Plant Physiology and Biochemistry 118 (2017) 362–369

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

journal homepage: www.elsevier.com/locate/plaphy

Research article

Seed priming and transgenerational drought memory improves tolerance against salt stress in bread wheat

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ARTICLE INFO

Article history:
Received 9 April 2017
Received in revised form
6 July 2017
Accepted 6 July 2017
Available online 8 July 2017

Keywords:
Salinity
Seed priming
Terminal drought
Tolerance
Wheat

ABSTRACT

This study was conducted to evaluate the potential of seed priming following terminal drought on tolerance against salt stress in bread wheat. Drought was imposed in field sown wheat at reproductive stage (BBCH growth stage 49) and was maintained till physiological maturity (BBCH growth stage 83). Seeds of bread wheat, collected from crop raised under terminal drought and/or well-watered conditions, were subjected to hydropriming and osmopriming (with 1.5% $CaCl_2$) and were sown in soil-filled pots. After stand establishment, salt stress treatments *viz.* 10 mM NaCl (control) and 100 mM NaCl were imposed. Seed from terminal drought stressed source had less fat (5%), and more fibers (11%), proteins (22%) and total soluble phenolics (514%) than well-watered seed source. Salt stress reduced the plant growth, perturbed water relations and decreased yield. However, an increase in osmolytes accumulation (4–18%), malondialdehyde (MDA) (27–35%) and tissue Na^+ contents (149–332%) was observed under salt stress. The seeds collected from drought stressed crop had better tolerance against salt stress as indicated by better yield (28%), improved water relations (3–18%), osmolytes accumulation (21–33%), and less MDA (8%) and Na contents (35%) than progeny of well-watered crop. Seed priming, osmopriming in particular, further improved the tolerance against salt stress through improvement in leaf area, water relations, leaf proline, glycine betaine and grain yield while lowering MDA and Na^+ contents. In conclusion, changed seed composition during terminal drought and seed priming improved the salt tolerance in wheat by modulating the water relations, osmolytes accumulation and lipid peroxidation.

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1. Introduction

Salt stress causes both hyperosmotic and hyper-ionic stresses, which restricts plant growth and causes considerable reduction in crop yield (Mahajan and Tuteja, 2005; Farooq et al., 2015). However, plants may undergo different physiological and morphological adaptations for acquiring tolerance to salt stress. Salt tolerance is the potential of a plant to bear up the adverse effect of salinity in their leaves and/or rhizosphere without affecting their normal functioning (Shannon and Grieve, 1999; Farooq et al., 2015).

Any stress during grain development phase may change the composition and quality of grains by accumulation of certain secondary metabolites. However, this change in grain composition may help the plants to tolerate reoccurrence of the same or other stresses. Plants exposed to one stress can be able to improve its ability to tolerate to consequent or other stresses even in the next generation (Ćuk et al., 2010). The plants may retain the transgenerational stress memory in morphological, physiological and metabolic terms (Walter et al., 2013). Such stress comebacks involve modifications in the metabolome and proteome with increased expression of compatible solutes and proteins (Joyce et al., 2003). Therefore, cells formerly exposed to one stress may improve tolerance to the same and/or another type of stress (Wehmeyer and Vierling, 2000).

Seed priming, a controlled hydration technique, which allows germination metabolism without actual germination (Farooq et al., 2006). Seed priming has been quite effective in improving salt tolerance in wheat (Jafar et al., 2012). After priming, seed stored proteins are solubilized and lipid peroxidation is reduced while

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http://dx.doi.org/10.1016/j.plaphy.2017.07.007
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antioxidant activities are enhanced (Afzal et al., 2008; Jafar et al., 2012). Seed priming also enhances the accumulation of osmolytes through altered metabolic processes (Delavari et al., 2010) and state transition from non-germinated to germinated and then again germinated to non-germinated state in response to wetting, drying and re-wetting of seed (Chen and Arora, 2013). Although, several inorganic salts, organic substances and plant growth promoting substances may be used to control the hydration process during seed priming (Farooq et al., 2006, 2008; Afzal et al., 2008; Jafar et al., 2012); use of calcium salts has been more effective and economical in improving the crop performance under optimal and less than optimal conditions (Farooq et al., 2006, 2008; Jafar et al., 2012).

Any stress during the terminal growth stage may increase the production and accumulation of secondary metabolites in developing seeds as a defence mechanism. These metabolites may help in tolerance against abiotic stresses during next growing season exhibiting the memory of the preceding stress. However, to best of our knowledge no study has been conducted to explore the influence of terminal drought on the wheat performance in next generation after seed priming under less than optimum conditions. This study was, therefore, carried out to evaluate the effect of seed priming, using seeds collected from crop raised under terminal drought and/or well-watered conditions, on tolerance against salt stress in bread wheat.

2. Materials and methods

2.1. Experimental details

The study was comprised of two separate phases. In first phase, wheat seed was collected after exposure to terminal drought stress at reproductive stage of wheat sown in field at Agronomic Research Area, University of Agriculture Faisalabad latitude 31°N, longitude 73°E and altitude 184.4 masl), Pakistan. Experimental soil was sandy loam with pH 7.6, electrical conductivity 1.01 dS m^{-1}, nitrogen 0.06%, phosphorus 5 ppm, potassium 166 ppm and soil organic 0.92%.

Seed of wheat cultivar Punjab-2011 was sown on November 11, 2012. The crop was raised under well-watered conditions throughout the growing season or drought stressed during reproductive stage using randomized complete block design, with four replications. Drought was imposed at reproductive stage (BBCH growth stage 49) and was maintained till physiological maturity (BBCH growth stage 83). Fertilizers were applied at 100-90-75 kg NPK ha^{-1} using urea (46% N), di-ammonium phosphate (18% N, 46% P_2O_5) and sulfate of potash (50% K_2O), respectively as sources. Whole of the P, K and one third of the N were applied as basal dose. Remaining N was applied at in two equal splits at tillering and panicle initiation stage. In total, three irrigations (each of three acre inches) were applied to the crop during the vegetative growth period in addition to soaking irrigation of four acre inches. At reproductive stage, was applied to well-watered crop whole no irrigation was applied to droughted crop. The crop was harvested on April 24, 2013 at harvest maturity and seeds were collected and stored for further experiments.

In second phase, seed collected from well-watered and droughted wheat crop were subjected to priming. The seed priming treatments were selected based on our previous studies (Farooq et al., 2008; Jafar et al., 2012). For seed priming, seeds were soaked in aerated water (hydropriming) and 1.5% (w/v) solution of $CaCl_2$ for 12 h keeping seed to solution ratio 1:5 (w/v). Aeration was provided by aquarium pump. After removing from the water and/or solution, seeds were thoroughly rinsed with water and dried in forced air under shade till original weight. Primed and non-primed (control) seeds were sown (15 in each pot) in soil filled earthen pots (30 cm diameter and 45 cm depth containing 15 kg soil) on November 15, 2013. After constant germination count, salt stress was imposed at 10 mM NaCl (control) and 100 mM NaCl (salt stress) (Mazhar et al., 2016). The experiment was conducted in factorial completely randomized design with six replications. Fertilizers were applied at the same rate using same sources as used for the phase I. During the experimentation, water was applied as per the requirement of the crop. The crop was harvested on April 20, 2014 at harvest maturity. The weather data during experimentation are given in Table 1.

2.2. Observations and measurements

2.2.1. Seed analysis

For determining the composition of seed collected from phase I, the seeds from both well-watered and droughted crop were analysed for ash, crude fat, crude protein, crude fiber and total phenolics. Wheat seeds were ashed on flame and placed into muffle furnace at 550 °C for 4 h and weighed. The ash contents were estimated following AOAC (1990). For crude fat, ether was added in wheat flour and crude fat was determined by soxhelt apparatus. After fat extraction, flour samples were analysed for crude fiber by adding H_2SO_4 and NaOH. The mixture was boiled for 30 min, washed with hot water, oven dried and placed in muffle furnace for 4 h at 550 °C. Crude fiber was calculated according to AOAC (1990). Crude protein in each sample was determined by Kjeldahl method. The samples were digested on hot plate and filtrate was distilled with concentrated NaOH and titrated against 0.1 N H_2SO_4. Crude protein was estimated following AOAC (1990). Total soluble phenolics were determined by soaking the flour in 80% acetone overnight. It was followed by addition of Folin-Ciocalteu reagent and Na_2CO_3 solution at 25 °C. Total soluble phenolic are reported as gallic acid equivalent (GAE) (Singleton and Rossi, 1965).

2.2.2. Plant water relations

To record data on plant water relation traits, in phase II, flag leaf samples were taken at booting stage (90 DAS). Leaf water potential (ψ_w) was measured with pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). The same leaf, which was used for determination of water potential, was frozen in a freezer at −20 °C for seven days. The frozen leaf material was thawed, cell sap was extracted and osmotic potential (ψ_s) was measured with an osmometer (Digital Osmometer, Wescor, Logan, UT, USA). Leaf pressure potential (ψ_p) was computed as a difference of ψ_w and ψ_s. For relative leaf water contents (RWC), fresh leaves samples were harvested, weighed, soaked for 4 h to record saturated weight, and dried. RWC were determined following Barrs and Weatherley (1962).

2.2.3. Mineral and biochemical analyses

For mineral and biochemical analyses, flag leaves were harvested at booting stage (90 DAS) in phase II. For mineral analysis, the leaf samples were oven-dried at 70 °C, soaked over-night in di-acid mixture and digested on hot plate. The digested samples were fed to the flame photometer to determine Na^+ and K^+ following Chapman and Pratt (1961).

Free leaf proline contents were estimated by homogenizing the fresh leaf samples in sulfosalicylic acid and glacial acetic acid. Ninhydrin solution was added to the filtrate. Afterwards, filtrate was incubated and cooled in ice bath, toluene was added and vortexed. The chromophore containing toluene was aspirated from the aqueous phase and the proline concentration was determined as described by Bates et al. (1973).

To determine glycine betaine contents, fresh leaf samples were

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