Potassium Consumption by Rice Plant from Different Sources under Salt Stress

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(received February 28, 2009; revised July 7, 2010; accepted July 15, 2010)

Abstract. The study on usage of K⁺ by two rice cultivars (Cv. Shaheen and KS-282) from KNO₃, KH₂PO₄ and K₂SO₄ (5 mM each), with 60 mM NaCl under hydroponics conditions, showed that fresh mass of shoot (FMS), fresh mass of root (FMR), root/ shoot ratio of fresh and dry mass, relative water contents (RWC) and relative growth rate (RGR) were affected significantly (P=0.01) inconsistent relating to K⁺ sources under salt stress. The intake of K⁺ was the highest with application of KH₂PO₄ than KNO₃ and K₂SO₄ application. The transport of K⁺ was the highest with KH₂PO₄ than KNO₃ and K₂SO₄ application in Shaheen, whereas in *var*. KS-282 with K₂SO₄, transport of K⁺ was higher than the other two sources. The utilisation of K⁺ was higher with KNO₃ than KH₂PO₄ and K₂SO₄ application in Shaheen, whereas in *var*. KS-282 with K₂SO₄ application in Shaheen, whereas in KS-282, K⁺ utilisation with KH₂PO₄ was higher than the other two sources. It was inferred that K⁺ consumption in shoot and root system of rice was dependent physio-genetically on potassium sources.

Keywords: rice cultivars, potassium sources, potassium uptake, salt stress

Introduction

Potassium is a mandatory nutrient for the growth of plants; it is closely associated with diverse tissue and cell-specific actions related to plant growth and development, such as germination, cell hydration, leaf movements, ionic balance, stomatal action, vascular transport, osmosis, nutrient storage and enzyme homeostasis (Cochrane and Cochrane, 2009; Gierth, 2005; Mengel and Kirkby, 2001; Blumwald, 2000; Quintero et al., 1998; Clarkson and Hanson 1980). Salinity reduces plant growth by affecting the availability, transport, and partitioning of nutrients besides nutrient deficiencies or imbalances, due to the competition of Na⁺ with nutrients such as K⁺, Ca²⁺ (Yuncai and Urs, 2005). Sodium ion stress often results in deficiency of K⁺ because of the physicochemical similarities between Na⁺ and K⁺ (Maathuis and Amtmann, 1999). The primary mechanism for maintaining ample tissue K⁺ levels under salt stress seems to be dependent upon selective K⁺ uptake and distribution in the shoots (Carden *et al.*, 2003). Uptake of K+by HAK/KUP/KT transporters is inhibited by Na⁺ (Santa-Maria et al., 1997). Sodium ion creates ionic imbalance, injury to tissue and water deficit. At low K⁺ level, moderate levels of Na⁺ promote plant growth by replacing K⁺ role as provider of turgor (Rodriguez-Navarro, 2000). Under salinity stress, Na⁺ transport is preferred (Yamaguchi et al., 2003). Vacuolar proteins OsNHX1 from rice have dual Na⁺ and K⁺ specificity (Ohnishi et al., 2005; Fukuda et al., 2004). In several studies K⁺ concentration in leaf was found to be associated with the tolerant phenotype (Wu *et al.*, 2005). Higher K⁺: Na⁺ ratio improves the resistance of plant to salinity (Asch *et al.*, 1999). Reasonable amounts of K⁺ is required to maintain cell-membrane integrity and function (Wei *et al.*, 2003). Rice growth to applied potassium is influenced by different sources of potassium and interaction of potassium with other nutrients (Singh *et al.*, 2003).

The present study is based on the hypothesis that consumption of potassium is source dependent; it also records its fate in different varieties of rice

Materials and Methods

Seeds of Oryza sativa (Cv. Shaheen and KS-282) were germinated in quartz sand moist with distilled water. Potassium was applied @ 5 mM as KNO₃, K₂SO₄ and KH₂PO₄. To create salt stress, 60 mM NaCl was applied. One week old seedlings were foam-plugged in lids of plastic pots containing continuously aerated one litre full strength nutrient solution (Hoagland and Arnon, 1950), which was replaced weekly. Light intensity was 450 µmol/m²/s. Photoperiod was adjusted to 16 h light period, temperature was maintained at 30 ± 2 °C and pH of the solution was adjusted to 6.0 with HCl or Ca(OH), and was monitored regularly. The treatments were applied in triplicates. Harvests were taken on the 22nd and the 33rd day after seedling transplantation. . After recording of fresh mass (FM), the plants were rinsed with deionised water and were separated into shoot and root portions. Plant samples were dried at 65 °C to constant mass. Dry mass (DM) of each sample

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was recorded and was ground to pass a 40-mesh Wiley Mill. Ground samples of root and shoot were separately digested in 1:2 perchloric-nitric di-acid mixture (Chapman and Pratt, 1961). Relative water contents (RWC) were calculated according to Misra and Dwievi (2004) and relative growth rate (RGR), as given by Gardner *et al.* (1985). Potassium ion in the digested material was determined by atomic absorption spectroscopy. Average rate of K⁺ intake by root and specific utilisation rate was calculated as given by Hunt (1978). Average rate of K⁺ transport was calculated according to Pitman (1972). The data were statistically analysed according to two factors; CRD and treatment means were compared using LSD test (Gomez and Gomez, 1984).

Results and Discussion

Both the rice varieties (Shaheen and KS- 282) showed significant (P= 0.01) response to various sources of potassium i.e., KNO_3 , K_2SO_4 and KH_2PO_4 under non-salt stress (NSS) and salt stress (SS) of 60 mM NaCl for growth parameters and K⁺ consumption.

Under NSS condition, in Shaheen fresh mass of shoot (FMS) and fresh mass of root (FMR) were higher with KH_2PO_4 than KNO_3 and K_2SO_4 application, whereas in KS-282, FMS was higher with KNO_3 than KH_2PO_4 and K_2SO_4 and FMR was higher with KH_2PO_4 than K_2SO_4 and KNO_3 application (Table 1). Under SS condition, FMS and FMR of Shaheen

Table 1. Fresh and dry mass of shoot and root of rice underK⁺ sources and Na⁺ interaction

Treatments applied (mM)		Fresh mass (mg/plant)		Dry mass (mg/plant)						
K ⁺ source	NaCl	Shoot	Root	Shoot	noot Root					
Cv. Shaheen										
KNO3	0	126.1 ^e	28.3 ^j	21.9^{f}	2.8 ^g					
K,SO ₄	0	110.8 ^j	32.2 ^g	20.2 ^j	3.6 ^b					
KH,PO4	0	133.9 ^c	52.7 ^b	21.2 ^g	2.9^{f}					
KNO ₃	60 mM	121.8 ^g	34.0^{f}	22.7^{d}	2.9^{f}					
K ₂ SO ₄	60 mM	223.2ª	186.9 ^a	18.8^{k}	3.3°					
KH,PO4	60 mM	123.2^{f}	38.9 ^d	20.8^{i}	2.1 ⁱ					
2 4 Cv. KS-282										
KNO ₃	0	136.2 ^b	30.3 ⁱ	21.0^{h}	3.0 ^e					
K ₂ SO ₄	0	104.4 ^k	26.3 ^k	25.8^{a}	2.9^{f}					
KH,PO4	0	121.8 ^g	32.1 ^h	23.7 [°]	3.1 ^d					
KNO ₃	60 mM	116.2 ⁱ	25.3.1 ^d	22.5 ^e	1.9 ⁱ					
K ₂ SO ₄	60 mM	130.1 ^d	51.4°	24.5 ^b	5.7 ^a					
KH ₂ PO ₄	60 mM	117.7 ^h	37.5 ^e	20.8 ⁱ	2.3 ^h					

Means sharing similar letter(s) in a column do not differ significantly at P < 0.01.

and KS-282 were higher with K_2SO_4 than KNO_3 and KH_2PO_4 application. Under NSS and SS conditions, in Shaheen dry mass of shoot (DMS) was higher with KNO_3 than K_2SO_4 and KH_2PO_4 application, whereas in KS-282, DMS was higher with K_2SO_4 than KNO_3 and KH_2PO_4 application. Under NSS conditions in Shaheen, dry mass of root (DMR) was higher with K_2SO_4 than KNO_3 and KH_2PO_4 application, whereas in KS-282, DMS was higher with KH_2PO_4 than KNO_3 and $K2SO_4$ application. Under SS conditions, DMR of both the varieties and DMS of Shaheen was higher with K_2SO_4 than KNO_3 and KH_2PO_4 application, whereas DMS of Shaheen was higher with KNO_3 than K_2SO_4 and KH_2PO_4 application.

Potassium ion is involved in facilitating enzymatic activities and its counter anion acts in tissue building process. Under salt stress, potassium ion reduces water stress effects by countering sodium ion uptake in the root system, whereas sulphate ion plays its role in protein building for tissue development process by keeping itself in synergistic relationship with K⁺ in shoot and root portion, as found in sunflower by Zaman et al., (2002). The partitioning of dry matter between root and shoot is a heritable characteristic and the expression of these characteristics can be altered by environmental conditions (Cassman, 1980). Therefore, as an environmental factor, salt stress also affects portioning of dry mass between shoot and root. The system becomes complex, depending upon the nature and extent of salt stress besides notional sources. This phenomenon became evident when the dry mass of shoot of Shaheen increased with the treatment of KNO₂ under salt stress than that of KS-282. Forde (2002) found that nitrate acts as a signal to regulate dry matter partitioning between the shoot and the root of higher plants.

Under NSS condition, in Shaheen and KS-282, fresh mass of root/shoot ratio (FMRSR) was higher with KH₂PO₄ than KNO₃ and K₂SO₄ application, whereas under SS condition, in both the varieties, FMRSR was higher with K₂SO₄ than KNO₂ and KH₂PO₄ application.(Table 2). In this study at 60 mM NaCl application, FMRSR was the highest (0.84) with K₂SO₄ than KNO₃ or KH₂PO₄ in Shaheen than KS-282. The ratio was 52 percent higher in Shaheen than in KS-282. The lowest FMRSR (0.22) was the same in both the varieties, with KNO, application under non-salt stress condition. FMRSR parameter indicates comparative growth between root and shoot instantly at the time of harvest. Fresh mass of plant material consists of tissue besides water and other chemicals. As water maintains physicochemical properties of a cell or an organ, therefore, in fresh mass consideration, water contents of an organ cannot be ignored. With extra inclusion of inorganic or organic compounds, water potential is affected, thus functioning of an organ may also be

Treatments applied (mM)		R/S ratio		RGR (µg/g/d)		RWC (%)	
K ⁺ source	NaCl	FM	DM	Shoot	Root	Shoot	Root
			Cv. Sł	naheen			
KNO ₃	0	0.22^{d}	0.13 ^e	26.99 ^b	9.99 ^{gh}	84.00^{ab}	89.96 ^{bc}
K_2SO_4	0	0.29^{bcd}	0.18 ^c	8.22 ^d	11.28 ^{gh}	84.77 ^{ab}	90.77^{abc}
KH ₂ PO ₄	0	0.39 ^{bc}	0.14 ^d	35.95 ^b	16.56 ^{fgh}	83.25 ^b	93.99 ^a
KNO ₃	60 mM	0.28^{bcd}	$0.13^{\rm f}$	9.04 ^d	74.14 ^a	76.89 ^{de}	89.36 ^c
K_2SO_4	60 mM	0. 84 ^a	0.18 ^b	6.29 ^d	4.31 ^h	61.89 ^f	91.49 ^{abc}
KH,PO4	60 mM	0. 32 ^{bcd}	0.10^{h}	7.09^{d}	27.47 ^{ef}	77.99 ^{cd}	93.18 ^{ab}
2 7			Cv.	KS-282			
KNO ₃	0	0.22 ^d	0.14 ^d	14.94 ^{cd}	31.45 ^{ef}	87.22 ^a	91.68 ^{abc}
K ₂ SO ₄	0	0.25 ^{cd}	0.11 ^g	10.59 ^d	47.96 ^{cd}	78.59 ^{cd}	90.74^{abc}
KH ₂ PO ₄	0	0.26^{bcd}	0.13 ^{ef}	25.50 ^{bc}	54.97 ^{bc}	81.28 ^{bc}	90.37 ^{bc}
KNO ₃	60mM	0.22 ^d	0.08^{i}	57.54 ^a	22.30 ^{fg}	73.30 ^e	91.17 ^{abc}
K ₂ SO ₄	60 mM	0.40^{b}	0.23 ^a	30.27 ^b	65.24 ^{ab}	82.78 ^b	89.98 ^{bc}
KH ₂ PO ₄	60 mM	0.32^{bcd}	0.11 ^g	25.29 ^{bc}	38.21 ^{de}	78.93 ^{cd}	92.71 ^{abc}

Table 2. Root /shoot ratio of fresh and dry mass, relative growth rate (RGR) of shoot and root, and relative water content (RWC) of rice under K^+ and Na^+ interaction

Means sharing similar letter(s) in a column do not differ significantly at P < 0.01.

affected. Under NaCl, stress water contents of plant tissue are affected (Zaman *et al.*, 2006).

Dry mass root/ shoot ratio (DMRSR) parameter indicates comparative growth between root and shoot. Dry mass of plant material consists of tissues and chemicals. This indicates the net out-come of the resultant metabolic activities. Under specific ion effect, DMRSR may be affected, which is a consequence of the nature of an ion. Sodium ion interferes in biochemical processes and reduces plant growth in rice (Kumar et al., 2008). Under NSS condition, in Shaheen DMRSR was higher with K₂SO₄ than KNO₃ and KH₂PO₄ application, whereas in KS-282, FMRSR was higher with KNO₃ than K₂SO₄ and KH₂PO₄ application. Under SS condition, in Shaheen and KS-282, DMRSR was higher with K₂SO₄ than KNO₃ and KH₂PO₄ application. Under NaCl stress, KS-282 had 28 percent higher DMRSR than that in Shaheen. The role of K₂SO₄ was prominent under salt stress. Under salt stress KS-282 had the lowest (0.08) DMRSR with KNO₃ application.

As compared to NSS, under SS condition in shoot of both the varieties, the role of K_2SO_4 was more prominent than KNO₃ and KH₂PO₄ regarding increase in fresh mass and dry mass root/shoot ratio. Commonly, the root/shoot ratio of plants increase when water availability is limiting. Lesser availability of water causes lesser flow of nutrients to the shoot system from root (Zaman *et al.*, 2008). In this study, role of different

sources of K⁺ were compared under normal and salt stress conditions with abundant supply of water under hydroponic conditions. The inclusion of electrolyte NaCl resulted in change of root/shoot ratio. The mode of action of K⁺ sources was variable at fresh and dry mass levels for root and shoot ratio. This observation supports the theory that the action of K⁺ sources might be active not passive in the mode of function. According to Yajun and Cosgrove (2000), the root/shoot ratio increases because the roots are less sensitive than shoots to growth inhibition by low water potential. This may be due to continued root elongation for water uptake from the soil, irreversible cell wall enlargement besides osmotic adjustment of cell turgor pressure and adjustment of cell wall. In this study ψ_{w} may have decreased due to addition of NaCl than the control but the role of Na⁺ cannot be ruled out. Meloni et al. (2001) reported that increased NaCl levels resulted in a significant increase in root/shoot ratio in cotton.

Relative growth rate (RGR) indicates change in dry biomass as a function of time period. Under NSS condition, RGR of shoot (RGRS) of both the cultivars, was higher with KH_2PO_4 than KNO₃ and K_2SO_4 application, whereas under SS condition, in Shaheen and KS-282, RGRS was higher with KNO₃ than K_2SO_4 and KH_2PO_4 application. Under NSS condition, RGR of root (RGRR) of both the varieties was higher with KH_2PO_4 than KNO₃ and K_2SO_4 application. Under SS condition, RGRR of Shaheen was higher with KNO₃ than K_2SO_4 and KH_2PO_4 application, whereas in KS-282, RGR was higher with K_2SO_4 than KNO_3 and KH_2PO_4 application. In shoot of KS-282, RGR was 6 times higher than that of Shaheen under SS condition with KNO_3 application, whereas in root of Shaheen, RGR was 3 times higher than that of KS-282 under SS condition with KNO_3 application, The response of the two varieties may be function-dependent on genetic make up and the genetic factors might have been switched on/off as per micro environment conditions of the root system. Also varietal response to respective treatments for RGR was variable depending upon temporal requirements of metabolic activities. Variations of RGR in both the species were similar to the findings which emphasized a wide variation in relative growth rate when plant species are grown under salt stress conditions (Poorter, 1989).

Water retention is an important property of a plant tissue that indicates its health and turgidity. The higher the water retention capacity of a tissue, the higher would be the metabolic activities. Under stress conditions, this attribute may be affected. In this study under NSS condition, relative water contents (RWC) of shoot in Shaheen was equivalent to that observed in case of KNO₂ and K₂SO₄ application than with KH₂PO₄. In shoot of KS-282, RWC was higher with KNO₃ than with K₂SO₄ and KH₂PO₄ application under NSS condition. Under SS condition, in shoot of Shaheen, RWC was higher with the application of KH₂PO₄ than with that of KNO₃ and K₂SO₄, whereas in shoot of KS-282 under SS condition, RWC was higher with the application of K₂SO₄ than with that of KNO₃ and KH₂PO₄ application. Under NSS condition, relative water contents (RWC) of root in Shaheen was higher with KH₂PO₄ than KNO₃ and K₂SO₄ application. In roots of KS-282, RWC was higher with KH₂PO₄ than with K₂SO₄ and KNO₂ application under NSS condition. Under SS condition in roots of Shaheen and KS-282, RWC was higher with KH₂PO₄ than with KNO₃ and K₂SO₄ application. Being a hydroponic study, it can be assumed that mass flow of water to the root system was not interrupted. The difference in RWC in these varieties of rice may be due to the treatments applied. The same difference was prominent when salt stress was obligatory applied. According to Bohnert et al. (1995), two major roles of water in plants are as a solvent and transport medium and as an electron donor in the photosynthesis reaction. It can be, therefore, inferred that the more efficient is the photosynthetic system, the more is the formation of metabolites. Siddique et al. (2000) observed that the higher the RWC, the higher was the photosynthetic rate. The differences in RWC reflect that either intake and transport or utilisation of K⁺ also might have been affected by RWC.

All the factors that affect the growth of plants may influence the intake of nutrients by the root system. Under stress condition, the phenomenon becomes more complex. In this study under SS, the intake of K⁺ was the highest with KH₂PO, than KNO, and K₂SO, application in Shaheen and KS-282. Under NSS condition, in Shaheen, the intake of K⁺ was the highest with KH₂PO₄ than KNO₃ and K₂SO₄ application, whereas in KS-282 the intake of K⁺ was the highest with K₂SO₄ than KNO₃ and KH_2PO_4 application (Fig. 1). For a healthy growth of a plant, it is necessary that the root and the shoot system must be in co-ordination. Higher intake of nutrients by a root system according to the growth requirements of a plant, and higher nutrient transport, lead to improved metabolic activities. In this study under SS in Shaheen, the transport of K⁺ was the highest with KH₂PO₄ than KNO₃ and K₂SO₄ application, whereas in KS-282, with K₂SO₄ application, K⁺ was higher than the other two sources. Under NSS condition, in Shaheen, the intake of K^+ remained the same with KNO₃ and K_2SO_4 than with KH,PO₄ application, whereas in KS-282, the intake of K⁺ was higher with K₂SO₄ than KNO₃ and KH₂PO₄ application (Fig. 2). The worth of an ion is dependent on the aspect

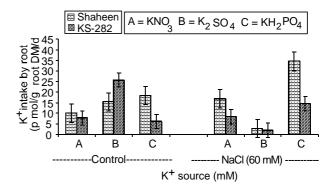


Fig. 1. Average rate of potassium ion intake by roots in two varieties of rice under K⁺ and Na⁺ interaction.

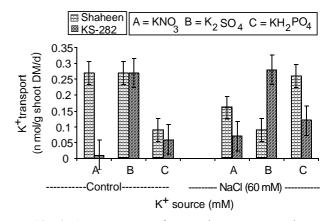


Fig. 2. Average rate of potassium transport in two varieties of rice under K⁺ and Na⁺ interaction.

whether it kept on accumulating in a tissue or it played its part in a metabolic activity. In this study, under SS, the utilisation of K⁺ was the highest with KNO₃ than KH₂PO₄ and K₂SO₄ application in Shaheen, whereas in KS-282 with KH₂PO₄ application, utilization of K⁺ was higher than the other two sources. Under NSS condition, in Shaheen, the utilisation of K⁺ remained higher with KH₂PO₄ than with KNO₃ and K₂SO₄ application whereas in KS-282 the utilisation of K⁺ was the highest with K₂SO₄ than KNO₃ and KH₂PO₄ application (Fig. 3).

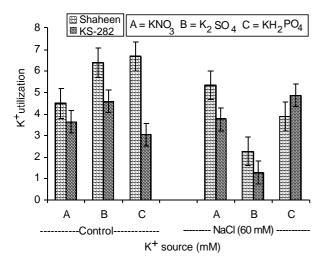


Fig. 3. Average rate of potassium utilization (mg of dry matter produced/µg of K absorbed) in two varieties of rice under K⁺ and Na⁺ interaction.

Under salt stress, rice variety Shaheen was more efficient than variety KS-282 in intake of K⁺ from KH₂PO₄ than KNO₂ and K₂SO₄, whereas, KS-282 remained more capable than Shaheen in intake of K⁺ from K₂SO₄ than KNO₃ and KH₂PO₄. Utilization rate of K⁺ by Shaheen remained higher from KNO₃ whereas in case of KS-282 it was higher from KH₂PO₄ than KNO₂ and K₂SO₄. Uptake and translocation of cations play essential roles in plant nutrition, signal transduction, growth and development (Pardo et al., 2006). In this study even in a particular variety, under NaCl stress the acquisition of K⁺ from different sources remained variable for intake, translocation and utilisation. It might be that salt stress affects nutrient acquisition by interfering with K⁺ uptake by carriers and channels as revealed by Maathuis and Amtmann (1999). Since phosphorus is an important component of ATP, the induction of vacuolar ATPase (proton-motive force for the cation exchanger) has been recorded in glycophytes and halophytes (Pardo et al., 2002); hence, the use of KH₂PO₄ might have been more useful than the two other K⁺ sources for plant root K⁺ attainment. The K⁺ inward-rectifying channel AKT1 is a target for Na⁺-induced failure of K⁺ uptake (Qi and Spalding, 2004). Lacan and Durand (1996) have shown that excised soybean roots treated with NaCl reabsorbed Na⁺ from the xylem vessels in exchange of K⁺. This net Na⁺/K⁺ exchange at the xylem/symplast interface was strongly linked because Na⁺ in the xylem sap enhanced K⁺ release, whereas, increased xylematic K⁺ prompted Na⁺ reabsorption. Na⁺ removed from the xylem sap was subsequently excreted to the external medium.

This study, showed that these two varieties of rice, i.e. Shaheen and KS-282, consumed potassium ion from K_2SO_4 , KNO₃ and KH_2PO_4 applied in the root medium. The intake, transport and utilization of K⁺ had a marked effect on root/shoot ratio, RGR and RWC depending upon its source. It was inferred that K⁺ consumption in shoot and root system of rice was dependent physio-genetically on potassium sources.

References

- Asch, F., Dinghuhn, M., Wittstock, C., Doerffling, K. 1999. Sodium and potassium uptake of rice panicles as affected by salinity and season in relation to yield components. *Plant and Soil*, **207:** 133-145.
- Blumwald, E. 2000. Sodium transport and salt tolerance in plants. *Current Opinion in Cell Biology*, **12**: 431-434.
- Bohnert, H.J., Nelson, D. E., Jensen, R.G. 1995. Adaptation to environmental stresses. *The Plant Cell*, **7**: 1099-1111.
- Carden, D.E., Walker, D.J., Flowers, T.J., Miller, A.J. 2003. Single-cell measurements of the contributions of cytosolic Na⁺ and K⁺ to salt tolerance. *Plant Physiology* 131: 676-683.
- Cassman , K.G., Whitney, A.S., Stockinger, K.R. 1980. Root growth and dry matter distribution of soybean as affected by phosphorus stress, nodulation, and nitrogen sources. *Crop Science*, **20**: 239-244.
- Chapman, H.D., Pratt, P.F. 1961. Methods of Analysis for Soils, Plants and Water, pp. 56-65, Division of Agricultural Science, University of California, Davis. CA, USA.
- Clarkson, D.T., Hanson, J.B. 1980. Mineral nutrition of higher plants. Annual Review of Plant Physiology, 31: 239-298.
- Cochrane, T.T., Cochrane, T.A. 2009. The vital role of potassium in the osmotic mechanism of stomata aperture modulation and its link with potassium deficiency. *Plant Signaling and Behavior,* **4:** 240-243.
- Forde, B.G. 2002. Local and long-range signaling pathways regulating plant responses to nitrate. *Annual Review of Plant Biology*, **53**: 203-224.
- Fukuda, A., Nakamura, A., Tagiri, A., Tanaka, H., Miyao, A., Hirochika, H., Tanaka, Y. 2004. Function, intracellular

localization and the importance in salt tolerance of a vacuolar Na⁺/H⁺ antiporter from rice. *Plant and Cell Physiology*, **45:** 146-159.

- Gardner, F.P., Pearce, R.B., Mitchell, R.L. 1985. *Physiology* of Crop Plants, pp. 202-203, Iowa State University Press, USA.
- Gierth, M., Maser, P., Schroeder, J.I. 2005. The potassium transporter AtHAK5 functions in K⁺ deprivation-induced high-affinity K⁺ uptake and AKT1 K⁺ channel contribution to K⁺ uptake kinetics in arabidopsis roots. *Plant Physiology*, **137**: 1105-1114.
- Gomez, K.A., Gomez, A.A. 1984. *Statistical Procedure for Agricultural Research*, pp. 20-28, 2nd edition, John Wiley and Sons, NewYork, USA.
- Hoagland, D.R., Arnon, D.I. 1950. The Water Culture Method for Growing Plants Without Soil, University of California, College of Agriculture, Barkeley, California, USA.
- Hunt, R. 1978. *Plant Growth Analysis*, Studies in Biology No. 96. Edward Arnold, London, UK.
- Kumar, V., Shriram, V., Nikam, T.D., Jawali, N., Shitole, M.G. 2008. Sodium chloride-induced changes in mineral nutrients and proline accumulation in indica rice cultivars differing in salt toleranc. *Journal of Plant Nutrition*, **31:** 1999-2017.
- Lacan, D., Durand, M. 1996. Na⁺/K⁺ exchange at the xylem/ symplast boundary. *Plant Physiology*, **110**: 705-711.
- Lindhauer, M.G. 1985. Influence of K⁺ nutrition and drought on water relations and growth of sunflower (*Helianthus anuus* L). Z. *Pflanzenernahr. Bodenk*, **148**: 654-669.
- Maathuis, F.J.M., Amtmann, A. 1999. K⁺ nutrition and Na⁺ toxicity: the basis of cellular K⁺/Na⁺ ratios. *Annals of Botany*, 84: 123-133.
- Meloni, D.A., Oliva, M.A., Ruiz, H.A., Martinez, C.A. 2001. Contribution of proline and inorganic solutes to osmotic adjustment in cotton under salt stress. *Journal of Plant Nutrition*, 24: 599-612.
- Mengel, K., Kirkby, E.A. 2001. Principles of Plant Nutrition, 849 pp., 5th edition, Kluwer Academic Publishers, London, UK.
- Misra, N., Dwivedi, U.N. 2004. Genotypic difference in salinity tolerance of green gram cultivars. *Plant Science*, 166: 1135-1142.
- Ohnishi, M., Fukada-Tanaka, S., Hoshino, A., Takada, J., Inagaki, Y., Iida, S. 2005. Characterization of a novel Na⁺/ H⁺ antiporter gene InNHX2 and comparison of InNHX2 with InNHX1, which is responsible for blue flower coloration by increasing the vacuolar pH in the Japanese morning glory. *Plant and Cell Physiology*, **46**: 259-267.
- Pardo, J.M., Cubero, B., Leidi, E.O., Quintero, F.J. 2006. Alkali cation exchangers: roles in cellular homeostasis

and stress tolerance. *Journal of Experimental Botany*, **57:** 1181-1199.

- Parks, G.E., Dietrich, M.A., Schumaker, K.S. 2002. Increased vacuolar Na⁺/H⁺ exchange activity in *Salicornia bigelovii* Torr. in response to NaCl. *Journal of Experimental Botany*, **53**: 1055-1065.
- Pitman, M. G. 1972. Uptake and transport of ions in barley seedlings III. Correlation between transport to the shoot and relative growth rate. *Australian Journal of Biological Sciences*, 25: 905-919.
- Poorter, H. 1989. Plant growth analysis: towards a synthesis of the classical and the functional approach. *Physiologia Plantarum*, **75:** 237-244.
- Qi, Z., Spalding, E.P. 2004. Protection of plasma membrane K⁺ transport by the salt overly sensitive1 Na⁺-H⁺ antiporter during salinity stress. *Plant Physiology*, **136**: 2548-2555.
- Quintero, J.M., Fournier, J.M., Ramos, J., Benlloch, M. 1998. K⁺ status and ABA affect both exudation rate and hydraulic conductivity in sunflower roots. *Physiologia Plantarum*, **102:** 279-284.
- Rodriguez-Navarro, A. 2000. Potassium transport in fungi and plants. *Biochimica et Biophysica Acta*, **1469**:1-30.
- Santa-Maria, G.E., Rubio, F., Dubcovsky, J., Rodriguez-Navarro, A. 1997. The HAK1 gene of barley is a member of a large gene family and encodes a high-affinity potassium transporter. *The Plant Cell*, **9**: 2281-2289.
- Siddique, M.R.B., Hamid, A., Islam, M.S. 2000. Drought stress effects on water relations of wheat. *Botanical Bulletin of Academia Sinica*, **41**: 35-39.
- Singh, B., Singh, Y., Imas, P., Jian-Chang, X. 2003. potassium nutrition of the rice-wheat cropping system. *Advances in Agronomy*, 81: 203-259.
- Wei, W.X., Bilsborrow, P.E., Hooley, P., Fincham, D.A., Lombi, E., Forster, B.P. 2003. Salinity induced differences in growth, ion distribution and partitioning in barley between the cultivar Maythorpe and its derived mutant golden promise. *Plant and Soil*, **250**: 183-191.
- Wu, Y.Y., Chen, Q.J., Chen, M., Chen, J., Wang, X.C. 2005. Salt-tolerant transgenic perennial ryegrass (*Lolium perenne* L.) obtained by *Agrobacterium tumefaciens*mediated transformation of the vacuolar Na⁺/H⁺ antiporter gene. *Plant Science*, **169**: 65-73.
- Yajun, W., Cosgrove, D.J. 2000. Adaptation of roots to low water potentials by changes in cell wall extensibility and cell wall proteins. *Journal of Experimental Botany*, **51**: 1543-1553.
- Yamaguchi, T., Apse, M.P., Shi, H., Blumwald, E. 2003. Topological analysis of a plant vacuolar Na⁺/H⁺ antiporter reveals a luminal C terminus that regulates antiporter

cation selectivity. *Proceedings of the National Academy of Sciences of USA*, **100:** 12510-12515.

- Yuncai, H.U., Urs, S. 2005. Drought and salinity: A comparison of their effects on mineral nutrition of plants. *Journal* of Plant Nutrition and and Soil Science, 168: 541-549.
- Zaman, B., Salim, M., Rehana, A., Niazi, B.H., Mahmood, I. A., Ali, A. 2008. Growth responses and ionic relations in two *Brassica* species under water stress conditions. *Pakistan Journal of Scientific and Indstrial Research*,

51: 31-35.

- Zaman, B., Asghar, R., Salim, M., Ali, S., Niazi, B.H., Arshad, A., Mahmood, I.A. 2006. Growth and ionic relations of *Brassica campestris* and *B. juncea* (L.) Czern & Coss. under induced salt stress. *Pakistan Journal of Agricultural Science*, 43: 103-107.
- Zaman, B., Ali, A., Salim, M., Niazi, B.H. 2002. Role of sulphur for potassium/sodium ratio in sunflower under saline conditions. *Helia* (Pakistan), 25: 69-78.