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Effect of increasing salinity on growth and mineral composition of wheat varieties and role of sodium exclusion capacity in salt tolerance mechanisms

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A few wheat varieties including two Japanese wheat varieties were evaluated for their salt tolerance at seedling stage, their behavior to increasing salinity levels and role of Na exclusion capacity in salt tolerance mechanisms. The wheat varieties were grown in nutrient solution and subjected to 0 (control), 25, 75 and 125 mM NaCl salinity levels for 7 days. Although the shoot growth was reduced while Na contents were increased progressively with increasing salinity in all varieties, the varieties were quite different in their response. Salt tolerant varieties maintained less reduction in their root and shoot growth and better water relations in their shoots than salt sensitive varieties under saline conditions. The wheat varieties were quite different in their Na exclusion capacity. Poor growth in salt sensitive varieties might be due to higher accumulation of Na in their shoots resulting from low Na exclusion capacity of roots, higher Na transport to shoot and/or inferior compartmentation capability.

Key words: growth and mineral composition, increasing salinity, Na exclusion capacity, salt tolerance, wheat varieties

1 INTRODUCTION

Salinity is the major threat to the performance of agriculture particularly in arid and semiarid regions of the world. The process of gradual soil salinization and preponderance of saline water sources point to a future reliance on salt tolerant crop species. Salinity is not necessarily prohibitive to plant life. It may be possible to combine salt tolerance and economic utility within crop species. This approach would lead to not only improved yield on inland saline fields but it might even allow the use of sea water to irrigate crops on sandy coastal soil Wheat (*Triticum aestivum* L.) is a moderately salt tolerant plant and thus has the potential to grow under salt-affected conditions. There are many evidences that considerable intraspecific diversity exists in wheat regarding salt tolerance. However, the efforts for exploiting the genetic variability in wheat varieties have been hampered mainly by the lack of understanding the mechanisms of salt tolerance. If the salt tolerant varieties are identified as well as their mechanisms of salt tolerance are understood, they can be incorporated into breeding programs to improve agronomic quality.

Salinity reduces the plant growth through its various detrimental effects. The harmful effects of high Na concentration in the growth medium on plant growth can be divided into three groups, (a) osmotic effect; inhibition of water uptake due to low water potential of the external medium, (b) specific ion effect/toxicity: disturbance of normal metabolism caused by high Na concentration in plant tissues and (c) ion imbalance effect/induced nutrient deficiency: inhibition of the absorption of other essential cations by plants. Under saline conditions, acclimation requires osmotic adjustment(i.e. ion accumulation); therefore, accumulator

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species may be expected as tolerant ones. The ability of salt-stressed plants to adjust rapidly to the changes in water potential involves accumulation of K, Ca, Na and/or Cl ions (Amzallag and Lerner, 1995). However, higher accumulation of ions especially Na causes toxicity effects leading to poor growth under saline conditions. Na accumulation especially in shoot tissues is inversely related to plant salt tolerance. It is reported that ion excess affects membrane permeability, enzyme activity, protein synthesis, nitrogen absorption, photosynthesis and other such processes leading to poor growth.

In glycophytes, different strategies occur depending on the species that may lead to salt tolerance. Salt tolerance variation among wheat varieties is attributed to differences in maintenance of low Na and Cl uptake and their accumulation, lower Na/K and Na/Ca ratios in shoots. However, higher salt tolerance in wheat varieties is also attributed to higher accumulation of Na and Cl (Maftoun and Sepaskhah, 1989; Saneoka et al., 1999).

In present study, a few Japanese and Pakistani wheat varieties were evaluated for their salt tolerance under increasing salinity at seedling stage. The role of Na exclusion capacity and maintenance of water relations in varietal differences was investigated to develop better understanding of salt tolerance mechanisms in wheat varieties under saline conditions.

2 MATERIALS AND METHODS

2.1 Plant material and seed germination

Two Japanese (Chikugo Izumi and Shirasagi Komugi) and four Pakistani (Blue Silver, LU-31, PB-81 and PARI-73) wheat varieties were evaluated for their salt tolerance at seedling stage. The seeds previously treated with fungicide (Benelate-T) were germinated in petri dishes 9 cm in diameter on two layers of filter paper saturated with distilled water in an incubator in the dark at 25°C. Each variety was replicated in sufficient numbers of petri dishes to get required number of healthy, same age and size seedlings for transplantation.

2.2 Seedling transplantation, growth and salinity imposition

Seven-day old seedlings were transplanted into holes of 15 mm thick polystyrene sheet floating on 7 liters of 5% aerated Hoagland's nutrient solution contained in plastic containers (35×27×12 cm) holding plants in position by foam collars with roots fully submerged in the solution. The polystyrene sheet was also covered with a vinyl sheet extending around in all directions to cover the nutrient solution container fully for avoiding any direct physical effect of saline solution on plant leaves. Each treatment consisted of five plants while each treatment was tetra-replicated. The seedlings were grown in a cultivation chamber (Model CFH-405, TOMY SEIKO Co. Ltd., Tokyo, Japan) at 23°C /15°C day/night temperature and light intensity of about 3×10^4 lx for 12 hours. After a seedling growth of eight days under normal conditions, salinity of 0 (control), 25, 75 and 125 mM NaCl was imposed by the addition of NaCl to the nutrient solution. The nutrient solution was replaced after three days during initial growth stage and after two days during the later growth period.

2.3 Growth measurement and plant analysis

The plants were harvested after seven days of growth under saline conditions. Each plant was separated into root and shoot portions and root and shoot length was recorded. The samples were washed in three replacements of distilled water to remove any external salt. Then the root and shoot samples were blotted dry with blotting paper before measuring root and shoot fresh weight. The samples were dried to their constant weight at 80°C for two days in an electric drying oven and dry weight was recorded. The ground plant samples were processed according to the procedures recommended by Ishihara (1975) for extraction and determination of mineral ions. The concentration of calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na) was measured using Polarized Zeeman Atomic Absorption Spectrophotometer (Model Z-6100, Hitachi Ltd.). Na/K and Na/Ca ratios were calculated from ion contents of roots and shoots on dry weight basis.

2.4 Statistical analysis

The statistical analysis of the data was carried out by SAS computer software package (SAS, 1998) and comparisons of all pairs of varieties were conducted by Tukey-Kramer's test.

3 RESULTS

3.1 Effect of salinity on root and shoot growth of various wheat varieties

The root and shoot growth was more reduced in Blue Silver, PB-81 and PARI-73 proving as salt sensitive varieties while less reduced in Chikugo Izumi, Shirasagi Komugi and LU-31 proving as relatively salt tolerant varieties under saline conditions. It was observed that salinity improved the dry weight of roots in all varieties at 25 mM NaCl salinity level, improved only in relatively salt tolerant varieties at 75 mM NaCl while reduced in all varieties except two Japanese wheat varieties (Chikugo Izumi and Shirasagi Komugi) at 125 mM NaCl (Table 1). The root growth was significantly higher in salt sensitive varieties than salt tolerant varieties under control conditions. However, the root growth was much more reduced in salt sensitive varieties than salt tolerant varieties at higher salinity levels. Moreover, the root growth was improved in salt tolerant varieties while depressed in salt sensitive varieties at moderate (75 mM NaCl) salinity level. Although some varieties were statistically alike in their absolute root dry weight under saline conditions, they were entirely different in their response to salinity in terms of relative root dry weight (% of respective controls). PARI-73 that showed slight improvement in root dry weight at low salinity and was statistically alike with salt tolerant varieties, experienced 62% reduction and proved to be the most sensitive among all varieties at high salinity in terms of root sensitivity to salinity.

Generally salinity reduced the shoot dry weight and magnitude of reduction increased with increasing salinity level (Table 1). Moreover, the shoot dry weight was much more reduced than root dry weight in all varieties. The shoot dry matter production capacity was significantly higher in all the three salt sensitive wheat varieties than salt tolerant wheat varieties as in case of

Table 1 Effect of salinity on root and shoot growth of wheat varieties at various salinity levels. Values in ( ) are % of respective controls.

Variety	Salinity levels (mM NaCl) 0 (Control)	25		75		125	
Root dry weight (mg plant^{-1})							
Chikugo Izumi	17.7 b	24.9 a	(141)	25.7 a	(146)	17.6 ab	(100)
Shirasa Komugi	18.5 b	26.3 a	(143)	23.5 ab	(128)	18.8 a	(103)
Blue Silver	22.2 a	26.5 a	(119)	19.8 cd	(89)	12.3 cd	(55)
PB-81	23.2 a	24.2 a	(105)	21.7 bc	(94)	14.6 bc	(63)
PARI-73	22.3 a	24.3 a	(109)	18.2 d	(82)	8.5 d	(38)
LU-31	19.1 b	20.1 b	(106)	19.8 cd	(104)	16.6 ab	(87)
Shoot dry weight (mg plant^{-1})							
Chikugo Izumi	54.4 c	47.5 bc	(88)	44.3 a	(82)	31.9 ab	(59)
Shirasa Komugi	50.3 c	45.3 c	(90)	35.8 cd	(71)	32.6 ab	(65)
Blue Silver	62.6 b	45.0 c	(72)	37.0 cd	(59)	27.7 bc	(44)
PB-81	70.4 a	52.3 a	(74)	42.9 ab	(61)	30.0 ab	(43)
PARI-73	62.6 b	50.6 ab	(81)	33.9 cd	(54)	19.1 cd	(31)
LU-31	49.8 c	50.6 ab	(102)	38.2 bc	(77)	33.7 a	(68)
Shoot FW/DW ratio							
Chikugo Izumi	6.2 ab	7.0 a	(113)	6.2 bc	(101)	6.3 ab	(103)
Shirasa Komugi	6.4 a	6.9 a	(108)	6.4 bc	(101)	6.4 a	(100)
Blue Silver	6.2 ab	6.7 a	(108)	6.4 bc	(103)	5.6 bc	(90)
PB-81	5.5 c	6.0 b	(109)	6.0 cd	(108)	5.1 c	(92)
PARI-73	6.5 a	6.7 a	(102)	6.6 ab	(101)	5.3 c	(81)
LU-31	5.7 bc	6.0 b	(104)	6.9 a	(121)	6.7 a	(118)

Different letters within columns indicate a significant differences among varieties at p=0.05 by TukeyKramer test.

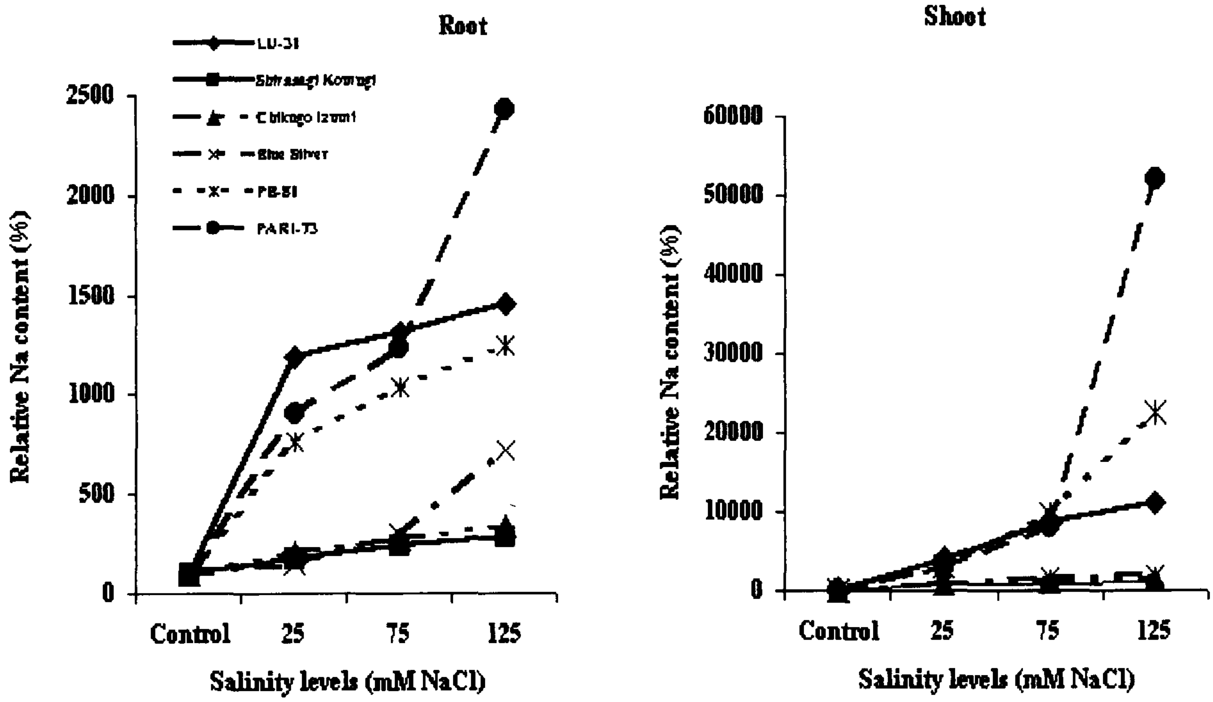

Fig.1. Relative Na content (% of respective control) of root and shoot of wheat varieties at 25, 75 and 125mM NaCl salinity levels.

root dry matter under control conditions. There were significant differences among varieties in absolute shoot dry weight at all salinity levels and even varieties statistically alike at a specific salinity level were entirely different in their relative shoot dry weight (% reduction relative to respective control). Most of the varieties experienced reduction in their shoot dry weight even at low salinity level except the most salt tolerant variety where slight improvement was recorded. High salinity level (125 mM NaCl) was enough to reduce shoot dry weight sufficiently in all varieties. There were significant differences among varieties in their absolute and especially relative shoot dry weight. The relative reduction varied from 32 to 69% compared to respective controls in various varieties. LU-31and Shirasagi Komugi were relatively more tolerant among all varieties at high salinity level. In contrast, PARI-73 with the highest reduction of 69% in shoot dry weight proved to be the most sensitive at high salinity.

3.2 Effect of salinity on shoot water relations of various wheat varieties

Fresh weight/dry weight (FW/DW) ratio is a good indicator of water relations in plant tissues and a highe r ratio is desirable for less disturbed water relations under saline conditions. The behavior of wheat varieties was different regarding effects of salinity on FW/DW ratio under saline conditions. FW/DW rati o was the highest in the most salt sensitive variety PARI-73 under control conditions (Table 1). This ratio was improved in all varieties at low (25 mM NaCl) and moderate (75 mM NaCl) salinity levels. However, this ratio was much reduced in salt sensitive varieties especially the most salt sensitive variety at 125 mM NaCl level indicating disturbed water relations leading to poor growth. On the other hand, this ratio was either maintained or improved in salt tolerant varieties at high salinity level co mpared to respective controls.

3.3 Effect of salinity on Na content and ionic ratios in roots and shoots of various wheat varieties

3.3.1 Sodium (Na)

As the varieties were quite different in their tissue ionic contents under control conditions, therefore, the relative ion contents (% of respective control) were considered more reliable criteria than absolute contents for the evaluation of varietal differences under saline conditions. Salinity increased the Na content of root and shoot, and there was progressive increase in these contents with increasing salinity level in all varieties (Fig.

1). Na contents were much higher in shoots than roots in all varieties under saline conditions. The behavior of wheat varieties to Na uptake and its accumulation in plant tissues was quite different under saline conditions. Some salt tolerant wheat varieties like Shirasagi Komugi and Chikugo Izumi restricted the accumulation of Na in their roots and shoots behaving as Na excluders while some salt sensitive varieties like PARI-73 and PB-81 accumulated a lot of Na in their tissues and behaved as Na includers/accumulators. The most salt tolerant variety LU-31 accumulated some Na in its root tissues but restricted its transport to shoots maintainin g much lower than salt sensitive varieties and thus behaved as poor includer. On the other hand, a relatively salt sensitive variety Blue Silver behaved as good Na excluder at low salinity levels but failed to restrict Na accumulation at high salinity and thus behaved as poor excluder.

3.3.2 Root/shoot ratio for relative Na content

It was observed that although relative Na content were increased more in shoots than roots of all varieties under saline conditions as evident from lower root/shoot ratio (Table 2), the increase was lower in salt tolerant than salt sensitive varieties especially at high salinity level. All the varieties were alike in the transport of Na from roots to shoots at low salinity. The transport of Na and its accumulation was increased progressively and significantly in salt sensitive varieties with increasing salinity while salt tolerant varieties restricted the transport to shoots. Blue Silver being a Na excluder variety did not transport much Na to shoot especially at high salinity compared to other salt sensitive varieties resulting in major accumulation in roots that led to root degradations. In spite of higher root/shoot ratio at high salinity than salt tolerant varieties, it showed poor growth that might be the consequences of inferior compartmentation capacity of this variety.

Table 2 Varietal differences in root/shoot ratio of relative Na content at various salinity levels.

Variety	Salinity levels (mM NaCl)							
	Control		25mM		75mM		125mM	
Chikugo Izumi	1.00	a	0.27	b	0.27	b	0.26	b
Shirasa Komugi	1.00	a	0.23	b	0.27	c	0.27	c
Blue Silver	1.00	a	0.20	b	0.19	b	0.40	c
PB-81	1.00	a	0.26	b	0.10	c	0.06	d
PARI-73	1.00	a	0.33	b	0.15	c	0.05	d
LU-31	1.00	a	0.30	b	0.15	c	0.13	c

Different letters within rows indicate a significant differences among salinity levels at p=0.05 by TukeyKramer test.

3.3.3 Na/K ratio

Salinity increased Na/K ratio in roots and shoots of all varieties and there was a progressive increase in this ratio with increasing salinity in most varieties. Relative Na/K ratio was much higher in shoots than roots in all varieties under saline conditions (Fig. 2). The varieties were quite different in relative Na/K ratio at various salinity levels. Na/K ratio was more increased in Na includer varieties than Na excluder vari eties in both roots and shoots at all salinity levels. Although Na includer but salt tolerant variety LU-31 exhibited much increase in relative Na/K ratio in roots under saline conditions, it maintained relative Na/K ratio much lower than salt sensitive varieties in its shoots.

3.3.4 Na/Ca ratio

Relative Na/Ca ratio was enhanced by salinity in all varieties and this ratio was progressively increased with increasing salinity in Na includer varieties (Fig. 3). Although Na includer but salt tolerant varie ty LU-31 exhibited the highest relative Na/Ca ratio in roots under saline conditions, it maintained this ratio much lower than salt sensitive varieties in its shoots especially at the high salinity level as in case of relative Na/K ratio. On the other hand, Na includer salt sensitive variety PARI-73 showed much lower relative Na/Ca ratio in its roots but failed to restrict its transport to shoot leading to the highest accumulation in its shoots at high salinity level.

4 DISCUSSION

Growth response to salinity is often regarded as a basis of evaluation for salt tolerance. The data indicated that relative parameters (growth and tissue ioni c composition) were more reliable criteria than absolute parameters for the evaluation of relative salt tolerance due to different growth habits of wheat varieties even under control conditions. It was observed that low salinity improved the root growth in almost all varieties while shoot growth was improved only in relatively most salt tolerant variety. The improvement i n plant growth at low salinity level may be attributed to improved water relations. Root growth was seriously inhibited in salt sensitive varieties under high salinity conditions.

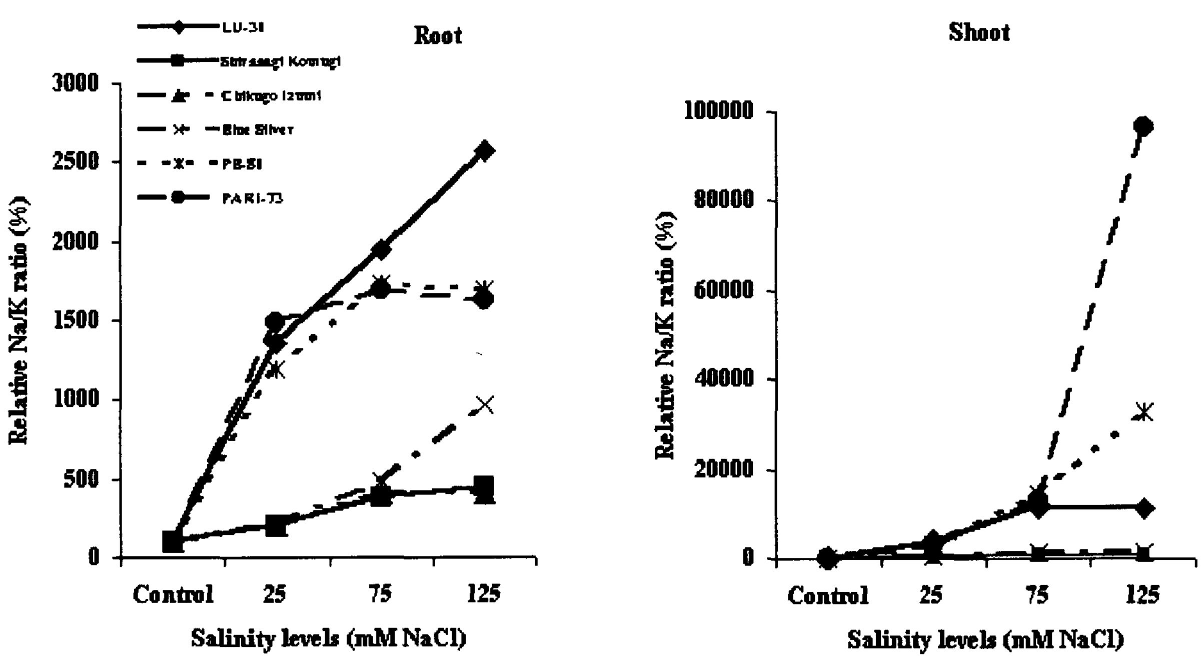

Fig.2. Relative Na/K ratio (% of respective control) of root and shoot of wheat varieties at 25, 75 and 125mM NaCl salinity levels.

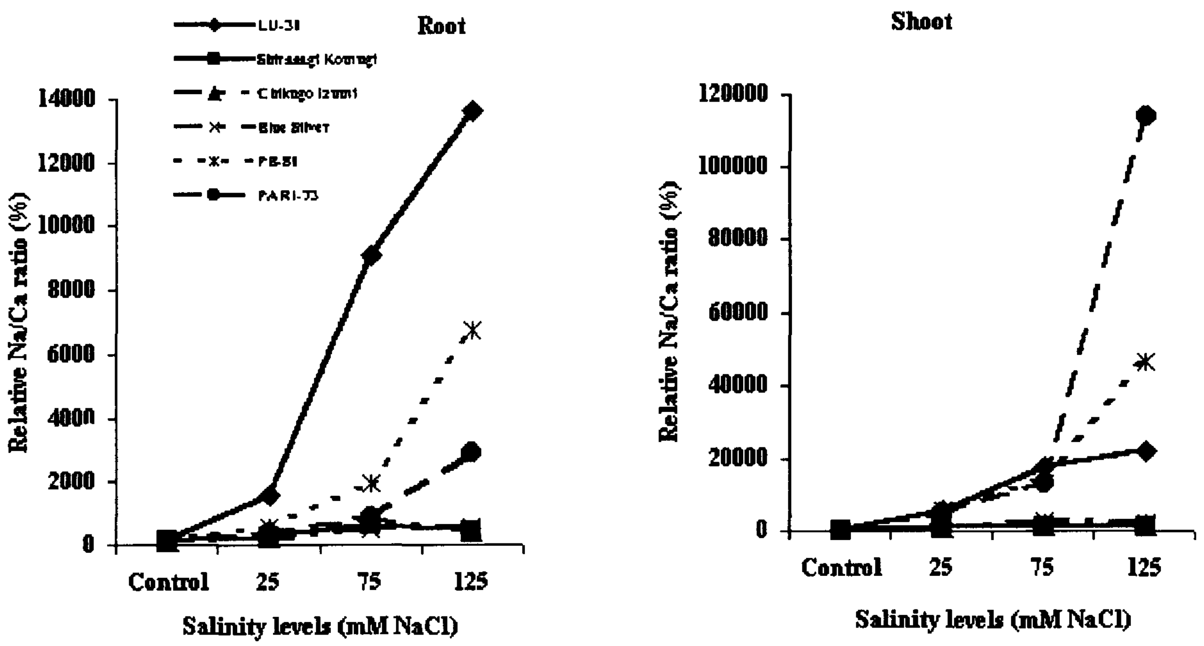

Fig.3. Relative Na/Ca ratio (% of respective control) of root and shoot of wheat varieties at 25, 75 and 125mM NaCl salinity levels.

Generally root growth was less affected than shoot growth leading to increase in root/shoot ratio under saline conditions. On the other hand, shoot growth was stimulated or the effect of salinity was negligible in salt tolerant varieties only at low salinity. Generally, this stimulation of growth is attributed to improvement in osmoregulation in wheat plants with regard to specific ion absorption (Maftoun and Sepaskhah, 1989). The shoot growth of salt sensitive varieties was much inhibited even at low salinity. The differences in growth among salt tolerant and salt sensitive var ieties were widened with increasing salinity levels. It was observed that osmoregulation occur successfully in almost all varieties at low salinity level as evident from high FW/DW ratio in some salt sensitive varieties. However, the capacity of shoot cells to compartmentalize the toxic ions is also important to keep ion balance conducive for metabolic processes. For example, PARI-73 showed the higher FW/DW ratio in shoots indicating that water relation was not the only limiting factor for growth inhibition at low salinity level. However, the lack of superior compartmentation capacity of this variety may have resulted in detrimental effects of toxic ions to metabolic processes leading to poor growth. On the other hand, a salt tolerant variety LU-31 showed a much lower FW/DW ratio in shoots apparently indicating an impaired water relation in shoots but actually no growth reduction was exhibited rather slight growth improvement was revealed at low salinity probably due to superior compartmentation capacity. These results were consistent with the conclusions of Kingsbury et al. (1984). These observations suggest that just osmoregulation alone is not a major growth controlling factor under saline condition but the compartmentation capacity also play its due role in growth stimulation or inhibition even at low salinity level.

It seems that the real differences among the varieties in the ionic contents exist in their capacity to transport these mineral ions especially Na to their shoots and their accumulation. The differences in the transport of mineral ions from roots to shoots between salt tolerant and salt sensitive varieties were also exhibited in another study based on X-ray microanalysis (Kamboh, 2000). However it was observed that the role of essential mineral ions also depends upon genetic requirement of the varieties, concentrations of other ions especially the Na and ions used for osmotic adjustment in shoots. It was revealed that salt tolerant varieties restricted the transport of Na from roots to shoots along with superior compartmentation capacity in shoots under increasing salinity levels. On the other hand, salt sensitive varieties failed to check transport and accumulation of Na in shoots and/or their inferior compartmentation capacity led to poor growth.

The role of Na exclusion or accumulation in salt tolerance of wheat varieties was not clearly understood. Some researchers advocated that salinity causes detrimental effects on plant growth of wheat varieties through toxic effects of Na accumulation in plant tissues, therefore, lower Na accumulation in plant tissue result in higher salt tolerance of wheat varieties. In contrast, Salama et al. (1994) and Saneoka et al. (1999) advocated that higher accumulation of Na in salt tolerant varieties led to better growth through better osmotic adjustment in plant tissues. It was observed that salt tolerant varieties might exhibit either behavior depending upon the variety. However, they maintain growth by better osmotic adjustment avoiding the toxic effects of higher levels of

Table 3 Categorization of some selected wheat varieties into various salt tolerance groups on the basis of their performance (shoot parameters) at 125 mM NaCl

Variety	Na exclusion/ inclusion group	Growth limiting factor: Water relations	Growth limiting factor: Na exclusion capacity	Salt tolerance group
Shirasagi Komugi	Excellent excluder	Good	Good	Salt tolerant
Chikugo Izumi	Good excluder	Good	Good	Moderately salt tolerant
Blue Silver	Moderate excluder	Poor	Good	Moderately salt sensitive
PB-81	Moderate includer	Poor	Moderate	Moderately salt sensitive
PARI-73	High includer	Poor	Poor	Salt sensitive
LU-31	Poor includer	Best	Moderate	Salt tolerant

Na in shoots probably through superior compartmentation capacity. The wheat varieties were classified into various salt tolerance groups on the basis of their Na exclusion capacity and maintenance of water relations in their tissues as presented in Table 3. Generally, accumulation of Na in plant tissues showed a negative relationship with shoot yield especially at high salinity. Na includer wheat varieties like PARI-73 and PB-81 behaved as salt sensitive and their poor shoot yield at high salinity might be due to ion excess (toxicity) as well as disturbed ionic ratios in the tissues. Thus the salt tolerance of ion includer wheat varieties depends upon successful exclusion of Na ions. The ion excluder varieties consisting of most salt tolerant varieties like Shirasagi Komugi and Chikugo Izumi showed comparatively low Na concentration in root. Consequently there was low Na accumulation in shoots indicative of the involvement of Na exclusion leading to lower increase in Na/K and Na/Ca rat ios in roots and shoots of these varieties. These ionic ratios play major role in cell elongation, radial cell expansion, rate of cell production and cellular stability (Kurth et al., 1986). LU-31 that behaved as poor includer proved to be the most salt tolerant at high salinity but accumulated more Na in root tissues than some salt sensitive varieties. This variety was capable of restricting the transport of Na to its shoot and thus maintaining accumulation of Na much lower than salt sensitive varieties in its shoots where it may be toxic. However, maintenance of the highest FW/DW ratio among all varieties indicate that the water relations were not disturbed and possibly superior compartmentation capacity helped in better osmotic adjustment without toxic effects of salt accumulation. On the other hand, Blue Silver behaved as poor excluder as Na exclusion by roots was much impaired at high salinity leading to poor growth. Therefore, disruption of Na exclusion capacity, poor compartmentation capability and disturbed water relations seem to be the cause of poor growth at high salinity. The measure of Na accumulation in wheat varieties at high salinity suggest that Na is compartmented in a pool in the salt tolerant varieties that seems to be of much lower capacity in salt sensitive varieties. Higher salt tolerance in salt tolerant wheat varieties is attributed to their superior compartmentation of toxic ions especially Na presumably in the vacuole leading to enable these varieties to maintain their cytoplasmic met abolic apparatus in a stable and more nearly normal state than the sensitive varieties. Moreover, a measure of true cytoplasmic tolerance of salt may also be a factor for lower salt tolerance in sensitive varieties (Kingsbury et al., 1984; Salama et al., 1 994). There is possibility that exclusion mechanism operative in salt sensitive varieties at low salinity was disrupted at high salinity in these varieties resulting in their failure to restrict higher build up of Na in the tissues.

As a conclusion, the results of present study elucidate that salt tolerance in wheat varieties may be contributed by the different capabilities of root and shoot i.e. Na exclusion by roots, restriction of Na transport to the shoots, lower accumulation of Na in shoots, maintenance of better water relations in shoots by the proper osmotic adjustment and keeping the cell environment conducive for near normal metabolic processes through superior compartmentation capacity of toxic ions especially such as the Na.

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