PATTERN OF POTASSIUM AND SODIUM DISTRIBUTION IN TWO COTTON VARIETIES

Liaqat Ali, Rahmatullah,Tariq Aziz, M. Aamer Maqsood, Shamsa Kanwal and M. Ashraf
Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad

The present investigation was aimed at assessing the ion accumulation and response in two cotton varieties under hydroponics, grown at K^+, Na^+ levels i.e. 3 mM K, 2.25 mM K +0.75 mM Na, 0.3 mM K+2.7 mM Na and 0.3 mM K using Johnsons's nutrient solution. Dry matter partitioning and ions (K^+, Na^+) distribution in older leaves (OL), younger leaves (YL), stem, primary (PR) and secondary roots (SR) were measured and compared between two cotton varieties at 10, 20, and 30 days of transplanting. The results explained that dry matter, ionic absorption and K:Na ratio were affected by translocation of K^+:Na^+ within different plant parts. Maximum total biomass (6.22 g plant^{-1}) was produced by NIBGE-2 followed by MNH-786 after 30 days of transplanting. Average dry matter of stem (2.54 g) i.e. 41% of total dry matter (TDM) was noted in NIBGE-2 that was higher than dry matter of OL (2.24 g), YL (1.0 g), PR (0.22 g) and SR (0.21 g). Maximum mean K:Na ratio was computed in YL of both varieties as compared to other plant parts at K+Na levels @ 2.25+0.75mM. There was significant relationship (R^2=0.83, 0.90, n=4 i.e. mean of 3 replicates) between stem dry matter and K^+ contents in stem for NIBGE-2 and MNH-786 respectively, at 30 days after transplanting.

Keywords: Cotton (*Gossypium hirsutum* L), K^+, Na^+ levels, Dry matter partitioning and ions (K^+ ,Na^+) distribution

INTRODUCTION

The potassium (K^+) is an essential macro-nutrient required by both plants and animals. After entering a plant, K^+ has to be transported to distant organs through the xylem. Potassium moves from the root symplast to the xylem sap and from this to the apoplastic space outside the bundle sheath, a process that involves many types of cells. Although plants have an absolute requirement for K^+ whereas, Na^+ is beneficial for vacuolar processes in the cell and the replacement of K^+ by Na^+ in the vacuole does not produce toxicity (Subbarao *et al*., 2003). The main feature of the relatively salt tolerant genotype is higher accumulation of Na^+ in leaves and an apparent capacity for K^+ redistribution to younger leaves (Leidi and Saiz, 1997). The low K^+ concentration together with high Na^+ concentration in older leaves of salt tolerant cotton cultivar indicated vacuolar Na^+ accumulation and active Na^+/K^+ exchange leading to K^+ retranslocation (Jeschke, 1984). Salt tolerant lines have higher concentrations of K^+ and K^+/ Na^+ ratios in the leaves than those of the salt sensitive lines at higher NaCl concentrations (Ashraf and Ahmad, 2000). In plant species which hardly translocate Na^+ to the shoot, some replacement of K with in the root takes place and makes this K^+ available for translocation in to the shoot (El-Sheikh and Ulrich, 1970; El-Sheikh, 1967). Although a very low K content in the root is the result of this replacement (Marschner, 1971).

Absorption of K^+ and Na^+ can be attributed to two mechanisms (Rains and Epstein, 1967; Jacobson *et al*., 1961). The first mechanism is related to high affinity for K^+ and the presence of K^+ prevents the uptake of Na^+. Sodium absorption takes place only after K^+ is completely depleted. The second mechanism was not highly selective, transported Na $^+$as well as K^+ and operated at high Na^+ and K^+ concentrations. The relatively high translocation rate of ions found in maize may be due to the higher carbon translocation rate observed for C_4 plants as opposed to C_3 plants. Approximately 13-36 % of the Na^+ and Cl^+ imported into leaves through xylem were exported by the phloem (Lohaus *et al*., 2000).

Higher K : Na ratio in younger leaves suggests K^+ re-absorption/translocation from the xylem (Jeschke and Stelter 1983; Pitman 1984). Maintenance of high cytosolic K: Na ratio is critical for the function of cells (Rubio *et al*., 1995; Zhu *et al*., 1998). Elevated levels of cytosolic Na^+ or a high Na^+: K^+ ratio exerts metabolic toxicity by competition between Na^+ and K^+ for the binding sites of many enzymes (Tester and Davenport, 2003). Protection of this Na^+ sensitive metabolic mechanism under saline conditions partly depends on the ability to keep cytosolic Na^+ levels low. For plant cells, the most important way of keeping the cytosolic Na^+ concentration at a low level is to minimize Na influx into the cytosol, and to maximize the Na^+ efflux from cytosol, either into the apoplast or into the vacuole (Nie *et al*., 1995; Blumwald *et al*., 2000; Zhu, 2001; Qiu *et al*., 2004). Sodium entry into plant cells may be restricted by selective ion uptake. In parallel with the HAK transporters, some HKT transporters mediate high affinity Na^+ uptake without

contransporting K^+. HKT transporters have two functions: (i) to take up Na^+ from the soil solution to reduce K^+ requirements when K^+ is a limiting factor, and (ii) to reduce Na^+ accumulation in leaves by both removing Na from the xylem sap and loading Na^+ into the phloem sap (Rodriguez-Navarro and Rubio, 2006). Plants reduces the effects of nutrient deficiency by changes in their growth characteristics and morphology, and by increasing biomass allocation to roots (Poorter and Nagel, 2000; Gorny, 2001). Cotton cultivars differ in K^+ translocation within different plant parts in relation to its ambient concentration in nutrient solution.

Thus the present study was planned to evaluate K^+,Na^+ translocation within different plant parts in two cotton varieties at 10, 20, and 30 days after transplanting.

MATERIALS AND METHODS

The experiment was conducted in hydroponics in a wire house of the Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad during May, 2006. The cotton seeds of two selected cotton varieties i.e. NIBGE-2 and MNH-786 were sown in thoroughly washed river-bed sand taken in polyethylene lined iron trays. Distilled water was used for maintaining optimum moisture for germination. One week after germination, uniform seedlings were transplanted in foam–plugged holes of thermopal sheets floating on continuously aerated 2 L half strength modified Johnson' s nutrient solution (Johnson *et al*., 1957) in polyethylene lined plastic beakers. The solution contained 6 mM N, 2mM Ca, 0.25mM P, 1mM Mg, 2mM S, 50µM Cl, 25µM B, 2µM Mn, 2µM Zn, 1µM Cu, 0.5µM Mo and 50µM Fe. Four treatments of K+Na in mM were: 3+0, 2.25+0.75, 0.3+2.7 and 0.3+0. There were three replicates of each treatment. Hydrogen ion activity (pH) of nutrient solution was monitored daily in all the twenty four beakers and adjusted daily at 5.5±0.5. Plants were harvested thrice at 10, 20 and 30 days after transplanting. After each harvest, K^+ and Na^+ levels were maintained to their original level by replacing the existing nutrient solution. Plants were washed in distilled water and blotted dry by using filter paper sheets and separated into younger leaves, older leaves, stem, primary roots and secondary roots before air drying after each harvest. The samples were stored in paper bags. Top four leaves were considered as younger leaves. The plant samples were air dried in wire house for two days. Air dried samples were then oven dried at 72^oC for 48 hours in a forced air driven oven to record dry matter yield (g $plant^{-1}$) of all plant parts using top loading balance. Dried samples of first, second and third harvests were ground to fine powder in a mechanical grinder (MF 10 IKA, Werke, Germany) by passing through a 1 mm sieve. Ground samples were homogenized. A 0.5 g portion of plant sample was digested in diacid mixture of nitric acid and perchloric acid (3:1) at 150^0C (Miller, 1998). The digested samples were diluted with distilled water as per requirement and K^+ and Na^+ in different plant parts were determined by flame photometer (Jenway PFP 7).

The data were subjected to statistical analysis using computer software "MSTAT-C" (Russell and Eisensmith (1983) and following the methods of Gomez and Gomez (1984). Completely randomized factorial design was employed for analysis of variance (ANOVA). Duncan's multiple range tests was used for mean separation (Duncan, 1955).

RESULTS

Biomass production (g $plant^{-1}$)

Dry matter of all plant parts (older leaves, younger leaves, stem, primary roots & secondary roots) for both varieties differed significantly ($p<0.01$) due to K^+,Na^+ levels, varieties and time interval (Table 1, 2, 3) at the three harvests. Dry matter of both varieties was highest at third harvest i.e. 30 days after transplanting (DAT). Maximum biomass was accumulated by NIBGE-2 and minimum was observed in MNH-786 at each harvest. Average dry weight of stem (2.54 g $plant^{-1}$) i.e. 41% of total dry weight (6.22 g $plant^{-1}$) increased over other plant parts by NIBGE-2 as compared to that of MNH-786 at 30 days after transplanting. Many scientists reported significant variations among varieties of several crops for dry matter production grown with varying levels of K^+,Na^+ supply (Leidi and Saiz, 1997; Jeschke, 1984; Ashraf and Ahmad, 2000; Lohaus *et al*., 2000; Kader and Lindberg, 2005; Subbarao *et al*., 2003). Interaction between varieties, levels of Na and K and time interval was found non-significant ($p<0.01$) for dry matter of older, younger leaves, stem, total dry matter, primary and secondary roots.

Table 1. Dry matter of older and younger leaves of two cotton varieties after 10, 20 and 30 days of transplanting in solution with various proportions of K and Na

Treatments	Dry matter of older leaves (g plant^{-1})								Dry matter of younger leaves (g plant^{-1})							
	Genotypes															
	NIBGE-2				MNH-786				NIBGE-2				MNH-786			
	10 *	20	30	mean	10	20	30	mean	10	20	30	mean	10	20	30	mean
K @3.0mM	0.33	1.84	2.53	1.57 ns	0.28	1.34	1.90	1.17ns	0.24 ns	0.90	1.04	0.73 a	0.16	0.65	0.70	0.50 cd
K+Na@ 2.25+0.75mM	0.23	1.45	2.21	1.30	0.16	1.02	1.60	0.93	0.19	0.77	0.85	0.61 b	0.14	0.63	0.70	0.49 cd
K+Na@ 0.3+2.7mM	0.18	1.10	1.93	1.07	0.15	0.89	1.36	0.80	0.12	0.67	1.03	0.61 b	0.10	0.46	0.76	0.44 d
K @0.3mM	0.20	1.48	2.28	1.32	0.16	1.00	1.70	0.95	0.15	0.78	1.05	0.66 b	0.13	0.59	0.88	0.53 c
Mean	0.24 e	1.47 c	2.24 a		0.19 e	1.06 d	1.64 b		0.18 d	0.78 b	1.00 a		0.13 d	0.58 c	0.76 b	

ns = non-significant
Means with different letter(s) in columns and rows differ significantly according to Duncan's Multiple Range Test (p=0.05)
*Days after transplanting

Table 2. Dry matter (stem and total) of two cotton varieties after 10, 20 and 30 days of transplanting in solution with various proportions of K and Na

Treatments	Stem dry matter (g plant^{-1})								Total dry matter (g plant^{-1})							
	Genotypes															
	NIBGE-2				MNH-786				NIBGE-2				MNH-786			
	10 *	20	30	mean	10	20	30	mean	10	20	30	mean	10	20	30	mean
K @3.0mM	1.14 ij	2.24 def	2.92 a	2.10 ns	0.93 jkl	1.50 h	2.82 ab	1.75 ns	1.92	5.34	7.04	4.77 ns	1.52	3.84	6.02	3.79ns
K+Na@ 2.25+0.75mM	1.01 jk	1.13 ij	2.65 bc	1.60	0.75 lm	1.11 ij	2.28 de	1.38	1.61	3.63	6.36	3.87	1.24	3.04	4.93	3.07
K+Na@ 0.3+2.7mM	0.72 lm	1.32 hi	2.18 ef	1.41	0.61 m	1.06 j	1.79 g	1.15	1.41	3.87	6.13	3.80	1.16	2.89	4.80	2.95
K @0.3mM	0.91 jkl	1.07 j	2.42 cd	1.47	0.80 klm	0.92 jkl	2.03 fg	1.25	1.16	2.99	5.34	3.16	0.96	2.51	4.15	2.54
Mean	0.94 c	1.44 b	2.54 a		0.77 c	1.15 b	2.23 a		1.53 e	3.96 c	6.22 a		1.22 f	3.07 d	4.98 b	

ns= non-significant
Means with different letter(s) in columns and rows differ significantly according to Duncan's Multiple Range Test (p=0.05)
* Days after transplanting

Table 3. Dry matter of primary and secondary roots of two cotton varieties after 10, 20 and 30 days of transplanting in solution with various proportions of K and Na

Treatments	Dry matter of primary roots (g plant^{-1})								Dry matter of secondary roots (g plant^{-1})							
	Genotypes															
	NIBGE-2				MNH-786				NIBGE-2				MNH-786			
	10 *	20	30	mean	10	20	30	mean	10	20	30	mean	10	20	30	mean
K @3.0mM	0.13 ns	0.15	0.27	0.18	0.09	0.13	0.23	0.15	0.09	0.19	0.26	0.18 a	0.07	0.12	0.19	0.13 cd
K+Na@ 2.25+0.75mM	0.11	0.15	0.23	0.16	0.09	0.10	0.20	0.13	0.06	0.13	0.19	0.13 c	0.05	0.11	0.15	0.10 ef
K+Na@ 0.3+2.7mM	0.08	0.15	0.18	0.14	0.07	0.12	0.14	0.11	0.05	0.14	0.18	0.12 cd	0.04	0.10	0.13	0.09 f
K @0.3mM	0.09	0.13	0.21	0.14	0.06	0.10	0.18	0.12	0.08	0.14	0.22	0.15 b	0.06	0.12	0.15	0.11 de
Mean	0.10 d	0.15 c	0.22 a		0.08 e	0.11d	0.19 b		0.07 d	0.15 b	0.21 a		0.05 e	0.11 c	0.16 b	

ns= non-significant
Means with different letter(s) in columns and rows differ significantly according to Duncan's Multiple Range Test (p=0.05)
* Days after transplanting

Table 4. K:Na ratio in older and younger leaves of two cotton varieties after 10, 20 and 30 days of transplanting in solution with various proportions of K and Na

Treatments	K:Na ratio in older leaves								K:Na ratio in younger leaves							
	Genotypes															
	NIBGE-2				MNH-786				NIBGE-2				MNH-786			
	10 *	20	30	mean	10	20	30	mean	10	20	30	mean	10	20	30	mean
K+Na@ 2.25+0.75mM	0.67 c	0.54 d	0.97 a	0.73	0.82 b	0.47 de	0.95 a	0.75	2.10 ns	1.83	1.58	1.84	2.29	1.84	1.44	1.86
K+Na@ 0.3+2.7mM	0.42 e	0.26 f	0.47 de	0.38	0.45 e	0.27 f	0.48 de	0.40	0.79	0.52	0.58	0.63	0.78	0.56	0.57	0.64
Mean	0.55 c	0.40 d	0.72 a		0.64 b	0.37 d	0.72 a		1.45	1.18	1.08		1.54	1.20	1.01	

ns= non-significant
Means with different letter(s) in columns and rows differ significantly according to Duncan's Multiple Range Test (p=0.05)
* Days after transplanting

Table 5. K:Na ratio in stem of two cotton varieties after 10, 20 and 30 days of transplanting in solution with various proportions of K and Na

Treatments	K:Na ratio in stem							
	Genotypes							
	NIBGE-2				MNH-786			
	10 *	20	30	mean	10	20	30	mean
K+Na@ 2.25+0.75mM	0.83 bc	0.80 c	0.88 ab	0.84 a	0.90 ab	0.72 d	0.91 a	0.84 a
K+Na@ 0.3+2.7mM	0.31 f	0.44 e	0.41 e	0.39 b	0.23 g	0.44 e	0.40 e	0.36 b
Mean	0.57	0.62	0.65		0.57	0.58	0.66	

Means with different letter(s) in columns and rows differ significantly according to Duncan's Multiple Range Test (p=0.05)
* Days after transplanting

Table 6. K:Na ratio in primary and secondary roots of two cotton varieties after 10, 20 and 30 days of transplanting in solution with various proportions of K and Na

Treatments	K:Na ratio in primary root								K:Na ratio in secondary root							
	Genotypes															
	NIBGE-2				MNH-786				NIBGE-2				MNH-786			
	10 *	20	30	mean	10	20	30	mean	10	20	30	mean	10	20	30	mean
K+Na@ 2.25+0.75mM	0.34 ns	0.20	0.29	0.28 a	0.41	0.22	0.26	0.30 a	0.29	0.21	0.28	0.26 a	0.32	0.24	0.31	0.29 a
K+Na@ 0.3+2.7mM	0.12	0.09	0.13	0.11 b	0.12	0.09	0.10	0.10 b	0.12	0.10	0.11	0.11 b	0.12	0.08	0.11	0.10 b
Mean	0.23 ab	0.15 c	0.21 abc		0.27 a	0.16 c	0.18 bc		0.21	0.16	0.20		0.22	0.16	0.21	

ns= non-significant
Means with different letter(s) in columns and rows differ significantly according to Duncan's Multiple Range Test (p=0.05)
* Days after transplanting

Table-7. Relative growth rate of shoot and root of two cotton varieties after 10, 20 and 30 days of transplanting in solution with various proportions of K and Na

Treatments	Relative growth rate of shoot (g g^{-1} SDW day^{-1})						Relative growth rate of root (mg mg^{-1}RDW day^{-1})					
	10 - 20 DAT			20 – 30 DAT			10- 20 DAT			20 – 30 DAT		
	Genotypes						Genotypes					
	NIBGE-2	MNH-786	Mean	NIBGE-2	MNH-786	Mean	NIBGE-2	MNH-786	Mean	NIBGE-2	MNH-786	Mean
K @3.0mM	1.553 ns	1.216	1.384 a	1.710	1.596	1.653 a	5.310 ns	5.013	5.162 a	5.696	5.485	5.590 a
K+Na @ 2.25+ 0.75mM	1.175	1.005	1.090 b	1.654	1.419	1.536 b	5.159	4.856	5.007 b	5.540	5.328	5.434 b
K +Na @ 0.3+2.7mM	1.253	0.967	1.110 b	1.619	1.404	1.512 b	5.153	5.016	5.085 ab	5.401	5.194	5.297 c
K @0.3mM	1.038	0.835	0.937 c	1.498	1.266	1.382 c	5.084	4.855	4.969 b	5.373	5.147	5.260 c
Mean	1.255 a	1.006 b		1.620 a	1.421 b		5.176 a	4.935 b		5.503 a	5.288 b	

ns= non-significant
Means with different letter(s) in columns and rows differ significantly according to Duncan's Multiple Range Test (p=0.05)
DAT= Days after transplanting

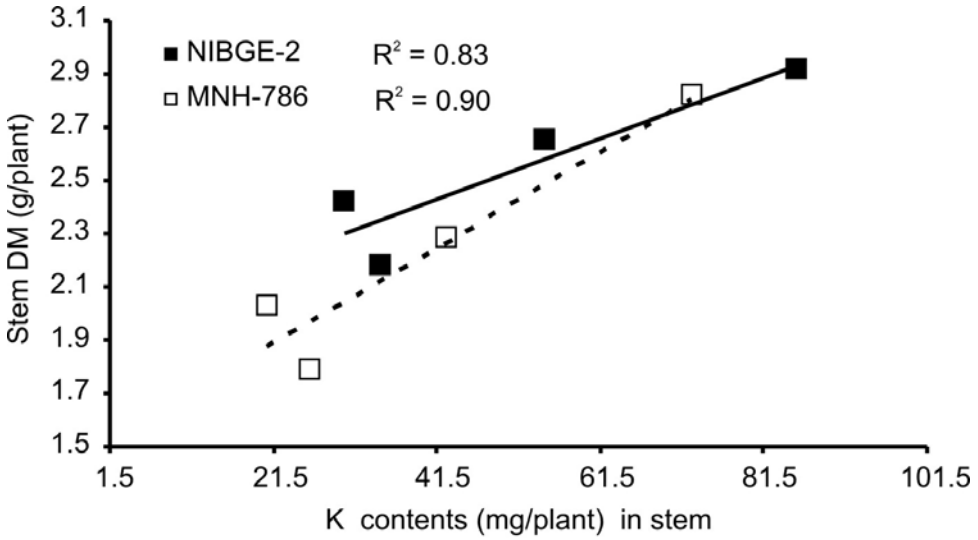

Fig.1 Correlation of stem dry matter (g/plant) with K contents (mg/plant) of stem of both genotypes at 30 DAT

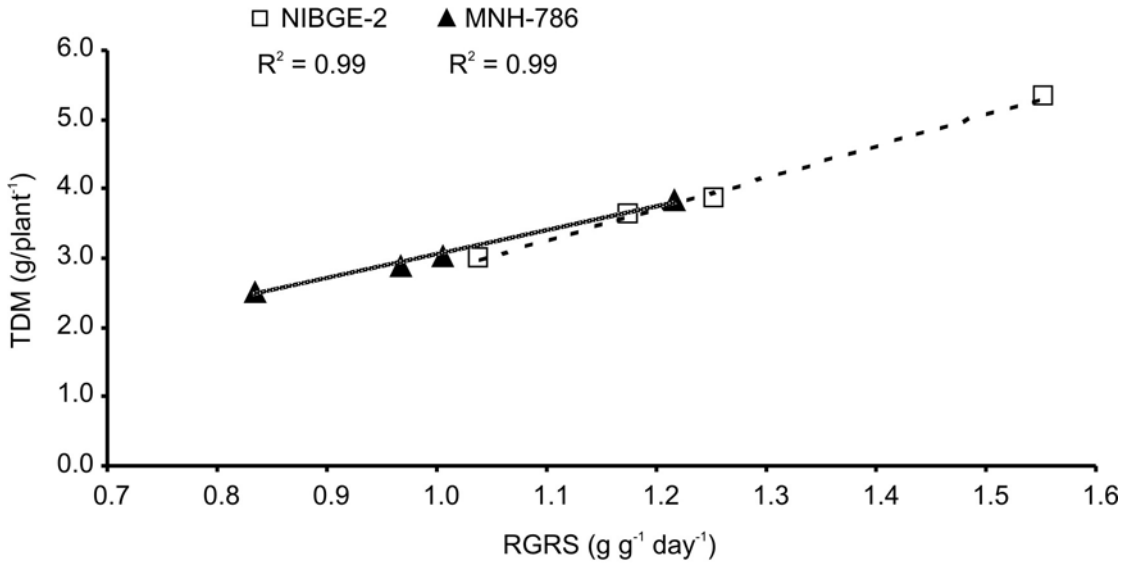

Fig. 2 Relationship between relative growth rate of shoot and total dry matter of both genotypes at 10-20 DAT

Relative growth rate of shoot (RGR) (g g^{-1} SDW day^{-1})

Relative growth rate (RGR) of shoot differed significantly ($p<0.01$) due to treatments and varieties (Table 7). NIBGE-2 had the highest RGR followed by MNH-786. RGR of shoot increased by 29% and 39% at 20 to 30 DAT in NIBGE-2 and MNH-786 respectively as compared to that at 10 to 20 DAT. There were significant variations observed in plants with regard to RGR of shoot when grown at various proportions of K and Na. Maximum RGR (1.653 g g^{-1}SDW day^{-1}) revealed at adequate K i.e. 3.0 mM and it increased by 19% at 20 to 30 DAT as compared to 10 to 20 DAT. Whereas, minimum RGR (1.382 g g^{-1}SDW day^{-1}) was observed at deficient K (0.3 mM). Growth responses to nutrient limitation are well documented (Poorter and Nagel, 2000; Gorny, 2001).

Relative growth rate of root (RGR) (mg mg^{-1}RDW day^{-1})

Both the treatments and varieties significantly ($p<0.01$) varied relative growth rate (RGR) of root (Table 7). NIBGE-2 manifested highest RGR followed by MNH-

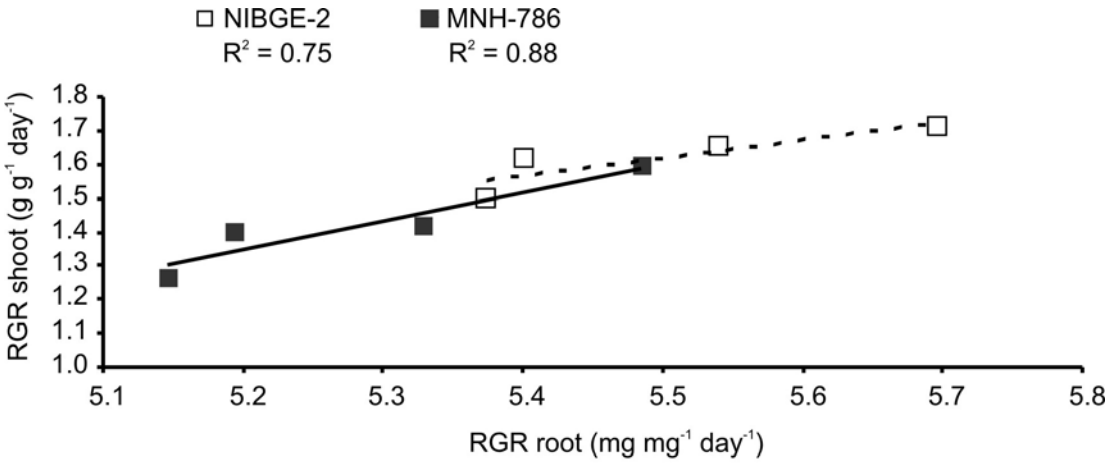

Fig. 3 Relationship between RGR of shoot and RGR of root in both genotypes at 20-30 DAT

786. An increase of 6% and 7% in RGR of root was observed at 20 to 30 DAT in NIBGE-2 and MNH-786 respectively as compared to that at 10 to 20 DAT. Significant differences were observed in plants with respect to RGR of root when grown at various proportions of K and Na. Maximum RGR (5.590 mg mg^{-1}RDW day^{-1}) was obtained at adequate K i.e. 3.0 mM and it increased by 8% at 20 to 30 DAT as compared to 10 to 20 DAT. Whereas, minimum RGR (5.260 mg mg^{-1} RDW day^{-1}) was revealed at deficient K (0.3 mM).

K:Na ratio

Influence of K^+,Na^+ levels and time interval varied K:Na ratio in older leaves, younger leaves , stem, primary roots, and secondary roots significantly ($p<0.01$) (Table 4, 5 and 6). K: Na ratio in younger leaves of both varieties varied non-significantly. Maximum K: Na ratio (1.86) was measured in younger leaves of MNH-786 at K^+,Na^+ levels of 2.25+0.75 mM. K: Na ratio in younger leaves decreased with increasing time intervals from 10 to 30 days in both varieties. Minimum K:Na ratio (0.28) measured in primary roots of NIBGE-2 at K^+,Na^+ levels of 2.25+0.75 mM. Interaction did not influence K:Na ratio significantly in primary roots and secondary roots.

DISCUSSION

It can be conceived from data presented in Table 2 that 40% of total dry matter was partitioned in the stem of the variety NIBGE-2. The proportion of total K concentration partitioned in stem progressively increased from 9.58 to 15.55 and from 15.55 to 19.60 mg g^{-1} at 10 to 20 and 20 to 30 days after transplanting in NIBGE-2, higher (62 % and 26%) than that of MNH-786, respectively followed by in younger leaves. Two mechanisms were implicated in the absorption of K^+ and Na^+ (Rains and Epstein, 1967; Jacobson *et al*., 1961). The first mechanism attributed to high affinity for K^+ and was not effective for Na^+ in the presence of K^+. This mechanism was available for Na^+ absorption after K^+ was completely depleted. The second mechanism was not highly selective in transporting Na^+ as well as K^+ and operated at high Na^+ and K^+ concentrations. The results for K:Na ratio are in conformity with (Rubio *et al*., 1995; Zhu *et al*., 1998; Tester and Davenport, 2003). Higher K: Na ratio was observed in younger leaves of cultivar MNH-786 at 10 and 20 days after transplanting (Table 4). Higher K: Na ratio in younger leaves was interpreted as an indication of potassium re-absorption/translocation from the xylem (Jeschke and Stelter 1983; Pitman 1984). Thus variation in K/Na selectivity of xylem transport from roots to the leaves proved to be one important cause of inter-specific differences in cotton varieties. NIBGE-2 effectively retained Na^+ in primary roots, suggesting preference for K^+ towards leaves during xylem transport.

Nutrient stress resulted in a reduction of relative growth rate (RGR) of shoot and root of both varieties. Na addition to K caused increase in RGR of shoot as compared to that at deficient K only. It was due to replacement of K by Na in some non-specific functions. There was significant relationship (R^2=0.83 and 0.90, n=4) of stem dry matter with K contents in stem for NIBGE-2 and MNH-786 respectively (Fig. 1). A substantial increase in total dry matter of both varieties significantly (R^2= 0.99 and 0.99, n=4) related with increase in RGR of shoot (Fig. 2). An increase in relative growth rate of shoot of both varieties caused increase in relative growth rate of root (R^2= 0.75 and 0.88, n=4) (Fig. 3).

CONCLUSION

Both the cotton varieties behaved differently with respect to growth and K^+,Na^+ distribution pattern within different plant parts when grown at different levels of K and Na, at 10, 20, and 30 days after transplanting. Due to low Na concentration in leaves, more Na was retained in the primary roots. Higher K accumulation was found in different plant parts e.g. in stem, younger leaves and older leaves of the shoot. It resulted more dry matter of stem out of total dry matter of the cotton varieties.

ACKNOWLEDGEMENT

Authors are grateful to Higher Education Commission of Pakistan for providing financial support under the project "Development of S&T Manpower through Indigenous Ph. D. Scholarship Scheme."

REFERENCES

Ashraf, M. and S. Ahmad. 2000. Influence of sodium chloride on ion accumulation, yield components ad fiber characteristics in salt tolerant and salt sensitive lines of cotton. Field Crop Res. 66: 115-127.

Blumwald, E., G.S. Aharon and M.P. Apse. 2000. Sodium transport in plant cells. Biochemica Biophysica Acta. 1465: 140-151.

Duncan, D.B. 1955. 'Multiple Range and Multiple F-tests.' Biometrics. vol. 11: 1-42.

El-Sheikh, A.M. 1967. Alkali metal interactions in the nutrition of sugar beets. Ph. D dissertation. University of California, Berkeley.

El-Sheikh, A.M. and A. Ulrich. 1970. Interaction of rubidium, sodium and potassium on the nutrition of sugar beet plants. Plant Physiol. 46: 645-649.

Gomez, K.A. and A.A. Gomez. 1984. Statistical Procedures for Agricultural Research. John Wiley & Sons, NY, USA.

Gorny, A.G. 2001. Variation in utilization efficiency and tolerance to reduced water and nitrogen supply among wild and cultivated barleys. Euphytica. 117: 59-66.

Hunt, R. 1978. Pant growth analysis. Edwards Arnold (Publishers) Ltd., London.

Jacobson, L., R.J. Hannapel., D.P. Moore and M. Schaedle. 1961. Influence of Ca on selectivity of ion absorption process. Plant Physiol. 36: 58-61.

Jeschke, W.D. 1984. K^+-Na^+ exchange at cellular membranes, intracellular compartmentation of cation and salt tolerance. In: Salinity tolerance in plants. Strategies for Crop Improvement. (Eds.), R. C. Staples and G. H. Toenniessen. John Wiley and Sons, New York. p. 37-66.

Jeschke, W.D. and W. Stelter. 1983. Ionic relations of garden orache, *Atriplex hortensis:*Growth and ion distribution at moderate salinity and the function of bladder hairs. J. of Exp. Botany. 34: 795-810.

Johnson, C.M., R.R. Strout, T.C. Broyer and A.B. Carlton. 1957. Comparative chlorine requirements of different plant species. Plant and Soil. 8: 327-353.

Kader, M.A. and S. Lindberg. 2005. Uptake of sodium in protoplasts of salt sensitive and salt tolerant cultivars of rice, determined by the fluorescent dye SBFI. J. Exp. Botany. 422: 3149-3158.

Leidi, E.O. and J.F. Saiz. 1997. Is salinity tolerance related to Na accumulation in upland cotton seedlings? Plant and Soil. 190: 67-75.

Lohaus, G.M., K. Hussmann, H. Pennewiss, J. Schneider, J. Zhu and B. Sattelmacher. 2000. Solute balance of a maize source leaf as affected by salt treatment with special emphasis on phloem retranslocation and ion leaching. J. Exp. Botany. 51: 1721-1732.

Marschner, H. 1971. Why can sodium replace K in plants? In: Potassium in Biochemistry and Physiology. Proc. Colloc. Int. Potash Inst., 8th Bern, Switzerland. P: 50-63.

Miller, R.O. 1998. Nitric-Perchloric wet digestion in an open vessel. In: hand book of reference methods for plant analysis. (Ed.) Y.P. Kalra, CRC Press Washington, D.C., U.S.A. p. 57-62.

Nie, X., R.A. Bressan, P.M. Hasegawa and J.M. Pardo. 1995. Ion homeostasis in NaCl stress environments. Plant Physiol. 109: 735-742.

Pitman, M.G. 1984. Transport across the root and shoot/ root interactions. In: Salinity Tolerance in Plants: Strategies for Crop Improvement (ed. R.C. Staples & G.H. Toennissen), John Wiley and Sons Inc., New York, NK. p. 93-123.

Poorter, H. and O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO2, nutrients and water: a quantitative review. Australian J. Plant Physiology. 27: 597-607.

Qiu, Q., Y. Guo, F.J. Quintero, J.M. Pardo, K.S. Schumaker and J.K. Zhu. 2004. Regulation of vacuolar Na^+/H^+ exchange in *Arabidopsis thaliana* by the salt overly sensitive pathway. J. Biol. Chem. 279: 207-215.

Rains, D.W. and E. Epstein. 1967. Sodium absorption by barley roots: Role of the dual mechanisms of alkali cation transport. Plant Physiol. 42: 314-318.

Rodriguez-Navarro, A. and F. Rubio. 2006. High affinity potassium and sodium transport systems in plants. J. Exp. Botany. 57: 1149-1160.

Rubio, F., W. Gassmann and J.I. Schroeder. 1995. Sodium driven potassium uptake by the plant potassium transporter HKT1 and mutations conferring salt tolerance. Science. 270: 1660-1663.

Russel, D.F. and S.P. Eisensmith. 1983. MSTAT-C. Crop and Soil Science Department, Michigan State University, East Lansing, M1.

Subbarao, G.V., O. Ito, W.L. Berry and R.M. Wheeler. 2003. Sodium a functional plant nutrient. Critical Reviews in Plant Sciences. 22: 391-416.

Tester, M. and R. Davenport. 2003. Na tolerance and Na transport in higher plants. Annals of Botany. 91: 503-527.

Zhu, J.K. 2001. Plant salt tolerance. Trends in plant Science. 6: 66-71.

Zhu, J.K., J. Liu and L. Xiong. 1998. Genetic analysis of salt tolerance in *Arabidopsis*: evidence for a critical role to potassium nutrition. The Plant Cell. 10: 1181-1191.