LONG TERM SALINITY STRESS IN RELATION TO LIPID PEROXIDATION, SUPER OXIDE DISMUTASE ACTIVITY AND PROLINE CONTENT OF SALT-SENSITIVE AND SALT-TOLERANT WHEAT CULTIVARS

Azam Borzouei¹, Mohammad Kafi², Elahe Akbari-Ghogdi³, and MirAhmad Mousavi-Shalmani¹

Salinity is a widespread root medium problem limiting productivity of cereal crops worldwide. The ability of plants to tolerate salt is determined by multiple biochemical pathways that facilitate retention and/or acquisition of water, protect chloroplast functions, and maintain ion homeostasis. Therefore, the ability of salt-sensitive (‘Tajan’) and salt-tolerant cultivar (‘Bam’) of Triticum aestivum L. to adapt to a saline environment were evaluated in a set of greenhouse experiments under salt stress during three growth stages (tillering, 50% anthesis, and 10 d after anthesis). Plants were irrigated by different saline waters with electrical conductivities of 1.3, 6, 8, 10, and 12 dS m⁻¹, which were obtained by adding NaCl:CaCl₂ in 10:1 molar ratio to fresh water. Differences in growth parameters, lipid peroxidation, superoxide dismutase (SOD) activity, and proline accumulation were tested in order to put forward the relative tolerance or sensitivity of cultivars. Results indicated that both parameters differ according to the cultivar’s ability in coping oxidative stress caused by salinity. We observed a greater decline in the growth parameters and grain yield under salt stress in ‘Tajan’ than in ‘Bam’. Malondialdehyde content was also higher in ‘Tajan’. The improved performance of the ‘Bam’ under high salinity was accompanied by an increase in SOD (EC 1.15.1.1) activity and proline content at all growth stages. Growth parameters, lipid peroxidation and proline accumulation results are also in good correlation with supporting this cultivar is being relatively tolerant.

Key words: Triticum aestivum, salt stress, NaCl, malondialdehyde.

¹Agricultural, Medical and Industrial Research School, Nuclear Science and Technology Research Institute, PO Box 31485-498 Karaj, Iran.
²Corresponding author (aborzouei@nrcam.org, aborzouei@gmail.com).
³Ferdowsi University of Mashhad, Faculty of Agriculture, PO Box 91775-1163 Mashhad, Iran.
⁴University of Tehran, Department of Agronomy and Plant Breeding Sciences, Tehran, Iran.

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H₂O₂ and O₂. Then, the produced hydrogen peroxide is scavenged (Rios-Gonzalez et al., 2002; Tuna et al., 2008) by various enzymes like peroxidase (POX), ascorbate peroxidase (APX), catalase (CAT) and glutathione reductase (GR) (Asada, 1992; Noctor and Foyer, 1998). Increase in the activities of these enzymes closely relates to the salt tolerance of many plants as reported in various researches (Zeng et al., 2003a; Lehner et al., 2008; Liu et al., 2011). Evidence suggests that membranes are the primary sites of salinity injury to cells and organelles because ROS can react with unsaturated fatty acids to cause peroxidation of essential membrane lipids in plasmalemma or intracellular organelles (Esfandiari et al., 2007). Cell membrane stability has long been taken as an indicator of stress tolerance (Ashraf and Ali, 2008). This attribute has recently been used as an effective selection criterion for salinity tolerance in plant species such as Brassica napus (Ashraf and Ali, 2008) and wheat (Sairam et al., 2002; Farooq and Azam, 2006).

Iod and osmotic homeostasis is necessary for plants to be salt tolerant. Osmotic homeostasis is accomplished by accumulation of compatible osmolytes in the cytosol for intracellular osmotic homeostasis (Zeng et al., 2003b; Raza et al., 2007). These N containing compounds (NCC) such as amino acids (proline and glycinebetaine) have pivotal roles in osmotic adjustment, protection of cellular macromolecules, storage form of N, maintenance of cellular pH, detoxification of the cells, and scavenging of free radicals (Tejera et al., 2006; Siddiqui et al., 2010). Proline accumulation might be used as an indicator in selection for withstanding saline stress through the participation in osmoregulation (Ueda et al., 2007; Tammam et al., 2008). Expression of one or more additional genes for proline accumulation can be induced by stress (Misra and Saxena, 2009). Moreover, proline accumulation under stress conditions may be caused by induction of proline biosynthesis enzymes, reduction the rate of proline oxidation conversion to glutamate, decline utilization of proline in proteins synthesis and enhancing proteins turnover (Tammam et al., 2008).

With this background, it was postulated that the growth of wheat species differing in salt tolerance may display differing responses with respect to their oxidative capacity and accumulation of osmoprotectants at different growth stages. Therefore, the main objective of the present experiment was to evaluate the effects of salt stress on the activity of superoxide dismutases, which constitute the first line of defense against ROS, lipid peroxidation, and proline accumulation at three growth stages of two wheat genotypes differing in salt tolerance, in order to better understand the mechanisms relevant in salt tolerance.

MATERIALS AND METHODS

Plant material, growth and treatment conditions

Healthy seeds of two cultivars of wheat (Triticum aestivum L.) ‘Tajan’ (salt-sensitive) and ‘Bam’ (salt-tolerant) were selected for the study. These genotypes were selected on the basis of results of our earlier experiment (Akbari Ghogdi et al., 2012). The seeds of two wheat cultivars were obtained from the Seed and Plant Improvement Institute (SPII), Karaj, Iran. Before sowing, seeds were surface sterilized with 1% sodium hypochlorite solution for 10 min, and washed three times with sterilized distilled water. The earthen pots of 30 cm diameter were filled with sandy loam soil and FYM (farmyard manure) in 6:1 ratio. Each pot was fertilized with 60, 60, and 60 kg ha⁻¹ of N, P, and K, respectively, in the form of urea, single super phosphate, and muriatic of potash at sowing. Remaining 60 kg N ha⁻¹ was given 25 d after sowing (DAS). After seedling establishment, five seedlings were retained. Plants were irrigated by different saline waters with electrical conductivities (1.3, 6, 8, 10, and 12 dS m⁻¹) obtained by adding NaCl:CaCl₂ in 10:1 molar ratio to fresh water. Observations for biochemical parameters were recorded at tillering or 50 DAS, 50% anthesis and 10 d after anthesis (DAA).

The experiment was carried out under greenhouse conditions in Agricultural, Medical and Industrial Research School, Nuclear Science and Technology Research Institute, Karaj, Iran, where the average PAR measured at noon ranged from 848 to 1254 μmol m⁻² s⁻¹, day/night relative humidity 58/74%, and day/night temperature 24/8 °C.

Growth parameters and extract preparation

At the end of the experiment, three plants from each treatment were sampled randomly. Root volume was measured and fresh weights (FW) of shoots and roots were weighed. For dry weight (DW) determination samples were oven dried at 70 °C for 72 h and then weighed.

For enzyme assays and estimation of lipid peroxidation, frozen leaf samples were ground to a fine powder with liquid nitrogen and extracted with ice-cold 50 mM phosphate buffer (pH 7.0). The extracts were centrifuged at 4 °C for 30 min at 20000 x g and the supernatants were used as the crude extracts (Dionisio-Sese and Tobita, 1998).

Lipid peroxidation and proline content

Lipid peroxidation was determined by estimating the malondialdehyde (MDA) content in 1 g leaf FW according to Koca et al. (2007). Malondialdehyde is a product of lipid peroxidation by thiobarbituric acid reaction. The concentration of MDA was calculated from the absorbance at 532 nm (correction was done by subtracting the absorbance at 600 nm for unspecific turbidity) by using extinction coefficient of 155 mM⁻¹ cm⁻¹.

To determine free proline level, 0.5 g of leaf samples from each group were homogenized in 3% (w/v)
Enzyme assays and protein determination
Total SOD (EC 1.15.1.1) activity was determined by measuring its ability to inhibit the photochemical reduction of nitrotrazolium blue chloride (NBT), as described by Giannopolitis and Ries (1977). The reaction mixture (1.5 mL) contained 50 mM phosphate buffer (pH 7.8), 0.1 µM EDTA, 13 mM methionine, 75 µM NBT, 2 µM riboflavin, and 50 µL enzyme extract. Riboflavin was added last and tubes were shaken and illuminated with a two 20 W fluorescent tubes. The reaction was allowed to proceed for 15 min after which the lights were switched off and the tubes covered with a black cloth. Absorbance of the reaction mixture was read at 560 nm. One unit of SOD activity (U) was defined as the amount of enzyme required to cause 50% inhibition of the NBT photoreduction rate and the results expressed as U mg\(^{-1}\) protein. Protein concentration was determined according to Bradford (1976), using bovine serum albumin (BSA) as a standard.

Statistical analysis
The experimental design was a completely randomized factorial, three (harvest periods) \(\times\) five (salt levels: 1.3, 6, 8, 10, and 12 dS m\(^{-1}\)) \(\times\) two (genotypes), with three replicates. The data were analyzed statistically with SPSS-17 statistical software (SPSS, Chicago, Illinois, USA). Means were statistically compared by Duncan’s multiple range test (DMRT) at \(P < 0.05\) level.

RESULTS AND DISCUSSION
Salt treatment significantly reduced dry weight of shoots and roots (\(P < 0.001\)) of both cultivars. Under salt stress, ‘Bam’ produced significantly higher root dry weight compared to ‘Tajan’ (Table 1). In both cultivars root volume decreased under the effect of salt treatment which it was more remarkable at 12 dS m\(^{-1}\) NaCl treatment.

Root FW decreased in both cultivars but this was more prominent in ‘Tajan’ at 10 and 12 dS m\(^{-1}\) NaCl. Shoot FW was also affected by salt treatment and same tendency (decline) can be seen at 12 dS m\(^{-1}\) NaCl treatment for both cultivars (Table 1). The results revealed that ‘Bam’ which is considered as salt-tolerant showed higher root volume, fresh and dry weight of shoots and roots, under both distressed and non-stressed conditions (Table 1).

Plants have the ability to tolerate salinity, but the extent to which they can counteract this menace depends on the nature of a species or even a cultivar (Ashraf and Ali, 2008). Shoot and root growth inhibition is a common response to salinity and plant growth is one of the most important agricultural indices of salt stress tolerance as indicated by different studies (Munns, 2002; Koca et al., 2007). In order to classify salt stress tolerance or sensitivity of both cultivars, growth parameters like volume, dry and fresh weight of roots and shoots were tested under the effect of NaCl treatment. Increase in the salinity from 1.3 to 8 dS m\(^{-1}\) NaCl had no effect on plant root and shoot weights, while further increase from 10 dS m\(^{-1}\) onwards significantly reduced root and shoot weights. Root and shoot weights of both cultivars were affected by salinity, besides growth inhibition was more prominent in ‘Tajan’ under severe salt stress conditions. Root volume exhibited the same trend under the same conditions in both cultivars. However, ‘Bam’ had higher root volume under the highest NaCl treatment. In the current investigation the highest level of salinity has a more pronounced effect on root weight with respect to shoot weight as roots are directly

Table 1. The effect of NaCl treatments on growth parameters (root and shoot fresh and dry weights, root volume) and grain yield on wheat cultivars Bam and Tajan.

| NaCl treatment | Root fresh weight | Root dry weight | Shoot fresh weight | Shoot dry weight | Root volume | Grain yield |
|----------------|-------------------|----------------|-------------------|-----------------|-------------|------------|
|                | g plant\(^{-1}\)  | cm\(^{3}\)      | g plant\(^{-1}\)  | cm\(^{3}\)      | g m\(^{-2}\) |
| ‘Bam’          |                   |                |                   |                 |             |
| 1.3            | 27.54 ± 2.42a     | 5.37 ± 0.39a   | 64.55 ± 3.61a     | 16.62 ± 1.23a   | 36.75 ± 2.23a | 57.55 ± 2.42a |
| 6              | 23.50 ± 2.42ab    | 4.76 ± 0.39a   | 57.81 ± 3.61b     | 14.99 ± 1.23abc | 35.70 ± 2.23a | 45.30 ± 2.42ab |
| 8              | 20.83 ± 2.42abc   | 4.63 ± 0.39ab  | 52.80 ± 3.61bc    | 14.52 ± 1.23abc | 32.25 ± 2.23ab | 42.95 ± 2.42ab |
| 10             | 17.83 ± 2.42cde   | 4.56 ± 0.39ab  | 50.51 ± 3.61bc    | 14.35 ± 1.23abc | 31.75 ± 2.23ab | 41.90 ± 2.42b  |
| 12             | 12.31 ± 2.42e     | 3.52 ± 0.39cd  | 48.83 ± 3.61bcd   | 14.03 ± 1.23bc  | 26.00 ± 2.23bc | 38.08 ± 2.42d  |
| ‘Tajan’        |                   |                |                   |                 |             |
| 1.3            | 20.33 ± 2.42bcd   | 3.90 ± 0.39bc  | 47.62 ± 3.61bcd   | 15.82 ± 1.23ab  | 23.50 ± 2.23cd | 36.10 ± 2.42c  |
| 6              | 19.31 ± 2.42cde   | 3.66 ± 0.39cd  | 42.53 ± 3.61cde   | 14.53 ± 1.23abc | 22.75 ± 2.23cd | 34.58 ± 2.42c  |
| 8              | 14.11 ± 2.42de    | 3.01 ± 0.39    | 42.16 ± 3.61cde   | 14.20 ± 1.23abc | 18.00 ± 2.23de | 31.72 ± 2.42cd |
| 10             | 13.25 ± 2.42de    | 2.90 ± 0.39    | 38.57 ± 3.61de    | 14.15 ± 1.23abc | 18.00 ± 2.23de | 31.02 ± 2.42cd |
| 12             | 12.57 ± 2.42e     | 2.34 ± 0.39    | 36.72 ± 3.61e     | 13.10 ± 1.23c   | 16.00 ± 2.23e  | 22.05 ± 2.42e  |

Values followed by different letters in the same column are significantly different at \(P \leq 0.05\). Within each column, values followed by same letters are not significantly different according to LSD test at \(P = 0.05\).

Standard error.

sulfsalicylic acid and then homogenate filtered through filter paper (Bates et al., 1973). Mixture was heated at 100 °C for 1 h in water bath after addition of acid ninhydrin and glacial acetic acid. Reaction was then stopped by ice bath. The mixture was extracted with toluene and the absorbance of fraction with toluene aspirated from liquid phase was read at 520 nm. Proline concentration was determined using calibration curve and expressed as µmol proline g\(^{-1}\) FW.
exposed to salt solution. The reduction in root and shoot growth may be due to toxic effects of the higher level of NaCl concentration as well as unbalanced nutrient uptake by roots (Glyn Bengough et al., 2011).

Growth processes are especially salt sensitive, so that growth rates and biomass production provide reliable criteria for assessing the degree of salt stress and ability of a plant to withstand it as reported by Ben Amor et al. (2005). Similar to our findings, dry weight was less affected in salt tolerant sugar beet, sesame, wheat and moderately salt tolerant cotton (Ghoulam et al., 2002; Meloni et al., 2003; Katerji et al., 2005; De Azevedo Neto et al., 2006; Koca et al., 2007).

Lipid peroxidation in leaves of both wheat genotypes, MDA content increased with age and salinity levels in both genotypes (Figure 1). At all three stages, with increasing level of salinity stress, MDA content increased in the sensitive variety (‘Tajan’), thus indicating an increase in lipid peroxidation. However, ‘Tajan’ showed higher MDA content in control and all salinity treatments at 10 DAA as compared with ‘Bam’ (Figure 2). ‘Tajan’ maintained highest MDA at third stage and 12 dS m⁻¹, while ‘Bam’, on the other hand, did not exhibit this increase in lipid peroxidation at first and second stages.

Salinity stress is an intricate stress which includes osmotic stress, specific ion effect, nutrient deficiency, etc., thereby affecting various physiological and biochemical mechanisms associated with plant growth and development. Salinity has a pronounced effect on plasma membrane lipid peroxidation, which is an indication of membrane damage and leakage under salt stress conditions (Sairam et al., 2002; Ashraf and Ali, 2008). The increased production of activated oxygen species (ROS) such as superoxide (O₂⁻), hydrogen peroxide (H₂O₂), hydroxyl radical (OH•) (Lehner et al., 2008), and singlet oxygen (¹O₂) in chloroplasts of plants under salt stress has been described. However, stability of biological membranes has been taken as an effective screening tool to assess salinity stress effects (Abdul Jaleel et al., 2007). For example, Farooq and Azam (2006) reported an increase in cell membrane injury under salt stress in different wheat varieties. It has been suggested that decrease in membrane stability reflects the extent of lipid peroxidation caused by ROS (Heidari and Jamshidi, 2011). In the present study salt stress affected both cultivars by means of lipid peroxidation, but ‘Tajan’ had higher rates of increment at 10 and 12 dS m⁻¹ salinity levels on second and third growth stages. Lower MDA level was remarkable in ‘Bam’ at highest NaCl concentrations on last growth stages. However, the reverse trend was true in ‘Tajan’.

An increase in the activity of antioxidative enzymes under salt and water stresses could be indicative of an increased production of ROS and a build-up of a protective mechanism to reduce oxidative damage triggered by stress experienced by plants (Shao et al., 2005a).

SOD activity in leaves of both cultivars was highest at tillering stage in both control and salinity treatments as compared with other two growth stages. SOD activity in ‘Bam’ was greater than that of ‘Tajan’ at all three stages and treatments. At vegetative stage, leaves of both varieties exhibited an increase in SOD activity with increasing magnitude of salinity stress; whereas at second and third stages a slight increase in SOD activity can be observed at higher salinity level (Figure 2).

SOD is one of several important antioxidant enzymes with the ability to repair oxidation damage caused by ROS. Its activity modulates the relative amounts of O₂⁻ and H₂O₂, the two Haber-Weiss reaction substrates.
and decreases the risk of OH⁻ radical formation, which is highly reactive and may cause oxidative damage to cellular components (Agarwal et al., 2005). Thus, SOD is considered a key enzyme for maintaining normal physiological conditions and coping with oxidative stress in the regulation of intracellular levels of ROS (Ashraf and Ali, 2008).

Our results show that SOD activity in leaves of salt-stressed plants was greater than control plants. In both cultivars SOD activity increased as the NaCl amount increased but the rate of increment was higher in ‘Bam’. Enhancement of SOD activity is a good implication of this cultivar ability in better coping with ROS (Noreen and Ashraf, 2009). Several authors investigating salt-tolerant and salt-sensitive cultivars have suggested that the salt tolerance character is related to increased SOD activity in salt-tolerant cultivars (Sairam et al., 2002; De Azevedo Neto et al., 2006; Noreen and Ashraf, 2009). Decline in SOD activity at second and third growth stages could be related to proline accumulation (Koca et al., 2007).

Salinity caused a considerable increase in proline content in both wheat cultivars. ‘Bam’ showed generally higher proline content at all the stages (Figure 3). The magnitude of difference in proline content in ‘Bam’ over ‘Tajan’ increased with increasing salinity level at third stage. Proline content also increased very significantly at 50% anthesis and 10 d after anthesis as compared with pre-anthesis stage (Figure 3).

In our study, both ‘Bam’ and ‘Tajan’ exhibited increased proline accumulation with increasing salt concentration. However, at medium and high salt concentrations, ‘Bam’ had significantly higher proline accumulation. Proline accumulation was more remarkable at the end of experimental period at the highest NaCl treatment.

One distinctive feature of most plants growing in saline environments is the accumulation of increased amounts of low molecular weight water-soluble metabolites in their cells, such as proline (Siddiqui et al., 2010), possibly for osmotic adjustment (Moradi and Ismail, 2007). Proline is generally regarded as a compatible solute involved in cellular osmotic adjustments, whose accumulation increases when plants are in drought- and salt stressed conditions (Ueda et al., 2007; Wang and Han, 2009). Moreover, stabilizing proteins, regulating cytosolic pH and scavenging of hydroxyl radicals could be more effective under severe stress conditions (Koca et al., 2007).

Under control condition grain yield per pot was higher in ‘Bam’. Salinity significantly reduced the grain yield and the effect increased with salinity level. At 12 dS m⁻¹ NaCl treatment ‘Tajan’ showed significantly lower yield (22.05 g m⁻²) than ‘Bam’ (38.08 g m⁻²). The percentage reduction due to salinity over control was lower in ‘Bam’ (19.9), as compared with ‘Tajan’, which showed higher decline (38.9).

CONCLUSIONS

Considering data obtained on grain yield as agronomic index of salinity stress tolerance, it is clear that ‘Bam’ is more tolerant to salinity stress, than ‘Tajan’. Additionally, ‘Bam’ could induce antioxidative enzyme system more efficiently and higher proline accumulation resulted in retarded growth inhibition and lower lipid peroxidation under saline conditions at long-term salinity. It is thus perceptible that no single parameter or group of parameters could be recommended as individual factor responsible for salinity stress tolerance of wheat genotypes. A combination of characters like higher antioxidant activity leading to lower oxidative stress, higher osmotic concentration and selective uptake of useful ions and prevention of over accumulation of toxic ions contributes to salinity stress tolerance of tolerant wheat genotypes.
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Palabras clave: Triticum aestivum, estrés salino, NaCl, malondialdehído.
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