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The Effect of Priming and Salinity on Physiological and Chemical Characteristics of Wheat (*Triticum aestivum* L.)

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Abstract

In order to study of the effect of priming and salinity on physiological and chemical characteristics of wheat (*Triticum aestivum* L.), an experiment was carried out at the Experimental Farm of Shiraz University. Results showed that primed plants significantly reduced its gas exchanges by accelerating senescence under a series of salt stress, which became more serious along with the increasing of salt concentrations, especially at 21 d after anthesis. Under each level of salt stress, dry matter accumulation of primed plants was always higher than the non-primed plants. Primed plants had higher potassium selectivity against sodium than non-primed plants with the former could maintain relatively stable balance of ions, potassium/sodium was found not to be the limited factor for salt tolerant plants, but it was in salt-sensitive plants. Net photosynthesis (*P*n) significantly positively correlated with leaf potassium/sodium (K^+/Na^+), relative water content (RWC), and leaf area duration ($P < 0.01$). So those four parameters might be ideal criterions of salt tolerance in wheat. In conclusion, salt stresses caused significant declines in growth period of wheat by accelerating leaf senescence at reproductive stage. Primed plants of wheat successfully preserved normal growth by maintaining *P*n, K^+/Na^+, leaf area duration (LAD) and dry matter accumulation (DMA), while non-primed plants decreased considerably in those parameters. The improvement of photosynthesis and related traits in reproductive stage was a key to the growth of wheat under saline conditions.

Keywords: Priming; Salinity; Wheat; Physiological and Chemical Characteristics

1. Introduction

According to the studies %7 of the world lands is saline and %3 is high saline, because of low precipitation, high evaporation and irrigation by saline waters, soil salinity is getting increased (Teimouri et al, 2009). The most important problems for economic crops production in arid regions is high concentration of ions specially NaCl either in soil or in irrigation water (Moeinrad, 2008). Salinity reduces the ability of plants to take up water and this quickly causes reductions in growth rate, along with a suite of metabolic changes identical to those caused by water stress (Abbasdokht, 2011). High salinity adversely affects germination, growth, physiology and productivity by causing ionic and osmotic stresses as well as oxidative damage (Iterbe-Ormaetxe et al., 1998). Moreover, salt stress has also been found responsible for an increased respiration rate, ion toxicity (Sudhir and Murthy, 2004), changes in C and N metabolism (Kim et al., 2004), mineral distribution, membrane instability (Marschner, 1986) and permeability (Gupta et al., 2002), decreased biosynthesis of chlorophyll and inefficiency of photosynthesis (Munns, 2002), all of which ultimately leading to lowered economic productivity.

Differences between closely related plants are particularly interesting to identify a small number of factors responsible for salt tolerance (Gehlot *et al.*, 2005). Salinity stress has been studied in relation to regulatory mechanisms of osmotic and ionic homeostasis (Ashraf &

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Harris, 2004). The response of plants to a salinity stress may vary with the genotype; nevertheless some general reactions occur in all genotypes. Increased tolerance to salinity stress in crop plants is necessary in order to increase productivity with limited water supplies and high salinity. Tolerant genotypes respond to salinity stress with complex changes in their physiological and molecular status (Morsy *et al.*, 2007). During the course of salinity stress, active solute accumulation of osmotic solutes such as soluble carbohydrates, proteins and free amino acids is claimed to be an effective stress tolerance mechanism. The adaptability of plant species to high salt concentrations in soil by lowering tissue osmotic potential was accompanied by accumulation of these osmotic solutes (Zhu, 2002; Jaleel *et al.*, 2008). Studies of Heikal *et al.* (2000), Ismail and Azooz (2002) revealed that salt tolerance of wheat, was correlated with higher accumulation of ionic and osmotic solutes in salt-tolerant than that of salt-sensitive plants. Differences in the accumulation patterns of Na^+ and K^+ were found under salinity stress. The salt tolerant plants maintained a high K^+ content and higher K^+/Na^+ ratio compared with the salt sensitivity plants (Azooz *et al.*, 2004; Rejili *et al.*, 2007). High K^+/Na^+ ratio is more important for many species than simply maintaining a low concentration of Na^+ (Cuin *et al.*, 2003). Salinity stress is known to trigger oxidative stress in plant tissues through the increase in reactive oxygen species (Apel & Hirt, 2004). Chloroplasts are the major organelles producing the reactive oxygen species (ROS) such as, the superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2) and singlet oxygen (O^-_1) during photosynthesis (Asada, 1992). Salt stress induces a significant reduction in photosynthesis. This reduction depends on photosynthesizing tissue (leaf area) and photosynthetic pigments (Dubey, 2005; Raza *et al.*, 2006). The production of ROS can be particularly high, when plants are exposed to salinity stress (Athar *et al.*, 2008; Ashraf, 2009). ROS cause chlorophyll degradation and membrane lipid peroxidation. So, malondialdehyde (MDA) accumulation as product of lipid peroxidation and chlorophyll retention are two oxidative stress indicators that are tested tools for determining salt tolerance in plants (Yildirim *et al.*, 2008). To scavenge ROS, plants posses specific mechanisms, which include activation of antioxidant enzymes (Jaleel, *et al.*, 2006) and non- enzymatic antioxidants such as, carotenoids and ascorbic acid (Mittler, 2002).

Abbasdokht et al. (2004) reported that high quality of germination in crops will result high yield. There are many strategies to overcome the negative effects of drought and salinity. A good strategy is the selection of cultivars and species for salinity and drought conditions. But an alternative strategy for the possibilities to overcome salt and drought stresses is by seed priming. Effects of priming or pre-treatment of seed persist under suboptimum field conditions, such as salinity (Muhyaddin and Weibe, 1989; Wahid et al., 2006), low or high temperature (Bradford et al., 1990; Pill and Finch-Savage 1988; Wahid and Shabbir 2005) and low soil moisture availability (Lee et al., 1998; Du and Tuong, 2002). Different seed priming tools have been successfully integrated (Taylor et al., 1998; Basra et al., 2004; Farooq et al., 2006b). Seed priming is beneficial in many respects. Seed priming techniques such as hydropriming, hardening, osmoconditioning, smohardening, and hormonal priming have been used to accelerate emergence of roots and shoots, more vigorous plants, and better drought tolerance in many field crops like wheat (Iqbal and Ashraf, 2007), chickpea (Kaur et al., 2002), sunflower (Kaya et al., 2006) and cotton (Casenave and Toselli, 2007).

Although reports are available on the physiological enhancements of direct-seeded rice (Du and Tuong, 2002; Ruan et al., 2002), no comprehensive study has evaluated the response of wideranging seed priming treatments for enhancing seedling establishment, plant allometry. Information is also scarce on the physiological implications of priming- triggered enhancement in germination, growth or yield, and their inter-relationships using primed seeded winter wheat. It is surmised that the priming of seed is beneficial in improving the agronomic characters of wheat under saline conditions. Here we tested this prediction by evaluating the effects of seed priming strategy on the relationships among leaf physiology, gas exchange, growth parameters and duration of growth stage.

2. Materials and Methods

The experiment was conducted at the Experimental Farm of Shiraz University in 2009. Wheat seeds were primed with KNo_3 solution (1.2 MPa) for three days at $25^\circ C$. After priming, seeds were put in wire mesh strainer and washed with tap water for 3 min and then rinsed with distilled water. Following this, seeds were dried between two filter papers and set to germinate. Seeds of primed and non-primed of winter wheat *(Triticum aestivum* L.) were planted into soil pools with different NaCl concentrations (0.0%, 0.3%, 0.6%, 0.9% w/w). During the experiment, no water was lost except water evaporations of soil and plants. In avoiding the influence of rainfall on the salt concentrations, plastic films were used as rain roofs. All the pools were illuminated by natural light, with the photosynthetic active radiation. All the pools were filled with light loam soil, which has the organic matter content, available nitrogen, available phosphorus, and available potassium being 0.72% (w/w), 110.11, 70.11 and 65.73 mg kg^{-1}, respectively. Soil salt concentrations were adjusted with pure salt (NaCl). Plants were irrigated five times throughout the growing period. All samples and measurements on physiological variables were taken at a 7 days interval from anthesis. In order to carry on photosynthesis, green plants need a supply of carbon dioxide and a means of disposing of oxygen. In order to carry on cellular respiration, plant cells need oxygen and a means of disposing of carbon dioxide. Net photosynthetic rate and stomatal conductance were measured on flag leaves of the primed and non-primed plants receiving different salt treatments at 7 d intervals after anthesis. Only on clear days were the measurement done. Leaf water status is intimately related to several leaf physiological variables, such as leaf turgor, growth, stomatal conductance, transpiration, photosynthesis and respiration (Kramer & Boyer, 1995). Water content and water potential have been widely used to quantify the water deficits in leaf tissues. Leaf water content is a useful indicator of plant water balance, since it expresses the relative amount of water present on the plant tissues. Dynamic trends of relative water contents (RWC) in flag leaves and dry matter accumulation (DMA) in spikes were determined at 7 d intervals after anthesis subjected to each treatment. Samples were taken immediately after the measurements of gas exchanges were finished. In determining relative water contents, flag leaf samples were washed in distilled water and weighted after drying by filter paper to obtain their fresh mass (f.m.), the turgid leaf samples were blotted, dried and weighed to gain the turgid mass (t.m.) values. All the leaf samples were then dried at 75 °C for 72 h, with their dry masses (d.m.) being determined. Leaf RWC in different stages were calculated by the following formula (Muranaka et al., 2002) To measure DMA, we separated 25 spikes from 25 individuals of each treatment and dried at 75 ◦C for 72 h, finally, the dry matter weight was obtained after cooling the samples to room temperature.

RWC (%) = [(f.m. - d.m.)/(t.m. – d.m.)] * 100

Leaf area index (LAI) is defined as the leaf area per unit of ground area, and is a measure of the leafiness of a crop and Leaf area duration (LAD) is the integral of LAI over time. LAD is calculated by multiplying LAI with the time (in days or weeks) during which the leaf area is photosynthetically functional.

LAD= [(LAI1 + LAI2)/2] x Number of days

Leaf area was measured by leaf area analyzer. Leaf area index (LAI) was computed as the ratio between total leaves photosynthetic area and the corresponding land area at different stages. Flag leaf samples were firstly dried at 75 °C for 72 h, then ground to determine the sodium and potassium contents. About 0.5 g ground flag leaves were put in to digesting tubes, 10 ml concentrated nitride acid and 3ml perchlorate acid was added. All the samples were further soaked for 12 h, and then burned at 300 °C for 6 h, with the extractions being completed to 50 ml with distilled water finally ions contents were measured using an atomic absorption spectrophotometer. The experiment was carried out as factorial based on randomized complete block design (RCBD) with four replications. The treatments included salinity and seed priming (primed ad non-primed seeds). Statistical analysis of data was processed using analysis of variance (ANOVA) in MSTAT-C. The effects of salt stress on plant growth parameters were verified using one-way ANOVA. Pearson’s correlation test was also carried out to study the relationships among leaf physiology, gas exchange, growth parameters and duration of growth stage.

3. Results and Discussion

The effect of salinity on plant growth is due to an osmotic effect and/or ion toxicity. However, variation of adaptive mechanisms exists in different species (Rehman et al., 1996). Results showed that dry matter accumulation were similar in primed and non-primed plants in control; however, significant differences appeared in dry matter accumulation of the primed and non-primed plants under salt stress (dry matter collected from 25 spikes). Reproductive stage is the most sensitive period for winter wheat to obtain high yield (Yu et al., 2001). Generally, longer reproductive period of wheat can capture more light energy and produce more CO_2 assimilations.At the beginning of reproduction stage, dry matter accumulation of primed plants increased more rapidly than non primed plants and non-primed plants decreasing more rapidly than the primed plants in late reproductive stage at all levels of salt stress. There was significant difference between primed and non primed plants at 0.3% and 0.6% and 0.9 % salt concentrations in dry matter accumulation. No significant differences in dry matter accumulation were found in primed plants at 0.6% and 0.9% salt concentrations compared with the 0.3% and control. Dry matter accumulation of primed and non-primed plants at levels of 0.0%, 0.3% and 0.6% salt concentration increased linearly from 7 to 28 days after anthesis. Those parameters of non-primed plants showed significant reductions in comparison with control at all levels of salt concentration, with serious reductions being especially noted at salt levels of 0.6% and 0.9%. Under each level of salt stress, dry matter accumulation of primed plants was always higher than the non-primed plants. There were no significant differences between primed and non-primed plants in net photosynthetic rate and stomatal conductance in control plants under normal soil conditions. However, gas exchanges of primed plants maintained normal capacities at 0.3% salt concentrations, while decreased under 0.6% and 0.9% salt concentration. The primed plants significantly reduced its gas exchanges by accelerating senescence under a series of salt stress, which became more serious along with the increasing of salt concentrations, especially at 21 days after anthesis. Gas exchanges declined to nearly zero under 0.6% and 0.9% salt concentrations. The values of net photosynthetic rate and stomatal conductance in primed plants were higher than in non-primed plants at all levels of salt concentration, particularly, at 0.3% and 0.6% salt concentrations. Primed plants maintained higher leaf area index and leaf area duration than non-primed plants during the reproductive period at all levels of salt concentration (Fig. 1). LAI and LAD are two very important marks to measure their growing situation. Leaf area index and leaf area duration of primed plants were larger than non primed plants in control, however, both decreased under salt stress condition and the reduction appeared more critical with increasing of salt concentrations (i.e., 0.6% and 0.9%). The primed plants displayed no significant reductions in leaf area index and leaf area duration in comparison with control at salt concentrations of 0.3% and 0.6%, only a rapid decrease being noted at 0.9% salt concentration. While those parameters of the non-primed plants were significantly decreased at all levels of salt stress, particularly, at 0.6% and 0.9% salt concentration. On the other hand, both parameters in the primed plants were higher than non-primed plants at all levels of salt concentration. Leaves of primed and non-primed plants dried to death and lost their photosynthetic capacities at the end of reproductive stage at the level of 0.9% salt concentration.

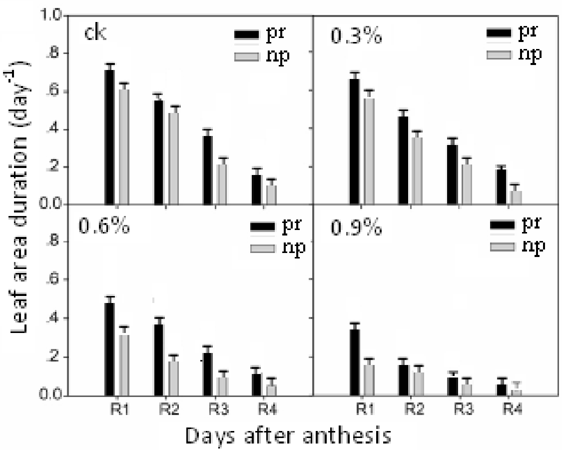

Fig.1. Changes of LAD at primed (pr) and non-primed (np) at 0.0%, 0.3%, 0.6% and 0.9% salt concentration

The relative water contents of primed and non primed plants during their reproductive stages were similar to those of control plants. Primed plants had no significant reductions under 0.3% and 0.6% salt concentrations compared with control, only appeared rapid decrease at level of 0.9%. While non-primed plants had significant reductions at all levels of salt concentration. The relative water content of primed plants appeared higher than non-primed plants at all levels of salt concentration, specially, at the late of reproductive stage. Salinity not only affects yield potential of a plant but almost every aspect of physiology and biochemistry of a plant (Parvaiz *et al.*, 2008; Zhu, 2002).Some believed that one of the key features of salt-tolerant plant was the ability for cells to maintain optimal K^+/Na^+ ratio (Tester and Davenport, 2003). Flag leaf potassium contents of the primed plants peaked at 14 days after anthesis at all levels of salt concentration, thereafter decreased along with increasing of salt concentrations (Fig. 2).

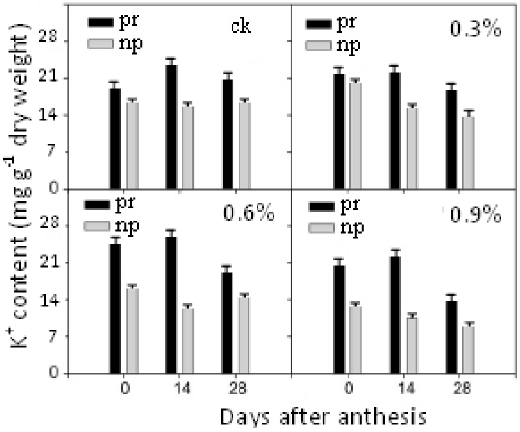

Fig. 2. Effects of different levels of salinity stress on K^+ in flag leaves of primed (pr) and non-primed (np) plants after anthesis

However, the non-primed plants always decreased its leaf potassium content since anthesis, especially along with increases of salt concentrations. Sodium contents appeared to increase for primed and non-primed plants. Nonetheless, sodium contents in the primed plants flag leaves were much lower than in the non-primed plants, which increased slightly with the enhancement of in vitro sodium concentration. Sodium contents significantly increased in non-primed plants, specially, at mature period (Fig. 3).

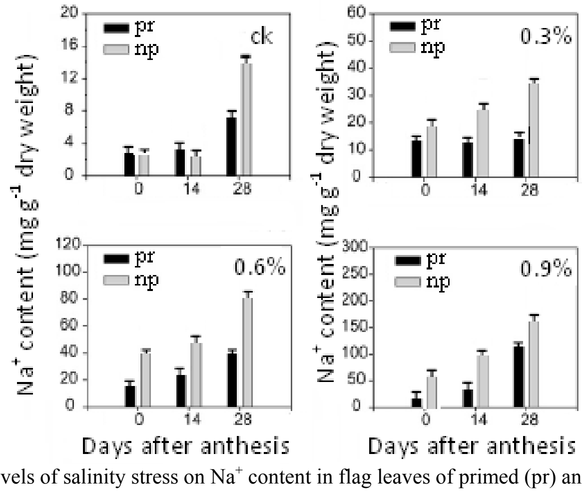

Fig. 3. Effects of different levels of salinity stress on Na^+ content in flag leaves of primed (pr) and non-primed (np) plants after anthesis

The primed plants maintained higher potassium/sodium ratios, but the non-primed plants decreased the ratios remarkably with increase of salt concentrations (Fig. 4). Our results showed that the K^+/Na^+ ratio fell slightly in the primed plants at 0.3% and 0.6% salt concentrations, although it decreased dramatically at 0.9%. However, the ratio in the non-primed plants decreased considerably at all salt concentrations. Such a phenomenon might owing to both excessive Na^+ accumulation in plant tissue and enhanced K^+ leakage from the cell (Poustini and Siosemardeh, 2004).

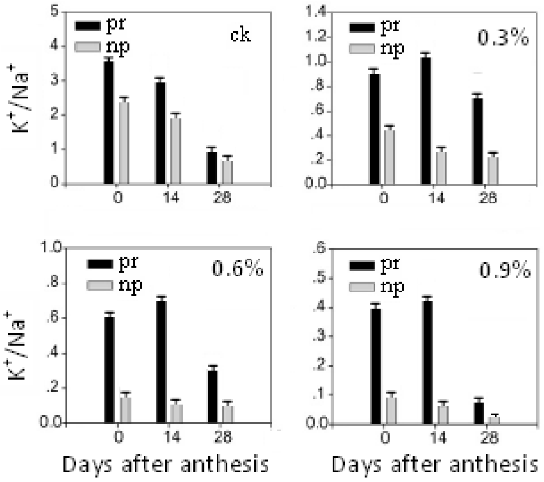

Fig. 4. Effects of different levels of salinity stress on K^+/Na^+ ratio in flag leaves of primed (pr) and non-primed (np) plants after anthesis

Vegetative growth period and reproductive growth period of primed and non-primed plants are shown in fig. 5. The primed plants had longer Vegetative growth period and reproductive growth period than the non-primed plants in control, and those differences appeared more apparent under salt stress. The primed plants maintained regular growth at 0.3% and 0.6% salt concentrations compared with control, while reproductive growth period reduced rapidly at salt concentration of 0.9%. Nevertheless, Reproductive growth period of the non-primed plants decreased dramatically at all levels of salt stress, especially at 0.6% and 0.9%. The total growth stages of the primed plants were very close to control at 0.3%, 0.6% and 0.9% salt concentrations, while the vegetative growth period and reproductive growth period of the non-primed plants decreased remarkably. Primed and non-primed plants accelerated senescence at 0.9% salt concentration, even so, total growth stage in primed plants still kept longer than in the non-primed plants.

There were no significant differences in vegetative growth period of both plants at 0.0% and 0.3% salt concentrations, with slight declines in vegetative growth period appeared in the non-primed plants at 0.6% and 0.9% salt concentrations. Considerable decreases were found in the reproductive growth period of non-primed plants in comparison with the primed plants at all levels of salt concentration (Fig. 5). This may allow the reproduction growth period to be salt-tolerant independently of the vegetative growth. Our finding was common with the report of Poustini and Siosemardeh (2004). Therefore, we believed that the tolerance of wheat plants to salt was determined by their reproductive phases, rather than by the vegetative stages. Primed plants, maintained normal growth period under 0.3% and 0.6% salt concentrations only significant decrease in growth period happened under 0.9% salt concentration. Nevertheless, the non-primed plants showed earlier senescence/death at both 0.6% and 0.9% salt concentrations at late reproductive stage. Significantly positive relationships ($P<0.01$) among net photosynthesis and stomatal conductance, leaf area index, leaf area duration, and relative water content of flag leaf, reproductive growth period and total growth period were determined. While significantly positive relationships ($P < 0.05$) were observed between Net photosynthesis and leaf area duration (Table 1). Significantly positive correlations ($P<0.01$) were also found between Net photosynthesis and stomatal conductance, flag leaf relative water content. Other significant correlations ($P<0.01$) included positive correlations among net photosynthesis, leaf area index, leaf area duration, relative water content, dry matter accumulation of spikes, reproductive growth period and total growth period, potassium/sodium, stomatal conductance, leaf area duration and relative water content in primed plants (Table 1). It has been reported that two major physiological traits enable the plant to tolerate salinity: (a) compensatory growth following adjustment to salinity and (b) ability to increase both leaf area ratio and net assimilation rate to achieve this increased growth (Wiynarah 1990). Structural components of plants including leaf structure that undergo changes due to salinity are intimately linked to physiological and biochemical activities of the plant (Cushman and Bohnert 1995, Bohnert and Jensen 1996).

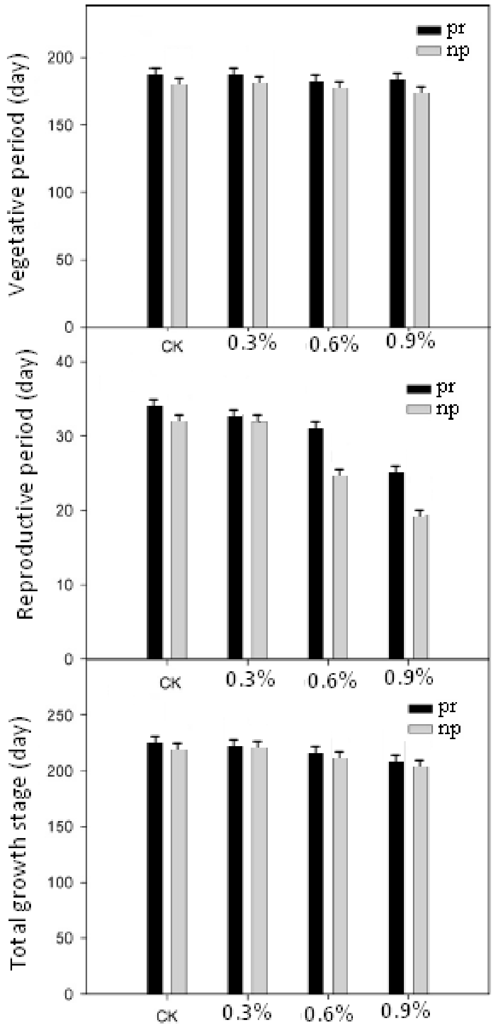

Fig. 5. Effects of salt stresses on vegetative growth period (VGP), reproductive growth period (RGP) and total growth period (TGP) of primed (pr) and non-primed (np) plants

4. Conclusion

Adverse changes in morphological structures associated with physiological modifications due to salinity may be the main elicitors of growth decline under salt stress. Salt accumulation in the expanding leaves has been correlated with photosynthetic decline and with ultra-structural and metabolic damages and sequential death of leaves and growth vigor may be related to the survival efficiency of different varieties (Yeo *et al.* 1990). So, leaf characters and physiological growth attributes may be important criteria for a tolerant variety. Although studies on the responses of plants to salt stress have been conducted, most of the researches were conducted on developing or mature leaves with scant regard to the senescence phase (Grandjean and Futher, 1989; Grover, 1993). The process of leaf senescence is known to take place under the active control genes that forms an integral part of leaf development (Biswal and Biswal, 1999). This study revealed that seed priming strategies, with significant differences, promoted plant growth, agronomic and physiological characters throughout the ontogeny of wheat. Net photosynthetic rate and stomatal conductance in primed plants maintained higher levels than the non-primed plants at 0.3% and 0.6% NaCl concentrations, with the latter plants decreasing gas exchanges drastically under salt concentration even less than 0.6%. Such a result indicated that the primed plants could acclimate the deleterious effects of salinity by maintaining almost normal photosynthesis. In fact, the sharper decreases in net photosynthetic rate than in stomatal conductance indicate that stomatal limitations rather than stress-induced dysfunctions at the chloroplast level accounted largely for the inhibition of CO_2 assimilation under salinity stresses. However, both primed and non-primed plants decreased considerably their net photosynthetic rate and stomatal conductance at salt level of 0.9%. The occasion leading to the decrease in photosynthetic capacity might be associated with the loss of RuBP carboxylase/oxygenase (Grover, 1993) in the relatively later senescence phases.The results indicated that high concentration salinity stress aggravated the senescence for both plants by causing significant reductions in net photosynthetic rate and stomatal conductance. Even though we found that the primed plants could relieve the senescence under salt concentrations less than 0.6% as evidenced by the nearly normal gas exchanges, while the non-primed plants did not have this ability. The decreases of relative water content, leaf area index and leaf area duration in non-primed plants happened earlier than control under salt stress, which were linear with the days of the late of reproductive stage. Those decreases can largely cause reductions in photosynthetic area, the duration of photosynthesis and dry matter accumulation. LAI of the primed plants showed rapid decreases at 14 days after anthesis, because primed plants grew faster and formed denser canopy than the non-primed plants, with senescence accelerated in lower section leaves. Although both plants displayed rapid senescence at salt concentration of 0.9%, these higher parameters of relative water content, leaf area index and leaf area duration were always noted in the primed plants at all levels of salt stress. The primed plants here could avoid this harmful effects by maintaining lower leaf Na^+ content, higher K^+ versus Na^+ through selective ion transport from soil to leaf. On the other hand, high toxic ion (Na^+) concentrations in non-primed plants caused a sharp decrease in K^+ content and K^+/Na^+ ratios at all levels of salt concentration, specially at 0.6% and 0.9% salt stress concentrations, indicating physiological injures happened from ion poisoning.

Table 1. Correlations among studied parameters of primed (pr) and non-primed plants (np) exposed salt stress

Seed Teatment	Items	gs	K^+/Na^+	LAI	LAD	RWC	TGP
Primed (pr)	*P*n	0.81^{**}	0.61^{*}	0.75^{**}	0.73^{**}	0.82^{**}	0.72^{**}
	gs		0.69^{*}	0.73^{**}	0.79^{**}	0.77^{**}	0.83^{**}
	K^+/Na^+			0.64^{*}	0.66^{*}	0.73^{**}	0.87^{**}
	LAI				0.86^{**}	0.83^{**}	0.86^{**}
	LAD					0.82^{**}	0.83^{**}
	RWC						0.88^{**}
Non-primed (np)	n	0.73^{**}	0.77^{**}	0.81^{**}	0.81^{**}	0.88^{**}	0.9^{**}
	gs		0.73^{**}	0.81^{**}	0.83^{**}	0.85^{**}	0.88^{**}
	K^+/Na^+			0.84^{**}	0.86^{**}	0.8^{**}	0.77^{**}
	LAI				0.81^{**}	0.88^{**}	0.96^{**}
	LAD					0.72^{**}	0.9^{**}
	RWC						0.83^{**}

*P*n = net photosynthetic rate; *g*s = stomatal conductance; K^+/Na^+ = potassium/sodium; LAI = leaf area index; LAD= leaf area duration; RWC= relative water content of flag leaf; RGP = reproductive growth period; TGP = total growth period. * and ** Correlation is significant at 0.05 and 0.01 levels.

References

Abbasdokht, H. 2011. The effect of hydropriming and halopriming on germination and early growth stage of wheat (*Triticum aestivum* L.). Desert, 16: 61-68.

Abbasdokht, H., D. Mazaheri, M.R. Chaichi, H. Rahimian, M.A. Baghestani, H. Mohammad Alizadeh, F. Sharifzadeh. 2004. The evaluation of redroot pigweed (*Amaranthus retroflexus* L.) competition at different density and different time of germination on some of agronomical traits of soybean (*Glycine max* L.). Desert. 8, 104-120.

Apel, K. and H. Hirt, 2004. Reactive oxygen species: Metabolism, oxidative stress and signal transduction. Annu. Rev. Plant Biol., 55: 373–399.

Asada, K., 1992. Ascorbate peroxidase-a hydrogen peroxide-scavenging enzyme in plants. Physiol. Planta, 85: 235–241.

Ashraf, M. and P.J.C. Harris, 2004. Potential biochemical indicators of salinity tolerance in plants. Plant Sci., 166: 3–16.

Ashraf, M., 2009. Biotechnological approach of improving plant salt tolerance using antioxidants markers. *Biotech. Adv*., 27: 84–93.

Athar, H., A. Khan and M. Ashraf, 2008. Exogenously applied ascorbic acid alleviates salt-induced oxidative stress in wheat. Environ. Exp. Bot., 63: 224–231.

Azooz, M.M., M.A. Shaddad and A.A. Abdel-Latef, 2004. Leaf growth and K^+/Na^+ ratio as an indication of the salt tolerance of three sorghum cultivars grown under salinity stress and IAA treatment. Acta Agron. Hungarica, 52: 287–296.

Basra, S.M.A., Farooq, M., Hafeez, K., Ahmad N, 2004. Osmohardening: a new technique for rice seed invigoration. Inter Rice Res Notes 29, 80–81.

Biswal, B., Biswal, U.C., 1999. Leaf senescence: physiology and molecular biology. Curr. Sci. 77, 775–782.

Bohnert, H.J. and R.G. Jensen. 1996. Strategies for engineering water stress tolerance in plants. Trends in Biotechnol. 14: 89-97.

Bradford, K.J., Steiner, J.J., Trawatha, S.E, 1990. Seed priming influence on germination and emergence of pepper seed lots. Crop Sci 30, 718–721.

Casenave E.C, Toselli, M.E., 2007. Hydropriming as a pre-treatment for cotton germination under thermal and water stress conditions. Seed Sci. Technol. 35: 88-98.

Cuin, T.A., A.G. Miller, S.A. Laurie and R.A. Leigh, 2003. Potassium activities in cell compartments of salt-grown barley leaves. J. Exp. Bot., 54: 657–661.

Cushman, J.C. and H.J. Bohnert. 1995. Transcriptional activation of CAM genes during development and environmental stress. In: Crassulacean Acid Metabolism. K. Winter and J.A.C. Smith (Eds.). Springer, Heidelberg, Germany.

Du, L.V., Tuong, T.P, 2002. Enhancing the performance of dry-seeded rice: effects of seed priming, seedling rate, and time of seedling. In: Pandey S, Mortimer M, Wade L, Tuong, T.P., Lopes, K., Hardy, B (eds) Direct seeding: research strategies and portunities. Farooq M, Basra SMA, Hafeez K, Ahmad N, 2005. Thermal hardening: a new seed vigor enhancement tool in rice. Acta Bot Sin 47,187–193.

Dubey, R.S., 2005. Photosynthesis in plants under stressful conditions. *In:* Pessarkli, M. (ed.), *Photosynthesis Handbook,* 2nd edition, pp: 717– 718. C.R.C. Press, New York, USA.

Farooq, M., Basra, S.M.A., Hafeez, K, 2006b. Rice seed invigoration by osmohardening. Seed Sci. Technol 34,181–186.

Gehlot, H.S., A. Purohit and N.S. Shkhawat, 2005. Metabolic changes and protein patterns associated with adaptation to salinity in *Sesamun indicum* cultivars*. J. Cell Mol. Biol.,* 4: 31–39.

Grandjean, A., Futher, J., 1989. Growth and leaf senescence in spring wheat (*Triticum aestivum* L.) grown at different ozone concentrations in open-top field chambers. Physiol. Plant 77, 389–394.

Grover, A., 1993. How do senescing leaves lose photosynthetic activity? Curr. Sci. 64, 226–234.

Gupta, N.K., Meena, S.K. Gupta, S. Khandelwal, S.K., 2002. Gas exchange, membrane permeability, and ion uptake in two Species of indian jujube differing in salt tolerance. Photosyntetica, 40, 535-539.

Heikal, M.M., A.M. Ismail and M.M. Azooz, 2000. Interactive effects of salinity and some vitamins on some metabolic processes in two broad bean lines. Acta Agron. Hung., 48: 327–336.

Iqbal, M. Ashraf, M., 2007. Seed treatment with auxins modulates growth and ion partitioning in salt-stressed wheat plants. J. Integr. Plant Biol. 49: 1003-1015.

Ismail, A.M. and M.M. Azooz, 2002. Response of *Vicia faba* to salinity and vitamins. *Indian J. Plant Physiol*., 7: 303–306.

Iterbe-Ormaetxe, I., Escuredo, P.R. Arrese-Igor, C. Becana, M., 1998. Oxidative damage in pea plants exposed to water deficit of paraquat. Plant Physiol., 161, 173-181.

Jaleel, C.A., P. Kishorekumar, A. Manivannan, B. Sankar, M. Gomathinayagam and R. Panneerselvam, 2008. Salt stress mitigation by calcium chloride in *Phyllanthus amarus*. Acta Bot. Croat., 67: 53–62.

Jaleel, C.A., R. Gopi, G.M. Alagu Lakshmanan and R. Panneerselvam, 2006. Triadimefon induced changes in the antioxidant metabolism and ajmalicine production in *Catharanthus roseus* (L.) *G. Don. Plant Sci.,* 171: 271–276

Kaur S, Gupta AK, Kaur, N., 2002. Effect of osmo- and hydropriming of chickpea seeds on seedling growth and carbohydrate metabolism under water deficit stress. Plant Growth Regul. 37: 17-22.

Kaya, M.D., Okcu, G. Atak, M. Cikili, Y. Kolsaric, O., 2006. Seed treatments to overcome salt and drought stress during germination in sunfower (*Helianthus annuus* L.). Europ. J. Agronomy., 24, 291-295

Kim, Y., Arihara, J. Nakayama, T. Nakayama, N. Shimada, S. Usui, K., 2004. Antioxidative responses and their relation to salt tolerance in *Echinochloa oryzicola* vasing and *Steraia virdis* (L.) Beauv. Plant Growth Regul., 44, 87-92.

Kramer, P.J. & Boyer, J.S. 1995. Water relations of plants and soils**.** San Diego, Academic Press, 495 p.

Lee, S.S., Kim, J.H., Hong, S.B., Yun, S.H, 1998. Effect of humidification and hardening treatment on seed emergence of rice. Kor J Crop Sci 43, 157–160.

Marschner, H., 1986. Mineral nutrition in higher plants. Academic Press, London, 477-542.

Mittler, R., 2002. Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci., 7: 405–410.

Moeinrad, H. 2008. The relationship between some physiological traits and salt tolerance in pistachio genotypes. Desert. 13, 129-136.

Morsy, M.R., L. Jouve, J. Hausman, L. Hoffmann and J. McD Stewart, 2007. Alteration of oxidative and carbohydrate metabolism under abiotic stress in two rice (*Oryza sativa* L.) genotypes contrasting in chilling tolerance. J. Plant Physiol*.*, 164: 157–167.

Muhyaddin, T., Weibe, H.J, 1989. Effect of seed treatments with polyethyleneglycol (PEG) on emergence of vegetable seeds. Seed Sci Technol 17, 49–56.

Munns, R., 2002. Comparative physiology of salt and water stress. Plant, Cell and Environment. 25, 239-250.

Muranaka, S., Shimizu, K., Kato, M., 2002. A salt-tolerant wheat maintains photosynthetic activity by suppressing sodium uptake. Photosynthetica 40, 509–515.

Parvaiz, A., and S. Satyawati (2008). Salt stress and phyto-biochemical responses of plants-a review. Plant Soil Environ. 54: 89–99.

Pill, W.G., Finch-Savage W.E, 1988. Effects of combining priming and plant growth regulator treatments on the synchronization of carrot seed emergence. Ann Appl Biol 113, 383–389.

Poustini, K., Siosemardeh, A., 2004. Ion distribution in wheat cultivars in response to salinity stress. Field Crops Res. 85, 125–133.

Raza, S.H., H.R. Athar and M. Ashraf, 2006. Influence of exogenously applied glycine betine on photosynthetic capacity of differently adapted wheat cultivars under salt stress. Pakistan J. Bot., 38: 341–351.

Rehman, S., Harris, P.J.C., Bourne, W.F., Wilkin, J. 1996. The effect of sodium chloride on germination and the potassium and calcium contents of Acacia seeds. Seed Science and Technology 25: 45–57.

Rejili, M., A.M. Vadel, A. Guetet and M. Neffatti, 2007. Effect of NaCl on growth and the ionic balance K^+/Na^+ of two populations of *Lotus creticus* (L) (Papilionaceae). South Africa J. Bot., 73: 623–631.

Ruan, S., Xue, Q., Tylkowska, K, 2002. Effects of seed priming on emergence and health of rice (*Oryza sativa L.*) seeds. Seed Sci. Technol 30, 451–458.

Sudhir, P., Murthy, S.D.S., 2004. Effects of salt stress on basic processes of photosynthesis. Photosynthetica, 42**,** 481- 486.106

Taylor, A.G., Allen, P.S., Bennett, M.A., Bradford, J.K., Burris, J.S., Misra, MK, 1998. Seed enhancements. Seed Sci Res 8, 245–256.

Teimouri, A., M. Jafari, H. Azarnivand. 2009. Effect of proline, soluble carbohydrates and water potential on resistance to salinity of three Salsola species. Desert. 14, 15-20.

Tester, M., Davenport, R., 2003. Na^+ tolerance and Na^+ transport in higher plants. Ann. Bot. 91, 503–527.

Wahid, A., Parveen, M., Gelani. S., Basra, S.M.A, 2006. Pretreatment of seeds with H_2O_2 improves salt tolerance of wheat seedling by alleviation of oxidative damage and expression of stress proteins. J Plant Physiol (published online).

Wahid, A., Shabbir, A, 2005. Induction of heat stress tolerance in barley seedlings by pre-sowing seed treatment with glycinebetaine. Plant Growth Regul 46, 133–141.

Wiynarah, K. 1990. Growth responses of *Phaseolus vulgaris* to varying salinity regimes. Environ. and Expt. Bot. 30: 141-147.

Yeo, A.R., M.E. Yeo., S.A. Flowers and T.J. Flowers. 1990. Screening of rice (*Oryza sativa* L.) genotypes for physiological characters contributing to salinity resistance, and their relationship to overall performance. Theoretical and Applied Genetics. 79:377-384.

Yildirim, B., F. Yaser, T. Ozpay, D.T. Ozpay, D. Turkozu, O. Terziodlu and A. Tamkoc, 2008. Variations in response to salt stress among field pea genotypes (*Pisum sativum* sp. arvense L.). J. Anim. Veter. Adv., 7: 907–910.

Yu, Z.W., Li, H.P., Wang, P., 2001. Crop Cultivation. The press of Chinese Agriculture, pp. 120-160.

Zhu, J.K., 2002. Salt and drought stress signal transduction in plants. Annl. J. Plant Biol., 14: 267–273.