Modification of foliar solute concentrations by calcium in two species of wheat stressed with sodium chloride and/or potassium chloride

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The effects of saline-stresses due to different salts on growth and on foliar solute concentrations in seedlings of two species of wheat that differed in salt tolerance, *Triticum aestivum* L. cv. Probred and *Triticum turgidum* L. (Durum group) cv. Aldura, were studied. *Triticum aestivum* is the more salt tolerant species. The salts used were NaCl, KCl, a 1:1 mixture of NaCl and KCl, and these same monovalent cation salts but mixed with $CaCl_2$ at a ratio of 2:1 on a molar basis of monovalent to divalent cation salts. Growth inhibition of both species was a function of media osmotic potentials. There was a small additional inhibition of growth if KCl replaced NaCl as the salinizing salt. $CaCl_2$ had little or no effect on growth inhibition beyond an osmotic effect except at the most severe stress level, i.e. when Ca^{2+} concentrations may be excessive. The amounts of water-soluble Ca^{2+} were about 10 times higher in leaves of plants grown in the presence of $CaCl_2$ than in its absence, but its concentrations even then were approximately 10% or less of those of the monovalent cations. Including $CaCl_2$ in growth media resulted in a reduction in the amount of Na^+ in leaves compared to the amounts in plants grown at the same osmotic potential but in the absence of $CaCl_2$. *Triticum aestivum* was a better Na^+-excluder than *T. turgidum*. With $CaCl_2$ in media, $(Na^+ + K^+)$ remained relatively constant or increased by small amounts as media osmotic potentials decreased. In the absence of $CaCl_2$, $(Na^+ + K^+)$ increased by large amounts when media osmotic potentials were at −0.6 and −0.8 MPa. It is concluded that the accumulation system in leaves for monovalent cations was under feed-back control, and that this control mechanism was inhibited by high media concentrations of Na^+ and/or K^+. Sucrose was present at a constant amount under all growth conditions. Proline started accumulating when $(Na^+ + K^+)$ exceeded a threshold value of 200 μmol (g fresh weight)$^{-1}$. Its concentration was 5 to 13% of that portion of $(Na^+ + K^+)$ that exceeded the threshold value.

Key words – Betaine, calcium chloride, control mechanisms, inorganic solutes, osmotic adjustment, potassium chloride, proline, salt tolerance, sodium chloride, sucrose, *Triticum aestivum, Triticum turgidum,* wheat.

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Introduction

Salt tolerance of plants may be measured according to several different criteria (Maas and Hoffman 1977). These tolerances are usually expressed as if they were a quantitatively constant property of the organism. Actually, salt tolerance measurements are affected by environmental conditions and other parameters. A few examples from the many in the literature are temperature and humidity (Bernstein 1974, Nieman and Poulsen 1967), light intensity (Maas and Nieman 1978, Meiri et al. 1982), ionic effects (Bernstein 1975, Grieve and Fujiyama 1987, Maas and Nieman 1978) and physiological age or stage of growth (Maas and Grieve 1987, Maas et al. 1983, 1986, Schubert and Läuchli 1986).

The present article is concerned with describing the

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nodifying effects, if any, of the ionic composition of alinized media (Ca^{2+} combined with Na^+ and/or K^+) on oncentrations of several tissue solutes believed to be nvolved in osmotic adjustment in *Triticum aestivum* and *T. turgidum*. These two wheat species were selected for his study, because they differ in their salt tolerances; *T. aestivum* is the more salt tolerant one (Francois et al. 1986). One conclusion drawn from a previous study with these same species (Weimberg 1987) was that both species were efficient Na^+-excluders, but that *T. aestivum* excluded Na^+ to a greater degree than did *T. turgidum*. The question arises as to how well the plants would respond to salinity if KCl partially or totally replaced NaCl as the salinizing salt. In addition, in the previous study, the plants were treated with a salt mixture composed of a 2:1 ratio on a molar basis of NaCl and $CaCl_2$, respectively. Therefore, it seemed of interest to determine the effects not only of K^+ but also of Ca^{2+} on growth and on solute accumulation in leaves of young salt-stressed plants.

Age affects the salt tolerance of these two species of wheat (Francois et al. 1986, J. A. Poss and E. V. Maas, unpublished results) as well as solute concentrations in leaves of saline-stressed plants (Weimberg 1987). These solute concentration data were obtained with plants that were 55 and 96 days old, two stages of growth that were well advanced into the plants' growth cycle. To complete a study of the interrelationship of age and salinity on growth and solute concentrations in leaves, the present article reports results obrained with younger plants; 3-week-old wheat seedlings.

Abbreviations – ($Na^+ + K^+$), the sum of foliar Na^+ and K^+; OP, osmotic potential.

Materials and methods

Batches of 10 g of seeds (approximately 200 seeds) of *Triticum aestivum* L. cv. Probred, and *T. turgidum* L. (Durum group) cv. Aldura, were soaked in aerated water for 6 h. Each batch was spread on moist cheese cloth supported by a stainless steel wire screen and placed in a 4-l plastic pot over 0.5 m*M* $Ca(NO_3)_2$. The liquid was 5 to 10 mm below the screen. The procedure for germinating the seeds in the dark and then growing the seedlings in liquid media in the light in growth chambers, the composition of the liquid media, the light intensity and the photoperiods were the same as described previously for *Sorghum bicolor* (Weimberg et al. 1984).

The seedlings were 4 days old when they were transferred to culture media and allowed to grow in the light. For the first 24 h after transfer, the plants were grown without any saline stress. Then media were salinized with one of the following 6 stock salt solutions: NaCl (2.3 *M*), NaCl + $CaCl_2$ (1.33 and 0.66 *M*, respectively), KCl (2.3 *M*), KCl +$CaCl_2$ (1.33 and 0.66 *M*, respectively), NaCl + KCl (1.15 *M* of each) and NaCl + KCl + $CaCl_2$ (0.66 *M* of each). A volume of 10 ml of any stock solution added to one l of media reduced the osmotic potential (OP) of the medium by 0.1 MPa. The OP's of the media were reduced by 0.1 MPa at 12 h intervals until the desired level of salinity was reached. Also, liquid lost from the growth medium was replaced by water every 24 h to keep the volume constant.

Plants were harvested 21 days after germination was begun and after the lights had been turned on for 6 h on the day of harvest. Growth was measured as the fresh weight of shoots immediately after the tissue had been cut from the plant. Whole shoots were used for weight measurements, but only the top 5 to 8 cm of the shoots were used for extraction. This top portion of shoots

Tab. 1. Shoot weights ±SD (n = 4) of 3-week-old seedlings grown under saline conditions. Shoot weights of plants grown under non-saline conditions were 33.5±2.7 and 40.3±2.6 g (100 plants)$^{-1}$ for *T. turgidum* and *T. aestivum*, respectively. Plants of *T. aestivum* were not grown at −0.2 MPa. No plants of *T. turgidum* survived in the −0.8 MPa growth condition. Osmotic potentials are those due to the added salts.

Medium osmotic potential, −MPa	Shoot weight, g (100 plants)$^{-1}$					
	NaCl	NaCl+$CaCl_2$	KCl	KCl+$CaCl_2$	NaCl+KCl	NaCl+KCl+$CaCl_2$
T. turgidum						
0.1	33.9±3.1	32.9±2.8	33.4±2.5	38.6±3.2	31.8±3.9	38.0±4.0
0.2	27.0±4.0	28.6±3.5	27.7±3.8	27.7±4.1	26.8±3.8	26.9±5.0
0.3	27.6±3.1	28.1±3.3	24.8±3.2	27.5±2.9	26.4±3.5	28.3±4.0
0.4	25.6±4.1	23.9±2.5	21.7±3.9	22.6±3.6	22.3±3.8	24.2±6.8
0.6	22.6±2.9	22.0±2.2	15.5±1.8	18.3±3.1	21.6±1.5	18.4±3.1
T. aestivum						
0.1	38.7±2.6	38.6±3.2	35.5±5.0	40.0±5.8	37.9±3.3	36.4±3.9
0.3	34.5±3.1	33.0±2.6	27.9±3.1	30.7±3.8	32.9±3.8	31.5±3.5
0.4	30.0±3.5	27.0±3.8	26.6±3.0	25.3±4.1	30.2±3.2	23.3±3.9
0.6	26.1±3.0	21.7±2.5	20.8±2.8	22.3±2.8	24.0±2.6	24.7±2.4
0.8	21.9±2.1	22.7±1.8	14.5±1.9	16.6±1.9	20.8±1.9	14.2±2.9

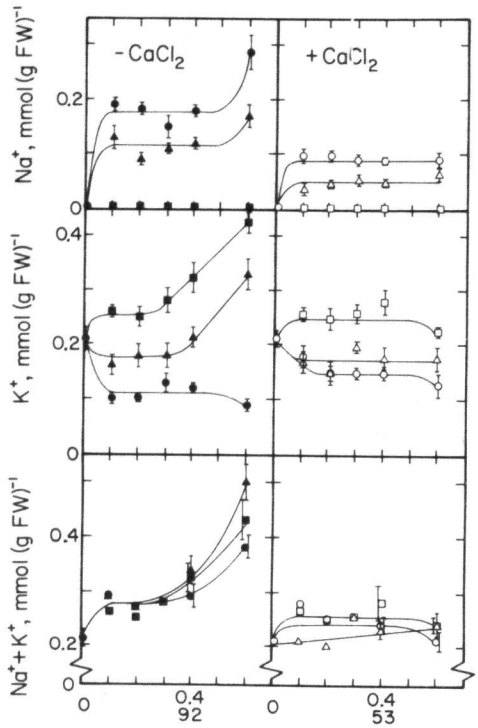

Fig. 1. Monovalent cation concentrations in leaves of *Triticum turgidum* stressed with salts of differing ionic composition. Symbols representing media salts are: ●, NaCl; ○, NaCl + $CaCl_2$; ■, KCl; □, KCl + $CaCl_2$; ▲, NaCl + KCl; and △, NaCl + KCl + $CaCl_2$. The OP's and concentrations of monovalent salts in media, given on the x-axis, are in addition to the OP of, and cation concentrations in, basic growth media. The OP of non-stressed media is approximately −0.04 MPa and cation concentrations are: Na^+, none; K^+, 3 m*M*; and Ca^{2+}, 2.5 m*M*. All values are means (n = 4). Standard deviations are shown for most data points but are omitted for (Na^+ + K^+) values at the milder stress conditions, because they overlapped to a considerable degree. Standard deviations are shown for the remaining (Na^+ + K^+) data but, for clarity, the SD bars for NaCl grown plants are shifted slightly to the right of the data points, the SD bars for KCl grown plants are shifted slightly to the left, and the bars for plants grown in a 1:1 mixture of NaCl and KCl are drawn through the data point.

consisted predominantly of the first leaf which was the only mature leaf on 3-week-old seedlings. Amounts of ca 4 g of leaf tissue (but accurately weighed) were cut from the shoots, rinsed quickly in water to remove surface salts and then extracted with toluene (Weimberg et al. 1981, 1984). Solute concentrations in crude extracts were assayed by the same techniques employed earlier for *S. bicolor* (Weimberg et al. 1984) and wheat species (Weimberg 1987). The solutes measured were Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, glucose, fructose, sucrose, betaine and proline.

The entire experiment was repeated once. The plants in the second replicate were grown ca 6 months after the first set of plants. Tissues were harvested and extracted in duplicate in each replicate. Thus, all the growth and solute concentration data reported in this article are the mean of the 4 measurements ± SD.

Results

Growth

The fresh weight of leaves of saline-stressed plants of *Triticum aestivum* and *T. turgidum* were measured when the plants were 21 days old (Tab. 1). Only healthy-looking plants were selected for harvesting. At all levels of stress, some plants in each pot were wilting, and these were avoided at harvest time. The proportion of wilting plants increased as the severity of the stress increased until, at −0.8 MPa for *T. turgidum* and −1.0 MPa for *T. aestivum*, 100% of the plants had wilted and collapsed by day 21. In media containing either 100 or 50% NaCl but lacking added $CaCl_2$, the decrease in weight of both species caused by salinity was a function of the OP of the medium. When NaCl was replaced

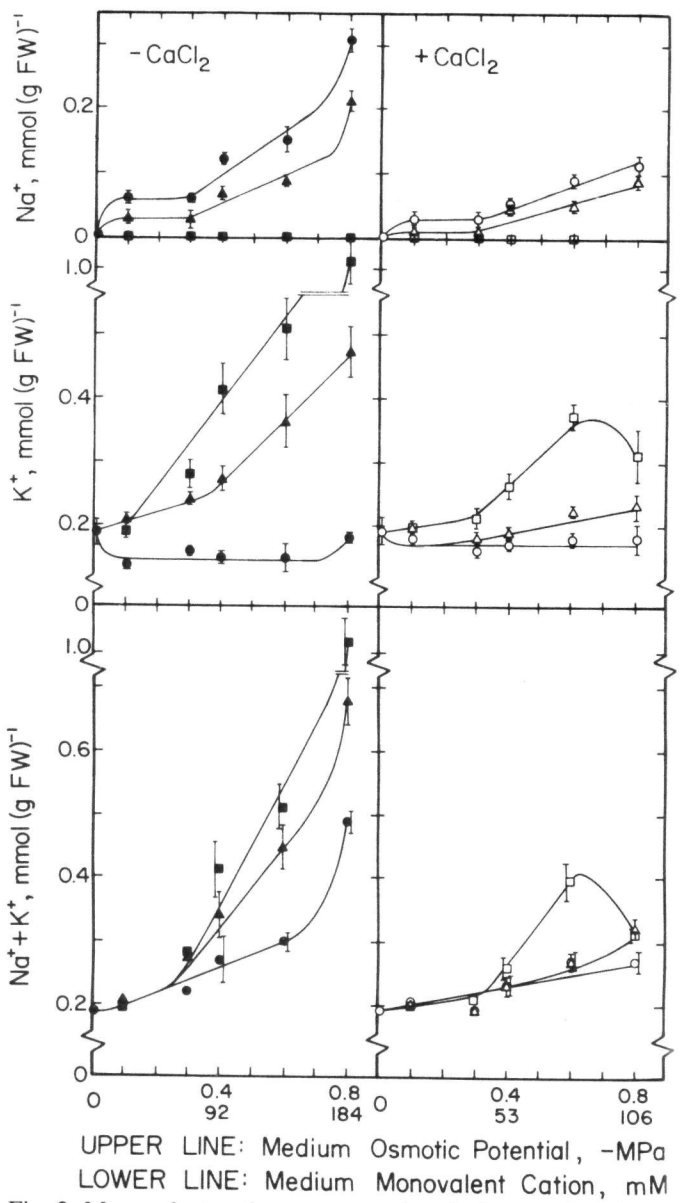

Fig. 2. Monovalent cation concentrations in leaves of *Triticum aestivum* stressed with salts of differing ionic composition. Conditions, symbols and SD bars are the same as for Fig. 1.

completely by KCl, there was a somewhat greater inhibition of growth at each level of OP than with media containing some Na^+. *Triticum aestivum* was the more salt tolerant of the two species, because growth was less inhibited by salt than in *T. turgidum* at each stress level, but the differences in growth were not as pronounced as with older plants (J. A. Poss and E. V. Maas, unpublished results). This result could be due to the fact that the plants in this experiment were grown in liquid media, while the plants in the study by Poss and Maas were grown in sand and were irrigated at intervals with growth media.

Replacing a portion of either NaCl or KCl with $CaCl_2$ but keeping media OP's constant had no effect on growth. If the salinizing salts contained all 3 cations, the growth inhibition by this type of salinity was the same as with $CaCl_2$ plus KCl.

Sodium ions

At 3 weeks of age, the two species of wheat were not as successful in excluding Na^+ from shoots as the older plants (Weimberg 1987). The 2 species accumulated Na^+ in differing patterns (Figs 1 and 2). When stressed with NaCl without added $CaCl_2$, the amounts of accumulated Na^+ in *T. turgidum* were the same at −0.1 to −0.4 MPa. However, the concentration of foliar Na^+ at −0.6 MPa was nearly twice that at the more moderate stress levels. In *T. aestivum,* the concentrations of foliar Na^+ at −0.1 and −0.3 MPa were less than in *T. turgidum* at −0.1 to −0.4 MPa. Na^+ increased with decreasing OP's until, at −0.6 MPa, the amount of foliar Na^+ in *T. aestivum* was equal, perhaps fortuitously, to the amount in *T. turgidum* at −0.4 MPa. In *T. aestivum,* Na^+ concentrations at −0.8 MPa were double those at −0.6 MPa and essentially equal to the amount in *T. turgidum* at −0.6 MPa.

Media salinized with NaCl plus $CaCl_2$ contain 42% less Na^+ than media salinized to the same OP with NaCl alone. In *T. turgidum* plants stressed with NaCl plus $CaCl_2$, the concentration of foliar Na^+ was still constant at −0.1 to −0.4 MPa, but it was 30 to 50% less than in plants stressed with NaCl alone (Fig. 1). At −0.6 MPa, foliar Na^+, instead of increasing, remained constant at the same value as at −0.1 MPa. In *T. aestivum,* the concentrations of Na^+ were also 30 to 50% less than in plants stressed with NaCl alone at any one OP ranging from −0.1 to −0.6 MPa (Fig. 2). At −0.8 MPa, Na^+ did not double in concentration but increased by a smaller increment that was consistent with the pattern of increase observed at the milder levels of stress.

Media salinized with a 1:1 mixture of NaCl and KCl contain 50% less Na^+ than media salinized with only NaCl. The pattern of change in foliar Na^+ concentrations under these conditions was the same as that described above; however, the amounts of Na^+ were 30–50% less. Including $CaCl_2$ in media reduced the amount of Na^+ in tissue even further but had no effect on the overall pattern. Plants grown in the absence of NaCl but salinized with KCl contained, of course, only trace amounts of foliar Na^+.

The sum of sodium and potassium ions ($Na^+ + K^+$)

The two species accumulated K^+ in controlled patterns that were related to the sum of the concentrations of $Na^+ + K^+$ in shoot tissue. In the curves for ($Na^+ + K^+$) levels in *T. turgidum* grown in media with $CaCl_2$ (Fig. 1), the standard deviations for the data points at each stress level overlapped, indicating that there are no significant differences in the 3 curves. The ($Na^+ + K^+$) levels remained constant at an average value of 0.24 ± 0.02 mmol (g fresh weight)$^{-1}$ for all saline treatments, beginning with −0.1 MPa, in which the medium contained $CaCl_2$. However, if $CaCl_2$ was omitted, ($Na^+ + K^+$) was constant at an average value of 0.28 mmol (g fresh weight)$^{-1}$ in plants exposed to OP's of −0.1 to

Tab. 2. Ratio of Cl^- to ($Na^+ + K^+$) in leaves of salt-stressed plants. SD are omitted but they ranged from ± 0.02 for the smaller values to ± 0.08 for the largest values. Osmotic potentials are the decreased potentials due to added salts.

Medium osmotic potential, −MPa	Ratio of $Cl^-/(Na^+ + K^+)$ in leaves					
	NaCl	NaCl+ $CaCl_2$	KCl	KCl+ $CaCl_2$	NaCl+KCl	NaCl+KCl+ $CaCl_2$
T. turgidum						
0.1	0.44	0.44	0.45	0.50	0.46	0.67
0.2	0.48	0.52	0.52	0.56	0.44	0.70
0.3	0.43	0.75	0.76	0.70	0.47	0.77
0.4	0.48	0.75	0.50	0.75	0.49	0.74
0.6	0.45	0.76	0.79	0.65	0.70	0.71
T. aestivum						
0.1	0.44	0.50	0.43	0.69	0.49	0.75
0.3	0.46	0.58	0.46	0.67	0.52	0.89
0.4	0.59	0.70	0.70	0.69	0.53	0.74
0.6	0.63	0.81	0.69	0.63	0.47	0.74
0.8	0.57	0.85	0.90	1.16	0.49	0.84

−0.3 MPa but increased 40 to 90% as media OP's decreased further to −0.6 MPa.

$(Na^+ + K^+)$ in *T. aestivum* growing in media containing $CaCl_2$ increased approximately 50% as media OP decreased from −0.1 to −0.8 MPa (Fig. 2). There is one result at −0.6 MPa in plants treated with KCl that did not fit this pattern. If $CaCl_2$ was omitted, the increase in $(Na^+ + K^+)$ over this same range of media OP's was 250% with media salinized with NaCl, 350% for a 1:1 mixture of NaCl and KC1 and 500% with KCl.

Ca^{2+} and Mg^{2+} ions

The amounts of these two cations that could be extracted by a toluene-water treatment from leaves of non-stressed plants of both species averaged 4±2 μmol (g fresh weight)$^{-1}$. Salinity in the absence of $CaCl_2$ had no effect on their concentrations. Therefore, these ions are unimportant in both species in terms of providing sufficient water-soluble solute to affect osmotic adjustment of the tissue. Addition of $CaCl_2$ to growth media caused a 7- to 10-fold increase in extractable Ca^{2+}, but the amount was constant under all saline conditions.

Chloride ions

Ca^{2+} had only a small influence on the amounts of Cl^- that accumulated at any one level of stress. Cl^-: $(Na^+ + K^+)$ ratios, in general, ranged from 1:2 to 3:4 if media lacked $CaCl_2$ and were 3:4 if $CaCl_2$ was included (Tab. 2). The only exception was in *T. aestivum* subjected to −0.8 MPa due to KCl or KCl plus $CaCl_2$. At this level of stress, the ratios shifted to 1:1 under both growth conditions.

Betaine

Unlike older plants (Weimberg 1987), the young plants of this experiment lacked detectable amounts of betaine except for *T. turgidum* subjected to the most severe level of KCl stress in the absence of $CaCl_2$. Under this condition, a trace amount of ca 1 μmol (g fresh weight)$^{-1}$ was measured.

Sucrose, glucose and fructose

Salinity had no effect on the concentrations of these sugars. Sucrose concentrations in leaves of both species were equal under all growth conditions at an average of 25±4 μmol (g fresh weight)$^{-1}$. The other sugars were barely detectable in extracts.

Proline

Proline increased linearly in relation to $(Na^+ + K^+)$ in both species in media without added $CaCl_2$. Its concentration was 6% of that part of $(Na^+ + K^+)$ that exceeded 200 μmol (g fresh weight)$^{-1}$ (Fig. 3). The only exception

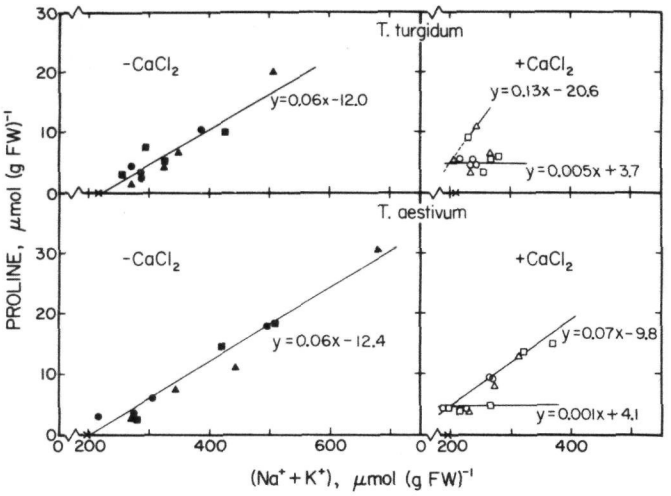

Fig. 3. Proline content of leaves as a function of $(Na^+ + K^+)$. Results with non-stressed plants are shown by the symbol X. All other symbols are the same as for Fig. 1.

was in *T. aestivum* plants grown in KCl media at −0.8 MPa. The proline level in leaves under this condition was 70 μmol (g fresh weight)$^{-1}$, about 40% higher than would be expected from the calculated linear pattern. Consequently, this data point is omitted from Fig. 3, and it was not included in the calculation of the linear regression line for *T. aestivum*. The calculated linear regression line showed a theoretical threshold value of 200 μmol (g fresh weight)$^{-1}$ in both species below which there should be no proline in the tissue. In actual fact, such a low concentration of $(Na^+ + K^+)$ was almost never measured even in non-stressed plants.

Including $CaCl_2$ in growth media caused the appearance of some compound in extracts that interfered with the proline assay. However, this interfering substance was present at a constant amount in all plant extracts (see the linear regression lines with nearly zero slopes in Fig. 3). Another linear regression line was calculated for the proline data points for *T. aestivum* that exceeded the value of the interfering substance. This line had a slope of 6% and intersected the line for the interfering substance at a point where $(Na^+ + K^+)$ was near 200 μmol (g fresh weight)$^{-1}$ (Fig. 3). Thus, the pattern for proline accumulation in *T. aestivum* was the same for plants grown in the absence and presence of $CaCl_2$. There was one difference in the conditions, though. Plants grown in media salinized with only monovalent salts accumulated proline when $(Na^+ + K^+)$ exceeded the threshold value and was independent of the degree of stress. Plants grown in the presence of $CaCl_2$ required both that the concentration of $(Na^+ + K^+)$ exceeded 200 μmol (g fresh weight)$^{-1}$ and that the plants were grown at a stress level of −0.6 MPa or lower.

Such a clear-cut similarity in proline accumulation patterns between plants of *T. turgidum* grown in the presence or absence of $CaCl_2$ was not obtained. For *T. turgidum* grown in the presence of $CaCl_2$, there were only 2 data points for proline accumulation that exceeded the value of the interfering substance (Fig. 3).

These were data points for plants grown at −0.6 MPa in media salinized with KCl + $CaCl_2$ or with a 1:1:1 mixture of all 3 salts. The slope of a straight line connecting these two points was 13%, a slope twice as high as the one for *T. turgidum* plants treated with monovalent cations alone. However, since there are only two data points available for calculating the slope, there is some justification for doubting the accuracy of this 13% value. On the other hand, evidence supporting the accuracy of this slope is that the extrapolated line crossed the line for the interfering substance at a point corresponding to a value for ($Na^+ + K^+$) that was very close to 200 μmol (g fresh weight)$^{-1}$.

Discussion

Inorganic ions flowing from the external environment in the root zone, through the plant, to the leaves where they accumulate, pass through several cell types, each with specific control and transport systems for the individual ions. Whole plant experiments, such as the present study, provide no information on such cellular systems. Instead, they measure the cumulative influence of these systems on ion levels in leaves. Although the pattern of accumulation of Na^+ and K^+ in leaves of *Triticum turgidum* and *T. aestivum* differed, there were enough similarities to permit the development of an explanation that would be applicable to both species. The proposed model is based on the assumption that the collective accumulating systems for monovalent cations in whole plants growing under steady-state environmental conditions behave as if they were a single system and, therefore, Na^+ and K^+ are competing for the same active sites (of undefined nature) for accumulation. Consequently, the differing relative amounts of Na^+ and K^+ in leaf tissue would be determined by the differing affinities of these active sites for K^+. In *T. aestivum*, the pattern of Na^+ accumulation conformed to what would be expected by the Law of Mass Action, i.e. Na^+ in shoots increased as media Na^+ levels increased, both when media K^+ concentrations remained constant and when media K^+ increased equally with Na^+ (Fig. 2). This was the pattern in plants of *T. aestivum* subjected to mild and moderate levels of stress due to monovalent cations in the absence of added Ca^{2+} and at all levels of stress (with the one exception noted in the text) if media were salinized with salt solutions containing one or both monovalent cations and Ca^{2+}.

The accumulating system in *T. turgidum* probably had a lower affinity for K^+ than the one in *T. aestivum*, because Na^+ concentrations were higher in *T. turgidum* than in *T. aestivum* at each stress level and so were the $Na^+ : K^+$ ratios (Fig. 1). In addition, the Na^+ accumulation pattern differed in the two species in that Na^+ levels in *T. turgidum* were apparently equal at all levels of stress due to monovalent cations plus added Ca^{2+}. If Ca^{2+} was omitted from the salinizing salt solutions, the amounts of Na^+ were higher but still equal at all stress levels except the most severe ones. The deviations from this pattern at severe stress levels will be discussed later. ($Na^+ + K^+$) was also constant, indicating that the accumulating system was under control of a feed-back mechanism [also called 'set points' (Pasternak 1987)] that limited the amount of ($Na^+ + K^+$) in shoots, and that the feed-back mechanism was independent of stress. Since the accumulating system of *T. turgidum* had a lower affinity for K^+, relative to the system in *T. aestivum*, it is possible that the ratios of Na^+ and K^+ being assimilated increased by only small increments as Na^+ concentrations in media increased. Thus, by the time the control system prevented the accumulation of more ($Na^+ + K^+$) [i.e. the steady-state level of ($Na^+ + K^+$) had been reached], the differences in the amounts of Na^+ accumulated as stress levels increased would be too small to be detected by the assay methods used in these experiments.

The feed-back control system in *T. aestivum* differed slightly from the system in *T. turgidum* in that ($Na^+ + K^+$) increased with decreasing media OP's. However, the 50% increase in ($Na^+ + K^+$) at −0.8 MPa compared to non-stressed plants was small compared to the increase of inorganic solute concentrations in growth media. In both species, the feed-back control mechanism, in turn, appeared to be inhibited by monovalent cations with K^+ being more toxic (or inhibitory) than Na^+. However, in these experiments, the only salinity conditions in which media monovalent cation concentrations were high enough to measurably affect the feed-back control systems were when salinity was due to monovalent salts without added Ca^{2+}. This pattern of a constant amount of ($Na^+ + K^+$) accumulating in plants growing in media salinized with increasing amounts of monovalent cations has also been reported in *Thinopyrum* (= *Agropyron*) *elongatum*, another member of the Triticeae (Weimberg 1986). The effect of Ca^{2+} on the system in *T. elongatum* has not yet been studied.

Proline accumulation in wheat seedlings (Fig. 3) followed the pattern reported in several other species (Voetberg and Stewart 1983, Weimberg 1986, Weimberg et al. 1984). In plants grown in media without added $CaCl_2$, there was a threshold value for ($Na^+ + K^+$) of 200 μmol (g fresh weight)$^{-1}$ before proline would begin to accumulate. Above the threshold value, proline concentrations increased proportionately with increasing concentrations of the inorganic foliar solutes. For plants grown in the presence of Ca^{2+}, the conditions for proline accumulation were not only that ($Na^+ + K^+$) exceed the threshold value, but also that the plants were simultaneously subjected to severe saline stress. Except for this latter added requirement, the pattern of proline accumulation was the same.

Betaine was absent in the extracts of these young plants. This may be contrasted to the presence of this compound in older plants in quantities proportional to the degree of stress to which the plants were subjected (Weimberg 1987). There are other reports in the litera-

ture of young plants lacking betaine while older plants did contain the compound (*Sorghum bicolor*: Grieve and Maas 1984, Weimberg et al. 1984; *Trinopyrum* (= *Agropyron*) *elongatum*: Weimberg 1986, Weimberg and Shannon 1988).

Sucrose was the one organic compound whose pattern of change due to salinity was qualitatively different at each of 3 stages of growth. In previous work (Weimberg 1987) it was shown that sucrose was essentially not present in 55-day-old non-stressed plants but its concentration increased as the plants were subjected to more severe stress conditions. This result resembled those observed in *S. bicolor* (Weimberg et al. 1984). In 96-day-old plants, sucrose was present in leaves of non-stressed plants and those subjected to mild stress, but the sugar then decreased as the stress conditions became more severe. In the present study with 3-week-old plants, sucrose was present in leaves at low concentrations that were unaffected by media OP's or the ionic composition of the salinizing salts. This result resembled sucrose levels as affected by salinity in seedlings of *T. elongatum* (Weimberg 1986).

It is unknown how extensive in the plant world are the patterns of uptake of monovalent cations as described here. This subject requires further investigation. However, it does appear that a different pattern exists in *Sorghum bicolor* (Weimberg et al. 1984). The concentrations of foliar K^+ remained relatively steady and Na^+ increased in *S. bicolor* treated with NaCl or Na_2SO_4 as media OP's decreased. This result indicates that Na^+ and K^+ do not compete for the same sites of their respective accumulating systems in *S. bicolor*. However, assuming that there is a feed-back control mechanism in *S. bicolor*, the mechanism was inhibited by high concentrations of media K^+.

From the data concerning inorganic monovalent cation concentrations in leaves, the function of these ions in osmoregulation may be interpreted in one of 2 ways. According to one interpretation, the constancy of ($Na^+ + K^+$) in *T. turgidum* and its small increase in *T. aestivum* as media OP's decreased indicate that the uptake and total amount of these ions in leaves are neither controlled by, nor controlling of, turgor. This was also concluded from the data for foliar solute concentrations in older wheat plants (Weimberg 1987) and from data concerning water relations in living wheat plants (Munns and Termaat 1986). This conclusion appears applicable to *T. elongatum* (Weimberg 1986) and tobacco cell suspensions (Binzel et al. 1987) as well. In other words, inorganic ions have no role in osmoregulation. If so, the mechanism of osmoregulation and the compounds utilized for osmotic adjustment in wheat are still unknown.

A different interpretation may be developed by comparing inorganic ion concentrations in leaves of saline-stressed wheat plants with those in *S. bicolor* (Weimberg et al. 1984). The ($Na^+ + K^+$) concentration in non-stressed plants of *S. bicolor* was approximately 100 μmol (g fresh weight)$^{-1}$. This value increased with decreasing media OP's and reached over 200 μmol (g fresh weight)$^{-1}$ when plants were stressed with NaCl or Na_2SO_4 at −0.8 MPa. The ($Na^+ + K^+$) concentration in *T. turgidum* (Fig. 1), *T. aestivum* (Fig. 2), and *T. elongatum* (Weimberg 1986) were always higher than 200 μmol (g fresh weight)$^{-1}$ even in non-stressed plants. Perhaps, then, the cellular OP's in these plants were constitutively low enough for the plants to have a favorable osmotic gradient for the flow of water into the plant until media OP's were lower than −0.6 or −0.8 MPa. In this way, plants could survive harmful effects of salinity to these levels without further osmotic adjustment. It is this latter interpretation that seems more compatible with current ideas on the role of solutes in osmotic adjustment.

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