11:30, at 0, 7, 9, 14 and 21 DAA. On each measurement occasion, five leaves were taken for each treatment.

2.4. Chlorophyll (Chl) content

Chl content was measured non-destructively with a SPAD 502 Chl Meter (Soil Plant Analysis Development; *Minolta*, Japan) using the same flag leaf as used for the P_N analysis. For each measurement, five SPAD readings were taken and averaged as the Chl content for the leaf under investiagtion.