Pak. J. Bot., 47(6): 2055-2061, 2015.

SALT TOLERANCE POTENTIAL OF UPLAND AND LOWLAND RICE IN PHYSIOLOGICAL PERSPECTIVES

SHEREEN, A.[*], M.U. SHIRAZI, M.A. KHAN AND S. MUMTAZ

Nuclear Institute of Agriculture (NIA), Tandojam, Sindh, Pakistan
Present Address: Nuclear Institute of Agriculture (NIA), Tandojam, Sindh, Pakistan
[*] *Corresponding author: aisha.shereen@yahoo.com*

Abstract

Studies were conducted to evaluate upland (UR) and lowland (LR) types of rice for their salt tolerance potential at early seedling stage under controlled laboratory conditions. The treatment of salinity (100 mM NaCl) along with non saline control was imposed for the period of two weeks. Shoot and root growth of all genotypes reduced with varying intensity under salinity. All UR types were more sensitive except UR-74 and UR-60 and exhibited comparatively less reduction in growth. These studies have revealed significant differential responses of UR and LR at physiological level. LR types of rice were remarkably different from UR types in their shoot sodium concentrations. LR types have exhibited comparatively low concentration of sodium and also found distinctly different in their proline production. Tolerant LR types have exhibited less relative increase in Na and better K: Na ratio in their shoot. Significant positive correlation (r = 0.93) was observed between sodium and proline concentrations in shoot. While, significant negative correlation (r = - 0.84**)** was observed between sodium and potassium sodium ratios in shoot. Tolerant varieties of both types of rice exhibited more sucrose and total soluble sugars under salinity stress indicating its protective role. These findings suggest that LR types of rice have better capability for selective uptake and osmotic adjustment in comparison to UR types under salinity stress.

Key words: *Oryza sativa*, Upland (UR) and lowland (LR) rice, Salinity stress, Ion uptake and osmoregulation.

Introduction

Abiotic stresses like salinity and drought are the main obstacles for crop productivity worldwide and will remain to be a great challenge in future for enhacing crop productivity especially of salt sensitive crops like rice. According to an estimate in Pakistan crop yield losses due to salinity are 20% (Rehman *et al., 2005*; Ashraf *et al.,* 2008). Irrigated rice is one of the most important cereal crops in Pakistan, covers an area of 2.57 mha. and produce 6.2 mt (Anon., 2013). Salt sensitivity of rice is a major constrain for rice production. In Pakistan, rice is grown over an area of about one million hectare of salt affected land (Qureshi *et al.,* 1991) causes 50% reduction in crop yield (Nishimura *et al.,* 2011; Hakim *et al.,* 2014). In future this problem will further aggravate especially in the absence of good quality water, will impose severe impact on rice productivity.

Salinity affects rice plants at all stages of development with varying degree. In spite of its sensitivity rice is considered most suitable crop for saline soils due to its higher range of inter and intra varietal variability for salt tolerance (Mishra *et al.,* 2001; Kanawapee *et al.,* 2011; Zhang *et al.,* 2013). Success in rice genetic improvement is mainly based on appropriate evaluation and use of genetic diversity. Tremendous 'hidden' diversity for biotic and abiotic stresses in the primary gene pool of rice has been reported earlier (Ali *et al.,* 2006) and there is a need to exploit this useful genetic variation for the development of salt tolerant varieties through genetic manipultions (Nejad *et al.,* 2008).

The upland rice (UR) a rich source of biodiversity is of key importance worldwide grown on substantial part of the agricultural land (Zhang *et al.,* 2013). A vast number of studies have been reported for its ability to tolerate water stress (Lian *et al.,* 2006; Naz *et al.,* 2006; Wang *et al.,* 2007; Sandhu *et al.,* 2012; Yaqoob *et al.,* 2012; Sabar & arif, 2014) but very few work on salt tolerance of UR types have been reported so far (Haq *et al.,* 2009 and Cha-um *et al.,* 2010). Polymorphism studies for A*dh* and L*dh* revealed that upland rice (UR) group may have special physiological pathways to adapt diverse environments (Chen *et al.,* 2003). Physiological traits at component level are the genetic basis of salt tolerance. Therefore understanding of physiological responses and their relationship with genotypes exhibiting differential tolerance under salinity stress would have an impact on selection of physiologically distinct genotypes in true sense. The study was conducted to compare variability among upland and lowland types of rice for their growth and physiological responses at early seedling stage under salt stress.

Materials and Methods

Five upland (UR no.46, 19, 74, 60 and 62) and four lowland (IR-8, IR-8 202/E, IR-8 154/N and Shua-92) rice genotypes were obtained from IRRI, Philippines and NIA, Tandojam.

Seeds were sterilized with 1.5% sodium hypochlorite for twenty minutes and were germinated on nylon net fitted in glass bowls(size:8cm Ø and 7cm height-) containing Yoshida culture solution(Yoshida *et al.,* 1976).The planted bowls were kept in controlled incubator in dark, maintained at temperature 30/28°C day and night temperature. After germination seedlings were exposed to 16 hrs photoperiod (fluorescent light, $22Wm^{-2}$ for day and 8 hr night. The exposure of salinity treatment 100 mM NaCl corresponding to EC 10.32 dS/m of culture solution was given to seedlings (two leaf stage) along with non saline control for the period of one week. The EC and pH at 5 was maintained throughout the experimental period.

The observation on growth parameters (fresh weights of shoot and root) were recorded. Shoots were analyzed for sodium and potassium (Flowers & Yeo. 1981), proline (Bates *et al.,* 1973) and sucrose and total soluble sugars (Riazi *et al.,* 1985). Data were statistically analyzed for ANOVA and Tukey HSD test was applied for comparison between treatment means using MSTAT-C.

Results and Discussion

The data for shoot fresh weight of all these rice genotypes have shown variable reduction under salinity (100 mM NaCl). Among LR types the least relative reduction was observed in IR-8 202/E (11%) while highest in IR-8 154/N (42%).Whereas, among UR types, UR-74 and UR-60 have shown comparatively less reduction (20%). The highest reduction (36.5%) was observed in UR-19 (Fig. 1a). The root growth of all these genotypes was comparatively less affected than shoot growth. Least effects were observed in Shua-92 and IR-8 202/E (LR type) While, among UR types, UR-46 exhibited comparatively less effects (Fig. 1b). Growth reduction under salinity is a general phenomena reported in many crop including rice (Habib *et al.,* 2010; Kanwal *et al.,* 2013; Habib & Ashraf, 2014). The reduction in growth may be attributed to both ionic and osmotic effects of high salt concentration that disturbs metabolism and cause reduction in plant growth and development (Nishimura *et al.,* 2011; Shereen *et al.,* 2011). The variability in salt tolerance potential might be due to differential capacity of genotypes for selective uptake of toxic ions mainly sodium and chloride and its limited transportation to photosynthetic organs (Munns & Tester, 2008; Jampeetong & Brix, 2009; Khan *et al.,* 2013).

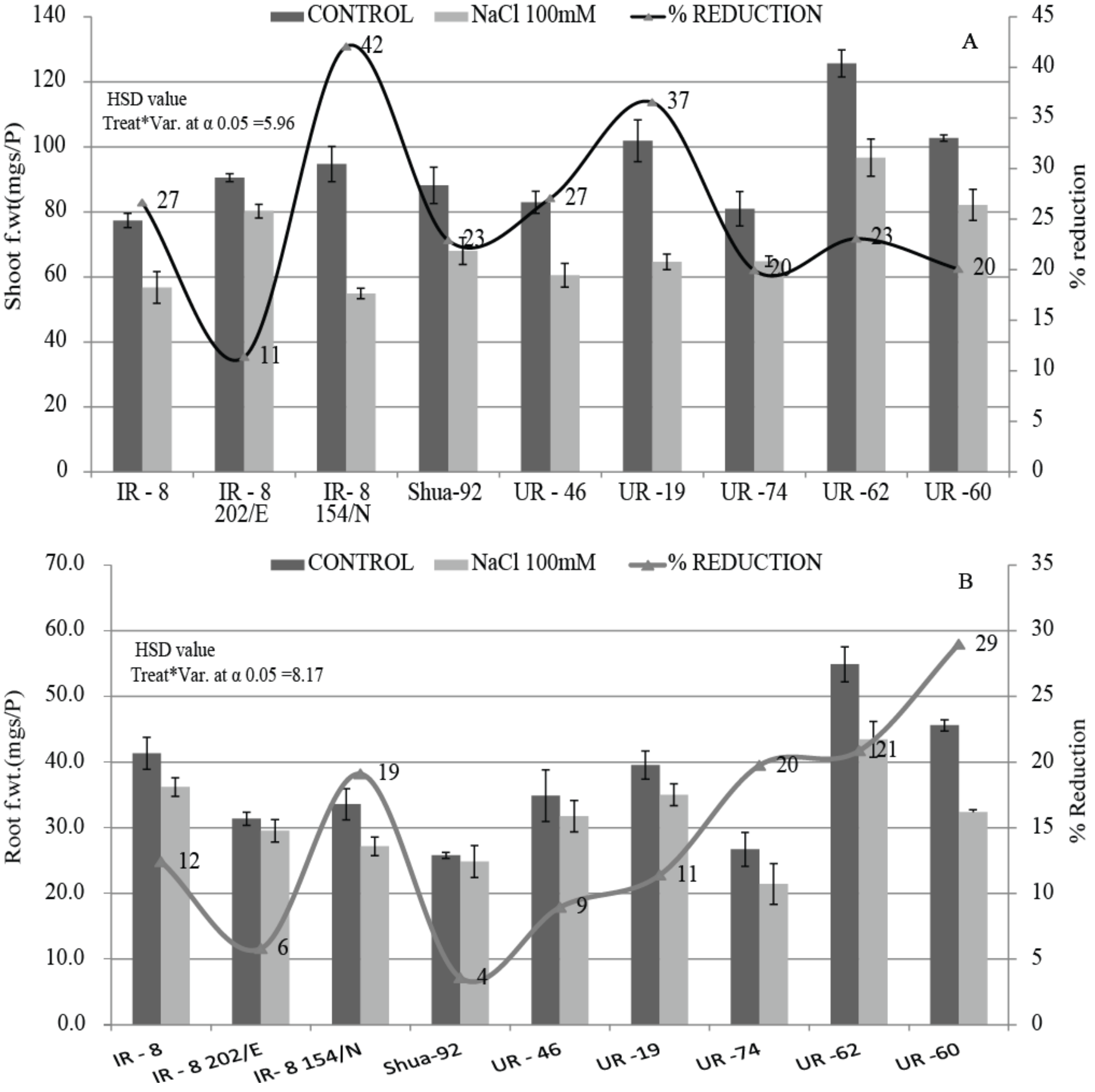

Fig. 1. Growth performance (Shoot and root Fresh weight) of LR and UR types of rice under salinity stress.

Plants exposed to salinity stress exhibits complex physiological, biochemical and molecular responses to overcome osmotic and ionic stress caused by high salinity. This is usually accomplished by uptake of inorganic ions as well as the accumulation of compatible solutes. Inorganic ions are sequestered in the vacuoles (Yeo, 1998), while organic solutes are compartmentalized in the cytoplasm to balance the low osmotic potential in the vacuole (Rontein *et al.,* 2002). However, salt stress responses and tolerance vary between species dependent on inherent differential ability to cope with high salt concentration in the growing medium (Munns & Tester, 2008; Jampeetong & Brix, 2009).

Data of shoot sodium concentrations and relative increase under salinity stress in comparison to their respective non-saline controls have shown that generally LR types exhibited comparatively less increase in shoot sodium concentrations than UR types (Fig. 2a). However variability within two rice types was observed. Among LR and UR types IR-8 154/N (LR type) and UR-19 have shown highest relative increase. The genotypes IR-8 202/E, Shua- 92 and IR-8 (LR types) were found significantly different in their low shoot sodium concentrations. These genotypes also exhibited less relative increase (4 times) in sodium under salinity. While all UR type genotypes exhibited more increase (≥ 6 times) in shoot sodium (Fig. 2a). Excess Na^+ in plant cells directly damage membrane systems and organelles, resulting in plant growth reduction and abnormal development prior to plant death (Siringam *et al.,* 2011). Generally salt tolerant varieties of rice maintain low shoot sodium concentrations than salt sensitive therefore the trait of low sodium in leaves could be used in breeding for salt tolerance (Joseph *et al.,* 2010)

A drastic reduction in K concentration and K: Na ratio was observed under salinity with varying intensities among genotypes (Fig. 2b & 2c). Comparatively more reduction was observed in UR types than LR types. Among LR types least reduction in K was observed in IR-8 202/E. A significant negative correlation was observed between shoot sodium and K concentration and K: Na ratio (Table 1). The increase in Na^+ while decrease in K^+ and K: Na ratio in plant tissues have already been reported in a number of crop plants such as in okra (Habib *et al.,* 2012), eggplant (Abbas *et al.,* 2010), rice (Habib *et al.,* 2013) and wheat (Kanwal *et al.,* 2013; Khan *et al.,* 2014). NaCl induced decrease in K: Na ratio could affect vital metabolic processes and activity of ROS scavenging system (Munns & Tester, 2008; Shereen *et al.,* 2011). Thus balanced K^+/Na^+ ratio plays a key role in maintaining physiological processes such as stomatal regulation, cell osmoregulation, and turgor maintenance, which further helps in normal functioning of photosynthetic process and protein synthesis (Shabala *et al.,* 2003). Maintenance of higher K: Na ratio and low concentration of sodium in plant tissues have been regarded as an important factor contributes in salt tolerance ability of crop plants (Zheng *et al.,* 2009).

The data of proline contents in shoot (µg/g F.wt) have shown significant increase in all genotypes (2-17 times increase) under salinity. The proline accumulation was comparatively higher in LR types (Fig. 3a). The highest increase was observed in IR-8 154/N (17 times) while least in Shua-92 (5 times). Among the UR types relatively higher increase was observed in UR-46 and UR-19. Significant positive correlation **(**r = 0.93**)** was observed between proline and sodium concentrations in shoot (Table 1). The response of genotypes IR-8 154/N was distinct in high sodium and high proline production with relatively less growth under salinity. The genotype IR-8 202/E exhibited comparatively less sodium and proline production with less reduction in growth found tolerant. While among UR type UR-46 and UR-19 were contrasting in their sodium uptake pattern. The trend of proline production was not in similar as was observed in LR types (low sodium and low proline). Proline overproduction under different stresses have been extensively studied and generally considered as a compatible solute that confers stress tolerance by contributing in osmotic adjustment, membrane and protein protection against reactive oxygen species (Mudgal *et al.,* 2010; Joseph *et al.,* 2015). However various contradictory differential responses of salt sensitive and salt tolerant rice genotypes related to proline production have reported. Increase proline synthesis was either positively correlated with salt tolerance (Kumar *et al.,* 2010; Deivanai *et al.,* 2011; Kumar *et al.,* 2013; Kumar *et al.,* 2015 and Wutipraditkul *et al.,* 2015).While Bagdi and Shaw, 2012 suggested that intensive accumulation of proline was a symptom of salt injury and a consequence of proteolysis and inversely correlated with salt tolerance. Recently some other studies have also reported higher accumulation of proline and sodium in salt sensitive rice cvs. (Demiral & Turkan, 2005; Theerakulpisut *et al.,* 2005; Kanawapee *et al.,* 2011; Kong-ngern *et al.,* 2012 and Lv, *et al.,* 2015) indicating that increase accumulation of proline in shoot is a general indicator for responses to salt stress.

Sucrose and total soluble sugars were increased in most of the genotypes subjected to salt stress. Both (UR and LR) types of rice have shown no pronounce difference in total soluble sugars and sucrose. There was a general increase in genotypes having good growth (tolerant). The highest increase was observed in Shua-92 followed by IR-8 and IR-8 202/E. The IR-8 154/N (sensitive) has shown decrease in sucrose concentrations under salinity. While among UR type highest increase was observed in UR-62 followed by UR-74 and UR- 46. The genotypes UR-19 showing sensitivity in growth has exhibited comparatively less increase in sucrose (Fig. 3b & 3c). Increased accumulation of sugars may be due to increase activity of sucrose phosphate synthase or decrease activity of acid invertase (responsible for hydrolysis of sucrose into simpler sugars so that starch may synthesize) may cause reduction in partitioning of sugars into starch ultimately results in metabolic alteration in expression in RUBISCO, feedback inhibition of carbon metabolism and reduced photosynthesis. Accumulation of sucrose and total soluble sugars may play an important role as energy resource, osmoregulation, signal transducion (Siringam *et al.,* 2012) and also in detoxification as a chelating agent to bound Na^+ with starch granules (Kanai *et al.,* 2007) under salt stress. In the present study higher increase of sugars in genotypes showing comparatively good growth under stress indicates its protective role in osmotic adjustment mechanism. These findings corroborate with the findings of Boriboonkaset *et al.,* 2013 for two contrasting rice genotypes with respect to salt tolerance.

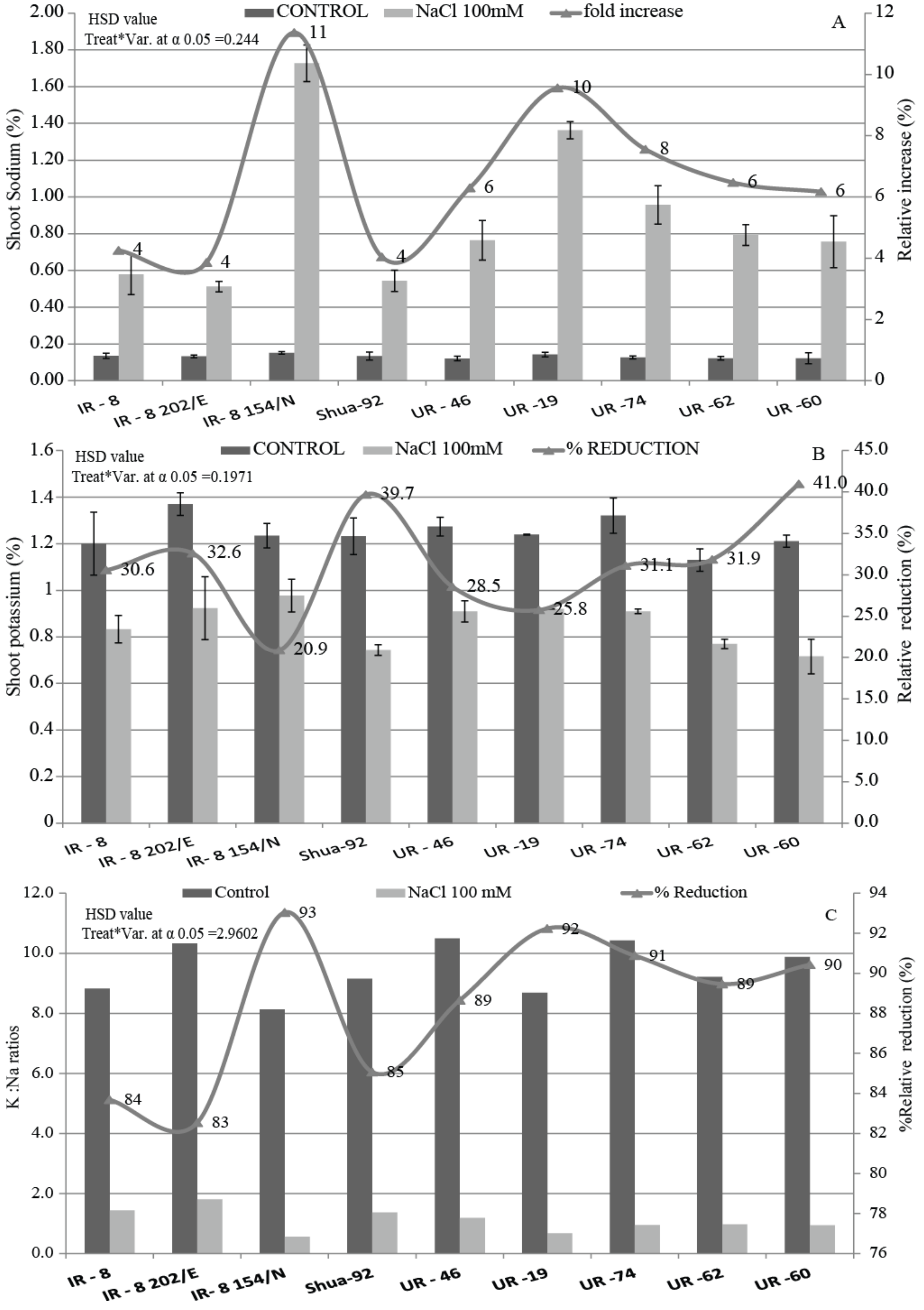

Fig. 2. Ions accumulation in UR and LR types of rice.

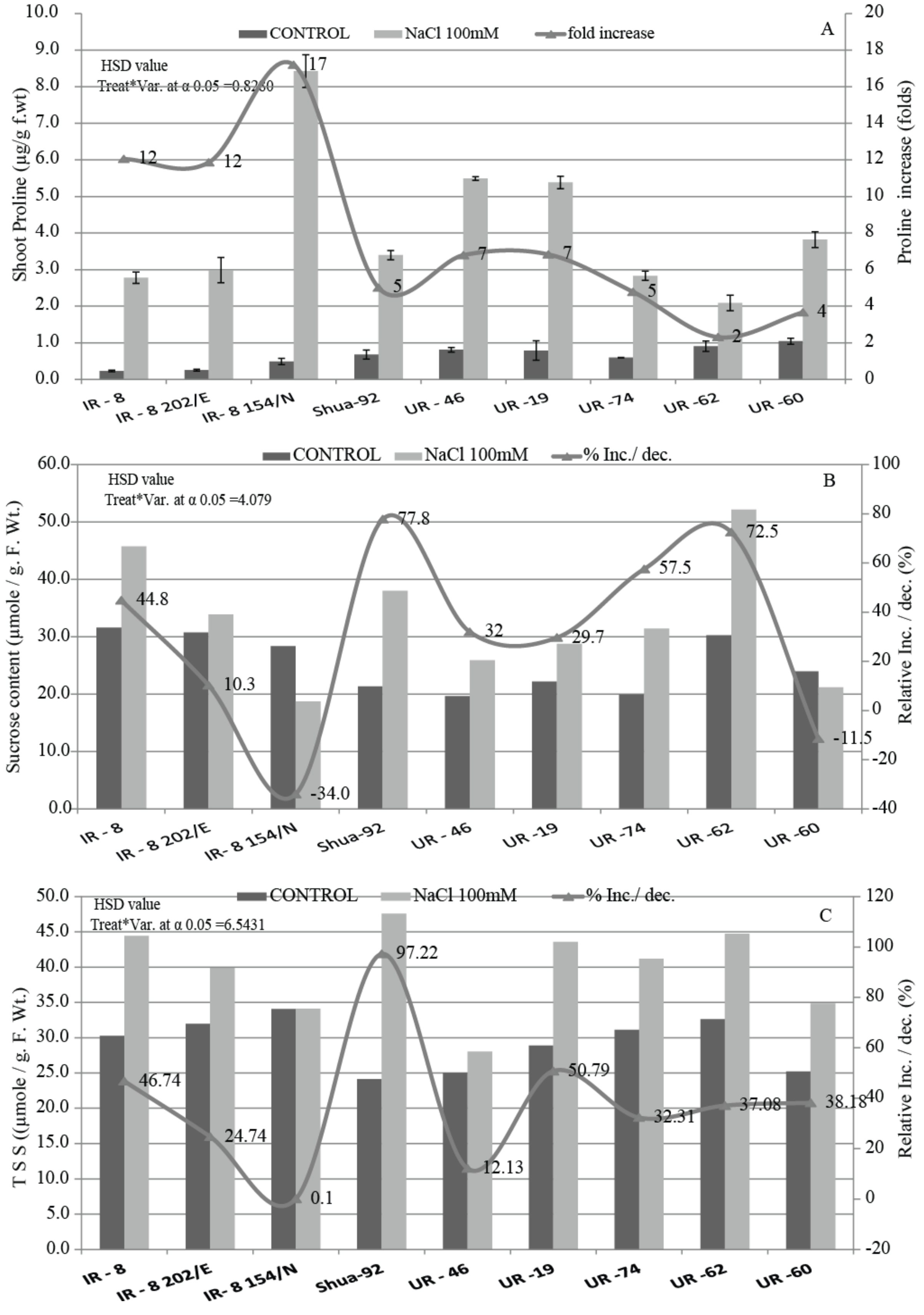

Fig. 3. Solutes accumulation in UR and LR types of rice under salinity stress.

Table 1. Correlation between different solutes accumulation in rice.

Parameters	Na	K	K/Na	Proline	Sucrose
K	-0.65**				
K/Na	-0.84**	0.93**			
Proline	0.93**	-0.64**	-0.81**		
Sucrose	0.08 NS	-0.52 *	-0.42 *	-0.05 NS	
Tot. Sol. Sugars	0.51*	-0.75**	-0.74 **	0.37 NS	0.74 **

** = Significant @1% prob., * = Significant @ 5% prob., NS = non-significant

Conclusions

Based on the findings of present study, we conclude that generally LR types have better capability for selective uptake and osmotic adjustment in comparison to UR types under salinity stress conditions. However, variability for physiological traits related to salt tolerance exists within UR and LR types of rice genotypes needs further exploration. Among all tested genotypes IR-8 -202/E was found tolerant. Low Na concentration in leaf and higher value of K: Na ratio may be used as selection criteria.

References

Abbas, W., M. Ashraf and N.A. Akram. 2010. Alleviation of salt-induced adverse effects in eggplant (*Solanum melongena* L.) by glycinebetaine and sugarbeet extracts. *Sci. Hort*., 125: 188-195.

Ali, A.J, J.L. Xu, A.M. Ismail, B.Y. Fu, C.H.M Vijaykumar , Y.M. Gao, J. Domingo, R. Maghirang, S.B. Yu, G. Gregorio, S. Yanaghihara, M. Cohen, B. Carmen, D. Mackill and Z.K. Li. 2006. Hidden diversity for abiotic and biotic stress tolerances in the primary gene pool of rice revealed by a large backcross breeding program. / Field Crops Research, 97: 66-76.

Anonymous. 2013. Agricultural Statistics of Pakistan, Ministry of Food, Agric. & Livestock (MINFAL), Govt. of Pakistan, Islamabad.

Ashraf, M., H.R. Athar, P.J.C. Harris and T.R. Kwon. 2008. Some prospective strategies for improving crop salt tolerance. *Adv. Agron*., 97: 45 -110.

Bagdi, D.L. and B.P. Shaw. 2012. Analysis of proline metabolic enzymes in *Oryza sativa* under salt stress. J.Expt. Biol. 34,677-681.

Bates, L.S., R.P. Waldern and L.D. Teare. 1973. Rapid determination of free proline for water stress studies. *Plant Soil*, 39: 205-207.

Boriboonkaset, T., C. Theerawitaya, N. Yamada, A. Pichakum, K. Supaibulwatana, S. Cha-um, T. Takabe and C. Kirdmanee. 2013. Regulation of some carbohydrate metabolism-related genes, starch and soluble sugar contents, photosynthetic activities and yield attributes of two contrasting rice genotypes subjected to salt stress. *Protoplasma*, 250: 1157-1167.

Cha-um, S., M. Ashraf and C. Kirdmanee. 2010. Screening upland rice (*Oryza sativa* L. ssp. *indica*) genotypes for salt-tolerance using multivariate cluster analysis. *Afr. J. Biotech*., 9(30): 4731-4740.

Chen, L.J., D.S. Lee and H.S. Suh.2003. Differential pattern of isozymes loci of A*dh* and L*dh* between UPL and LOL rice varieties. In: *Advances in Rice Genetics* iv. Proc. 4th Int. Rice Genetics Symposium. (Eds.): Khush, G.S., D.S Barar and B. Hardy. IRRI, Philippines. pp. 192-194.

Demiral, T. and I. Turkan. 2005. Comparative lipid peroxidation, antioxidant defense systems and proline content in roots of two rice cultivars differing in salt tolerance. *Environ. and Exp. Bot*., 53: 247-257.

Deivanai, S., R. Xavier, V. Vinod, K. Timalata and O.F. Lim. 2011. Role of exogenous proline in ameliorating salt stress at early stages in two rice cultivars. *J. Stress Physiol. & Biochem*., 7(4): 157-174.

Flowers, T.J. and A.R. Yeo.1981. Variability in the resistance of sodium chloride salinity within rice (*Oryza sativa* L.) varieties. *New Phytol*., 88: 363-373.

Habib, N. and M. Ashraf. 2014.Effect of exogenously applied nitric oxide on water relations and ionic composition of rice (*Oryza sativa* L.) plants under salt stress. *Pak. J. Bot*., 46(1): 111-116.

Habib, N., M. Ashraf and M.S.A. Ahmad. 2010. Enhancement in seed germinability of rice (*Oryza sativa* L.) by presowing seed treatment with nitric oxide (NO) under salt stress. *Pak. J. Bot*., 42(6): 4071-4078.

Habib, N., M. Ashraf and M. Shahbaz. 2013. Effect of exogenously applied nitric oxide on some key physiological attributes of rice (*Oryza sativa* L.) plants under salt stress. *Pak J. Bot*., 45(5): 1563-1569.

Habib, N., M. Ashraf, Q. Ali and R. Perveen. 2012. Response of salt stressed okra (*Abelmoschus esculentus* Moench.) plantsto foliar-applied glycine betaine and glycine betaine containing sugarbeet extract. *South Afr. J. Bot*., 83: 151-158.

Hakim, N.A., A.S. Juraimani, M.M. Hanafi, M.R. Ismail, A. Selamat, M.Y. Rafii and M.A. Latif. 2014. Biochemical and anatomical changes and yield reduction in rice (*Oryza sativa* L.) under varied salinity regimes. *Bio. Med. Research International*. Article ID 208584, 11 pages, http://dx.doi.org/10.1155/2014/208584

Haq, T., J. Akhtar, S. Nawaz and R. Ahmad. 2009. Morpho-physiological response of rice (O*ryza sativa* L.) varieties to salinity stress. *Pak. J. Bot*., 41(6): 2943-2956.

Jampeetong, A. and H. Brix. 2009. Effects of NaCl salinity on growth, morphology, photosynthesis and proline accumulation of Salvinia natans. *Aquat. Bot*., 91: 181-186.

Joseph, B., D. Jini and S. Sujatha. 2010. Biological and physiological perspectives of specificity in abiotic salt stress response from various rice plants. *Asian J. Agric. Sci*., 2(3): 99-105.

Joseph, E.A., V.V Radhakrishnan, K.V. Mohanan.2015.A study on the accumulation of proline an osmo protectant amino acid under salt stress in some native rice cultivars of north kerala, india. Universal Journal of Agricultural Research 3 (1): 15-22.

Kanai, M., K. Higuchi, T. Hagihara, T. Konishi, T. Ishii, N. Fujita, Y. Nakamura, Y. Maeda, M. Yoshiba and T. Tadano.2007. Common reed produces starch granules at the shoot base in response to salt stress. *New Phytol*., 176: 572-580.

Kanawapee, N., J. Sanitchon, P. Srihaban and P. Theerakulpisut. 2011. Genetic diversity analysis of rice cultivars (*Oryza sativa* L.) differing in salinity tolerance based on RAPD and SSR markers. *Electron. J. Biotechnol*., 14(6) On-*line* ISSN 0717-3458.

Kanwal, H., M. Ashraf and M. Hameed. 2013. Water relations and ionic composition in the seedlings of some newly developed and candidate cultivars of wheat (*Triticum aestivum* L.) under saline conditions. *Pak. J. Bot*., 45(4): 1221-1227.

Khan, S.K, J. Iqbal and M. Saeed. 2013. Comparative study of grain yield and biochemical traits of different rice varieties grown under saline and normal conditions. *J. Ani. & Pl. Sci*., 23(2): 575-588.

Khan, M.A., M.U. Shirazi, W, Mahboob, S.M. Mujtaba, M. A. Khan, S. Mumtaz and A. Shereen. 2014. Morpho-physiological adaptations of wheat genotypes to salinity stress. *Pak. J. Bot*., 46(6): 1981-1985.

Kong-ngern, K., S. Bunnag and P. Theerakulpisut. 2012. Proline, hydrogen peroxide, membrane stability and antioxidant enzyme activity as potential indicators for salt tolerance in rice (*Oryza sativa* L.). *Int. J. Bot*., 8(2): 54-65.

Kumar, V., V. Shriram, P.B. Kavi Kishore, N. Jawali and M.G. Shotole. 2010. Enhanced proline accumulation and salt stress tolerance of transgenic indica rice by over expression of P5CSF 129 A gene. *Plant Biotecnol Rep*., 4: 37-48.

Kumar, K., M. Kumar, S.R. Kim, H. Ryu and Y.G. Cho. 2013. Insight into the genomics of salt stress response in rice. *Rice*, 6: 27. http://www.the rice journal.com/content/6/1/27.

Kumar, P.D, Y. Murata, M.A. Hoque, and M.A. Ali. 2015. Effect of soil salinity and exogenous proline application on rice growth, yield, biochemical and antioxidant enzyme activities. EC Agriculture. 2(1):229-240.

Lian, H.L., X. Yu, D. Lane, W. Sun, Z.C. Tang and W.A. Su. 2006. Upland rice and lowland rice exhibited different *pip* expression under water deficit and aba treatment. *Cell Research*, 16: 651-660.

Lv, B.S., H.Y. Ma, X.W.Li, L.X.Wet, H.Y.Lv, H.Y.Yang, C.J.Jiang and Z.W.Liang. 2015. Proline accumulation is not correlated with saline-alkaline stress tolerance in rice seedlings. Agron. J.107(1): 51-60.

Mishra, B., R.K. Singh and D. Senadhira. 2001. Recent advances and future strategies for breeding salt tolerant rice varieties. In: *Rice Research for Food Security and Poverty Alleviation*. (Eds.): Peng, S. and B. Hardy. IRRI, Philippines, pp. 275-284.

Munns, R. and M. Tester. 2008. Mechanisms of salinity tolerance. *Ann. Rev. Plant Biol*., 59: 651-681.

Naz, F., S. Farooq, R. Arshad, M. Afzaal and M. Akram. 2006. Discriminating upland and lowland rice genotypes through proteomic approach. *Pak. J. Bot*., 38(5): 1731-1738.

Mudgal, V., N. Madaan and A. Mudgal. 2010. Biochemical mechanisms of salt tolerance in plants: A review. *Int. J. Bot*., 6: 136-143.

Nejad, G.M., A. Arzani, A.M. Rezai, R.K. Singh and G.B. Gregorio. 2008. Assessment of rice genotypes for salt tolerance using microsatellite markers associated with the saltol QTL. *Afr. J. Biotech*., 7: 730-736.

Nishimura, T., S. Cha-um, M. Takagaki and K. Ohyama. 2011. Survival percentage, photosynthetic abilities and growth characters of two indica rice (*Oryza sativa* L. spp. *indica*) cultivars in response to iso-osmotic stress. Span. *J. Agric. Res*., 9: 262-270.

Qureshi, R.H., M. Aslam, G. Mustafa and J. Akhtar. 1991. Some aspects of physiology of salt tolerance in wheat (*Triticum aestivum* L.). *Pak. J. Agric. Sci*., 28: 199-209.

Rehman, S., P.J.C. Harris and M. Ashraf.2005. Stress environment and their impact on crop production. In: (Eds.): Ashraf, M., and P.J.C. Harris. Abiotic stresses: Plant resistance through breeding and molecular approaches. Haworth press, New York, pp. 3-18.

Riazi, A., K. Matsuda and A. Arsalan. 1985. Water stress induced changes in concentration of proline and other solutes in growing regions. *J. Expt. Bot*., 36(172): 1716-1725.

Rontein, D., G. Basset and A.D. Hanson. 2002. Metabolic engineering of osmoprotectants accumulation in plants. *Metab. Eng*., 4: 49-56.

Sabar, M. and M. Arif. 2014. Phenotypic response of rice (*Oryza sativa*) genotypes to variable moisture stress regimes. *Int. J. Agric. Biol*., 16: 32- 40.

Sandhu, N., S. Jain, K.R. Battan and R.K. Jain. 2012. Aerobic rice genotypes displayed greater adaptation to water-limited cultivation and tolerance to polyethyleneglycol-6000 induced stress. *Physiol. Mol. Biol. Plants*, 18(1): 33- 43.

Shabala, S., L. Shabala and E.V. Volkenburgh. 2003. Effect of calcium on root development and root ion fluxes in salinised barley seedlings. *Funct. Plant Biol.*, 30(5): 507-514.

Shereen, A., R. Ansari, S. Raza, S. Mumtaz, M.A. Khan and M. Ali Khan. 2011. Salinity induced metabolic changes in rice (*Oryza sativa* L.) seeds during germination. *Pak. J. Bot*., 43(3):1659-1662.

Siringam, K. N. Juntawong, S. Cha-um and C. Kirdmanee. 2011. Salt stress induced ion accumulation, ion homeostasis, membrane injury and sugar contents in salt-sensitive rice (*Oryza sativa* L. spp. *indica*) roots under isoosmotic conditions. *Afr. J. Biotech*., 10: 1340-1346.

Siringam, K., N. Juntawong, S. Cha-um, T. Boriboonkaset and C. Kirdmanee. 2012. Salt tolerance enhances in indica rice (*Oryza sativa* L. spp. *indica*) seedlings using exogenous sucrose supplementation. *Plant Omics*, 5: 52-59.

Theerakulpisut, P., S. bunnag and K. Kong-Ngern. 2005. Genetic diversity, salinity tolerance and physiological responses to NaCl of six rice (*Oryza sativa* L.) cultivars. *Asian J. Pl. Sci*., 4(6): 562-573.

Wang, H., H. Zhang, F. Gao, J. Li and Z. Li. 2007.Comparison of gene expression between upland and lowland rice cultivars under water stress using cDNA microarray. *Theor. Appl. Genet*., 115(8): 1109-26.

Wutipraditkul,N., P.Wongwean and T.Buaboocha. 2015. Alleviation of salt induced oxidative stress in rice seedlings by proline and / or glycine-betaine. Biologia Plant. 59(3)547-553.

Yaqoob, M., N. Hussain and A. Rashid. 2012. Assessment of genetic variability in rice (*Oryza sativa* L.) genotypes under rainfed conditions. *J. Agric. Res*., 50(3): 311-320.

Yeo, A. 1998. Molecular biology of salt tolerance in the context of whole-plant physiology. *J. Exp. Bot*., 49: 915-929.

Yoshida, S., D.A. Forno, J.H. Cock and K.A. Gomez. 1976. Laboratory Manual for Physiological studies of Rice, 3rd edition, The International Rice Research Institute, Manila Philippines.

Zhang, L., C. Gui-lan and H. Long-zhi. 2013. Genetic diversity of rice landraces from lowland and upland accessions of China. *Rice Science*, 20(4): 259-266.

Zheng, C., D. Jiang, F. Liu, T. Dai, W. Liu, Q. Jing and W. Cao. 2009. Exogenous nitric oxide improves seed germination in wheat against mitochondrial oxidative damage induced by high salinity. *Environ. Exp. Bot*., 67(1): 222-227.

(Received for publication 23 December 2014)