# CHAPTER 10

# SODIUM-CALCIUM INTERACTIONS UNDER SALINITY STRESS

G.R. CRAMER
*Department of Biochemistry, Mail Stop 200*
*University of Nevada, Reno, NV 89557 USA*
*cramer@unr.edu*

**Abstract**

There are a wide range of responses of plants to salinity which involve interactions of Na with Ca. Plant processes such as growth, photosynthesis, mineral nutrition, water and ion transport are affected by these Na-Ca interactions. Many of these responses can be linked to the direct Na-Ca interactions at the surface of the plasma membrane and subsequent Ca signaling events.

## 10.1. General Effects of Salinity

Salinity affects plant growth through ionic and osmotic effects. Sometimes these effects are distinct from each other; sometimes these effects overlap. The difference in a plant's response to a given level of salinity is dependent upon the concentration and composition of the ions in solution as well as the genotype that is exposed to the salinity.

Once the importance of Ca in the external solution was fully appreciated (Epstein, 1961), there was a large increase in the number of experiments that focused on the interactions of Na with Ca in plants. Na-Ca interactions are particularly apparent in plants when the Na:Ca ratio in the external solution is above 17 (Greenway and Munns, 1980), but again the plant response will vary with genotype.

## 10.2. General Characteristics of Na and Ca

### 10.2.1. PHYSICAL PROPERTIES OF Na AND Ca

#### 10.2.1.1 *Na*

Sodium (Na), from the Latin word *sodanum*, meaning headache remedy, has a mass of 22.99 and a valence of 1 ($Na^+$). It is the sixth most abundant element on earth,

comprising about 2.6% of the earth's crust. Sodium salts readily dissolve in water. The crystal ionic radius of Na is 0.097 nm, its hydrated ionic radius has been estimated to be about 0.30 nm, and its heat of hydration is –322 kJ $mol^{-1}$. The heat of hydration is a measure of how easily a water layer can be stripped from the ion and is important in ion binding, particularly to ion channels.

2.1.1 *Ca*

Calcium (Ca), from the Latin word *calx*, meaning lime, has a mass of 40.08 and a valence of 2 ($Ca^{2+}$). It is more common than Na, being the fifth most abundant element in the earth's crust (approximately 3%). Ca salts can be quite soluble, but some (i.e. Ca phosphates) are very insoluble. This interaction with phosphate is in part why Ca activities are so low in the cytoplasm ($10^{-7}$ M). The crystal ionic radius of Ca is 0.099 nm, which is very similar to the crystal ionic radius of Na. Because Ca has a valence of 2, $Ca^{2+}$ has a much higher charge density than $Na^{+}$. The higher charge density increases the number of water layers attracted to the ion in solution. Therefore, both it's hydrated ionic radius, 0.44 nm, and its heat of hydration, –1580 kJ $mol^{-1}$ are much larger than those of Na.

10.2.2. CONCENTRATIONS VS. ACTIVITIES

Ions in saline solutions do not behave ideally. Therefore their activities are usually much lower than their concentrations due to ion pair formation and precipitation (Cramer and Läuchli, 1986). This effect is much more pronounced for Ca than it is for Na. Consequently the Na:Ca ratio in a solution on a concentration basis will be very different from the Na:Ca ratio on an activity basis. Since rates of reaction are dependent upon activities and not concentrations, the interactions of Na with Ca are best considered, when possible, on an activity basis.

10.2.3. Na:Ca RATIOS IN SOILS AND WATERS

Based upon the total salt concentration and the Na:(Ca + Mg) ratio, soils have been classified as saline, sodic or saline-sodic (Chapter 2). The total concentration of salts is usually measured by electrical conductivity, EC in units of dS $m^{-1}$, where 1 dS $m^{-1}$ is approximately equal to a 10 mM concentration of salt that disassociates into two monovalent ions when in solution (e.g. NaCl). Saline soils are commonly defined as those soils having an EC of 4 dS $m^{-1}$ or greater. Sodic soils are defined as those soils that have a sodium adsorption ratio (SAR) greater than 15. SAR is calculated as

$$SAR = \frac{[Na^{+}]}{[Ca^{2+} + Mg^{2+}]^{1/2}} \qquad (1)$$

where the brackets refer to the concentration in soil solution or the saturated paste extract. In sodic soils, soil colloids disperse, disrupting soil structure and water conductivity. Thus in saline-sodic soils, in which both the EC and SAR are high, this

physical change in soil structure has severe consequences on plant growth in addition to the direct effects of the saline solutions. Saline soils and sodic soils make up about 23% and 37%, respectively, of the cultivated land in the world (Chapter 2). Seawater has a SAR of about 56, whereas lake waters have an average SAR of 0.5 (calculated from Table 2.2 in Epstein, 1972).

#### 10.2.4. ION FUNCTION IN PLANTS

##### 10.2.4.1 $Na^+$

For most plants, Na is not essential (Marschner, 1995), but the growth of most plants is stimulated at low Na concentrations. Some halophytes require Na for growth, particularly $C_4$ and CAM plants, and some halophytes require very high concentrations of Na for maximal growth (Flowers *et al*., 1977). Na is generally used as an osmoticum in the vacuole, usually reducing the plant need for K (Marschner, 1995), whereas some halophytes have specific enzymatic needs for Na as well (Cramer, 1997).

##### 10.2.4.2 $Ca^{2+}$

Ca is an essential element in all plants (Marschner, 1995). The ability of Ca to form intermolecular linkages gives it an important role in maintaining the integrity and structure of membranes and cell walls (Hanson, 1984). Ca is also used as a second messenger in many signal transduction pathways within the cell (Bush, 1995).

## 10.3. Na-Ca Interactions

#### 10.3.1. EFFECTS ON PLANT GROWTH

The ameliorative effects of Ca on Na toxicity in plants has been reported as far back as 1902 (see references in LaHaye and Epstein, 1971). There were only a few papers that addressed this topic in the first half of the 20$^{th}$ century (see references in LaHaye and Epstein, 1971). Na-Ca interactions were largely overlooked until the importance of external Ca on the ion selectivity of ion transport was realized (Epstein, 1961). Since this discovery, there have been a very large number of papers published on Na-Ca interactions in plants, most notably in the last two decades. Because of the large number of papers, it is only possible to cite a few examples to illustrate the most important points. The reader is referred to several excellent reviews on Na-Ca interactions in plants for further information (Greenway and Munns, 1980; Läuchli and Schubert, 1989; Rengel, 1992; Lazof and Bernstein, 1999).

Although Ca ameliorates the Na-inhibition of growth for most plants, this is not always the case. During my graduate studies at the University of California, Davis, I tested the response to salinity and supplemental Ca of every species we were using in the lab at that time. Different species and different cultivars responded differently to supplemental Ca when salinized (Table 1).

TABLE 1. Growth response of different species to salinity with high (10 mM) or low (0.4 mM) $Ca^{2+}$ in the nutrient solution (0.1 modified Hoagland, pH 5.5). Eleven-day-old plants were salinized with 25 mM NaCl $day^{-1}$ increments until the final concentration of 100 mM NaCl was reached. Plants were harvested one week after the final concentration was reached. Data are means of 8 plants for each treatment. A rank of number 1 means the highest response to supplemental Ca (G.R. Cramer, unpublished results).

| Plant/ Genotype | Fresh Weight (g) | | | | High Ca/Low Ca (%) | | Rank for Positive Response to Ca | |
|---|---|---|---|---|---|---|---|---|
| | 0.4 mM $Ca^{2+}$ | | 10 mM $Ca^{2+}$ | | | | | |
| | Root | Shoot | Root | Shoot | Root | Shoot | Root | Shoot |
| Barley | | | | | | | | |
| Arivat | 2.51 | 2.80 | 3.66 | 3.62 | 146 | 129 | 11 | 10 |
| Calmariot | 1.32 | 1.17 | 2.04 | 1.77 | 155 | 151 | 10 | 5 |
| Triticale | | | | | | | | |
| Siskiyou | 0.99 | 0.86 | 2.13 | 1.68 | 215 | 195 | 4 | 2 |
| GTA 208 | 0.98 | 0.83 | 1.83 | 1.21 | 187 | 146 | 6 | 7 |
| Wheatgrass | | | | | | | | |
| *T. intermedium* | 0.05 | 0.06 | 0.12 | 0.12 | 240 | 200 | 1 | 1 |
| *T. ponticum* | 0.17 | 0.22 | 0.16 | 0.16 | 94 | 73 | 14 | 14 |
| Maize | | | | | | | | |
| Pioneer 3906 | 2.7 | 5.68 | 6.44 | 10.09 | 239 | 178 | 2 | 3 |
| Dekalb XL75 | 1.40 | 4.86 | 3.14 | 6.75 | 224 | 139 | 3 | 8 |
| Pioneer 3377 | 3.51 | 8.67 | 5.91 | 11.70 | 168 | 135 | 8 | 9 |
| Tomato | | | | | | | | |
| VF36 | 0.18 | 0.62 | 0.36 | 1.08 | 200 | 174 | 5 | 4 |
| Edkawi | 0.25 | 0.77 | 0.41 | 1.16 | 164 | 150 | 9 | 6 |
| Sorghum | | | | | | | | |
| *S. bicolor* | 1.60 | 1.34 | 1.70 | 1.60 | 106 | 119 | 13 | 11 |
| Kenaf | | | | | | | | |
| C-108 | 1.62 | 2.87 | 1.31 | 1.87 | 81 | 65 | 15 | 15 |
| Cotton | | | | | | | | |
| Acala S-J2 | 2.20 | 5.23 | 2.52 | 5.2 | 115 | 99 | 12 | 13 |
| Bean | | | | | | | | |
| *P. vulgaris* | 0.75 | 1.75 | 1.30 | 2.06 | 173 | 118 | 7 | 12 |

Most genotypes responded favorably to supplemental Ca when salinized. A couple of genotypes actually responded negatively (Kenaf and *T. ponticum*). Kenaf showed interveinal chlorosis in the lower leaves, similar to Mg deficiency symptoms. In addition, there were noticeable differences between cultivars within a species, especially within maize.

Other scientists have also found different genotype responses to supplemental Ca and salinity within rice (Yeo and Flowers, 1985; Grieve and Fujiyama, 1987; Muhammed *et*

*al*., 1987), *Brassica* species (Ashraf and Naqvi, 1992; Schmidt *et al*., 1993), *Hordeum* species (Suhayda *et al*., 1992), maize (Maas and Grieve, 1987; Alberico and Cramer, 1993), blueberry (Wright *et al*., 1992), sorghum (Grieve and Maas, 1988) and citrus (Zekri, 1993). It is hoped that the reader will keep in mind the differential responses of plants to Ca, especially when broad generalizations are made in this review and elsewhere.

The effect of supplemental Ca on salt-stressed roots has been related to the ion activities in the external solution (Cramer *et al*., 1986; Yermiyahu *et al*., 1997). Originally, root elongation was correlated to the Na:Ca activities in solution (Cramer *et al*., 1986) based upon a simple ion exchange theory at the surface of the plasma membrane (Cramer and Läuchli, 1986). Recently, a much more sophisticated approach has been fully developed which includes osmotic effects along with ionic effects (Yermiyahu *et al*., 1997; Kinraide, 1999). The latter approach appears to be widely applicable to many different ionic conditions.

The level of Ca in the external solution needed for maximal growth in saline conditions is usually between 5 and 10 mM Ca depending on the salinity level and genotype (see Table 2); concentrations of Ca above 10 mM can inhibit plant growth. The optimal Na:Ca ratio is somewhere between 10 and 20 for most plants tested (Table 2). To the best of my knowledge no such studies have been carried out in detail for halophytes.

TABLE 2. Ca concentrations necessary for maximal growth of salinized plants.

| Species | Na (mM) | Ca (mM) | Na:Ca | Reference |
|---|---|---|---|---|
| *Phaseolus vulgaris* | 80 | 5 | 16 | (Cachorro *et al*., 1993a) |
| | 50 | 3 | 17 | (LaHaye and Epstein, 1971) |
| | 24 | 1 | 24 | (Wadleigh and Bower, 1950) |
| *Zea mays* | 71 | 12.5 | 6 | (Maas and Grieve, 1987) |
| *Vaccinium ashei* | 100 | 1 | 100 | (Wright *et al*., 1992) |
| *Cucumis melo* | 40-100 | 5 | 8-20 | (Yermiyahu *et al*., 1997) |
| *Triticum aestivum* | 50 | 5 | 10 | (Hawkins and Lewis, 1993b) |
| *Vigna mungo* | 60 | 3.5 | 17 | (Nakamura *et al*., 1990) |
| | 80 | 6 | 13 | |
| | 100 | 5 | 20 | |
| | 150 | 7 | 21 | |
| *Sorghum bicolor* | 86 | 2.5 | 34 | (Grieve and Maas, 1988) |
| | 71 | 12.5 | 6 | |
| | 71 | 12.5 | 6 | |
| | 108 | 17.8 | 6 | |
| | 64.8 | 43.1 | 4 | |
| | 108 | 17.8 | 6 | |
| *Oryza sativa* | 86 | 4 | 18 | (Grieve and Fujiyama, 1987) |
| | 95 | 4.8 | 20 | (Muhammed *et al*., 1987) |
| Average | | 8.9 | 19 | |

The effects of supplemental Ca on the growth of salt-stressed roots are immediate (Cramer *et al*., 1988; Zhong and Läuchli, 1993b). If 80 mM NaCl was added before addition of supplemental Ca, then root growth was strongly inhibited and only slowly recovered over several hours (Cramer *et al*., 1988). However, if the Ca concentration in the nutrient solution was high, then root growth was unaffected by addition of 80 mM

NaCl to the nutrient solution (Cramer *et al*., 1988). In addition, differences in leaf growth of maize (Cramer, 1992) and bean (Ortiz *et al*., 1994) are discernable within hours after varying Na:Ca salinities.

Cell expansion is a function of water uptake and cell wall extension. It involves both biochemical and physical processes (Fig. 1). The current view is that a biochemical loosening of the cell wall under turgor pressure allows cell expansion to proceed followed by the nearly simultaneous absorption of water and solutes (Hsiao *et al*., 1976; Boyer, 1987; Cosgrove, 1987).

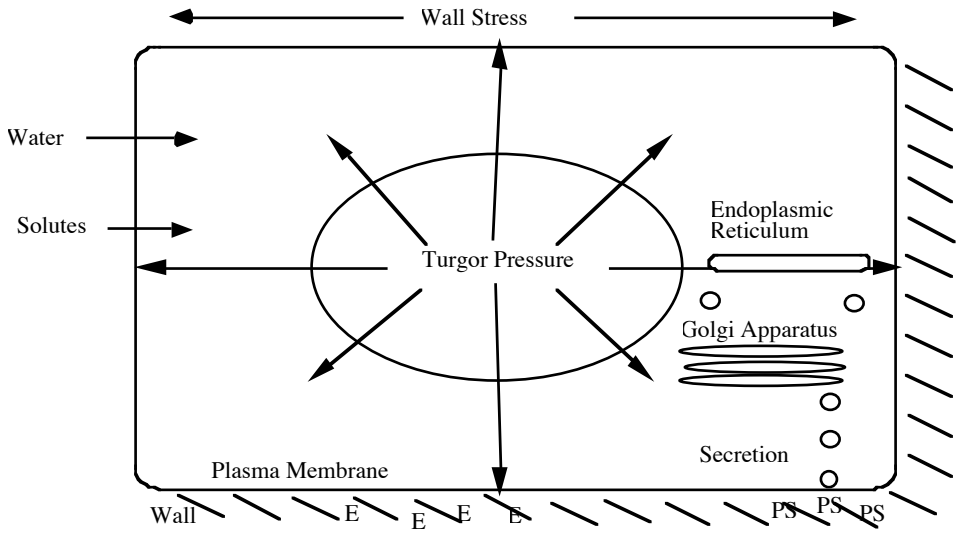


Figure 1. The expansion of a plant cell is dependent upon a physical stress that stretches the cell wall (turgor) and biosynthetic processes involving cell wall enzymes (E) and polysaccharides (PS).

A rigorous description of growth includes both mechanical and hydraulic aspects (Boyer, 1987):

$$\frac{1}{v}\frac{\partial v}{\partial t} = \frac{mL}{m+L}(\psi_o - \psi_s - Y) \qquad (2)$$

This is a variation of a previously derived equation (Lockhart, 1965), where m, L, $\psi_O$, $\psi_S$, and Y represent the cell wall extensibility, the hydraulic conductance, the xylem water potential, the cell osmotic potential, and the yield threshold, respectively. V is the cell volume and t is time. The term, mL/(m+L), is often referred to as the growth coefficient. The term, ($\psi_O$ - $\psi_S$ - Y), is the driving force for cell expansion. The yield threshold is the minimum turgor at which cells expand. Equation 2 is very useful for the analysis of growth limitations.

The way in which salinity and supplemental Ca affect growth has been analyzed for maize leaves (Cramer, 1992) using this mechanistic approach. Once steady-state conditions were reached after application of salinity, leaf growth was inhibited solely by an increase in the yield threshold of the cell wall (Cramer and Bowman, 1991). After a day of salinization, the cell wall extensibility was decreased as well (Cramer, 1992). In plants grown with a high Na:Ca ratio, the hydraulic conductance was reduced; supplemental Ca (10 mM) improved growth by restoring hydraulic conductance back to that of the control plants (Cramer, 1992).

Supplemental Ca can affect the length of the growth zones of salt-stressed plants. In sorghum leaves, the length of the growth zone is shortened by 100 mM NaCl salinity. If the Ca concentration of the nutrient solution is increased from 1 to 10 mM, then shortening of the growth zone by salinity is prevented (Bernstein *et al*., 1993). However, supplemental Ca did not influence the length of the growing zone in salt-stressed cotton roots (Zhong and Läuchli, 1993b).

### 10.3.2. EFFECTS ON CELL SHAPE, SIZE AND PRODUCTION

Figure 1 is a simplistic model for unidirectional (longitudinal) cell expansion. However, cells expand in a radial direction as well. The direction of expansion has pronounced effects on cell shape. The external Na:Ca ratio in solution can have significant effects on cell shape and cell production. In cotton roots, a high Na:Ca salinity causes cortical cells to become nearly isodiametric in contrast to controls (Kurth *et al*., 1986). Root cells exposed to low Na:Ca salinity become much longer and thinner. In both cases, however, there was no change in total volume of the cells. Supplemental Ca stimulated cell production in cotton roots by about 20%. In roots treated with 0.4 mM Ca, cell production was inhibited at 50 mM NaCl. In roots treated with 10 mM Ca, cell production was inhibited at 200 mM NaCl.

In maize roots, 100 mM NaCl reduced cell length in the root cortex by about half compared to controls (Zidan *et al*., 1990; Azaizeh *et al*., 1992). Plant roots grown with supplemental Ca (10 mM final concentration) without salinity had slightly reduced cell lengths compared to controls in one study (Azaizeh *et al*., 1992) and were not different from controls in another (Zidan *et al*., 1990). Plant roots grown with salinity and supplemental Ca had root cell lengths restored to slightly less than that of controls (Zidan *et al*., 1990; Azaizeh *et al*., 1992) and equivalent to the 10 mM Ca-grown roots in one study (Zidan *et al*., 1990). Cell volume was also reduced in salinity treatments without supplemental Ca, but not in treatments with supplemental Ca (Azaizeh *et al*., 1992). Root growth and cell production rates of salt-stressed maize were partially restored with supplemental Ca (Zidan *et al*., 1990). Possible mechanisms involved in the effects of Ca on cell expansion are discussed in Section 3.5.

### 10.3.3. EFFECTS ON PHOTOSYNTHESIS

Na-Ca interactions on photosynthesis have been observed. In *Citrus sinensis*, growth is very sensitive to $Cl^-$ concentrations (Bañuls and Primo-Millo, 1992). NaCl and KCl

salinity treatments significantly reduce photosynthesis, but isosmotic concentrations of $NaNO_3$ had no significant effects. When Ca concentrations were increased to 30 mM with Ca acetate, photosynthetic rates were similar to that of controls. The higher rates of photosynthesis were attributed to lower concentrations of $Cl^-$ in the leaves. In *Vaccinium ashei*, another species extremely sensitive to $Cl^-$, supplemental Ca increased photosynthetic rates in salt-stressed plants treated with $Na_2SO_4$, but not with NaCl (Wright *et al.*, 1993). In both species, growth was highly correlated with photosynthesis. Since these were long-term experiments, it is unclear which was the cause and which was the effect; photosynthesis can affect the growth rate of plants, but it can also be feedback-regulated by growth rates.

There are specific Na-Ca interactions on stomatal conductance. In abaxial epidermal peels of *Aster tripolium*, a halophyte, stomatal conductance is inhibited by external Na concentrations, whereas in *Commelina communis*, a nonhalophyte, external Na concentrations stimulate stomatal conductance (Perera *et al.*, 1994). When Ca is included in the medium in the presence of 50 mM NaCl, Ca concentrations prevents the reduction of stomatal conductance in *Aster tripolium* (Perera *et al.*, 1995). However, in the presence of 50 mM KCl, Ca concentrations reduce stomatal conductance (Perera *et al.*, 1995). These responses are likely to be due to Na-Ca interactions at the plasma membrane of the guard cells and their effects on Na, K, and Ca fluxes (Perera *et al.*, 1995).

In other plant species, no Na-Ca interactions have been observed on stomatal conductance and photosynthesis. In sunflower, there were differential responses between two lines. Transpiration and stomatal conductance was unaffected by varying Na:Ca ratios (all salt solutions were at 150 mM NaCl) in one line, whereas in another line there were significant reductions as the Na:Ca ratio was increased (Ashraf and O'Leary, 1997). Although the effect of varying Na:Ca ratios on photosynthesis was not statistically significant in sunflower, there was a slight trend towards reduced photosynthesis with increasing Na:Ca ratios (Ashraf and O'Leary, 1997).

Salinity reduced transpiration in barley, but supplemental Ca did not alter transpiration rates (Cramer *et al.*, 1989). In wheat (Hawkins and Lewis, 1993a) and cotton (Leidi *et al.*, 1991), no significant effects of supplemental Ca were observed in salt-stressed plants on stomatal conductance, transpiration, and photosynthesis. In salt-stressed maize, varying Na:Ca ratios did not have significant effects on transpiration and photosynthesis (Plaut and Grieve, 1988) or the net assimilation rate (Cramer *et al.*, 1994a). Thus, it would appear that in some species Na:Ca interactions affect growth without affecting photosynthesis.

### 10.3.4. EFFECTS ON WATER TRANSPORT

Water transport is a potentially limiting factor in plant growth (Boyer, 1985; Passioura, 1988; Steudle, 1989). Water transport is usually measured as the hydraulic conductivity (Lp), which is a measure of water flow across an individual unit area of membrane. Lp does not take into account the complex pathways of water transport through many cells

and whole tissues. Hydraulic conductance (L) does measure the average water conductance of a pathway and is related to Lp (L = Lp x A where A is the average area of the pathway).

Water transport into the root and to the leaf growing zone is affected by Na:Ca ratios. As mentioned above, salinity reduces hydraulic conductance (L) to the leaves of maize plants treated with NaCl salinity for 24 h (Cramer, 1992), but has no effect on plants treated for 4 h (Cramer and Bowman, 1991). Supplemental Ca fully prevents the inhibition of hydraulic conductance, but leaf elongation rates remain partially inhibited (Cramer, 1992).

The hydraulic conductivity of roots ($Lp_r$), which is the root hydraulic conductance divided by the effective root surface area, includes both apoplastic and symplastic water transport pathways of the root (Azaizeh *et al*., 1992). Both $Lp_r$ (Evlagon *et al*., 1990; Azaizeh and Steudle, 1991) and the Lp (Azaizeh *et al*., 1992) of root cells of maize are reduced by NaCl salinity. The inhibition of $Lp_r$ was partially (Evlagon *et al*., 1990) or fully (Azaizeh and Steudle, 1991) prevented by supplemental Ca. The inhibition of root cell Lp was also prevented by supplemental Ca (Azaizeh *et al*., 1992). Lp is inhibited much more than $Lp_r$ by salinity indicating that salinity and supplemental Ca primarily affect water transport across cell membranes rather than the apoplastic transport pathway (Azaizeh *et al*., 1992). The reduction of water transport across the plasma membrane may be due to salinity effects on cytosolic Ca and the dephosphorylation of water channels (see Sec. 3.7.).

### 10.3.5. EFFECTS ON CELL WALL

Nearly 50% of cellular Ca is bound in the cell wall to carboxyl groups, particularly in pectins (Demarty *et al*., 1984; Hanson, 1984). Ion exchange theory for cell walls is well developed (Grignon and Sentenac, 1991) and there are clear Na-Ca interactions in the cell wall (Demarty *et al*., 1984; Zid and Grignon, 1985). Under nonsaline conditions, Na:Ca ratios are correlated to differentiation in secondary walls (Ripoll *et al*., 1993). In salinized *Citrus aurantium*, Na competes with Ca for anionic sites in the leaf cell wall which have a high specificity for Ca (Zid and Grignon, 1985). In addition to the interference with cell wall Ca function, the localization of high concentrations of Na in the cell wall may lead to plant injury by reducing cell turgor (Oertli, 1968; Flowers *et al*., 1991).

In maize leaves, the short-term, steady-state limitations of cell expansion by salinity are associated with cell wall hardening (an increase in what appears to be the cell wall yield threshold) and not to hydraulic or turgor effects (Cramer and Bowman, 1991; Cramer and Schmidt, 1995; Neumann, 1995). Prior to steady-state conditions, turgor is rapidly reduced, but recovers to that in controls in a matter of hours (Thiel *et al*., 1988; Cramer and Bowman, 1991). Roots respond differently than leaves in that they are much less sensitive to salinity (Munns and Sharp, 1993). This can be attributed to an increase in cell wall loosening (Frensch and Hsiao, 1995; Wu *et al*., 1996b), the opposite response of leaves.

There are few data on the effect of Na:Ca ratios on cell wall extension properties of salinized plants (Lynch *et al*., 1988; Cramer, 1992). These data indicate that both the cell wall extensibility and yield threshold of the cell wall were not affected by varying Na:Ca ratios in a manner that would contribute to the reduction of growth and size of salt-stressed leaves. There are no reports on the effects of Na:Ca ratios on root cell wall extension properties. Thus, there is insufficient evidence to make any generalizations on this subject.

In barley, Na:Ca ratios in expanding leaf tissue increased with increasing salinity and leaf growth was reduced significantly (Lynch *et al*., 1988). Salinity did not decrease the *in vitro* plastic compliance of these tissues; a decrease in plastic compliance would be predicted by the high Na:Ca ratio in the tissue (Lynch *et al*., 1988). Similar observations have been made for *in vitro* assays in maize (G.R. Cramer, unpublished results). If anything, plastic compliance was increased by salinity, even though salinity significantly reduced leaf growth (Lynch *et al*., 1988). If cell walls are hardened in these plants, then it must be by some other mechanism, perhaps by a reduced secretion (Cramer and Jones, 1996) or reduced biosynthesis of cell wall components *in vivo*.

Na:Ca ratios do affect cell wall biosynthesis (Zhong and Läuchli, 1988; Zhong and Läuchli, 1993a). Salinity at a high Na:Ca ratio inhibits cellulose and noncellulosic polysaccharide biosynthesis of the cell walls of cotton roots (Zhong and Läuchli, 1988). At a low Na:Ca ratio, only noncellulosic polysaccharide biosynthesis of the cell wall is inhibited. High Na:Ca ratios increased the uronic acid content and decreased the cellulose content of the cell wall (Zhong and Läuchli, 1993a). Supplemental Ca prevented these changes in uronic acid and cellulose content. The neutral sugar content of the cell wall was unaffected by Na:Ca ratios, but there was a shift in polysaccharide molecular size (Zhong and Läuchli, 1993a). It was suggested that polysaccharide degradation and enzymatic activities in the cell wall might be inhibited by high Na:Ca ratios. However, cell wall enzymes involved in cell expansion from both halophytes and nonhalophytes are relatively salt tolerant compared to cytoplasmic enzymes and are unlikely to be the cause of reduced growth by salinity (Thiyagarajah *et al*., 1996). It has been suggested that changes in cell wall composition by salinity, particularly that of pectic polysaccharides, may be the result of a salinity-induced Ca deficiency (Kafkafi and Bernstein, 1996).

### 10.3.6. EFFECTS ON MEMBRANES

From the early observations of Na:Ca interactions on plant growth (see Sec. 3.1. above) and the development of the Gouy-Chapman theory for membranes, it was logical to hypothesize that Na:Ca interactions occurs at the surface of membranes (see LaHaye and Epstein, 1969 and references therein). Since membranes form compartments and are sites of many biological functions, interference of Na with Ca function in membranes of salt-stressed plants could have very serious consequences, particularly involving ion transport and compartmentation.

The first direct evidence for Na:Ca interactions at the membrane in salt-stressed plants was provided by the use of chlortetracycline (CTC) as a fluorescent probe for membrane-associated Ca (Cramer *et al*., 1985). In salt-stressed roots of cotton, Na displaced membrane-associated Ca, which was believed to be primarily located at the plasma membrane (Cramer *et al*., 1985). In other experiments where membrane-associated Ca was measured directly, NaCl-salinity also displaced membrane-associated Ca on protoplasts of corn (Lynch *et al*., 1987; Lynch and Läuchli, 1988) and barley (Bittisnich *et al*., 1989), and on plasma membrane vesicles of melon (Yermiyahu *et al*., 1994).

In corn root protoplasts, evidence was provided that part of the Ca-CTC fluorescence may come from internal membrane-bound compartments within the cell which may contain high Ca concentrations (Lynch *et al*., 1987; Lynch and Läuchli, 1988). Li blocks the release of Ca from internal stores caused by phosphoinositides. When cells were pretreated with Li, membrane-associated Ca was not reduced by 150 mM NaCl as much as in cells without Li pretreatment. Cells pretreated with Li and inositol (which is needed for the regeneration of phosphoinositides) behaved like cells without pretreatments; in other words, membrane-associated Ca was reduced to the same extent by salinity. Cytoplasmic Ca responded in a similar manner to Li, inositol and salinity (Lynch and Läuchli, 1988), consistent with the conclusion that salinity can release Ca from internal compartments that store Ca (Lynch *et al*., 1987).

Displacement of membrane-associated Ca is different at different Ca concentrations in the solution (Cramer *et al*., 1985; Lynch *et al*., 1987); there is a greater displacement of membrane-associated Ca by Na at low external Ca concentrations. In addition, salt-tolerant genotypes of barley (Bittisnich *et al*., 1989) and melon (Yermiyahu *et al*., 1997) had less displacement of membrane-associated Ca by NaCl-salinity than salt-sensitive genotypes of the same species. These data indicate that the partial alleviation of NaCl inhibition of growth by Ca may in part be related to the quantity of membrane-associated Ca.

Consistent with this hypothesis, the salt tolerance of four melon varieties was associated with the greater ability of their root membranes to bind Ca (Kafkafi, 1991). The ability to bind Ca was cleverly deduced from root responses to monovalent salts and comparison to ion selectivity at a surface according to Eisenman's series. Ion selectivity is a function of the relative energy of interaction between the ion's hydration energy and the surface charge density of the adsorbing surface (Kafkafi, 1991).

NaCl-salinity also reduces the surface potential of the plasma membrane (Suhayda *et al*., 1990), which is a function of the surface charge density and the ion activity in the surrounding solution. Salt reduced the surface potential directly by screening negative charges on the membrane and also indirectly in plants that had been salt-stressed for four days (presumably by reducing the surface charge density of the membrane over time). A reduction in charge density would reduce the cation activity at the outside surface of the

plasma membrane and therefore affect rates of ion transport across the plasma membrane.

Sophisticated models have been developed and applied to analyze Na:Ca interactions and estimate Ca-binding at the plasma membrane surface of plants (Kinraide, 1994; Yermiyahu *et al*., 1997; Murata *et al*., 1998a). These models use measurements of surface potential to estimate the surface charge density. They also calculate ion activities at the surface of the membrane based upon known ion chemistry in solution. From these parameters, the amount of Ca binding to the membrane can be computed. Using this indirect approach, these models estimate that Na reduces membrane-associated Ca (Kinraide, 1994; Yermiyahu *et al*., 1997; Murata *et al*., 1998a).

It was discerned from ion exchange analysis that Ca was displaced from two different classes of sites, one being a high-affinity binding site, probably associated with proteins, and the other being a low-affinity site, probably associated with phospholipids (Cramer and Läuchli, 1986). Other reports also provide evidence for multiple Ca-binding sites at the plasma membrane of other plant species (Yermiyahu *et al*., 1994; Murata *et al*., 1998a). Displacement of Ca from different sites will cause different effects.

In intact cotton roots, displacement of membrane-associated Ca from root hairs appears to be specific for Na; treatments with other monovalent cations, Ba (a divalent cation), or mannitol do not reduce membrane-associated Ca. Therefore, it is assumed that this effect is Na-specific. However, in corn root protoplasts isolated from the cortex, in addition to the displacement of membrane-associated Ca by Na, other monovalent cations displace membrane-associated Ca (Lynch *et al*., 1987). In this study, all monovalent cations substantially reduced membrane-associated Ca. Very small but significant differences were found between cations; the effect was in the following order: Li = K = Rb > Na > Cs. The lack of substantial difference between cations indicates that displacement of Ca was caused by an ionic strength effect, which was nonspecific. Likewise, it should be noted that all protoplasts were in isosmotic solutions; therefore these effects were truly ionic without any osmotic component. Based upon unpublished work on intact corn roots the authors suggested that the differential responses of ion specificity between corn and cotton were genetically based and not due to the differences in methods (i.e. intact cells vs. protoplasts). In support of this conclusion, Na-specific effects were recently identified in tobacco, but nonspecific ionic effects were identified in barley (Murata *et al*., 1998a). Thus, different genotypes seem to have inherently different responses.

One consequence of the displacement of membrane-associated Ca by Na is the immediate increase of K efflux across the plasma membrane of salt-stressed cotton roots at salt concentrations above 100 mM NaCl (Cramer *et al*., 1985). Supplemental Ca reduces this effect at concentrations above 150 mM NaCl. Isosmotic concentrations of mannitol have similar effects as saline treatments with supplemental Ca (10 mM) indicating that K efflux is affected by osmotic factors in these solutions and not associated with a Na-specific displacement of membrane-associated Ca (Cramer *et al*.,

1985). This effect may be related to the rapid depolarization of the membrane potential upon salinization (Cramer, 1997).

Salinity and supplemental Ca can alter lipid composition of plant membranes (Cachorro *et al*., 1993b; Yu *et al*., 1998). In beans and barley, salinity reduced total phospholipid content of the membrane (Cachorro *et al*., 1993b; Yu *et al*., 1998). This might account for the reduction in surface charge density described above. Furthermore, supplemental Ca increased the phospholipid content in both cases. Salinity and Ca also affected the fatty acid compositions. Specifically, the content of unsaturated fatty acids increased with salinity and was reduced by supplemental Ca (Cachorro *et al*., 1993b; Yu *et al*., 1998). An increase in the proportion of unsaturated fatty acids causes an increase in K permeability across membranes (Scarpa and de Grier, 1971). This effect is not likely to be related to the K efflux cited in the previous paragraph, since lipid composition would be unaffected in those short-term experiments.

### 10.3.7. EFFECTS ON ION TRANSPORT AND CONTENT

There is abundant evidence that salinity alters the ion transport and contents of plants (Cramer, 1997). In general, Na uptake and concentrations increase and Ca uptake and concentrations decrease in plant cells and tissues as the external Na concentration increases (Rengel, 1992; Cramer, 1997; Lazof and Bernstein, 1999). Likewise, as external Ca concentrations increase Na uptake and concentration decrease and Ca uptake and concentration increase. One consequence of these Na:Ca interactions is the reduction of K content in salinized plants, which can be prevented with supplemental Ca.

The issue of Na toxicity in plants has been addressed extensively in previous reviews and will not be addressed here (see Flowers *et al*., 1977 and references therein; Greenway and Munns, 1980; Cramer, 1997; Lazof and Bernstein, 1999). However, it should be noted that just because Na and Cl tissue concentrations increase with salinity (which is a function of increasing external concentrations and uptake) it does not necessarily mean that these concentrations are the cause of the growth reduction. In many cases, especially at low to medium salinity stresses, Na toxicity is probably not the cause of growth reduction (Cheeseman, 1988; Munns *et al*., 1988; Lazof and Läuchli, 1991; Cramer *et al*., 1994b; Bernstein *et al*., 1995; Leidi and Saiz, 1997).

The issue of Ca deficiency is not as extensively studied as Na toxicity. Ca deficiency can occur in some species at high Na:Ca ratios (Maas and Grieve, 1987; Muhammed *et al*., 1987; Ehret *et al*., 1990; Francois *et al*., 1991; Ho and Adams, 1994; Bernstein *et al*., 1995; Fortmeier and Schubert, 1995). Bulk tissue Ca concentrations and Ca influx are reduced by salinity (Lynch and Läuchli, 1985; Cramer *et al*., 1987; Lynch and Läuchli, 1988; Cramer *et al*., 1989; Cramer *et al*., 1994b; Davenport *et al*., 1997; Halperin *et al*., 1997; Lazof and Bernstein, 1999) and these factors certainly contribute to Ca deficiency.

Reduction of Ca by salinity has also been detected in the apical meristem and young leaves of lettuce by electron-probe microanalysis (Lazof and Läuchli, 1991) and all along the elongation zone of sorghum leaves (Bernstein *et al*., 1995). Ca content of

growing tissue under salinization can be reduced, and is restored in the same region under elevated Ca levels (Lazof and Bernstein, 1999). This reversal of the reduction in Ca level corresponds with partial reversal of the growth inhibition and prevention of the reduction in the growing zone length (Lazof and Bernstein, 1999).

In some cases, Ca imbalance may not be detectable by normal methods. Salinity may disturb normal Ca functions without disturbing overall Ca tissue concentrations. It can do this because cytoplasmic Ca activities are in the nM range, whereas overall tissue concentrations are in the mM range. It is very difficult to measure changes in Ca activity by conventional means (e.g. atomic absorption spectrophotometry); instead sophisticated fluorescent and luminescent techniques must be employed (Gilroy *et al*., 1989; Bush and Jones, 1990; Knight *et al*., 1997).

The effect of salinity on cytoplasmic Ca has been studied using these techniques. There are a variety of responses. Initial studies using maize root protoplasts indicated that salinity increased cytoplasmic Ca activities at high salinity (Bittisnich *et al*., 1989; Lynch *et al*., 1989). Recently, cytoplasmic Ca activities in whole seedlings of Arabidopsis were found to increase (at least transiently) in response to high salinity or mannitol (Knight *et al*., 1997). Cytoplasmic Ca activity peaked within 5 to 10 s after exposure to osmotic stress, declining thereafter. Measurements returned close to control values after 60 s. It is not known what happens after 60 s because measurements were terminated by 60 s. The characteristics of these transient responses seem to vary with environmental stimuli (Malhó *et al*., 1998) and may be responsible for different physiological responses to these stimuli. Furthermore, it appears that the previous history or exposure to other stimuli can affect the response of cytosolic Ca to a current stimulus (Knight *et al*., 1998).

In tissue culture cells of two *Brassica* species, salinity caused a multitude of responses. In some cells, cytoplasmic Ca was increased, in other cells there was no effect, and in other cells, cytoplasmic Ca was decreased (He, 1993). Salinity decreased cytoplasmic Ca activities in the roots of maize (Cramer, 1997) and *Arabidopsis* (Cramer and Jones, 1996; Cramer, 1997). In addition, mannitol treatments decreased cytoplasmic Ca activity in *Arabidopsis* roots (Cramer and Jones, 1996) and tobacco cells (Jones *et al*., 1998). One salinity treatment caused a transient increase in cytoplasmic Ca activity in *Arabidopsis* roots 6 s after exposure to salinity, but decreased below control values by 69 s (Cramer, 1997). It should also be noted that a sudden decrease in osmotic stress (hypoosmotic) causes a sudden transient increase in cytoplasmic Ca (Taylor *et al*., 1996; Takahashi *et al*., 1997; Taylor *et al*., 1997).

All of the above treatments were applied as rapid osmotic perturbations of the cells over a period of 15 minutes or less. These results indicate that this transient response of cytoplasmic Ca activity to salinity is variable depending upon the cell type, salinity concentration and length of exposure. To my knowledge, there are no long-term, steady-state studies on the effects of salinity on cytoplasmic Ca activities. With the inhibition of Ca transport into plant cells by salinity, it is difficult to see how cytoplasmic Ca activities can remain elevated over a substantial period of time.

What controls the changes in cytoplasmic Ca activity during salt stress and which adjacent Ca pools are affected? This is unclear. In intact plant cells tested so far, the response is osmotic, and not specifically related to Na antagonism (Cramer and Jones, 1996; Knight *et al*., 1997). In corn root protoplasts, which by necessity must be kept in isosmotic solutions, cytoplasmic Ca increased upon a substantial increase in ionic strength of the external medium (Lynch and Läuchli, 1988; Bittisnich *et al*., 1989). An increase in external Ca will also cause a rise in cytoplasmic Ca activity, suggesting that Ca influx across the plasma membrane contributes to the increase in cytoplasmic Ca activity. However, this rise in Ca is blocked if cells are already salinized (Cramer and Jones, 1996). Some Ca can be released from internal stores (Lynch and Läuchli, 1988). It is not known how salinity affects cytoplasmic Ca when external Ca concentrations are high. Further research is needed to understand Ca dynamics and compartmentation in salt-stressed plants over longer periods of time when growth rates are in steady-state conditions.

Great progress has been made in characterizing Na and Ca transport across membranes. It is now clear that Na can enter cells through ion channels (for a more extensive review see Amtmann and Sanders, 1998; Tyerman and Skerrett, 1999). In some cases these channels are more selective for Na than K (Roberts and Tester, 1997a). Increasing the external Ca reduces Na conductance through these channels (Roberts and Tester, 1997a; Tyerman *et al*., 1997) and this effect is highly correlated with effects on Na influx into roots (Tyerman and Skerrett, 1999). Na influx into membrane vesicles (Allen *et al*., 1995) and roots (Davenport *et al*., 1997) is more sensitive to Ca in a salt tolerant species of wheat than a salt-sensitive species. Multiple mechanisms for Na entry exist within plants with at least one mechanism insensitive to Ca (Amtmann and Sanders, 1998; Tyerman and Skerrett, 1999).

Ca entry into cells can also occur through ion channels (Muir *et al*., 1997; Piñeros and Tester, 1997; White, 1998b; White, 1998a). These channels are also permeable to Na (White, 1998a), but it is not certain how Na interacts with Ca in these channels. K also moves through a Ca channel and can interfere with Ca transport (Piñeros and Tester, 1997); it seems likely that Na would do the same.

An outward rectifying cation channel has also been discovered in maize stelar cells (Roberts and Tester, 1997b). These channels may control the transport of cations to the xylem (and therefore may control cation transport to the shoot). These channels are preferentially selective for K, but Na can also move through them to a lesser extent. Movement of Na through these channels would likely reduce K movement through them. These channels also appear to be permeable to Ca although Ca entry is predicted to be from the opposite side (apoplast). These ion interactions with the outward rectifying cation channel are consistent with the observed transport of these ions from the root to the shoot in salt-stressed maize (Cramer *et al*., 1994b). It is interesting to note that channels in root cortical cells have very different properties (Roberts and Tester, 1997b).

Calcium did not affect the K/Na selectivity of K outward rectifying cation channels in two wheat genotypes differing in salt tolerance (Schachtman *et al*., 1991) or in tobacco cells (Murata *et al*., 1998b). It is not known what type of cells these channels came from and therefore they cannot be properly compared to the maize channels described in the paragraph above.

In addition to the direct effects of Ca on ion transport, Ca may act on transport through a Ca signaling pathway. Recently, a genetic approach has been applied to salt-stressed *Arabidopsis* mutants (Wu *et al*., 1996a; Zhu *et al*., 1998). These mutants are hypersensitive to salt and defective in their K nutrition. One of these mutants, *sos3* (*s*alt-*o*verly-*s*ensitive *3*), requires increased Ca for its K nutrition and salt tolerance (Liu and Zhu, 1997). Under salinity stress, this mutant acquires more Na and less K. In addition, this mutant is unable to grow with low external K concentrations. With supplemental Ca the *sos3* mutant grows normally and has improved salt tolerance. *SOS3* encodes a protein that appears to be very similar to a subunit of Calcineurin B in yeast and neuronal calcium sensors in animals (Liu and Zhu, 1998). Because of these similarities it is believed that this protein is involved in a Ca signaling pathway which regulates Na and K transport and thus can alter the K/Na selectivity of the plant (Liu and Zhu, 1998).

Likewise, expression of a yeast calcinuerin in transgenic tobacco increased the plant's ability to survive salt stress (Pardo *et al*., 1998). Although plant growth during salinity stress was not significantly ameliorated, plant growth, particularly root growth, was substantially improved during recovery after the salt-stress was removed. Control shoots that were grafted on to transgenic rootstock also showed significant improvement in recovery after salt removal. It is believed that this yeast calcineurin functions primarily in the root by acting on ion transport mechanisms. This effect on root ion transport then alters ion transport to the shoot and thereby affects the salt tolerance of the shoot.

There are other reports supporting the involvement of Ca signaling in salt tolerance. A Ca-binding protein is induced in salt-stressed *Arabidopsis* (Jang *et al*., 1998). Likewise, mRNA levels of a Ca-ATPase in tomato (Wimmers *et al*., 1992) and a Ca-dependent protein kinase in mungbean (Botella *et al*., 1996) increase substantially after salinization. CAM induction by salinity in the halophyte, *Mesembryanthemum crystallinum*, appears to be dependent upon Ca-signaling mechanisms (Taybi and Cushman, 1999).

Is expression of the genes encoding these proteins induced because cytoplasmic Ca activities are increased or decreased? It has been generally assumed that Ca activities are increased and this triggers the induction of some Ca-dependent proteins, presumably to further enhance the response of the biochemical pathway to elevated Ca. However, it was pointed out above that if Ca activity is increased, this response is frequently short-lived (on the order of s). Thus, the increased activity of induced enzymes comes too late. Perhaps the amounts of proteins are increased to compensate for their reduced functions when cytoplasmic Ca activity is eventually reduced by salinity?

It is interesting to note that a plasma membrane water channel can be regulated by phosphorylation in response to apoplastic water potential and cytoplasmically-relevant

Ca concentrations (Johansson *et al*., 1996). Lower external water potentials and lower Ca concentrations decrease phosphorylation of the channel. Dephosphorylation of the channel reduces water conductance through the channel (Johansson *et al*., 1998). This may explain the role of Ca in controlling water conductance in plants described above (Sec 3.4.).

The pH gradient across the tonoplast is also affected by salinity and supplemental Ca (Martinez and Läuchli, 1993; Colmer *et al*., 1994). Salinity causes an alkalinization of the vacuole and supplemental Ca reduces this effect. It was suggested that reduced cytoplasmic Na concentrations by supplemental Ca, reduced Na/H antiport activity at the tonoplast and therefore reduce alkalinization of the vacuole.

Proton extrusion is increased in mungbean roots by salinity and supplemental Ca reduces this effect (Nakamura *et al*., 1992). The activities of the plasma membrane $H^+$-ATPase and the tonoplast $H^+$-ATPase and $H^+$-PPase are also affected. It was suggested that elevated cytoplasmic Na activities inhibit the tonoplast $H^+$-PPase, thereby stimulating the activity of the plasma membrane $H^+$-ATPase. However, it should be noted that decreased cytoplasmic Ca activities also stimulate the plasma membrane $H^+$-ATPase (Kinoshita *et al*., 1995; Lino *et al*., 1998) and it is very possible that salinity affects proton extrusion in this manner.

## 10.4. Summary

In summary, a large number of Na:Ca interactions occur in salt-stressed plants, particularly those in saline-sodic conditions (see Fig. 2 for a hypothetical model). One of the first sites of action occurs at the external solution/root cell plasma membrane interface. These Na:Ca interactions have important effects on membrane properties and ion transport, which lead to changes in cytoplasmic Ca activity and gene expression. Na:Ca interactions can affect growth, photosynthesis, plant nutrition, water and ion transport in plants. The nature of the response will vary depending on the plant genotype.

## 10.5. Acknowledgements

I would like to thank my former mentor, André Läuchli, for stimulating my interest in this exciting topic. I am very grateful. I would also like to thank Rana Munns, Nirit Bernstein, Jonathan Lynch, Malcolm Drew and Tim Colmer for their useful and insightful comments on an earlier draft of this manuscript.

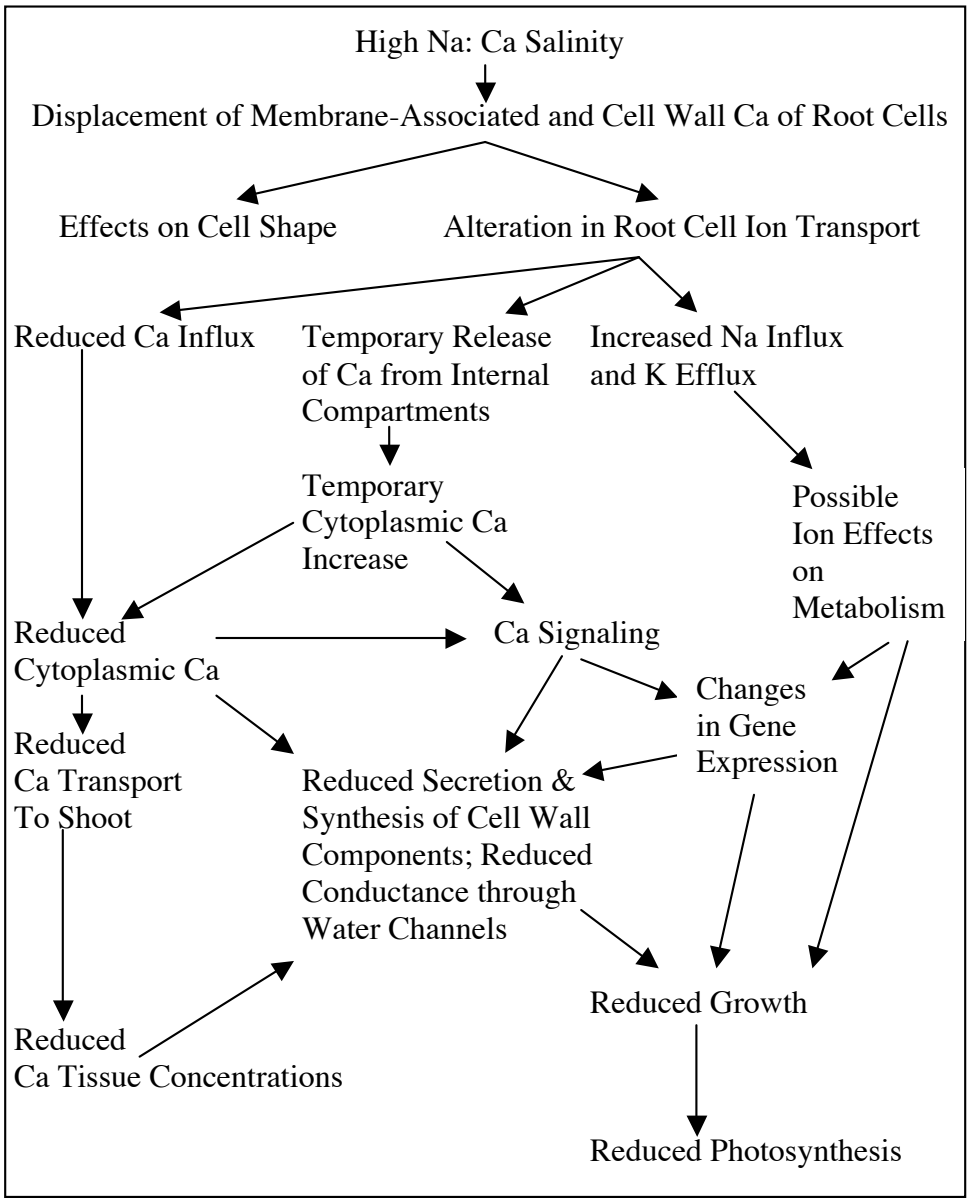


Figure 2. Schematic hypothetical model of the effects of NaCl salinity on Ca, physiology and growth.

**References**


Alberico, G. J. and Cramer, G. R. (1993) Is the salt tolerance of maize related to sodium exclusion? I. Preliminary screening of seven cultivars, *J. Plant Nutr.* **16**, 2289-2303.

Allen, G. J., Wyn Jones, R. G. and Leigh, R. A. (1995) Sodium transport in plasma membrane vesicles isolated from wheat genotypes with differing $K^+/Na^+$ discrimination traits, *Plant Cell Environ.* **18**, 105-115.

Amtmann, A. and Sanders, D. (1998) Mechanisms of $Na^+$ uptake by plant cells, *Adv. Bot. Res.* **29**, 75-112.

Ashraf, M. and Naqvi, M. I. (1992) Growth and ion uptake of 4 *Brassica* species as affected by Na/Ca ratio in saline sand culture, *Z. Pflanz. Bodenk.* **155**, 101-108.

Ashraf, M. and O'Leary, J. W. (1997) Responses of a salt-tolerant and a salt-sensitive line of sunflower to varying sodium/calcium ratios in saline sand culture, *J. Plant Nutr.* **20**, 361-377.

Azaizeh, H., Gunse, B. and Steudle, E. (1992) Effects of NaCl and $CaCl_2$ on water transport across root cells of maize (*Zea mays* L.) seedlings, *Plant Physiol.* **99**, 886-894.

Azaizeh, H. and Steudle, E. (1991) Effects of salinity on water transport of excised maize (*Zea mays* L.) roots, *Plant Physiol.* **97**, 1136-1145.

Bañuls, J. and Primo-Millo, E. (1992) Effects of chloride and sodium on gas exchange parameters and water relations of citrus plants, *Physiol. Plant.* **86**, 115-123.

Bernstein, N., Läuchli, A. and Silk, W. K. (1993) Kinematics and dynamics of sorghum (*Sorghum bicolor* L.) leaf development at various Na/Ca salinities. I. Elongation growth, *Plant Physiol.* **103**, 1107-1114.

Bernstein, N., Silk, W. K. and Läuchli, A. (1995) Growth and development of sorghum leaves under conditions of NaCl stress: possible role of some mineral elements in growth inhibition, *Planta* **196**, 699-705.

Bittisnich, D., Robinson, D. and Whitecross, M. (1989) Membrane-associated and intracellular free calcium levels in root cells under NaCl stress, in J. Dainty, M. I. de Michelis, E. Marré and F. Rasi-Caldogno, (eds.), *Plant Membrane Transport: The Current Position. Proceedings of the Eighth International Workshop on Plant Membrane Transport, Venice, Italy, 25-30 June 1989*, Elesevier Science Publishing Company, Inc., New York, pp. 681-682.

Botella, J. R., Arteca, J. M., Somodevilla, M. and Arteca, R. N. (1996) Calcium-dependent protein kinase gene expression in response to physical and chemical stimuli in mungbean (*Vigna radiata*), *Plant Mol. Biol.* **30**, 1129-1137.

Boyer, J. S. (1985) Water transport., *Annu. Rev. Plant Physiol.* **36**, 473-516.

Boyer, J. S. (1987) Hydraulics, wall extensibility and wall proteins, in D. J. Cosgrove and D. P. Knievel, (eds.), *Physiology of Cell Expansion During Plant Growth*, The American Society of Plant Physiologists, Rockville, pp. 109-121.

Bush, D. S. (1995) Calcium regulation in plant cells and its role in signaling, *Annu. Rev. Plant. Physiol. Plant. Mol. Biol.* **46**, 95-122.

Bush, D. S. and Jones, R. L. (1990) Measuring intracellular $Ca^{2+}$ levels in plant cells using the fluorescent probes, Indo-1 and Fura-2: progress and prospects, *Plant Physiol.* **93**, 841-845.

Cachorro, P., Ortiz, A., Barcelo, A. R. and Cerda, A. (1993a) Lignin deposition in vascular tissues of *Phaseolus vulgaris* roots in response to salt stress and $Ca^{2+}$ ions, *Phyton* **33**, 33-40.

Cachorro, P., Ortiz, A. and Cerda, A. (1993b) Effects of saline stress and calcium on lipid composition in bean roots, *Phytochem.* **32**, 1131-1136.

Cheeseman, J. M. (1988) Mechanisms of salinity tolerance in plants, *Plant Physiol.* **87**, 547-550.

Colmer, T. D., Fan, T. W. M., Higashi, R. M. and Läuchli, A. (1994) Interactions of $Ca^{2+}$ and NaCl stress on the ion relations and intracellular pH of *Sorghum bicolor* root tips: an *in vivo* $^{31}$P-NMR study, *J. Exp. Bot.* **45**, 1037-1044.

Cosgrove, D. J. (1987) Linkage of wall extension with water and solute uptake, in D. J. Cosgrove and D. P. Knievel, (eds.), *Physiology of Cell Expansion during Plant Growth*, The American Society of Plant Physiologists, Rockville, pp. 88-100.

Cramer, G. R. (1992) Kinetics of maize leaf elongation. II. Response of a Na-excluding cultivar and a Na-including cultivar to varying Na/Ca salinities, *J. Exp. Bot.* **43**, 857-864.

Cramer, G. R. (1997) Uptake and role of ions in salt tolerance, in P. K. Jaiwal, R. P. Singh and A. Gulati, (eds.), *Strategies for Improving Salt Tolerance in Higher Plants*, Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi, pp. 55-86.

Cramer, G. R., Alberico, G. J. and Schmidt, C. (1994a) Leaf expansion limits dry matter accumulation of salt-stressed maize, *Aust. J. Plant Physiol.* **21**, 663-674.

Cramer, G. R., Alberico, G. J. and Schmidt, C. (1994b) Salt tolerance is not associated with the sodium accumulation of two maize hybrids, *Aust. J. Plant Physiol.* **21**, 675-692.

Cramer, G. R. and Bowman, D. C. (1991) Kinetics of maize leaf elongation. I. Increased yield threshold limits short-term, steady-state elongation rates after exposure to salinity, *J. Exp. Bot.* **42**, 1417-1426.

Cramer, G. R., Epstein, E. and Läuchli, A. (1988) Kinetics of root elongation of maize in response to short-term exposure to NaCl and elevated calcium concentration, *J. Exp. Bot.* **39**, 1513-1522.

Cramer, G. R., Epstein, E. and Läuchli, A. (1989) Na-Ca interactions in barley seedlings: relationship to ion transport and growth, *Plant Cell Environ.* **12**, 551-558.

Cramer, G. R. and Jones, R. L. (1996) Osmotic stress and abscisic acid reduce cytosolic calcium activities in roots of *Arabidopsis thaliana*, *Plant Cell Environ.* **19**, 1291-1298.

Cramer, G. R. and Läuchli, A. (1986) Ion activities in solution in relation to $Na^+$-$Ca^{2+}$ interactions at the plasmalemma, *J. Exp. Bot.* **37**, 321-330.

Cramer, G. R., Läuchli, A. and Epstein, E. (1986) Effects of NaCl and $CaCl_2$ on ion activities in complex nutrient solutions and root growth of cotton, *Plant Physiol.* **81**, 792-797.

Cramer, G. R., Läuchli, A. and Polito, V. S. (1985) Displacement of $Ca^{2+}$ by $Na^+$ from the plasmalemma of root cells. A primary response to salt stress?, *Plant Physiol.* **79**, 207-211.

Cramer, G. R., Lynch, J., Läuchli, A. and Epstein, E. (1987) Influx of $Na^+$, $K^+$, and $Ca^{2+}$ into roots of salt-stressed cotton seedlings. Effects of supplemental $Ca^{2+}$, *Plant Physiol.* **83**, 510-516.

Cramer, G. R. and Schmidt, C. (1995) Estimation of growth parameters in salt-stressed maize: comparison of the pressure-block and applied-tension techniques, *Plant Cell Environ.* **18**, 823-826.

Davenport, R. J., Reid, R. J. and Smith, F. A. (1997) Sodium-calcium interactions in two wheat species differing in salinity tolerance, *Physiol. Plant.* **99**, 323-327.

Demarty, M., Morvan, C. and Thellier, M. (1984) Calcium and the cell wall, *Plant Cell Environ.* **7**, 441-448.

Ehret, D. L., Redmann, R. E., Harvey, B. L. and Cipywnyk, A. (1990) Salinity-induced calcium deficiencies in wheat and barley, *Plant Soil* **128**, 143-151.

Epstein, E. (1961) The essential role of calcium in selective cation transport by plant cells, *Plant Physiol.* **36**, 437-444.

Epstein, E. (1972) *Mineral Nutrition of Plants: Principles and Perspectives*, John Wiley and Sons, Inc., New York.

Evlagon, D., Ravina, I. and Neumann, P. (1990) Interactive effects of salinity and calcium on hydraulic conductivity, osmotic adjustment, and growth in primary roots of maize seedlings, *Isr. J. Bot.* **39**, 239-247.

Flowers, T. J., Hajibagheri, M. A. and Yeo, A. R. (1991) Ion accumulation in the cell walls of rice plants growing under saline conditions: evidence for the Oertli hypothesis, *Plant Cell Environ.* **14**, 319-325.

Flowers, T. J., Troke, P. F. and Yeo, A. R. (1977) The mechanism of salt tolerance in halophytes, *Annu. Rev. Plant Physiol.* **28**, 89-121.

Fortmeier, R. and Schubert, S. (1995) Salt tolerance of maize (*Zea mays* L.): the role of sodium exclusion, *Plant Cell Environ.* **18**, 1041-1047.

Francois, L. E., Donovan, T. J. and Maas, E. V. (1991) Calcium deficiency of artichoke buds in relation to salinity, *Hortsci.* **26**, 549-553.

Frensch, J. and Hsiao, T. C. (1995) Rapid response of the yield threshold and turgor regulation during adjustment of root growth to water stress in *Zea mays*, *Plant Physiol.* **108**, 303-312.

Gilroy, S., Hughes, W. A. and Trewavas, A. J. (1989) A comparison between Quin-2 and aequorin as indicators of cytoplasmic calcium levels in higher plant cell protoplasts, *Plant Physiol.* **90**, 482-491.

Greenway, H. and Munns, R. (1980) Mechanisms of salt tolerance in nonhalophytes, *Annu. Rev. Plant Physiol.* **31**, 149-190.

Grieve, C. M. and Fujiyama, H. (1987) The response of two rice cultivars to external Na/Ca ratio, *Plant Soil* **103**, 245-250.

Grieve, C. M. and Maas, E. V. (1988) Differential effects of sodium/calcium ratio on sorghum genotypes, *Crop Sci.* **28**, 659-665.

Grignon, C. and Sentenac, H. (1991) pH and ionic conditions in the apoplast, *Annu. Rev. Plant Physiol.* **42**, 103-128.

Halperin, S. J., Kochian, L. V. and Lynch, J. P. (1997) Salinity stress inhibits calcium loading into the xylem of excised barley (*Hordeum vulgare*) roots, *New Phytol*. **135**, 419-427.

Hanson, J. B. (1984) The function of calcium in plant nutrition, in P. B. Tinker and A. Läuchli, (eds.), *Advances in Plant Nutrition*, Praeger, New York, pp. 149-208.

Hawkins, H. J. and Lewis, O. A. M. (1993a) Combination effect of NaCl salinity, nitrogen form and calcium concentration on the growth, ionic content and gaseous exchange properties of *Triticum aestivum* L. cv. gamtoos, *New Phytol*. **124**, 161-170.

Hawkins, H. J. and Lewis, O. A. M. (1993b) Effect of NaCl salinity, nitrogen form, calcium and potassium concentration on nitrogen uptake and kinetics in *Triticum aestivum* L. cv. gamtoos, *New Phytol*. **124**, 171-177.

He, T. (1993) *Mechanisms of salt tolerance in rapid-cycling Brassica species used as model plant systems*, Ph.D., University of Nevada, Reno.

Ho, L. C. and Adams, P. (1994) The physiological basis for high fruit yield and susceptibility to calcium deficiency in tomato and cucumber, *J. Hort. Sci*. **69**, 367-376.

Hsiao, T. C., Acevedo, E., Fereres, E. and Henderson, D. E. (1976) Stress metabolism. Water stress, growth, and osmotic adjustment, *Phil. Trans. R. Soc. Lond. B*. **273**, 479-500.

Jang, H. J., Pih, K. T., Kang, S. G., Lim, J. H., Jin, J. B., Piao, H. L. and Hwang, I. (1998) Molecular cloning of a novel $Ca^{2+}$-binding protein that is induced by NaCl stress, *Plant Mol. Biol*. **37**, 839-847.

Johansson, I., Karlsson, M., Shukla, V. K., Chrispeels, M. J., Larsson, C. and Kjellbom, P. (1998) Water transport activity of the plasma membrane aquaporin PM28A is regulated by phosphorylation, *Plant Cell* **10**, 451-459.

Johansson, I., Larsson, C., Ek, B. and Kjellbom, P. (1996) The major integral proteins of spinach leaf plasma membranes are putative aquaporins and are phosphorylated in response to $Ca^{2+}$ and apoplastic water potential, *Plant Cell* **8**, 1181-1191.

Jones, D. L., Kochian, L. V. and Gilroy, S. (1998) Aluminum induces a decrease in cytosolic calcium concentration in BY-2 tobacco cell cultures, *Plant Physiol*. **116**, 81-89.

Kafkafi, U. (1991) Root growth under stress, in Y. Waisel, A. Eshel and U. Kafkafi, (eds.), *Plant Roots: The Hidden Half*, Marcel Dekker, Inc., New York, pp. 375-391.

Kafkafi, U. and Bernstein, N. (1996) Root growth under salinity stress, in Y. Waisel, A. Eshel and U. Kafkafi, (eds.), *Plant Roots: The Hidden Half*, Marcel Dekker, Inc., New York, pp. 435-451.

Kinoshita, T., Nishimura, M. and Shimazaki, K.-I. (1995) Cytosolic concentration of $Ca^{2+}$ regulates the plasma membrane $H^+$-ATPase in guard cells of fava bean, *Plant Cell* **7**, 1333-1342.

Kinraide, T. B. (1994) Use of a Gouy-Chapman-Stern model for membrane-surface electrical potential to interpret some features of mineral rhizotoxicity, *Plant Physiol*. **106**, 1583-1592.

Kinraide, T. B. (1999) Interactions among $Ca^{2+}$, $Na^+$ and $K^+$ in salinity toxicity: quantitative resolution of multiple toxic and ameliorative effects, *J. Exp. Bot*. **50**, 1495-1505.

Knight, H., Brandt, S. and Knight, M. R. (1998) A history of stress alters drought calcium signalling pathways in *Arabidopsis*, *Plant J*. **16**, 681-687.

Knight, H., Trewavas, A. J. and Knight, M. R. (1997) Calcium signalling in *Arabidopsis thaliana* responding to drought and salinity, *Plant J*. **12**, 1067-1078.

Kurth, E., Cramer, G. R., Läuchli, A. and Epstein, E. (1986) Effects of NaCl and $CaCl_2$ on cell enlargement and cell production in cotton roots, *Plant Physiol*. **82**, 1102-1106.

LaHaye, P. A. and Epstein, E. (1969) Salt toleration by plants: enhancement with calcium, *Science* **166**, 395-396.

LaHaye, P. A. and Epstein, E. (1971) Calcium and salt toleration by bean plants, *Physiol. Plant*. **25**, 213-218.

Läuchli, A. and Schubert, S. (1989) The role of calcium in the regulation of membrane and cellular growth processes under salt stress., in J. H. Cherry, (ed.) *Environmental Stress in Plants*, NATO ASI Series, pp. 131-138.

Lazof, D. and Läuchli, A. (1991) The nutritional status of the apical meristem of *Lactuca sativa* as affected by NaCl salinization: an electron-probe microanalytic study, *Planta* **184**, 334-342.

Lazof, D. B. and Bernstein, N. (1999) The NaCl induced inhibition of shoot growth: the case for disturbed nutrition with special consideration of calcium, *Adv. Bot. Res*. **29**, 113-189.

Leidi, E. O., Nogales, R. and Lips, S. H. (1991) Effect of salinity on cotton plants grown under nitrate or ammonium nutrition at different calcium levels, *Field Crop Res*. **26**, 35-44.

Leidi, E. O. and Saiz, J. F. (1997) Is salinity tolerance related to Na accumulation in Upland cotton (*Gossypium hirsutum*) seedlings?, *Plant Soil* **190**, 67-75.

Lino, B., Baizabal-Aguirre, V. M. and De la Vara, L. E. G. (1998) The plasma-membrane $H^+$-ATPase from beet root is inhibited by a calcium-dependent phosphorylation, *Planta* **204**, 352-359.

Liu, J. P. and Zhu, J. K. (1997) An *Arabidopsis* mutant that requires increased calcium for potassium nutrition and salt tolerance, *Proc. Natl. Acad. Sci. USA* **94**, 14960-14964.

Liu, J. P. and Zhu, J. K. (1998) A calcium sensor homolog required for plant salt tolerance, *Science* **280**, 1943-1945.

Lockhart, J. A. (1965) An analysis of irreversible plant cell elongation, *J. Theoret. Biol.* **8**, 264-275.

Lynch, J., Cramer, G. R. and Läuchli, A. (1987) Salinity reduces membrane-associated calcium in corn root protoplasts, *Plant Physiol.* **83**, 390-394.

Lynch, J. and Läuchli, A. (1985) Salt stress disturbs the calcium nutrition of barley (*Hordeum vulgare* L.)., *New Phytol.* **99**, 345-354.

Lynch, J. and Läuchli, A. (1988) Salinity affects intracellular calcium in corn root protoplasts, *Plant Physiol.* **87**, 351-356.

Lynch, J., Polito, V. S. and Läuchli, A. (1989) Salinity stress increases cytoplasmic Ca activity in maize root protoplasts, *Plant Physiol.* **90**, 1271-1274.

Lynch, J., Thiel, G. and Läuchli, A. (1988) Effects of salinity on the extensibility and Ca availability in the expanding region of growing barley leaves, *Bot. Acta* **101**, 355-361.

Maas, E. V. and Grieve, C. M. (1987) Sodium-induced calcium deficiency in salt-stressed corn, *Plant Cell Environ.* **10**, 559-564.

Malhó, R., Moutinho, A., Van der Luit, A. and Trewavas, A. J. (1998) Spatial characteristics of calcium signalling: the calcium wave as a basic unit in plant cell calcium signalling, *Phil. Trans. R. Soc. Lond. B.* **353**, 1463-1473.

Marschner, H. (1995) *Mineral Nutrition of Higher Plants. 2nd ed*, Academic Press Inc., San Diego.

Martinez, V. and Läuchli, A. (1993) Effects of $Ca^{2+}$ on the salt-stress response of barley roots as observed by *in vivo* $^{31}$P-nuclear magnetic resonance and *in vitro* analysis, *Planta* **190**, 519-524.

Muhammed, S., Akbar, M. and Neue, H. U. (1987) Effect of Na/Ca and Na/K ratios in saline culture solution on the growth and mineral nutrition of rice (*Oryza sativa* L.), *Plant Soil* **104**, 57-62.

Muir, S. R., Bewell, M. A., Sanders, D. and Allen, G. J. (1997) Ligand-gated $Ca^{2+}$ channels and $Ca^{2+}$ signalling in higher plants, *J. Exp. Bot.* **48**, 589-597.

Munns, R., Gardner, P. A., Tonnet, M. L. and Rawson, H. M. (1988) Growth and development in NaCl-treated plants. II. Do $Na^+$ or $Cl^-$ concentrations in dividing or expanding tissues determine growth in barley?, *Aust. J. Plant Physiol.* **15**, 529-540.

Munns, R. and Sharp, R. E. (1993) Involvement of abscisic acid in controlling plant growth in soils of low water potential, *Aust. J. Plant Physiol.* **20**, 425-437.

Murata, Y., Fujita, M., Nakatani, T., Obi, I. and Kakutani, T. (1998a) Effect of $Na^+$ on $Ca^{2+}$-binding on the plasma membrane of barley mesophyll cells: an electrophoretic study, *Plant Cell Physiol.* **39**, 452-457.

Murata, Y., Yoshihashi, M., Obi, I. and Kakutani, T. (1998b) $Ca^{2+}$ regulation of outward rectifying $K^+$ channel in the plasma membrane of tobacco cultured cells in suspension: a role of the $K^+$ channel in mitigation of salt-stress effects by external $Ca^{2+}$, *Plant Cell Physiol.* **39**, 1039-1044.

Nakamura, Y., Kasamo, K., Shimosato, N., Sakata, M. and Ohta, E. (1992) Stimulation of the extrusion of protons and $H^+$-ATPase activities with the decline in pyrophosphatase activity of the tonoplast in intact mung bean roots under high-NaCl stress and its relation to external levels of $Ca^{2+}$ ions, *Plant Cell Physiol.* **33**, 139-149.

Nakamura, Y., Tanaka, K., Ohta, E. and Sakata, M. (1990) Protective effect of external $Ca^{2+}$ on elongation and the intracellular concentration of $K^+$ in intact mung bean roots under high NaCl stress, *Plant Cell Physiol.* **31**, 815-821.

Neumann, P. M. (1995) The role of cell wall adjustment in plant resistance to water deficits, *Crop Sci.* **35**, 1258-1266.

Oertli, J. J. (1968) Extracellular salt accumulation, a possible mechanism of salt injury, *Agrochim.* **12**, 461-469.

Ortiz, A., Martinez, V. and Cerda, A. (1994) Effects of osmotic shock and calcium on growth and solute composition of *Phaseolus vulgaris* plants, *Physiol. Plant.* **91**, 468-476.

Pardo, J. M., Reddy, M. P., Yang, S. L., Maggio, A., Huh, G. H., Matsumoto, T., Coca, M. A., Paino-D'Urzo, M., Koiwa, H., Yun, D. J., Watad, A. A., Bressan, R. A. and Hasegawa, P. M. (1998) Stress signaling through $Ca^{2+}$/calmodulin-dependent protein phosphatase calcineurin mediates salt adaptation in plants, *Proc. Natl. Acad. Sci. USA* **95**, 9681-9686.

Passioura, J. B. (1988) Water transport in and to roots, *Annu. Rev. Plant. Physiol. Plant. Mol. Biol.* **39**, 245-265.

Perera, L. K. R. R., Mansfield, T. A. and Malloch, A. J. C. (1994) Stomatal responses to sodium ions in *Aster tripolium*: a new hypothesis to explain salinity regulation in above-ground tissues, *Plant Cell Environ.* **17**, 335-340.

Perera, L. K. R. R., Robinson, M. F. and Mansfield, T. A. (1995) Responses of the stomata of *Aster tripolium* to calcium and sodium ions in relation to salinity tolerance, *J. Exp. Bot.* **46**, 623-629.

Piñeros, M. and Tester, M. (1997) Calcium channels in higher plant cells: selectivity, regulation and pharmacology, *J. Exp. Bot.* **48**, 551-577.

Plaut, Z. and Grieve, C. M. (1988) Photosynthesis of salt-stressed maize as influenced by Ca:Na ratios in the nutrient solution, *Plant Soil* **105**, 283-286.

Rengel, Z. (1992) The role of calcium in salt toxicity, *Plant Cell Environ.* **15**, 625-632.

Ripoll, C., Pariot, C., Jauneau, A., Verdus, M. C., Catesson, A. M., Morvan, C., Demarty, M. and Thellier, M. (1993) Involvement of sodium in a process of cell differentiation in plants, *C R Acad Comptes Rendus de L Academie Des Sciences Serie III - Sciences de La Vie - Life Sciences [III]* **316**, 1433-1437.

Roberts, S. K. and Tester, M. (1997a) A patch clamp study of $Na^+$ transport in maize roots, *J. Exp. Bot.* **48**, 431-440.

Roberts, S. K. and Tester, M. (1997b) Permeation of $Ca^{2+}$ and monovalent cations through an outwardly rectifying channel in maize root stelar cells, *J. Exp. Bot.* **48**, 839-846.

Scarpa, A. and de Grier, J. (1971) Cation permeability of liposomes as a function of the chemical composition of the lipid bilayers, *Biochim. Biophys. Acta* **241**, 789-797.

Schachtman, D. P., Tyerman, S. D. and Terry, B. R. (1991) The $K^+/Na^+$ selectivity of a cation channel in the plasma membrane of root cells does not differ in salt-tolerant and salt-sensitive wheat species, *Plant Physiol.* **97**, 598-605.

Schmidt, C., He, T. and Cramer, G. R. (1993) Supplemental calcium does not improve growth of salt-stressed *Brassicas*, *Plant Soil* **156**, 415-418.

Steudle, E. (1989) Water flow in plants and its coupling to other processes: an overview., in S. Fleischer and B. Fleisher, (eds.), *Methods of Enzymology, Vol. 174, Part U: Cellular and Subcellular Transport: Eukaryotic (Nonepidermal) Cells*., Academic Press, New York, pp. 183-225.

Suhayda, C. G., Giannini, J. L., Briskin, D. P. and Shannon, M. C. (1990) Electrostatic changes in *Lycopersicon esculentum* root plasma membrane resulting from salt stress, *Plant Physiol.* **93**, 471-478.

Suhayda, C. G., Redmann, R. E., Harvey, B. L. and Cipywnyk, A. L. (1992) Comparative response of cultivated and wild barley species to salinity stress and calcium supply, *Crop Sci.* **32**, 154-163.

Takahashi, K., Isobe, M. and Muto, S. (1997) An increase in cytosolic calcium ion concentration precedes hypoosmotic shock-induced activation of protein kinases in tobacco suspension culture cells, *FEBS Lett.* **401**, 202-206.

Taybi, T. and Cushman, J. C. (1999) Signaling events leading to Crassulacean acid metabolism induction in the common ice plant, *Plant Physiol.* **121**, 545-555.

Taylor, A., Manison, N. and Brownlee, C. (1997) Regulation of channel activity underlying cell volume and polarity signals in *Fucus*, *J. Exp. Bot.* **48**, 579-588.

Taylor, A. R., Manison, N. F. H., Fernandez, C., Wood, J. and Brownlee, C. (1996) Spatial organization of calcium signaling involved in cell volume control in the *Fucus* rhizoid, *Plant Cell* **8**, 2015-2031.

Thiel, G., Lynch, J. and Läuchli, A. (1988) Short-term effects of salinity stress on the turgor and elongation of growing barley leaves, *J. Plant Physiol.* **132**, 38-44.

Thiyagarajah, M., Fry, S. C. and Yeo, A. R. (1996) *In vitro* salt tolerance of cell wall enzymes from halophytes and glycophytes, *J. Exp. Bot.* **47**, 1717-1724.

Tyerman, S. D. and Skerrett, I. M. (1999) Root ion channels and salinity, *Sci. Hort.* **78**, 175-235.

Tyerman, S. D., Skerrett, M., Garrill, A., Findlay, G. P. and Leigh, R. A. (1997) Pathways for the permeation of $Na^+$ and $Cl^-$ into protoplasts derived from the cortex of wheat roots, *J. Exp. Bot.* **48**, 459-480.

Wadleigh, C. H. and Bower, C. A. (1950) The influence of calcium ion activity in water cultures on the intake of cations by bean plants, *Plant Physiol*. **25**, 1-12.

White, P. J. (1998a) Calcium channels in the plasma membrane of root cells, *Ann. Bot*. **81**, 173-183.

White, P. J. (1998b) Voltage-dependent $Ca^{2+}$ uptake by right-side-out plasma membrane vesicles derived from maize shoots, *J. Plant Physiol*. **152**, 17-24.

Wimmers, L. E., Ewing, N. N. and Bennett, A. B. (1992) Higher plant $Ca^{2+}$-ATPase: primary structure and regulation of mRNA abundance by salt, *Proc. Natl. Acad. Sci. USA* **89**, 9205-9209.

Wright, G. C., Patten, K. D. and Drew, M. C. (1992) Salinity and supplemental calcium influence growth of rabbiteye and southern highbush blueberry, *J. Amer. Soc. Hort. Sci*. **117**, 749-756.

Wright, G. C., Patten, K. D. and Drew, M. C. (1993) Gas exchange and chlorophyll content of tifblue rabbiteye and sharpblue southern highbush blueberry exposed to salinity and supplemental calcium, *J. Amer. Soc. Hort. Sci*. **118**, 456-463.

Wu, S. J., Ding, L. and Zhu, J. K. (1996a) *SOS1*, a genetic locus essential for salt tolerance and potassium acquisition, *Plant Cell* **8**, 617-627.

Wu, Y. J., Sharp, R. E., Durachko, D. M. and Cosgrove, D. J. (1996b) Growth maintenance of the maize primary root at low water potentials involves increases in cell-wall extension properties, expansin activity, and wall susceptibility to expansins, *Plant Physiol*. **111**, 765-772.

Yeo, A. R. and Flowers, T. J. (1985) The absence of an effect of the Na/Ca ratio on sodium chloride uptake by rice (*Oryza sativa* L.), *New Phytol*. **99**, 81-90.

Yermiyahu, U., Nir, S., Ben-Hayyim, G. and Kafkafi, U. (1994) Quantitative competition of calcium with sodium or magnesium for sorption sites on plasma membrane vesicles of melon (*Cucumis melo* L.) root cells, *J. Membrane Biol*. **138**, 55-63.

Yermiyahu, U., Nir, S., Ben-Hayyim, G., Kafkafi, U. and Kinraide, T. B. (1997) Root elongation in saline solution related to calcium binding to root cell plasma membranes, *Plant Soil* **191**, 67-76.

Yu, B., Gong, H. and Liu, Y. (1998) Effects of calcium on lipid composition and function of plasma membrane and tonoplast vesicles isolated from roots of barley seedlings under salt stress, *J. Plant Nutr*. **21**, 1589-1600.

Zekri, M. (1993) Salinity and calcium effects on emergence, growth and mineral composition of seedlings of eight citrus rootstocks, *J. Hort. Sci*. **68**, 53-62.

Zhong, H. and Läuchli, A. (1988) Incorporation of [$^{14}$C]glucose into cell wall polysaccharides of cotton roots: effects of NaCl and $CaCl_2$, *Plant Physiol*. **88**, 511-514.

Zhong, H. and Läuchli, A. (1993a) Changes of cell wall composition and polymer size in primary roots of cotton seedlings under high salinity, *J. Exp. Bot*. **44**, 773-778.

Zhong, H. and Läuchli, A. (1993b) Spatial and temporal aspects of growth in the primary root of cotton seedlings: effects of NaCl and $CaCl_2$, *J. Exp. Bot*. **44**, 763-771.

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

Zid, E. and Grignon, C. (1985) Sodium-calcium interactions in leaves of *Citrus aurantium* grown in the presence of NaCl, *Physiol. Vég*. **23**, 895-903.

Zidan, I., Azaizeh, H. and Neumann, P. M. (1990) Does salinity reduce growth in maize root epidermal cells by inhibiting their capacity for cell wall acidification?, *Plant Physiol*. **93**, 7-11.