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Role of Calcium in Plants under Salt Stress

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Abstract: The role of Ca in preserving the structural and functional integrity of plant cell membranes, stabilization of cell wall structures and in regulation, transport and control of ion exchange behaviour is well documented. However, recently Ca has attracted attention as a second messenger in the signal conduction between environmental factors and plant responses. These functions are seriously impaired by reduced Ca^{2+} availability under saline and particularly sodic conditions. The uptake of Ca^{2+} from soil solution may decrease because of ion interactions, precipitation and increases in ionic strength that reduce the activity of Ca^{2+} leading to reduced growth and yields, under saline conditions. The available information on plant responses to nutritional imbalances due to high Na^+/Ca^{2+} ratios under salinity conditions has been discussed and the mechanisms governing sodium- calcium interactions in plants have been outlined.

Key words: Calcium, salinity, Ca-Na interactions, genotypic differences, physiological disorders.

Many plant species suffer a decline in growth when exposed to saline conditions. The deleterious effects of salinity are thought to result from osmotic effect on water availability, specific ion effects and ion imbalances due to interference with uptake of essential ions or a combination of these factors. Among many effects, high external sodium reduces the activity of Ca ions in the root medium and decreases the amount of available Ca for uptake by the plant (Cramer and Lauchli, 1986). Ca concentrations that are adequate under normal conditions may become nutritionally inadequate when external Na/Ca ratio is high (Bernstein, 1975) particularly under sodic conditions. Root growth and function is inhibited and the processes whereby Ca is transported from the root to the shoot may be impaired (Lynch and Lauchli, 1985).

In many salt sensitive species supplemental Ca partly reverses the detrimental effects of Na (LaHaye and Epstein, 1969; Kawasaki and Moritsugu, 1978 a,b; Ward *et al.*, 1986; Cramer *et al.*, 1987; Akhavan-Kharazian *et al.*, 1991; Garg *et al.*, 1997). Although it has been suggested that elevated Ca may protect the plants from salt toxicity by reducing the displacement of membrane associated Ca^{2+}, by reducing Na^+ uptake and translocation to the shoot and by improving K^+ uptake and translocation (Cramer *et al.*, 1985, 1989; Maas and Grieve, 1987; Gorham and Bridges, 1995) yet the experimental evidence available presently to support a correlation between low Ca and reduced growth is inconclusive (Bernstein *et al.*, 1993). Therefore an attempt has been made here to review the role of calcium in salt tolerance of plants and to understand the mechanisms underlying Ca-Na interactions.

Role of Calcium in Higher Plants

Calcium, an essential macro-nutrient, plays a vital nutritional and physiological role in plant metabolism. Calcium is involved in stabilization of cell walls and plasma membranes and cell division and elongation (Hanson, 1984; Kurth *et al.*, 1986). It regulates ion transport and controls ion-exchange behaviour and cell wall enzyme activities (Demarty *et al.*, 1984). These functions of Ca have been comprehensively reviewed by Hanson (1984), Kirkby and Pilbeam (1984) and Hepler and Wayne (1985). However, in recent years Ca has attracted much attention because of its function as a second messenger in the signal conduction between environmental factors and plant responses in terms of growth and development. Therefore, available information on this aspect is briefly outlined below.

Calcium Supply, Plant Growth and Composition

The Ca content in plant varies between 0.1 and >5% of the dry weight depending on the growing conditions, plant species and plant organ. The Ca requirement for optimum growth is much lower in monocotyledons than in dicotyledons (Loneragan and Snowball, 1969; Islam *et al.*, 1987). Another factor determining the calcium requirement for optimum growth is the concentration of other cations in the external solution. Because of its replacement by other cations from its binding sites at the exterior surface of the plasma membrane, the Ca requirement increases with increasing external concentration of heavy metals, aluminium and sodium chloride (LaHaye and Epstein, 1971).

Solomon *et al.* (1986) observed abnormal root morphology and anatomy of pea grown in nutrient cultures containing 120 mM NaCl as the sole salinizing salt. These ''salinity induced'' changes characterized by curvature of the root tip as well as constriction and thickening above the apex were completely reversed by the addition of 10 mM Ca^{2+} (Solomon *et al.*, 1989)

Growth parameters including root length, cell elongation, radial cell expansion and cellular stability of roots depend on the Na^+/Ca^{2+} ratio in the media in a number of crop plants (Gerard and Hinojosa, 1973; Kurth *et al.*, 1986; Cramer *et al.*, 1985, 1987; Zidan *et al.* 1990). The young leaves of new plants are affected before the older leaves and they are often distorted, and small with irregular margins and spotted or necrotic areas.

In many soils, Ca deficiency symptoms usually arise due to problems of internal distribution rather than low external supply from the soil. Restricted mobility of Ca^{2+} within the plant tissue also reduces its movement to growing meristems. However, the occurrence of low Ca concentrations in sodic soils is very common and well documented (Bernstein, 1975; Poonia and Bhumbla, 1973; Naidu and Rengasamy, 1993).

The Ca^{2+} requirement of a plant is generally low, i.e., 0.7 to 1.5 m mol l^{-1}. However, it depends on the presence of other ions. Therefore, Ca requirement is related to ion competition and is usually expressed in terms of ion ratios, rather than the absolute concentration of Ca^{2+} in the soil solution.

Severe Ca deficiency in barley results when Ca^{2+}/Mg^{2+} molar ratio or Ca^{2+}/TC ratio is less than 0.15 (Carter *et al.*, 1979; Carter and Webster, 1990). Howard and Adams (1965) related the critical requirement for the optimum growth of cotton roots to the molar ratio of Ca^{2+}/TC. Many later workers, however, suggested that ion activity was more accurate measure of Ca^{2+} availability (Wolt and Adams, 1979; Grattan and Grieve, 1992). It seems preferable to distinguish specific ion competition, e.g., Ca^{2+}/Na^{+} and Ca^{2+}/Mg^{2+} rather than Ca^{2+}/Tc.

Salinity Effects on Calcium Nutrition

Calcium deficiency is an important nutritional imbalance problem which occurs as a result of either excessive soil sodicity, pH or high soluble Na^{+}/Ca^{2+} or Mg^{2+}/Ca^{2+} ratio in the growth medium. Sodium induced Ca deficiency symptoms have been observed in a number of crop plants such as sorghum (Kawasaki and Moritsugn, 1979; Grieve and Maas, 1988), barley (Maas and Grieve, 1988) corn (Maas and Grieve, 1987) rice (Grieve and Fujiyama, 1987; Muhammed *et al.*, 1987), pea (Garg and Garg, 1980) and beans (LaHaye and Epstein, 1971; Cachorro *et al.*, 1994). In many cases increasing salinity or sodicity decreased Ca uptake and its transport to the shoot (Carter and Pearen, 1988; Hansen and Munns, 1988; Banuls *et al.*, 1991; Cachorro *et al.*, 1994).

Root growth

Root growth and function was restricted by high Na^{+}/Ca^{2+} in a number of plant species (Kent and Lauchli, 1985; Cramer *et al.*, 1985, 1986; Evalagon *et al.*, 1992). Solomon *et al.* (1989) observed abnormal root morphology and anatomy of pea grown on nutrient cultures containing 120 mM NaCl. These ''salinity induced'' changes were completely reversed by the addition of 10 mM Ca^{2+}.

Cramer *et al.* (1986) found that a wide range of NaCl concentrations did not inhibit the root growth of cotton, when supplemented with Ca. However, in the absence of Ca there was a drastic reduction in root growth. Azaizeh *et al.* (1992) found that NaCl had an adverse effect on water transport parameters of maize roots and supplemental Ca could compensate for these effects. Carter and Pearen (1988) found lower dry weight and reduced root penetration of barley in a saline-sodic soil but Ca addition had a compensating effect. Evalagon *et al.* (1992) reported 54% reduction in root growth of maize seedlings under 100 mM NaCl but when 10 mM $CaCl_2$ was also there, the reduction was only 20%. Supplemental Ca also overcame the adverse effect of NaCl on hydraulic conductivity. Cramer *et al.* (1989) concluded that the protection of root growth from salt stress by Ca is related to improved Ca status in the plants and maintenance of K^{+}/Na^{+} selectivity.

According to Kurth *et al.* (1986) Ca addition to the medium probably favours cell elongation over radial cell expansion and maintains high rates of cell production in cotton roots. Cramer *et al.* (1988) reported that addition of Ca after adding NaCl only partially restored, but adding Ca before adding NaCl completely protected the root growth of cotton from the inhibitory effects of salt.

Shoot growth

Although Ca deficiency generally impairs root growth more than top growth, there are several studies which show growth distorting effects on developing leaves under Na induced Ca deficiency (Maas and Grieve, 1987; Grieve and Maas, 1988; Ehret *et al*., 1990; Akhavan-Kharazian *et al*., 1991; Bernstein *et al*., 1993). However, addition of Ca partly or completely compensated these adverse effects. For example leaf elongation of salt-stressed barley seedlings was found to improve when Ca^{2+} supply was increased from 0.5 to 3 mM (Ward *et al*., 1986). Elzam and Epstein (1969) found a positive correlation between Ca levels and growth in *Agropyron* spp. exposed to salinity.

When LaHaye and Epstein (1969) grew highly sensitive bean plants in solution cultures at 50 mM NaCl and $CaSO_4$ concentrations of 1 mM or less, NaCl impaired the growth of the plants during the seven days of the experiment. Adding Ca^{2+} at concentrations of 3 or 10 mM completely protected the plants from adverse salinity effects. Similar findings were obtained with bean plants grown to maturity (LaHaye and Epstein, 1971). In several other studies also supplemental Ca partly restored the salinity induced growth reductions, e.g., barley (Ward *et al*., 1986), Corn (Maas and Grieve, 1987), beans (Akhavan-Kharazian *et al*., 1991), rapeseed (Porecelli *et al*., 1995) and clusterbean (Garg *et al*., 1997). However, in certain other studies there was no positive effect of Ca supply under salt stress, e.g., rice (Yeo and Flowers, 1985) and rapeseed (Schmidt *et al*., 1993). Kawasaki and Moritsugu (1978 a,b) found that Ca application (1 mM) significantly protected maize and barley plants from NaCl toxicity (0, 4, 20 and 40 mM), had no effect at all in rice and only a slight improvement in beans.

In citrus supplemental Ca could mitigate the adverse effects of NaCl on plant growth, defoliation and leaf injury (Banuls *et al*., 1991). Similarly Ben-Hayyim and Kochba (1983) had observed that salt inhibited cell growth in a salt-tolerant line of citrus when Ca was removed from the growth medium. Maximum cell production required an increase in Ca for each increase in NaCl (Ben-Hayyim *et al*., 1987). They observed that Ca^{2+}/Na^{+} ratio was crucial for optimum growth and a ratio of 0.5×10^{-4} per millimolar gave maximum protection from NaCl.

Ca-Na Interactions on Ion Concentrations

As salinity increases the requirements of plants for Ca increase (Gerard, 1971). In saline soils contrasted with sodic soils, Ca concentrations usually increase as the total salt concentration increases. At the same time, however, the uptake of Ca^{2+} from the soil solution may decrease because of ion interactions, precipitation and increases in the ionic strength that reduce the activity of Ca^{2+}. These combined effects are partially responsible for reduced yields under saline or sodic conditions (Bernstein, 1975; Rengasamy, 1987; Janzen and Chang, 1987; Puntamkar *et al*., 1988). In sodic soils, the low Ca concentration is a common feature (Naidu and Rengasamy, 1993). Garg and Garg (1980) found that increasing levels of Na_2CO_3 and $NaHCO_3$ drastically reduced the concentrations of Ca, magnesium and

Table 1. Effect of Na_2CO_3 and $NaHCO_3$ (dS m^{-1}) on concentration (%) of Ca, Mg, K, Na and K/Na ratio in shoot and root of pea (Garg and Garg, 1980)

Treatments (dS m^{-1})		Calcium	Magnesium	Potassium	Sodium	K/Na ratio
Shoot						
Control	0	4.13	2.00	2.29	0.44	5.20
Na_2CO_3	2	3.80	1.76	1.86	0.70	2.66
	4	3.20	1.59	2.22	0.97	2.29
	6	2.66	1.36	2.13	1.40	1.52
$NaHCO_3$	2	3.93	1.84	2.11	0.80	2.64
	4	3.53	1.51	1.82	1.21	1.50
	6	1.52	1.52	2.02	1.83	1.10
LSD (0.05)		0.46	0.26	0.21	0.12	–
Root						
Control	0	4.43	1.99	1.70	0.41	4.15
Na_2CO_3	2	4.00	2.48	1.56	1.24	1.26
	4	3.73	1.90	1.66	1.08	1.54
	6	3.40	1.48	1.81	1.40	1.29
$NaHCO_3$	2	3.66	2.37	1.48	1.21	1.22
	4	3.60	2.56	1.51	1.41	1.07
	6	3.46	2.00	1.43	1.65	0.87
LSD (0.05)		0.27	0.27	0.23	0.13	–

potassium in shoots as well as roots of pea (Table 1).

Kawasaki and Moritsugu (1978 a,b) found that at a high concentration of Ca (1 mM) barley, maize, bean and rice plants absorbed and translocated relatively more K and less Na than at a low concentration of Ca (0.1 mM) under increasing concentrations of NaCl (0, 4, 20, 40 mM) in nutrient solution. Consequently the K/Na ratios in the tops and roots were more wider at high than low Ca levels at all concentrations of NaCl (Table 2). A number of subsequent studies have established that increasing salinity decreased K^+ and Ca^{2+} concentrations and increased tissue concentrations of Na^+. However, elevated Ca enhanced the uptake and translocation of Ca and K from the roots to the shoots (Cramer *et al.*, 1987; Hansen and Munns, 1988; Zekri, 1993; Cachoroo *et al.*, 1994; Gorham and Bridges, 1995; Garg *et al.*, 1997). In most of these studies K^+/Na^+ ratio was enhanced by supplemental Ca under salt stress. It thus seems that addition of Ca increases the K^+/Na^+ and Ca^{2+}/Na^+ ratios in shoots and improves plant growth. Changes in tissue Ca^{2+} concentrations were correlated with the relative salt tolerance of certain species (Cramer *et al.*, 1991; He and Cramer, 1992).

The effects of Ca nutrition on chloride uptake under saline conditions are not consistent. While elevated Ca decreased chloride concentrations and its transport from root to the shoot in citrus plants (Banuls

Table 2. Effects of different levels of sodium chloride and calcium chloride on the ratio of potassium to sodium (K/Na) in maize, barley, rice and bean plants (Kawasaki and Moritsugu, 1978 a,b)

Na (mM)	Maize		Barley		Rice		Beans	
	0.1*	1.0	0.1	1.0	0.1	1.0	0.1	1.0
				Shoot				
0	399.1	558.8	89.3	141.3	78.5	87.4	194.3	253.7
4	56.4	132.2	4.7	7.6	20.7	21.3	104.6	107.0
20	6.6	10.4	0.9	1.6	3.6	4.6	28.7	30.7
40	1.9	4.1	0.6	0.9	1.0	0.9	7.4	20.7
				Root				
0	56.5	37.7	79.1	56.9	11.8	25.9	102.0	157.1
4	3.1	5.0	5.5	9.4	2.9	6.6	9.5	18.0
20	0.7	1.5	0.7	1.9	1.0	2.1	2.0	2.9
40	0.4	0.8	0.4	1.1	0.4	1.0	0.8	1.3

*Ca concentration (mM).

et al., 1991) there was no effect of Ca levels on chloride uptake in case of Beans (Cachorro *et al.*, 1994) and *Leucaena leucocephala* (Hansen and Munns, 1988). On the other hand increasing $CaCl_2$/NaCl ratios increased leaf chloride in soybean genotypes. Increased root permeability caused by a reduction in the availability of external Ca^{2+} may lead to increased Cl^- uptake which may decrease shoot growth (Subbarao *et al.*, 1990).

Salinity is known to severely inhibit nitrate uptake which may be limiting factor for growth in saline environment. Ward *et al.* (1986) found that increasing Ca^{2+} concentration in saline nutrient solutions resulted in increases in NO_3^- assimilation and seedling growth of barley seedlings. The enhancement of NO_3^- transport by Ca^{2+} under saline conditions was dependent on the presence of Ca^{2+} in the uptake solution along with the salt, since Ca^{2+} had no effect when supplied before or after salinity stress.

Nutritional Imbalances and Plant Responses

Nutritional imbalances in cereals and other plants by using iso-osmotic nutrient solutions salinized with various molar ratios of Na^+ and Ca^{2+} have been studied. These investigations include corn (Maas and Grieve, 1987; Plaut and Grieve, 1988), rice (Grieve and Fujiyama, 1987; Muhammed *et al.*, 1987), sorghum (Grieve and Maas, 1988), soybean (Grattan and Maas, 1988), pigeonpea (Subbarao *et al.*, 1990) and rapeseed (Porecelli *et al.*, 1995). The studies indicated that reduced Ca^{2+} availability in the leaf growth region and high Na^+/Ca^{2+} ratios in the region contributed to the inhibition of growth (Lynch, and Lauchli, 1988). Procelli *et al.* (1995) found that despite decreased K^+/Na^+ and Ca^{2+}/Na^+ ratios in the tissue under increased soil salinity, the seed yield and aerial biomass production were not affected in rapeseed. However, under soil sodicity (increased SAR) the K^+/Na^+ and Ca^{2+}/Na^+ ratios in plant tissue decreased considerably in accordance with seed and biomass production which indicated differential effects of sodicity from that of salinity.

Significant intergeneric differences in their response to different Na^+/Ca^{2+} molar ratios have been reported among cereals. A salt stress (OP = -0.6 MPa) with Na^+/Ca^{2+} = 52 reduced the relative dry matter yield of wheat less than that of rye or oats. At -0.4 MPa rice was more sensitive than corn at Na^+/Ca^{2+} = 5 (Maas and Grieve, 1987; Grieve and Fujiyama, 1987). In barley a wild variety exhibited higher salt tolerance than a cultivated variety (Suhayada *et al.*, 1992) due to maintenance of higher tissue concentration of Ca^{2+} and more effective compartmentalizing of Na^+ in the root rather than in the shoot. Likewise tolerant (ICPL-227) and sensitive (HY 3C) pigeonpea genotypes exhibited marked differences in Na^+ and K^+ concentrations at various Na^+/Ca^{2+} ratios under 6 and 8 dS m^{-1} salinity levels (Subbarao *et al.*, 1990).

Genotypic Differences

Genotypes within a given species may also differ in their susceptibility to Ca disorders at high substrate Na^+/Ca^{2+} ratios. Grieve and Maas (1988) compared the response of three sorghum genotypes and suggested that the Na^+ tolerance of Hegari was related to the efficiency of Ca^{2+} transport to the developing leaves. At Na^+/Ca^{2+} = 34.6 and OP = -0.40 MPa, many of the expanding blades of the sensitive cultivars NK 265 and NB 9040 were deeply serrated and tightly rolled with withered and necrotic tips. These symptoms have been associated with severe Ca deficiency (Kawasaki and Moritsugu, 1979) and this diagnosis was confirmed by mineral analysis.

In rice, dry matter production of two cultivars (M-9 and M-201) was sensitive to increasing Na^+/Ca^{2+} ratios (at OP = -0.4 MPa) but the correlation was significant only for M-201 (Grieve and Fujiyama, 1987). However, Ca nutrition was severely inhibited at high Na^+/Ca^{2+} ratios and laminae exhibited Ca deficiency symptoms in both the genotypes. Norlyn and Epstein (1984) observed that triticale lines differed in tolerance to high Na^+/Ca^{2+} during emergence and germination. Emergence of only one line improved when the Na^+/Ca^{2+} was reduced to 37, the other lines showed no effect of added Ca.

Physiological Disorders

Several investigations (Muhammed *et al.*, 1987, Grieve and Maas, 1988) have shown that as the injured cereal leaves mature and become less dependent on root pressure for their supply of water and nutrients, their Ca^{2+} demands are then met via increased transpiration rates. Consequently the Ca^{2+} concentration in the older leaves of salinized plants was as high as in those in the non saline controls. The limited capacity of plants to regulate Ca^{2+} distribution internally in relation to the demands of low transpiring organs (leaves, fruits, tubers) has been implicated in certain typical Ca^{2+} related physiological disorders as blossom end rot of tomatoes and peppers, black heart of celery and internal browning of lettuce and artichokes (Geraldson 1957; Francois *et al.*, 1991).

Calcium-Sodium Interactions

The importance of Ca for selective ion uptake is well documented (Epstein, 1961; Lauchli and Epstein, 1970; Hepler and Wayne, 1985). Ca plays an even more significant role under saline conditions. Therefore the interaction of Na^+ and Ca^{2+} in salt stressed plants has been the subject of many investigations. LaHaye and Epstein (1969, 1971) demonstrated that increasing Ca^{2+} levels in nutrient solutions protected bean plants from salt injury, presumably by restricting Na^+ influx and translocation. They postulated that Ca^{2+}/Na^+ interaction takes place at the plasmalemma and suggested that Na^+ acted by displacing Ca^{2+} from the membranes leading to increased membrane permeability and intra cellular Na^+ concentrations. Lynch and Lauchli (1985) suggested that sodium may inhibit the radial movement of Ca^{2+} from the external solution to the root xylem by screening of cation exchange sites in the apoplast. Cramer *et al.* (1985, 1987) concluded that the primary response to NaCl stress in cotton roots is the displacement of membrane associated Ca^{2+} by Na^+ leading to increased membrane permeability and to loss of K^+/Na^+ selectivity. The addition of 10 mM Ca^{2+} to the saline cultures preserved membrane integrity and prevented leakage of K^+. The maintenance of adequate K^+ and Ca^{2+} transport and K^+/Na^+ selectivity in the root may be related to salt tolerance in cotton and many other plant species. Kent and Lauchli (1985) suggested that K^+/Na^+ selectivity may be improved under saline conditions by increased Ca^{2+} concentrations. Cheeseman (1988) also suggested that Ca is essential for K^+/Na^+ selectivity markedly reducing K^+ efflux in salt stressed plants. On the other hand high Ca^{2+}/Na^+ ratio has a deleterious effect on the function of membranes within cells (Cramer and Lauchli, 1986; Cramer *et al.*, 1986). Bernstein *et al.* (1993) suggested that the improved growth of salinized leaves of sorghum under elevated Ca supply was due to increasing levels of the nutrients that reach the developing leaf. Therefore the Ca concentration in the growing region of a leaf under saline conditions seem very crucial (Ward *et al.*, 1986; Lynch and Lauchli, 1988).

More recently salinity-induced Ca deficiency has also attracted interest in terms of Ca^{2+} homeostasis at cellular level in the roots and in transmitting a signal of salinity stress in the roots to the shoots (Rengel, 1992). It has been suggested that high external Na^+ concentrations may displace Ca^{2+} from the binding sites on the outer surface of the plasma membrane of the root cells or more likely from intracellular membranes (Lynch and Lauchli, 1988) and thereby impair Ca^{2+} homeostasis in cells and its role as secondary messenger (Rengel, 1992).

Calcium-Magnesium Interactions

Calcium is strongly competitive with magnesium and binding sites on the root plasma membrane appear to have less affinity for the highly hydrated Mg^{2+} than for Ca^{2+}. Therefore high concentrations of substrate Ca^{2+} usually result in increased leaf-Ca along with marked reduction in leaf-magnesium. Hansen and Munns (1988) found that increased concentrations of $CaSO_4$ in the nutrient solution decreased Mg^{2+} in roots, stems and leaves of *Leucaena leucocephala*. Calcium induced Mg^{2+} deficiency has also been observed in sesame (Nassery *et al.*, 1979). There are evidences that such a Ca-Mg imbalance could lead to disturbances in photosynthesis. High concentrations of leaf-Ca may interfere with CO_2-fixation by inhibition of stroma enzymes, especially those that are Mg^{2+} activated (Brand and Becker, 1984). Plaut and Grieve (1988) found that CO_2-fixation rate of salt-stressed maize leaves was influenced by the Ca^{2+}/Na^{+} ratio in the solution cultures. At an osmotic potential of -0.4 MPa in the root media both the photosynthetic rate and the water use efficiency declined as substrate Ca increased. Blade Ca concentration also increased while blade sodium and magnesium decreased. It was suggested that photosynthetic activity was inhibited in part by internal Mg deficiency rather than by Na induced Ca deficiency. Reduction of the Ca^{2+}/Mg^{2+} ratio in the culture stimulated the CO_2-fixation rate.

Elevated Ca levels have been found to partly mitigate the adverse effects of salinity and sodicity in a number of crop plants. Different genotypes may have widely different responses. High levels of Na^{+} may adversely affect the nutritional status of plants by interfering with absorption and translocation of Ca^{2+}, resulting in salt toxicity caused by high Na^{+}/Ca^{2+} ratios. Supplemental Ca may protect the plants from salt injury by reducing displacement of membrane associated Ca^{2+}, by reducing sodium uptake and transport from the roots to the shoots, by improving potassium uptake and thereby effectively increasing K^{+}/Na^{+} ratio in the tissue or by a combination of these factors. Reduction in chloride concentration and improvement of NO_3 uptake by Ca application has also been found under saline conditions. Although several studies indicate a correlation between low Ca concentrations and reduced plant growth but the evidence is still inconclusive. However, maintenance of an adequate supply of Ca^{2+} in the soil solution is a very important factor in controlling the severity of specific ion toxicities.

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