

Ion distribution in leaves of salt-tolerant and salt-sensitive lines of spring wheat under salt stress

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SUMMARY

Two lines of spring wheat, salt-tolerant S24 and salt-sensitive Potohar, were grown until the onset of ear formation in sand culture containing 0 or 125 mol m⁻³ NaCl in full strength Hoagland's nutrient solution. Distributions of Na, K, Ca, Mg, and Cl in leaf laminae and leaf sheaths at varying ages were determined. Accumulation of Na and Cl in the laminae and sheaths of both lines increased significantly with age at 125 mol m⁻³ NaCl. However, the older laminae and all sheaths of Potohar contained more Na and Cl than those of S24 at the NaCl treatment. There was no effect of age on the distribution of K in laminae and sheaths under NaCl stress. In the salt treatment, lamina K concentration did not differ significantly between lines, whereas sheath K was significantly greater in Potohar than S24. An age-dependent distribution of Ca was observed in laminae of both lines at NaCl treatment, i.e. the younger laminae had slightly lower concentration of Ca than the older leaves. S24 had significantly lower Ca in the sheaths of varying age compared with Potohar, but no such difference was observed in lamina Ca. S24 maintained relatively lower concentrations of K in the sheaths and culms at the NaCl treatment, most of this ion absorbed being transported to the laminae. S24 and Potohar did not differ in K/Na or Ca/Mg ratios in laminae and sheaths, and the pattern of these ratios was uniform in relation to age under salt stress. It is concluded that maintenance of low Na and Cl concentrations in laminae, sheaths of all ages and of culms is an important component of salt tolerance in spring wheat, and the distribution of Na, Cl, Ca, and Mg in the laminae and that of Na, Cl and Mg in the sheaths are age-dependent.

Key-words: ion distribution, salt stress, salt tolerance, spring wheat.

INTRODUCTION

Based upon data from a large number of studies, it is now generally accepted that mesophytes respond to salt stress by partial exclusion of toxic ions from plant parts (Rains 1972; Greenway & Munns 1980; Wyn Jones 1981; Läuchli 1986; Schachtman &

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Munns 1992; Munns 1993; Ashraf 1994). By contrast, no relationship between Na exclusion from the shoots and salt tolerance was found (Alberico & Cramer 1993) for seven lines of maize. Accumulation of ions has been observed in some crop species when subjected to salt stress, e.g. *Lupinus* spp. (Van Steveninck *et al.* 1982), *Lolium perenne* (Ashraf *et al.* 1990), lentil (Ashraf & Waheed 1993), alfalfa (Croughan *et al.* 1978; Ashraf *et al.* 1986; Ashraf & O'Leary 1994).

In a number of studies (Qureshi *et al.* 1980; Wyn Jones 1981; Wyn Jones *et al.* 1984; Ashraf & McNeilly 1988; Gorham *et al.* 1990) a positive relationship has been found between partial exclusion of Na and Cl from plant parts and salt tolerance of spring wheat. In an experiment concerned with the evaluation of some newly developed lines of wheat it was found that the salt-tolerant genotype, S24, had appreciably lower concentrations of Na and Cl in leaves compared with the salt-sensitive genotype, Potohar (Ashraf & O'Leary 1996). Since it was an overall estimation of concentrations of different ions in shoots (a leaf of same age was sampled for ion analysis) of two lines differing in degree of salt tolerance, it was important to assess the extent of accumulation of different ions in leaves of varying ages in the two lines. K, Na, Mg, and Cl are known to move from older to younger leaves via phloem, whereas Ca is generally phloem immobile (Mengel & Kirkby 1987; Marschner 1995). It is thus possible that the two lines which differ in accumulation of different ions in shoots under saline substrate may differ in distribution of these ions from older to younger leaves. Ion distribution also differed between plant organs in different species/cultivars, Na and Cl concentrations of older leaves being greater than those of younger leaves in barley (Greenway 1962) and alfalfa (Ashraf & O'Leary 1994), Na in *Leptochloa fusca* (Bhatti *et al.* 1993), and Cl in beets and onions (Yankovitch 1949) and grapevines (Woodham 1956). Cl concentrations remained stable in laminae of varying ages in *L. fusca* (Bhatti *et al.* 1993). A contrasting pattern of accumulation of tissue K and Na in relation to leaf age, has been observed in different species, e.g. barley (Greenway 1962; Jeschke & Wolf 1985), *Ricinus communis* (Jeschke & Wolf 1988), *Atriplex* spp. (Jeschke & Stelter 1983; Aslam *et al.* 1986), and alfalfa (Ashraf & O'Leary 1994) with high K and low Na concentrations in young leaves, and high Na and low K in older leaves. Such partitioning of Na and K within the shoot was postulated to reflect the preference of phloem for translocation of K (Jeschke 1984). By contrast, no such age-dependent distribution of Na was found in the salt-tolerant sunflower line, Euroflor (Ashraf & O'Leary 1995). These contrasting reports led us to hypothesize that the salt-tolerant and salt-sensitive lines of spring wheat differ in the pattern of distribution of Na, Cl, K, Ca, and Mg in leaves of varying ages to effect the overall differential accumulation of these ions in shoots of these lines.

MATERIALS AND METHODS

Grains of the salt-intolerant spring wheat cv Potohar were obtained from the University of Agriculture Faisalabad, Pakistan, whereas those of the salt-tolerant genotype S24 were harvested from the selection of F_3 grain material derived from a cross, LU26S \times Kharchia, using a concentration (in electrical conductivity) of 24.0 dS m^{-1} of NaCl+CaCl₂ 1:1 ratio (on equivalent wt. basis). All samples were surface sterilized in 5% sodium hypochlorite solution for 8 minutes before experimentation.

In October 1993, 300 grains of each line were sown randomly about 5 mm deep in thoroughly washed sand contained in plastic containers ($32 \times 32 \times 7 \text{ cm}$) with drainage

holes in each bottom. The sand was irrigated on alternate days with 3 L of full strength Hoagland's nutrient solution prepared in tap water (chemical composition of tap water in mol m^{-3} $\text{K}=0.036$, $\text{Na}=1.08$, $\text{Ca}=0.78$, $\text{Mg}=0.08$, $\text{Cl}=0.83$, $\text{pH}=6.91$). The experiment was conducted in a naturally lit glasshouse in which PAR measured at noon ranged from 450 to $1350 \mu\text{mol m}^{-2} \text{s}^{-1}$, relative humidity day/night 60/80% and temperature 21/2°C. After 5 days, seven seedlings per line were transplanted into a plastic pot (21.5 cm diameter and 21.0 cm deep) which contained 6.35 kg of well-washed dry sand. All pots were irrigated for 14 days with full strength Hoagland's nutrient solution. Salt treatments in this solution were begun 19 days after the start of the experiment. The NaCl treatments used were 0 or 125 mol m^{-3} in full strength Hoagland's nutrient solution. This moderate salt treatment was used to get sufficient plant material for analysis since we analyzed five consecutive leaves of varying age individually from each plant, which would have not been possible under very high salt concentration.

The experiment was arranged in a completely randomized design with four replicates, and two salt treatments. Salt treatment was increased daily in aliquots of 50 mol m^{-3} in Hoagland's nutrient solution until the appropriate salt concentration was reached. Treatments continued with the addition of 2 L of the appropriate solution to each pot twice a week. Every day 200 mL of distilled water was added to each pot to compensate for evapotranspiration loss.

Just before the onset of the booting stage plants from each pot were harvested, and the shoots separated into leaf laminae, leaf sheaths and culms. Fresh weights of laminae, sheaths, and culms were recorded. Samples were then dried at 65°C for 1 week and dry weights recorded.

Analysis of ions

For the analysis of Na, K, Ca and Mg, 100 mg of well crushed dry material of the laminae, sheaths and culms was digested in 2–3 mL of concentrated HNO_3 . Lanthanum salt solution was used for the analysis of Ca and Mg. All four cations in the digests were determined with an atomic absorption spectrophotometer (Perkin Elmer 560). Well crushed dry material (50–100 mg) of each of the three different plant parts was extracted in 10 mL of double distilled water at 80°C for 4 hours. Cl concentrations in the extracts were determined with an Orion specific ion electrode.

Statistical analysis of data

Analysis of variance of data for all the parameters was computed using COSTAT computer package (CoHort Software, Berkeley CA), and least significant differences between the mean values were calculated following Snedecor and Cochran (1980).

RESULTS

Fresh and dry weights of laminae and sheaths of leaves of varying age of the salt-tolerant S24 and salt-sensitive Potohar spring wheat lines when grown in sand culture at 0 or 125 mol m^{-3} NaCl are presented in Fig. 1, and corresponding data for culms are presented in Fig. 2. Leaves are numbered in a basipetal direction, leaf 1 being the youngest and leaf 5 the oldest. Data for each variable have been statistically compared within each treatment, since the major objective of the study was to assess any possible relationship between the ion distribution in leaves and leaf age.

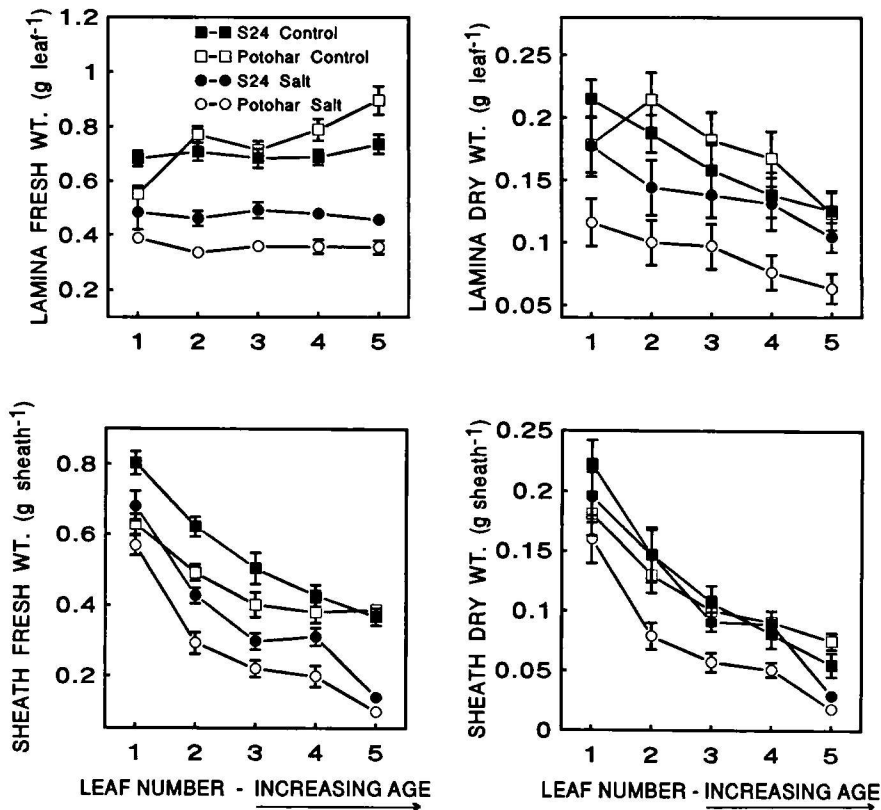


Fig. 1. Fresh and dry weights of laminae and sheaths of leaves of varying ages of a salt-tolerant (S24) and a salt-sensitive (Potohar) spring wheat line just prior to the booting stage in plants grown in sand culture salinized at 0 or 125 mol m⁻³ NaCl in Hoagland's nutrient solution.

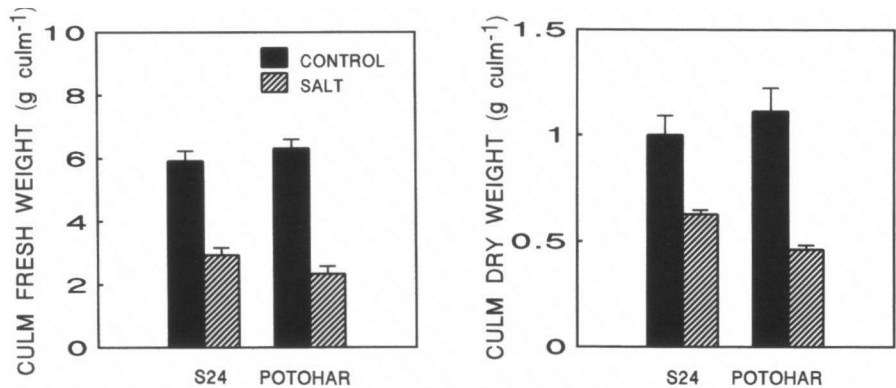


Fig. 2. Fresh and dry weights of culms of a salt-tolerant (S24) and a salt-sensitive (Potohar) spring wheat line just prior to the booting stage in plants grown in sand culture salinized at 0 or 125 mol m⁻³ NaCl in Hoagland's nutrient solution.

In the control treatment, fresh weights of laminae of different age of S24 remained unchanged, whereas those of Potohar were higher in the older laminae than the younger ones. By contrast, lamina fresh matter of both lines was similar at different ages in the NaCl treatment, although all five leaf laminae of S24 had significantly greater fresh weights than those of Potohar. Dry matter of laminae of both lines decreased consistently with age in both control and salt treatments. However, lamina dry weights of S24 were significantly greater than those of Potohar at the NaCl treatment. Fresh and dry matter of leaf sheaths of both lines decreased linearly with age in both treatments, although S24 had significantly heavier leaf sheaths than Potohar in the salt treatment. Culm fresh and dry weights did not differ between lines in the control treatment. By contrast, S24 had significantly greater culm fresh and dry weights than Potohar in the salt treatment.

Lamina Na and Cl concentrations (Fig. 3) increased with age in both lines at 125 mol m⁻³ NaCl, but were higher in the old leaf of Potohar than that of S24. Lamina K of both lines also increased with age in the control treatment, but in the salt treatment the increase in K was from lamina 1 to lamina 4 except lamina 5. Leaf lamina K concentration did not differ between lines at 125 mol m⁻³ NaCl, but in the control treatment Potohar had significantly greater lamina K than S24. Lamina Ca concentrations (Fig. 3) increased with age in both lines in both salt treatments. S24 and Potohar did not differ significantly in laminae Ca in the salt treatment, whereas in the control treatment Potohar had a significantly greater Ca concentration in two older leaves (no. 4 and 5) than those of S24. Lamina Mg concentrations in both lines (Fig. 3) increased with age in the control treatment, whereas no age effect was observed in salt treated plants. However, S24 had a significantly greater ($P < 0.05$) lamina Mg concentration than Potohar in the salt treatment. Lamina K/Na ratios (Fig. 3) of the lines did not differ under salt treatment, or with increasing age.

Sheath Na and Cl concentrations (Fig. 4) of both lines increased significantly ($P < 0.05$) with age under salt treatment, whereas in the control treatment no similar age effect was observed. At 125 mol m⁻³ NaCl, Potohar had significantly greater ($P < 0.05$) Na and Cl concentrations in all the leaf sheaths than S24. Sheath K in both lines and in both NaCl treatments increased with age. Potohar had significantly ($p < 0.05$) higher K in all sheaths than S24. There was no effect of age on sheath Ca concentration in either line. Overall, sheath Ca concentration in Potohar was higher than that of S24 without and with 125 mol m⁻³ NaCl. Sheath Mg (Fig. 4) decreased with age in both lines in the control treatment, whereas in the salt treatment no age effect was found. Potohar had significantly greater sheath Mg than S24 in 125 mol m⁻³ NaCl. Sheath K/Na ratios (Fig. 4) remained almost uniform in both lines in the salt treatment and no consistent pattern in sheath K/Na ratios was found in either line in the control treatment.

Culm Na, K, Mg and Cl concentrations (Fig. 5) were significantly higher in Potohar compared with S24 when grown at 125 mol m⁻³ NaCl, whereas culm Ca did not vary between lines. The lines also did not differ in culm K/Na ratios in the two treatments. Both lines maintained similar Ca/Mg ratios (data not presented) in the laminae, sheaths and culms in the control or salt treatment.

DISCUSSION

Both Na and Cl concentrations in the laminae and sheaths increased with age in both lines under salt stress conditions. Although the salt-sensitive Potohar accumulated

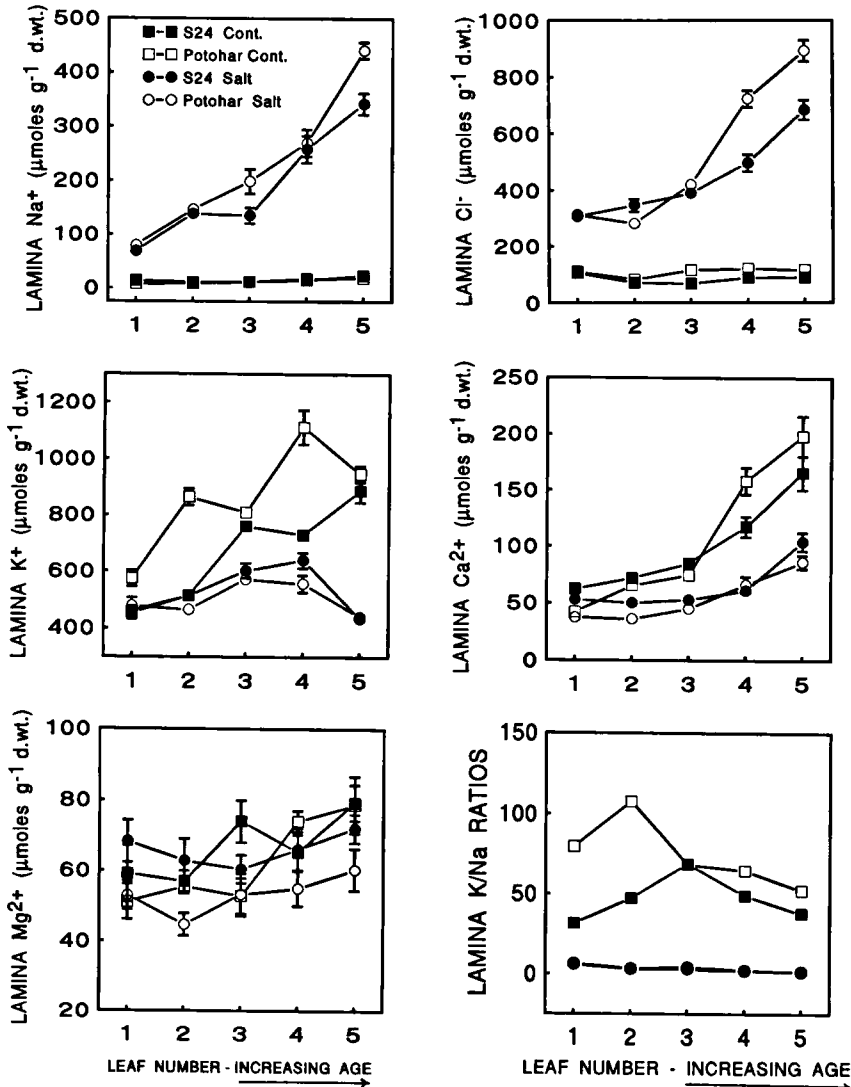


Fig. 3. Concentrations of various ions in the laminae of leaves of varying ages of a salt-tolerant (S24) and a salt-sensitive (Potohar) spring wheat line just prior to the booting stage in plants grown in sand culture salinized at 0 or 125 mol m⁻³ NaCl in Hoagland's nutrient solution.

higher concentrations of Na and Cl in the older laminae compared with the salt-tolerant S24 in the salt treatment, the concentrations of these ions did not differ in the younger laminae. Similarly sheath Na did not differ between lines, although in Potohar all sheaths of different age had greater Cl than those of S24 under saline medium.

It appears that in general, the salt-sensitive Potohar accumulated significantly greater concentrations of Na and Cl in sheaths, culms and only in older leaf laminae than the salt-tolerant S24. S24 accumulated a significantly lower amount of K in leaf sheaths and culms than the salt-sensitive Potohar under saline conditions, most of the K absorbed being transported to leaf laminae, whereas in Potohar the reverse was true. This pattern

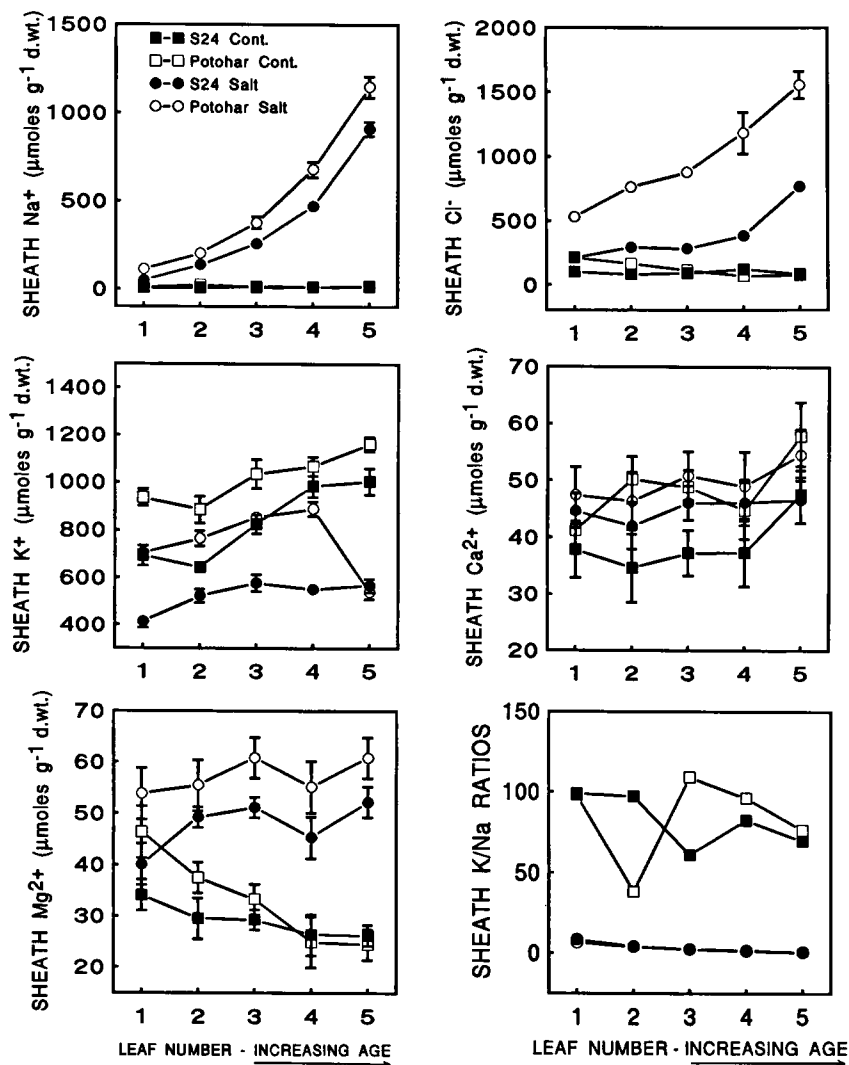


Fig. 4. Concentrations of various ions in the sheaths of leaves of varying ages of a salt-tolerant (S24) and a salt-sensitive (Potohar) spring wheat line just prior to the booting stage in plants grown in sand culture salinized at 0 or $125 \text{ mol m}^{-3} \text{ NaCl}$ in Hoagland's nutrient solution.

of age-dependent distribution of Na in the salt-tolerant S24 and salt-sensitive Potohar is in agreement with early findings in some mesophytes such as *Lupinus albus* (Jeschke *et al.* 1987) and rye, *Triticale* and *Aegilops* (Gorham 1990a, b).

Maintenance of almost uniform K/Na ratios in all laminae and sheaths under salt stress in contrast to control plants clearly shows that despite salt stress there was no age effect in either line. These results, however, are in contrast with previous findings in barley (Greenway 1962; Jeschke & Wolf 1985), *Atriplex* spp. (Jeschke & Stelter 1983; Aslam *et al.* 1986), *Ricinus communis* (Jeschke & Wolf 1988), and *Leptochloa fusca* (Bhatti *et al.* 1993), in all of which high K and low Na concentrations in young leaves and low K and high Na in older leaves were reported.

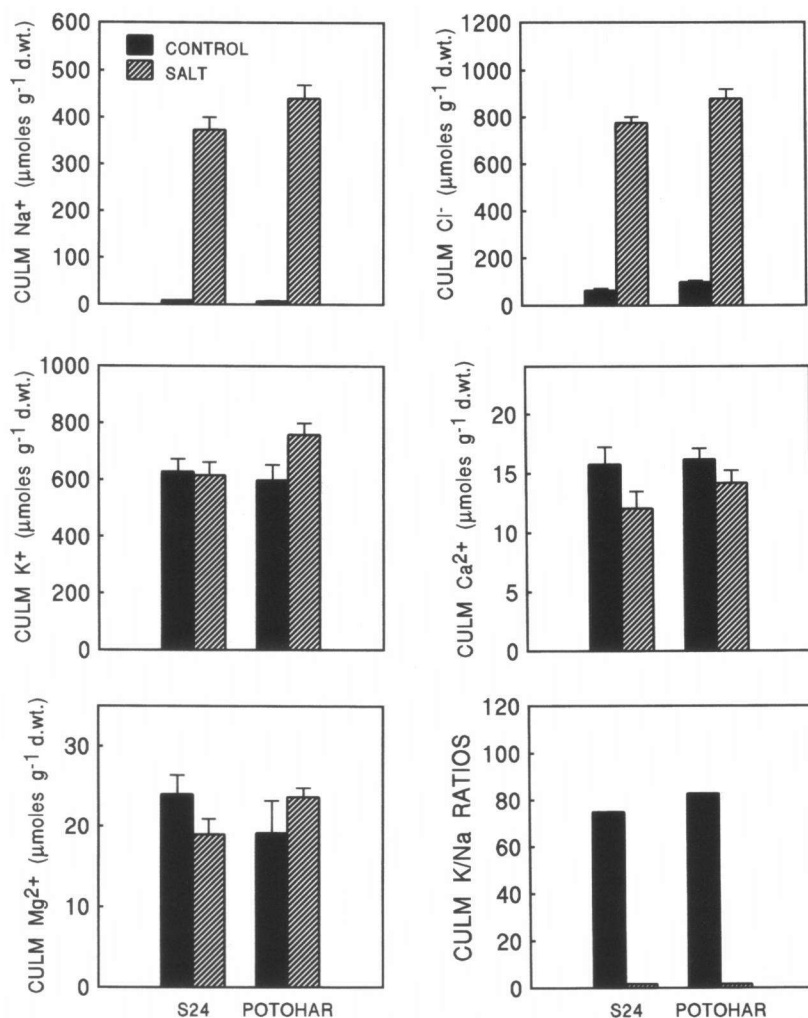


Fig. 5. Concentrations of various ions in the culms of a salt-tolerant (S24) and a salt-sensitive (Potohar) spring wheat line just prior to the booting stage in plants grown in sand culture salinized at 0 or 125 mol m⁻³ NaCl in Hoagland's nutrient solution.

The pattern of distribution of Na, Cl, and K in the laminae and sheaths of S24 and Potohar of wheat can be explained on the basis of the argument that salt-tolerant and salt-sensitive plants have similar patterns of ion distribution, and they only differ in degree (Jennings 1968). Maintenance of higher concentrations of Na in leaf laminae and sheaths of older leaves of Potohar can be related to the argument that turgor of old leaves depends on Na which is energetically less expensive than K (Jeschke 1984).

Efficiency of K translocation from older to younger leaves is considered an important component of salt tolerance (Jeschke & Wolf 1988; Bhatti *et al.* 1993). However, lack of difference in K distribution in laminae of the two lines of wheat examined in this work which differ in degree of salt tolerance, shows that there was not any difference in efficiency of K mobilization and re-translocation in the two lines. These results are

in close conformity with the earlier findings in alfalfa (Ashraf & O'Leary 1994) and sunflower (Ashraf & O'Leary 1995) in which salt-tolerant and salt sensitive lines did not differ in K distribution in laminae under salt stress.

The pattern of Ca concentration in the laminae appeared to be age-dependent in both lines, under both saline and non-saline conditions. This age-dependent increase in Ca concentrations in leaf laminae resembles that found in *R. communis* (Jeschke & Pate 1991) and *L. fusca* (Bhatti *et al.* 1993), although no age-dependent effect was observed in sheath Ca distribution. This pattern of Ca accumulation in leaf laminae may have occurred due to its low phloem mobility (MacRobbie 1971; Armstrong & Kirkby 1979; Marschner 1995). It is also possible that lower concentrations of Ca in younger leaves than in older leaves may have been due to the limited supply of Ca via xylem to young leaves (Marschner 1995). By contrast, since Mg is easily transported through the phloem (MacRobbie 1971; Mengel & Kirkby 1987; Marschner 1995), it readily moves from older leaves to younger and growing leaves. The pattern observed for Mg concentrations in the laminae of both lines was similar to that for Ca, except in non-stressed sheaths, suggesting that xylem import exceeded phloem export similarly in both lines. These results are at variance with those for white lupin and *R. communis* in which a considerable amount of xylem imported Mg was re-translocated from the laminae (Jeschke *et al.* 1987; Jeschke & Pate 1991).

From the partitioning of Ca and Mg concentrations in the laminae, it is noticeable that Mg concentrations exceeded those of Ca in younger leaves under salt stress and overall Ca/Mg ratios were lower in younger leaves than older leaves. This is similar to the findings of Jeschke and Pate (1991) who found that in *R. communis* Mg concentration exceeded that of Ca in young leaves. Low Ca concentrations in the young laminae can possibly occur due to the limited supply of xylem transported Ca to low transpiring organs such as young leaves (Marschner 1995). Ca concentrations in laminae of S24 and Potohar under salt treatment were significantly lower than those of the control treatment, contrasting with equivalent data for *L. fusca* (Bhatti *et al.* 1993) in which Ca concentrations of salt-stressed plants were almost equal to those of non-stressed plants. Interestingly a reduction in leaf Ca concentration under salt stress is a common phenomenon in most mesophytes (Greenway & Munns 1980).

From this examination of ion contents of different plant parts of a salt-tolerant and salt-sensitive wheat line, it is clear that in both lines leaf sheaths accumulated far more Na and Cl than culms and leaf laminae. A similar pattern of preferential partitioning of Na and Cl has been reported for barley (Greenway 1962). It is also evident that, at least for these two spring wheat lines, maintenance of low concentration of Na and Cl in leaf blades, sheaths, and culms is an important component of salt tolerance, and Na, Cl, Ca and Mg distribution between the leaf laminae and leaf sheaths is age-dependent. The results presented here so far substantially support the major hypothesis of the study that the salt-tolerant and salt-sensitive lines differed in the extent of distribution of Na and Cl in leaves of varying ages, which led to the overall low concentrations of Na and Cl in shoots of salt-tolerant, S24 and high in salt-sensitive, Potohar.

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