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Distribution of Mineral Ions in Root and Leaf Tissues and Their Role in Salt Tolerance of Wheat Varieties under Saline Conditions

Maqsood Ahmed KAMBOH*, Yoko OKI** and Tadashi ADACHI**

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The distribution of Ca, K, Na and Cl in root and leaves was studied in salt tolerant variety (Chikugo Izumi) and salt sensitive variety (PB-81) of wheat under saline conditions. The plants grown in 5% Hoagland's nutrient solution were subjected to 100 mM NaCl salinity for one week before observation with scanning electron microscope and analysis of selected samples with X-ray microanalyzer. Root growth was not affected in salt tolerant variety but reduced significantly in salt sensitive variety. Shoot growth was reduced in both varieties but much higher in salt sensitive variety. Salinity increased accumulation of Na and Cl in all root cells including vascular cells in salt sensitive variety. Salt tolerant variety not only reduced uptake of Na and Cl under saline conditions but also restricted their accumulation in cortex maintaining vascular cells relatively free of these ions. Salt sensitive variety failed to block transport of Na and Cl from root to leaves leading to much accumulation of these ions in leaves under salinity stress.

Key Words: Ion distribution, salinity, salt tolerance, wheat varieties, X-ray microanalysis.

1. INTRODUCTION

Salinity is one of the most important environmental factors limiting plant growth. Recent efforts in maintaining productivity under less favorable or marginal growth conditions have exhibited that considerable variation in salt tolerance exists among species of the same genus or among varieties of the same species. Most crop plants respond to salt stress as typical glycophytes and salt tolerance depend upon capability to maintain relatively low levels of Na and Cl especially in the foliage (Colmer et al., 1995).

The main physiological and biochemical traits contributing to the acquisition of resistance to salt stress are associated with different levels of organization. Hence resistance is not conferred by a single factor. Maintenance of membrane integrity, the selective uptake of essential minerals and compartmentation of excessive ions are part of mechanisms that contribute to salt tolerance. In non-halophyte plants, depending upon the species, different strategies occur that may lead to salt tolerance (Greenway and Munns, 1980).

Wheat is cultivated in many areas of the world exposed to salinity due to irrigation or saline subsoil and is regarded as moderately salt tolerant among glycophytic species. Salt tolerant varieties have been shown to possess selective uptake of K. It has also been observed that raising intracellular K concentrations reversed the inhibition of photosynthesis in osmotically stressed wheat leaves.

*Graduate School of Natural Science and Technology, Okayama University.
**Faculty of Environmental Science and Technology, Okayama University..

Detailed studies of Na and Cl distribution within roots especially those which are based on electron probe X-ray microanalysis have revealed mechanisms which depend on either the progressive exclusion of Na and Cl across the radial pathway from the epidermis to xylem e.g. of Na and Cl in barley (Yeo et al., 1977) or on removal of Na from the xylem elements by a K/Na exchange mechanism located in xylem parenchyma cells of root e.g. in maize (Yeo et al., 1977) and in soybeans (Lauchli and Weineke, 1978). The efficiency of these mechanisms may be genetically determined. However, under conditions of severe stress, the capacity for salt exclusion may be limited unless supplemented by a process of active salt extrusion by means of salt glands or by a process for the release of Na from roots.

There are some reports that provide information for the distribution of various mineral ions in wheat leaves under normal growth conditions based on scanning electron microscopy. However, there is little information in literature about the pattern of distribution and accumulation of these ions in roots and leaves of wheat plant under saline conditions. Therefore the present study was conducted to investigate the pattern of distribution and localization of various mineral ions in roots and leaves of wheat plant for the evaluation of varietal differences under saline conditions in an attempt to unveil the real mechanisms involved in salt tolerance of wheat varieties.

2. MATERIALS AND METHODS

2.1 Plant materials and seedling growth

Two wheat varieties were selected for this study which were previously screened as salt tolerant variety (Chikugo Izumi) and salt sensitive variety (PB-81). Seeds of these two varieties were treated with Benelate fungicide and germinated on two layers of filter paper moistened with distilled water in 90 mm petri dishes in an incubator at 25°C in the dark with an initial treatment of 5°C temperature overnight. Six days after seed germination, seedlings were transferred to growth tubes containing 5% Hoagland's nutrient solution with composition NH_4-N (5ppm), NO_3-N (5ppm), P (1.55ppm), K (10ppm), Ca (10.3ppm), Mg (2.4ppm), Fe (0.31ppm), Mn (0.025ppm), B (0.025ppm), Zn (0.035ppm), Cu (0.03ppm), Mo (0.025ppm). The seedlings were grown in a Cultivation Chamber (Model CF-405, Tomy Seiko Co. Ltd., Japan) with 12 hour light period, 23 °C /15°C day/ night temperature and a light intensity of 3×10^4 lx. Plants were held in position by foam collars (two piece foam corks). Salinity treatment of 100mM NaCl was applied after one-week growth in normal nutrient solution. Nutrient solution was replaced at three days interval during first week of growth and then on alternate days during remaining growth period. An identical study with similar plant material, experimental technique and growth conditions was carried out for salt tolerance screening and traditional analysis of root and shoot samples for Ca, Mg, K and Na by the procedures described by Ishihara (1975) with Polarized Zeeman Atomic Absorption Spectrophotometer (Model Z-6100, Hitachi Ltd.). Na/K ratios were estimated from ion concentrations in roots or shoots on the basis of dry weight. K/Na selectivity ratio ($S_{K,Na}$) was calculated according to Pitman (1976).

2.2 Specimen preparation and analysis

After a growth of 7 days in saline conditions, the plants were used for scanning electron microscopic studies. Root and leaf samples were harvested just prior to preparation and observation. Root samples were collected about 1 cm from the root apex while leaf samples from center of 2nd fully expanded younger leaf. Samples were cut into thin transverse cross sections with a sharp razor holding in between two pieces of vertically cut polystyrene stick, placed firmly on specific specimen stage with double sided adhesive tape and transferring immediately to specimen stage holder of Scanning Electron Microscope (Model S-3200N, Hitachi Ltd.). X-ray microanalysis was carried out by line analysis technique for qualitative analysis/distribution pattern for Ca, K, Cl and Na in various cell types of root and leaf samples at about -190°C with Energy Dispersive X-ray Microanalyzer (Model EMAX-5770W, Horiba Corporation Ltd.).

3. RESULTS

3.1 Effect of salinity on the growth of wheat varieties under saline conditions

It was observed that root growth was not affected rather slightly improved in salt tolerant variety Chikugo Izumi while significantly reduced in salt sensitive variety PB-81 at 100 mM NaCl salinity level compared to their respective controls (Table 1). In contrast shoot growth was reduced in both varieties at 100 mM NaCl level in comparison with their respective controls but the reduction was much higher in PB-81 than Chikugo Izumi. Similar types of observation were also recorded in a separate study where root growth was not affected in Chikugo Izumi up to 125 mM NaCl salinity level while root growth in PB-81 was reduced by 37% at this salinity level. Similarly, although shoot growth was sufficiently reduced in both varieties at 125 mM NaCl level but the reduction was much higher (57%) in PB-81 and lower (41%) in Chikugo Izumi compared to their respective controls. Poor yield in terms of root and shoot dry weight as well as development of leaf chlorosis in older leaves (visual observation) in salt sensitive variety (PB-81) under saline conditions, suggest dominance of salt toxicity effects.

3.2 Effect of salinity on the mineral composition of wheat varieties

Table 1 summarizes the data for Ca, Mg, K and Na contents in roots and shoots of Chikugo Izumi and Pb-81 under control and saline (100 mM NaCl) conditions. It clearly illustrates that Ca, Mg and K contents of roots of both varieties were reduced with salinity while Na contents were increased. However, the reduction in Ca and K contents in roots of Chikugo Izumi was lower than PB-81. The increase in Na contents was much higher in PB-81 than Chikugo Izumi, the increase being almost three times in Chikugo Izumi whereas 11 times in PB-81 at 100 mM NaCl salinity compared to their respective controls (Table 1). Consequently, Na/K and Na/Ca ratio were increased much more in roots of Pb-81 than in roots of Chikugo Izumi. Similarly, Ca, Mg and K contents were reduced in shoots of PB-81 while only Ca and Mg were reduced in Chikugo Izumi under saline conditions. Furthermore, the decrease was much higher in PB-81 than Chikugo Izumi compared to their respective controls. K contents in shoots of Chikugo Izumi were no reduced rather slightly improved under saline conditions. Although shoot Na contents were increased

Table 1 Effect of 100 mM NaCl salinity on growth and mineral composition of 20 days old plants of two wheat varieties. Values in ( ) are % of respective controls.

NaCl in external medium (mM)	Parameter	PB -81	Chikugo Izumi
	Roots		
	Dry weight (mg plant^{-1})	23.20	17.70
	Ca (mg g^{-1} dry wt.)	0.19	22.84
	Mg (mg g^{-1} dry wt.)	0.62	1.56
0	K (mg g^{-1} dry wt.)	0.03	122.85
	Na (mg g^{-1} dry wt.)	3.54	66.25
	Na/K	0.15	0.54
	Na/Ca	19.20	2.90
	$S_{K,Na}$	1.50	0.43
	Dry weight (mg plant^{-1})	18.80 (81)	19.70 (111)
	Ca (mg g^{-1} dry wt.)	0.08 (43)	11.32 (50)
	Mg (mg g^{-1} dry wt.)	0.47 (75)	0.28 (18)
100	K (mg g^{-1} dry wt.)	0.02 (58)	93.59 (76)
	Na (mg g^{-1} dry wt.)	39.15 (1104)	213.42 (322)
	Na/K	2.72 (1761)	2.28 (423)
	Na/Ca	528.71 (2754)	18.85 (650)
	$S_{K,Na}$	32.77 (2184)	39.88 (9274)
	Shoots		
	Dry weight (mg plant^{-1})	70.30	54.40
	Ca (mg g^{-1} dry wt.)	2.88	17.44
	Mg (mg g^{-1} dry wt.)	1.95	5.40
0	K (mg g^{-1} dry wt.)	0.15	61.40
	Na (mg g^{-1} dry wt.)	0.50	22.20
	Na/K	0.002	0.36
	Na/Ca	0.17	1.27
	$S_{K,Na}$	13.75	0.64
	Dry weight (mg plant^{-1})	35.9 (51)	37.00 (68)
	Ca (mg g^{-1} dry wt.)	1.53 (53)	12.70 (73)
	Mg (mg g^{-1} dry wt.)	1.14 (58)	4.39 (81)
100	K (mg g^{-1} dry wt.)	0.13 (91)	78.64 (128)
	Na (mg g^{-1} dry wt.)	55.47 (11187)	256.69 (1156)
	Na/K	2.89 (17292)	3.26 (903)
	Na/Ca	36.33 (21129)	20.21 (1588)
	$S_{K,Na}$	31.42 (228)	27.75 (4336)

in both varieties under saline conditions but the increase was almost 10 times higher in PB-81 than Chikugo Izumi. Consequently, Na/K and Na/Ca ratios in shoots were 20 and 13 times respectively higher in PB-81 than Chikugo Izumi (Table 1).

3.3 Effect of salinity on the distribution of mineral ions in various cells of plant tissues

3.3.1 Roots

Fig 1 shows the pattern of Na and Cl distribution in various cells of root of Pb-81 and Chikugo Izumi under control conditions. It was evident that Ca and Na ions were more or less uniformly distributed in all cells in PB-81 while K and Cl are more concentrated in epidermis and cortex, Cl being decreased inwardly (Fig. 1B). Furthermore K contents were much higher in all cell types especially cortex than any other ion under control conditions. In root of Chikugo Izumi, Ca was relatively more accumulated in epidermis than all inner cells, which were almost alike in Ca contents. Na was almost uniformly distributed in all cells under control conditions. As regard K and Cl contents in root cells of Chikugo Izumi, it was observed that they were relatively more accumulated in epidermis and outer cortex than the vascular bundles. Again K was the major ion dominating the all other ions in all cell types in root of Chikugo Izumi as in case of PB-81. It was observed that salinity reduced the Ca and K contents in almost all cell types of roots of both varieties while increased that of Na and Cl (Fig. 2). However, the accumulation of Na and Cl in root cells of Pb-81 was much higher than Chikugo Izumi in all cells in general and in cortex and vascular cells in particular. Ca and K were more or less uniformly distributed in all cell types of roots of the both varieties at 100 mM NaCl. The pattern of Na and Cl distribution in various cells was different in sensitive and tolerant wheat variety. In Chikugo Izumi root, most of the Na and Cl were restricted to the cortex and epidermis while endodermis and vascular tissues were almost free of these ions (Fig. 2 C&D). In contrast, in root of PB-81, Na replacing Ca and K more or less equally occupied almost all cells including vascular tissues. It was also observed that xylem vessels were very low in Cl and almost free of Na accumulations in Chikugo Izumi whereas these vessels exhibited much higher accumulation of Na and Cl along with other cell types in PB-81.

3.3.2 Leaves

The leaves of PB-81 under control conditions revealed that almost all ions were more or less uniformly distributed in all cells of leaf. However, the contents of Ca, K and Na were slightly low in vascular cells than epidermal or other surrounding cells while Cl was relatively low in epidermal cells than all inner cells. In case of Chikugo Izumi leaf under control conditions, all the ions were uniformly distributed in all cells of leaf except slightly higher accumulation of K, Na and Cl in abaxial (lower) epidermis and also of K in adaxial (upper) stereome cells. It was also observed that contents of all ions were higher in Chikugo Izumi than PB-81. However, K was the dominant ion in various cells of both varieties under control conditions (Fig.3). X-ray microanalysis of leaves of wheat varieties under 100 mM NaCl exhibited that contents of Na and Cl were increased in both varieties (Fig. 4). However, the increase was much higher in Pb-81 than Chikugo Izumi relative to their respective controls. It was observed that Ca was more or less uniformly distributed in all cells of Pb-81 leaf while Na mainly accumulated in adaxial epidermal and prickle cells (Fig. 4A). Although, K and Cl were uniformly distributed in almost all cells but special localization of Cl and to a lesser extent of K and Ca in specific epidermal cells of PB-81was also recorded. In Chikugo Izumi leaves under saline conditions, Ca was uniformly distributed in all cell types and sufficient Ca was present in xylem vessels. The pattern of K and Cl distribution was alike being both ions mostly accumulated in both epidermi layers and stereome cells. However, K was also sufficiently distributed in bundle

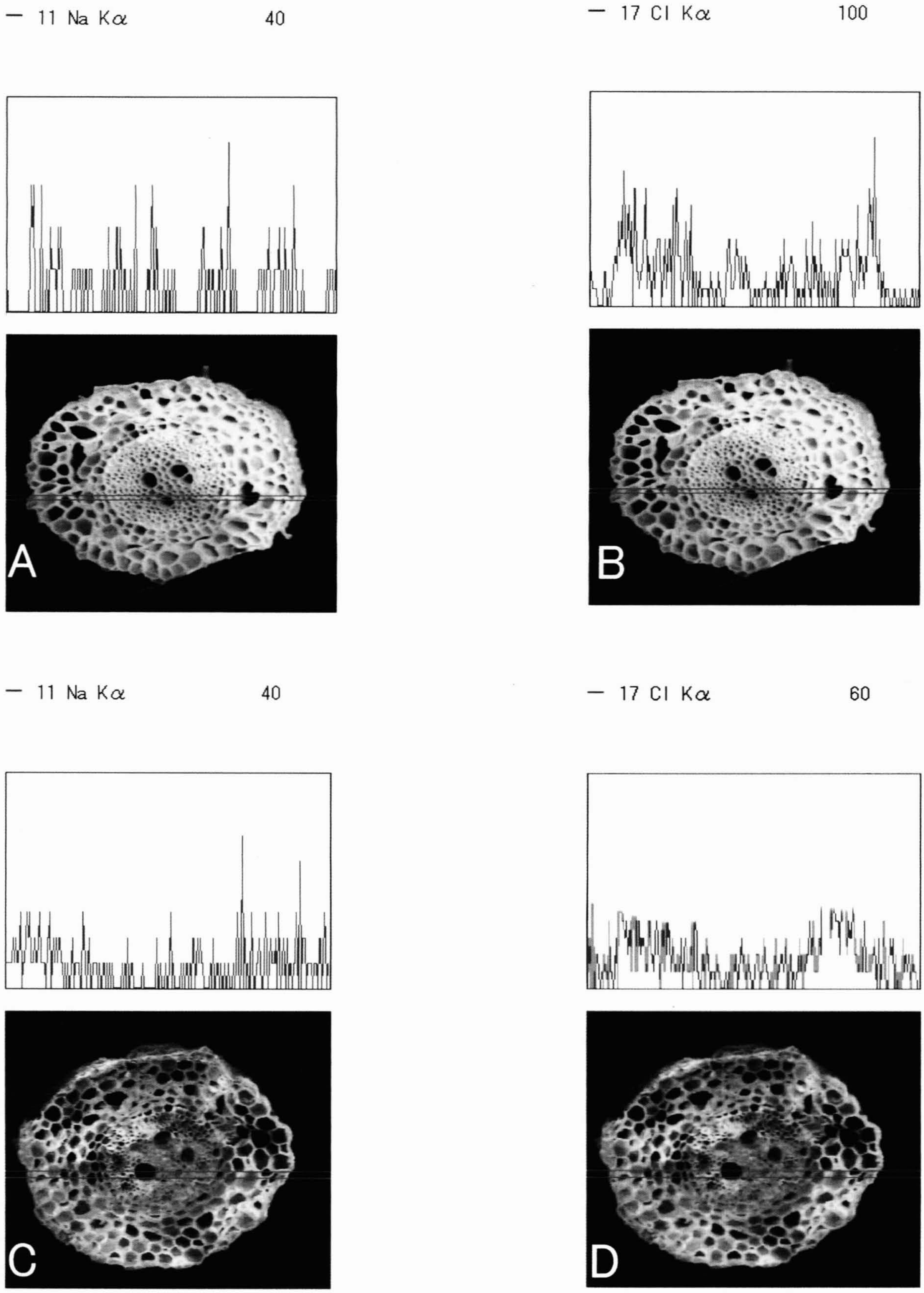

Fig. 1 X-ray microanalysis of Na and Cl in root cells from 10mm behind the root apex of PB-81 (salt sensitive) and Chikugo Izumi (salt tolerant) varieties of wheat under control conditions. The plants were 20 days old at the time of analysis and were grown in 5% Hoagland's nutrient solution. A and C are line analysis spectra for Na in leaves of PB-81 (×500) and Chikugo Izumi (×300) respectively while B and D represents line analysis spectra for Cl distribution in both varieties (×120).

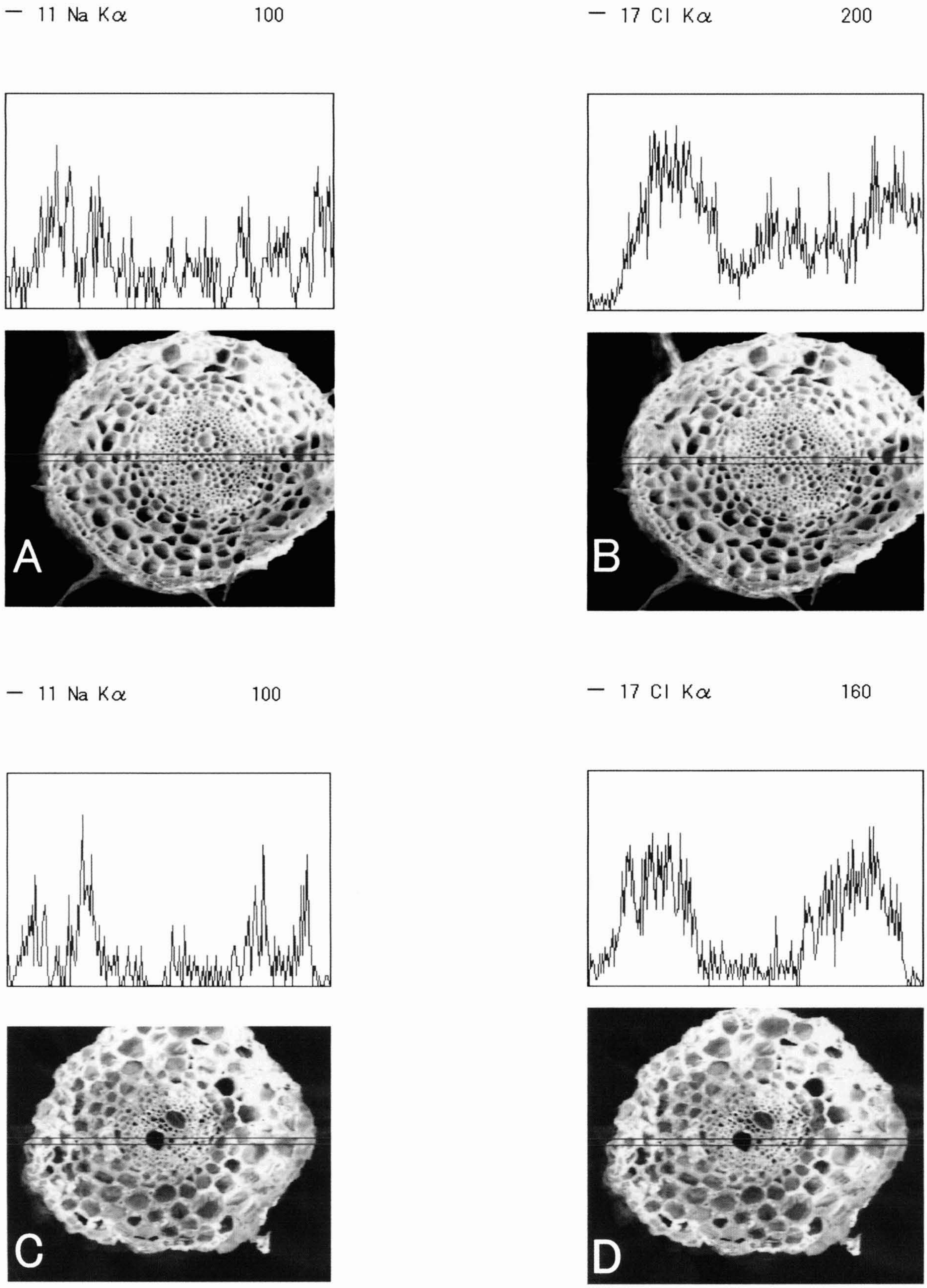

Fig.2 All details are same as in Fig. 1 except the plants were grown in nutrient solution containing 100 mM NaCl for the last one week before analysis.

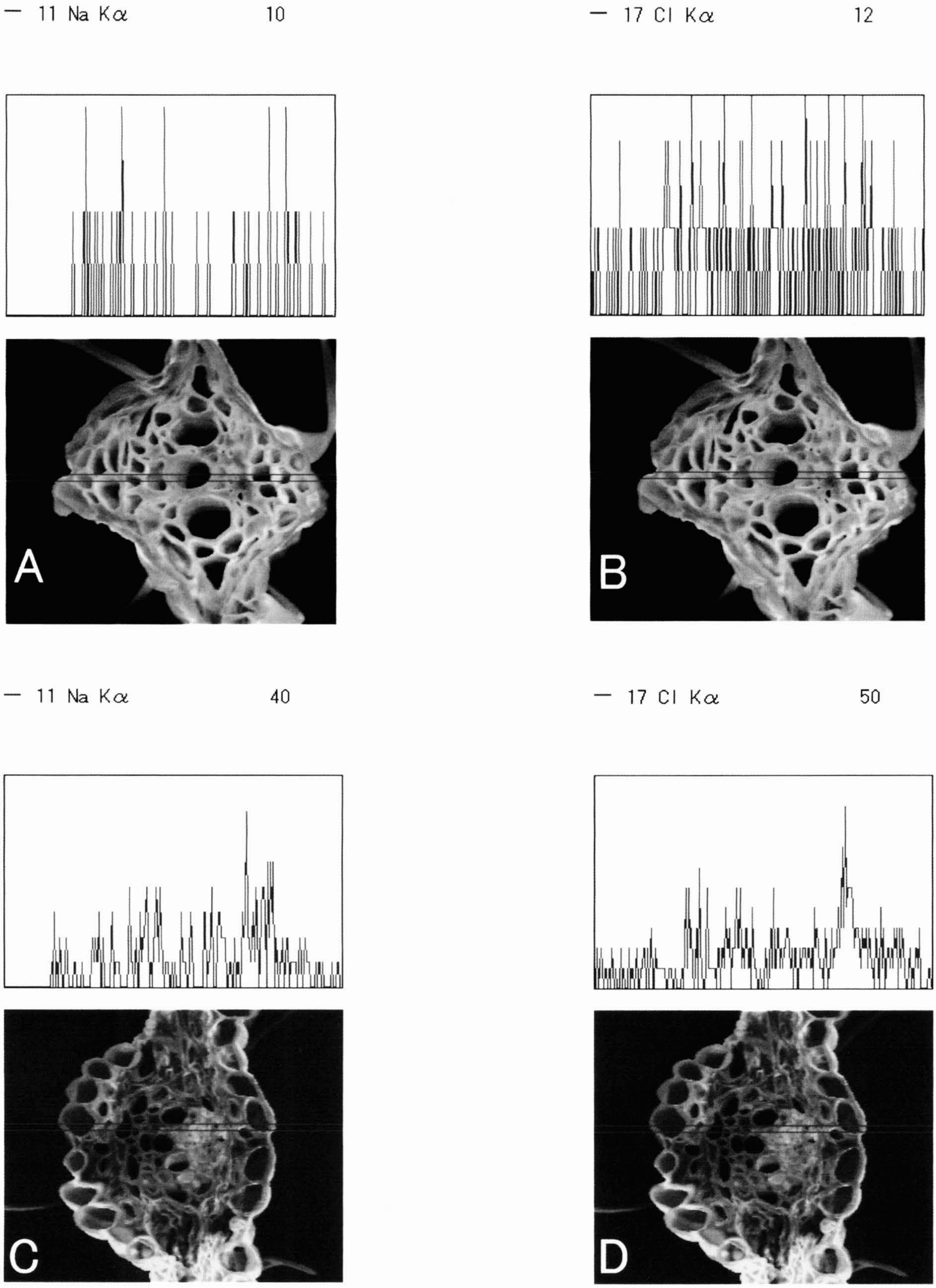

Fig.3 X-ray microanalysis of Na and Cl in leaf cells from second ffully expanded younger leaves of PB-81 (salt sensitive) and Chikugo Izumi (salt tolerant) varieties of wheat under control conditions. The plants were 20 days old at the time of analysis and were grown in 5% Hoagland's nutrient solution. A and C are line analysis spectra for Na in roots of PB-81 and Chikugo Izumi respectively while B and D represents line analysis spectra for Cl distribution in both varieties (×120).

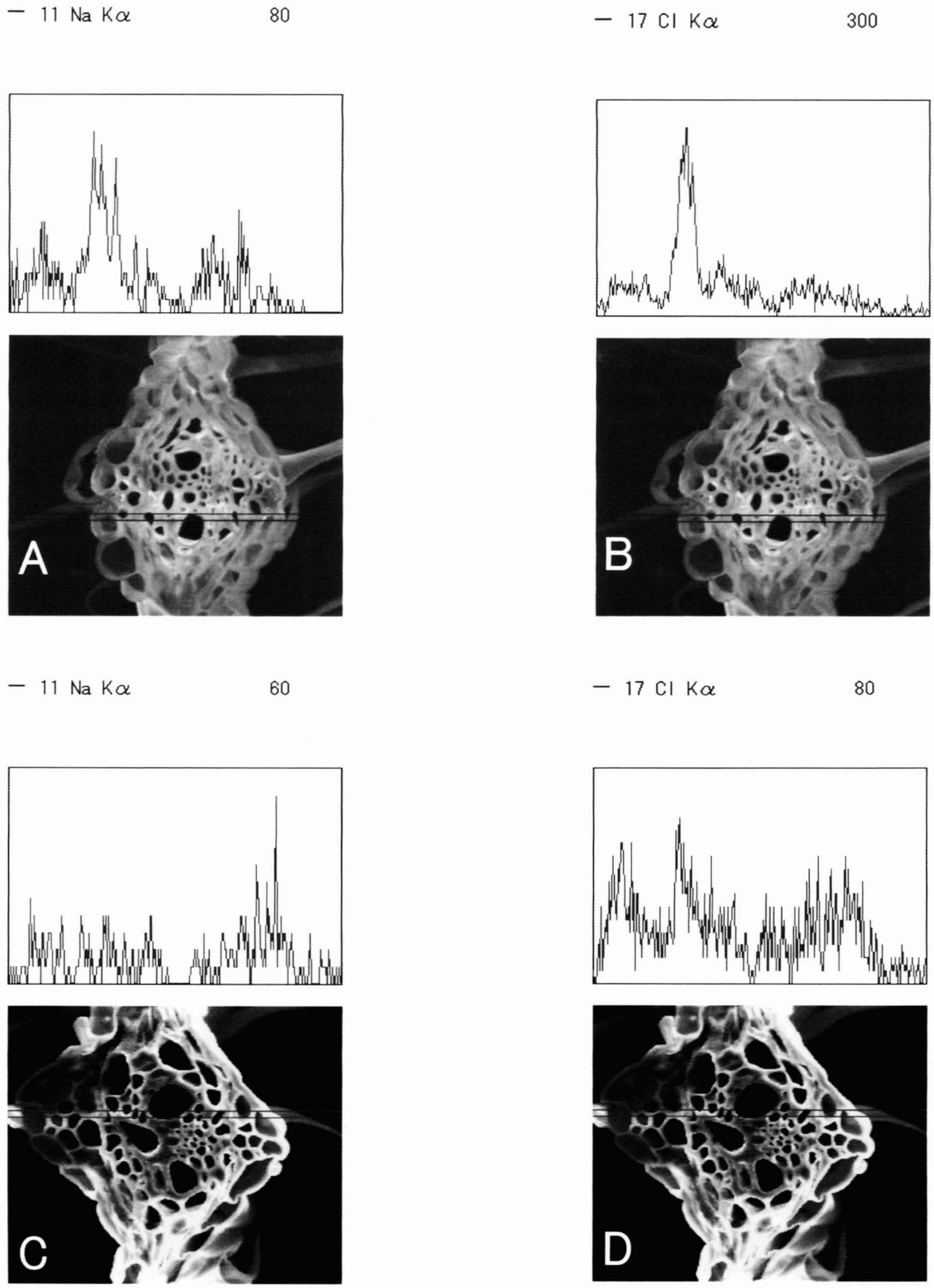

Fig.4 All details are same as in Fig. 3 except the plants were grown in nutrient solution containing 100 mM NaCl for the last one week before analysis, and PB-81 and Chikugo Izumi samples were observed at x400 and x450 magnification respectively.

sheath and vascular cells. Na was more accumulated in abaxial epidermis layer whereas vascular cells especially xylem vessels were low in Na accumulation. There was no special localization of any ion in Chikugo Izumi leaves as was observed in leaves of PB-81 under saline conditions.

4. DISCUSSION

In many crop plants, salinity tolerance may depend on the efficiency with which the root system can limit accumulation of Na and Cl in above ground parts of the plant (Hajibagheri et al., 1987). It has been well illustrated in soybeans (Lauchli and Wieneke, 1978), maize (Yeo et al., 1977; Hajibagheri et al., 1987), sugar beet (Marschner et al., 1981b) and rice (Kamboh et al., 1999) where in salt stressed plants, Na and Cl levels become relatively high in the roots and low in the leaves of salt tolerant varieties compared to salt sensitive varieties. Hence if the rate of transport of NaCl to the shoot exceeds that at which these ions can be accommodated in leaf cell vacuoles, then the plant will die either of ion toxicity or cellular dehydration (Greenway and Munns, 1980).

Data demonstrated that PB-81 was the salt sensitive variety while Chikugo Izumi relatively salt tolerant variety, both quite different in their Ca, Mg, Na and K uptake, Na/K, Na/Ca ratio and selectivity ratio in their roots and shoots under saline conditions. It was observed that the contents of mineral ions were much higher in Chikugo Izumi than PB-81 under both control and saline environments. It might be due to higher genetic requirement of mineral nutrition in Chikugo Izumi as similar observation has been recorded for some other Japanese wheat varieties compared to other exotic varieties. However, the changes in the contents of various mineral ions were quite different in both varieties under salt stressed conditions. The difference between varieties in selectivity of their roots may reflect differences in selectivity at the primary site of uptake (Jeschke, 1983). Under control conditions, the selectivity ratio was much higher in PB-81 than Chikugo Izumi in both roots and shoots indicating the existence of more successful ion selection in roots of PB-81. The selectivity ratio was not much different in roots and shoots of Chikugo Izumi but this difference was much higher between roots and shoots of PB-81. It suggested that PB-81 was also much more selective for K over Na in translocation to shoot retaining much Na in its roots under control conditions. Salinity impaired the selectivity of roots of PB-81 significantly under saline conditions. Consequently the selectivity ratio in roots of PB-81 was much lower than Chikugo Izumi. It indicated that the selectivity mechanism in root epidermis of PB-81 could not withstand the salinity effects that ultimately led to higher Na uptake from the saline medium. Furthermore, alike selectivity ratio in roots and shoots of PB-81 suggested that the Na was translocated to the shoot at the same rate at which it entered primary site of absorption. On the other hand, lower contents of Na and Cl in all cell types of Chikugo Izumi especially endodermis and vascular cells revealed that the selectivity mechanism is much more developed in roots of Chikugo Izumi at epidermis. A further lower content of Na in root endodermis and vascular cells than cortex cells and lower levels of Na while higher levels of K in leaf cells promote the possibility of the existence of some selectivity/exchange mechanism in endodermis cells of root of Chikugo Izumi. Such mechanisms are also reported at outer-middle cortex, inner cortex-endodermis interfaces and xylem vessels in *Plantago coronopus* (Harvey et al., 1985), in xylem parenchyma cells of maize root (Yeo et al., 1977; Hajibagheri et al., 1987). However, a more precise quantitative measurement of Na and K concentration in endodermis and other surrounding cells is required for the confirmation of the existence and contribution of the exchange mechanism. A much lower Na content rather freeness of xylem vessels in this respect indicated the possibility of some re-absorption mechanism at xylem vessels for the re-absorption of Na from xylem vessels by the surrounding cells as also has been reported by Yeo et al. (1977) in maize root. However, the lower selectivity ratio in shoots of Chikugo Izumi than roots did not support the possibility of much contribution of this re-absorption mechanism because such a system is likely to be rapidly saturated at such a high external salinity because of its small volume (Hajibagheri et al., 1987).

The major difference between the varieties for the response to salinity was the higher concentration of Na and Cl accumulated in endodermis and vascular cells and their transport to shoot in PB-81 than Chikugo Izumi. The salt tolerance of wheat varieties is related to their capability of restricting the transport of Na to the shoot where it is highly toxic as reported by Zsoldos et al. (1990). PB-81 also showed higher Na/K ratio in roots and shoots due to much higher decrease in K and increase in Na contents under saline conditions and proved to be salt sensitive. Higher Na and relatively lower K are reported to affect the salt tolerance of plants. Furthermore excess of Na over K may displace K from selective sites on carriers or channels that are essential in energy dependent influx as well as Na may displace Ca from the plasma lemma resulting in loss of membrane selectivity for K over Na (Cramer et al., 1985). It was evident from X-ray microanalysis data that K was the major ion in all cell types under control conditions which was replaced by Na significantly in salt sensitive variety PB-81. Moreover, higher accumulation of Cl in various cells of root and leaves of salt sensitive variety are also detrimental for normal metabolism of plant cells as it is reported to interfere in protein synthesis (Brady et al., 1984). The exhibition of much lower levels of Na and Cl in root vascular cells of Chikugo Izumi than PB-81 revealed the fact of lower translocation and accumulation of these ions in shoot of salt tolerant variety. It is reported that net transport of Na and Cl is much more important for the long-term survival of plants. Special localization of Na and Cl in specific epidermal cells of PB-81 may cause cell dehydration, interference in stomatal activity affecting guard cells turgidity, ion toxicity as exhibited from the development of toxicity symptoms and poor growth leading to leaf chlorosis and ultimately leaf death.

5. CONCLUSION

It was concluded that shoot growth is more affected than root growth under saline conditions. Moreover, Ca and K contents are more reduced in salt sensitive varieties than salt tolerant varieties. Similarly Na and Cl are less accumulated in shoots of salt tolerant varieties than salt sensitive varieties. It was concluded that salt tolerance of wheat varieties is related to their capacity of Na exclusion at root plasma membrane and endodermis layer that contributes to accumulation of

Na in shoots. Higher accumulation of Na in shoots of salt sensitive variety leads to poor growth probably due to impaired photosynthetic activity.

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