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Salinity–mineral nutrient relations in horticultural crops

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Abstract

The relations between salinity and mineral nutrition of horticultural crops are extremely complex and a complete understanding of the intricate interactions involved would require the input from a multidisciplinary team of scientists. This review addresses the nutrient elements individually and we emphasise research directed towards the organ, whole-plant and field level. We have attempted to synthesise the literature and reconcile results from experiments conducted in a variety of conditions such as soil and solution cultures, those using mixed and single-salt (only NaCl) compositions, and those conducted over short (days) and long periods (months) of time.

Crop performance may be adversely affected by salinity-induced nutritional disorders. These disorders may result from the effect of salinity on nutrient availability, competitive uptake, transport or partitioning within the plant. For example, salinity reduces phosphate uptake and accumulation in crops grown in soils primarily by reducing phosphate availability but in solution cultures ion imbalances may primarily result from competitive interactions. Salinity dominated by Na^+ salts not only reduces Ca^{2+} availability but reduces Ca^{2+} transport and mobility to growing regions of the plant, which affects the quality of both vegetative and reproductive organs. Salinity can directly affect nutrient uptake, such as Na^+ reducing K^+ uptake or by Cl^- reducing NO_3^- uptake. Salinity can also cause a combination of complex interactions that affect plant metabolism, susceptibility to injury or internal nutrient requirement.

Despite a large number of studies that demonstrate that salinity reduces nutrient uptake and accumulation or affects nutrient partitioning within the plant, little evidence exists that adding nutrients at levels above those considered optimal in non-saline environments, improves crop yield. Nutrient additions, on the other hand, have been more successful in improving crop quality such as the correction of Na-induced Ca^{2+} deficiencies by supplemental calcium. Nutrient additions may also reduce the incidences of injury as has been observed in the reduction of Cl-toxicity symptoms in certain tree crops by nitrate applications.

It is reasonable to believe that numerous salinity–nutrient interactions occur simultaneously but whether they ultimately affect crop yield or quality depends upon the salinity level and composition

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of salts, the crop species, the nutrient in question and a number of environmental factors.

Keywords: Crops; Fertility; Ion imbalance; Interactions; Mineral nutrients; Nutrition; Review; Saline; Salinity

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Contents

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1. Introduction

Most horticultural crops are glycophytes (Greenway and Munns, 1980) and have evolved under conditions of low soil salinity. The mechanisms they have developed for absorbing, transporting and utilising mineral nutrients from non-saline substrates may not operate as efficiently or as effectively under saline as non-saline conditions. Na^+ and/or Cl^- concentrations often exceed those of most macronutrients by one or two orders of magnitude, and by even more in the case of micronutrients. Therefore, high concentrations of Na^+ and Cl^- in the soil solution may depress nutrient-ion activities and produce extreme ratios of Na^+/Ca^{2+}, Na^+/K^+, Ca^{2+}/Mg^{2+}, and Cl^-/NO_3^-. As a result, the plant becomes susceptible to osmotic and specific-ion injury as well as to nutritional disorders that may result in reduced yield or quality.

Nutrient imbalances can result in salt-stressed plants in various ways. Imbalances may result from the effect of salinity on nutrient availability, competitive uptake, transport or partitioning within the plant or may be caused by physiological inactivation of a given nutrient resulting in an increase in the plant's internal requirement for that essential element (Grattan and Grieve, 1994). It is reasonable to believe that two or more of these processes may be occurring at the same time, but whether they ultimately affect crop yield or quality depends upon the salinity level, composition of salts, the crop species, the nutrient in question and a number of environmental factors.

The availability and uptake of nutrients by plants in saline environments are affected by many factors in the soil–plant environment. The solid phase of the soil and the concentration and composition of solutes in the soil solution controls the activity of the nutrient ion. Soil solution pH and pE[1] will influence the speciation and thus availability of certain nutrients. The concentration and ratios of accompanying elements can influence the uptake and transport of a particular nutrient and indirectly may affect the uptake and translocation of others. These interactions are complicated further by numerous environmental factors such as aeration, temperature, and stresses both biotic and abiotic.

Crops vary not only in the rate at which they absorb an available nutrient element, but also in the manner by which they distribute the element spatially within the plant. Certain ions in the salinising media such as sodium can have a profound effect on calcium mobility and distribution within certain plant organs. Similar examples can be made for other essential nutrients.

The interactive nature affecting nutrient availability, uptake and distribution are topics that are highly complex in the absence of salinity or other stresses (Marschner, 1995). The presence of salinity adds a new level of complexity to the mineral nutrition of crops.

In this paper, we review and synthesise the literature that pertains to salinity and mineral nutrition of horticultural crops. We have structured this review to address the major nutrient elements and the micro-nutrients, individually. This review includes references to both soil and solution culture studies as well as those using either mixed or single-salt (only NaCl) compositions. It is beyond the scope of this review to emphasise either biochemical or molecular level interactions between salinity and mineral nutrition. We have also excluded discussion on salinity–microbe interactions despite the importance of many symbiotic associations to plant nutrition. Our emphasis is placed at the organ and

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[1] pE is defined as the negative logarithm of the activity of the electron.

whole-plant level and on experiments conducted in the time frame between days and months.

2. Nutrient concentration and crop performance

In the absence of salinity, plant growth in relation to the concentration of an essential nutrient element in the root media is often described by the ‘‘generalised dose response curve’’ (Berry and Wallace, 1981). There is a nutrient-concentration window where plant growth is optimal. Concentrations below this optimal range are considered sub-optimal and growth is reduced. When the concentration or activity of the essential nutrient element exceeds this optimal range, growth may be inhibited due to either a toxicity or to a nutrient-induced deficiency. It is important to mention that these dose response curves can apply not only to vegetative and reproductive organs of a particular crop in a quantitative sense but can be modified to include a qualitative aspect as well. For example, excessive NO_3^- accumulation in spinach leaves may not affect yield but may pose a health risk to the consumer (Marschner, 1995). Therefore this window of nutrient adequacy would be narrowed and could be re-labelled ‘‘nutrient acceptability’’.

A substantial body of information in the literature indicates that a plant may not exhibit the same response function under saline conditions as it does under non-saline conditions. In some cases the optimal range may be widened, narrowed, or it may shift in one direction or the other depending upon the plant species or cultivar, the particular nutrient, the salinity level, or environmental conditions (Grattan and Grieve, 1994).

3. Reconciling the breadth and diversity of salinity–nutrient studies

Salinity and mineral–nutrient interaction studies are conducted in the laboratory, greenhouse, and in the field and correspondingly have a wide range of horticultural or physiological hypotheses that are to be tested.

3.1. Field studies

A major objective in most of the field studies examining salinity and mineral nutrition is overall plant performance such as productivity or market quality. An indicator of the crop’s production potential under saline conditions is the ‘salt-tolerance’ of the crop. As described by Maas and Hoffman (1977), the salt tolerance of a crop is determined by plotting its relative yield as a function of the average root-zone soil salinity. This allows one not only to compare salt tolerance among crops or cultivars but allows one to estimate a ‘yield potential’ given a certain level of soil salinity. Many of the salinity–fertility trials conducted in the field attempted to address whether or not fertilisation would increase crop salt tolerance.

Several scientists have reviewed the literature on salinity–fertility studies in the field and concluded that a bulk of the results were contradictory (Adams and Doerge, 1987; Feigin, 1985; Jurinak and Wagenet, 1981; Kafkafi, 1984). Many of the studies that were reviewed described experiments conducted in a variety of conditions but in most cases the soils or substrate were deficient in N, P and/or K^+. The reviewers found that plant growth was increased by nutrient application regardless of whether the plants were salt-stressed or not. This beneficial response does not, however, imply that fertilisation increases salt-tolerance.

The difficulty in interpreting these studies has been discussed in detail elsewhere (Bernstein et al., 1974; Grattan and Grieve, 1994) and will only be mentioned here briefly. In most field studies, two variables, salinity and nutrient deficiency limit plant growth. Generally, growth will be promoted more if the limiting factor, rather than the next limiting factor, is relieved. The difficulty in interpretation occurs since 'salt tolerance' is defined as one of the variables (i.e. soil salinity) and increases from non-limiting to severely limiting levels. In many experiments, the nutrient concentration is the limiting factor in non- or low-salinity conditions, yet when the identical concentration is present in a highly saline environment, salinity will be the limiting factor. This point was emphasised by Champagnol (1979) in his literature review on the relationship between salinity and phosphorus nutrition of plants. Therefore the addition of a nutrient may either increase or decrease crop salt-tolerance depending upon the level of salinity and the extent by which the nutrient in the system is limiting.

3.2. Soil vs. solution culture studies

Many of the studies in the area of plant nutrition and salinity interactions have been conducted in sand or solution cultures. A major difficulty in understanding plant nutrition as it is affected by soil salinity is reconciling results obtained in experiments conducted in the field and in solution cultures (Adams and Doerge, 1987). In the field, the concentrations of some nutrients in the soil solution, particularly P, K^+ and the micronutrients, are controlled by the solid phase and concentrations are much lower than those in nutrient solutions. In addition, certain nutrients in soil systems undergo transformations such as nitrification (ammonium to nitrate) which may be affected by salinity (Jurinak and Wagenet, 1981). To complicate matters further, field studies must contend with extreme variability in salinity, soil moisture, soil texture and soil nutritional status. These factors vary in location, depth and time.

In solution cultures, concentrations of salts and nutrients are easily controlled over the course of an experiment. Nutrient ratios, however, are much different from those found in soil solutions and root development and architecture are entirely different from that found in soils. It is obvious that plant responses and interactions observed in artificial media may not necessarily occur as they would under natural conditions. Nevertheless, solution culture studies are beneficial since they have advanced our understanding of crop salt-tolerance and have provided insight into physiological mechanisms responsible for nutrient uptake and discrimination.

Greenhouse and laboratory studies often have a different set of objectives than those conducted in the field. Variability can be reduced or eliminated using solution cultures where concentrations are uniform in space and time. These types of study are more conducive for shorter-term experiments and since variability is much less than at the field level, fewer measurements are required and more subtle differences between treatments can be detected.

Salinity–nutrition studies vary quite drastically at both spatial and temporal levels. Some studies examine response at the molecular level while others examine response at the field or regional level. The entire duration of some experiments may be minutes, as in short-term uptake studies using isotopes, while others may span seasons. The challenge comes in attempting to synthesise all these types of studies, with their different objectives, to attain a comprehensive understanding of how, why and to what extent salinity affects the mineral nutrition of crops.

3.3. Composition of the saline substrate

The composition of salts in water varies widely across the globe. In most waters the dominant cations are Na^+, Ca^{2+} and Mg^{2+} while the dominant anions are Cl^-, SO_4^{2-}, and HCO_3^-. Despite the variation in composition, there is an interesting relationship between salinity and the ratio of $Na^+/(Na^+ + Ca^{2+})$ in waters around the world (Gibbs, 1970). Waters very high in salinity, such as those in oceans and seas, have a ratio near one indicating that Na^+ is the major salinising cation. However the bulk of the waters with low (60 mg/l TDS[2] EC[3] = 0.1 dS/m) to intermediate salinity (1300 mg/l TDS; EC = 2.0 dS/m) have ratios between 0.1 to 0.7 indicating Ca^{2+} is a major contributor to the salinising media. This ratio increases as salts in waters are concentrated by evaporation with selective precipitation of Ca^{2+} over Na^+.

Unlike halophytes grown in coastal environments, most horticultural crops are subjected to irrigation water or soil solutions with $Na^+/(Na^+ + Ca^{2+})$ in the range of 0.1 to 0.7 suggesting that the composition of saline water in experimental studies should reflect this ratio. Surprisingly a large percentage of salinity studies on horticultural or agronomic crops use NaCl as the sole salinising agent. The use

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[2] Total dissolved solids.

[3] Electrical conductivity.

of unrealistic salinising compositions limit the extent to which the results can be interpreted.

The same argument can also be taken for the anions. The majority of salinity studies use Cl^- as the sole salinising anion yet most soil solutions contain a substantial amount of SO_4^{2-} and HCO_3^-. Nevertheless, a number of studies have examined crop response under solutions of variable anion composition, particularly sulphate and chloride salts, and these will be discussed briefly in the section of this paper dealing with sulphur. We argue that much more can be learned if a larger fraction of future salinity–nutrition studies, regardless of experimental scale or objectives, are conducted with more realistic ion ratios.

The remaining portion of this review will be directed towards crop performance and acquisition of the major nutrients elements (N, P, K^+, Ca^{2+}, Mg^{2+}, S) and micronutrient elements in saline environments.

4. Nitrogen

Nitrogen, in one form or another, accounts for about 80% of the total mineral nutrients absorbed by plants (Marschner, 1995). Moreover, inadequate nitrogen is often the growth-limiting nutritional stress in field soils. Consequently, addition of N usually improves plant growth and yield regardless of whether the crop is salt-stressed or not. In many field studies, horticulturists and agronomists set out to test the hypothesis that N-fertiliser additions alleviate, at least to some extent, the deleterious effect of salinity on plants.

Most salinity and N interaction studies in the field were conducted on soils deficient in N. Therefore, additions of N improved growth and/or yield of apple, *Malus pumila* Mill (El-Siddig and Lüdders, 1994), bean, *Phaseolus vulgaris* L. (Lunin and Gallatin, 1965; Ravikovitch and Porath, 1967; Wagenet et al., 1983), carrot, *Daucus carota* L. and cowpea, *Vigna unguiculata* L. Walp. (Ravikovitch and Porath, 1967), corn, *Zea mays* L. (Khalil et al., 1967; Ravikovitch and Porath, 1967; Ravikovitch, 1973), grape *Vitis vinifera* L. (Taylor et al., 1987), tomato, *Lycopersicon esculentum* L. (Ravikovitch and Porath, 1967; Papadopoulos and Rendig, 1983) and spinach, *Spinacia oleracea* L. (Langdale et al., 1971) when the degree of salinity was not severe. We have found no references to field studies on horticultural crops, however, that showed an increase in crop yield under saline soils where N was applied above a level considered optimal under non-saline conditions (i.e. N-fertilisation did not increase crop salt-tolerance).

Despite the lack of evidence indicating that N applied to saline soils or media above a level considered optimal under non-saline conditions improves plant growth or yield, a number of laboratory and greenhouse studies have shown that salinity can reduce N accumulation in plants (Cram, 1973; Pessarakli and Tucker, 1988; Feigin et al., 1991; Pessarakli, 1991; Al-Rawahy et al., 1992). This is not surprising since an increase in Cl^- uptake and accumulation is often accompanied by a decrease in shoot-NO_3^- concentration. Examples of such an effect have been found in cucumber, *Cucumis sativus* L. (Martinez and Cerdá, 1989), eggplant, *Solanum melongena* L. (Savvas and Lenz, 1996), melon, *Cucumis melo* L. (Feigin et al., 1987), and tomato (Kafkafi et al., 1982; Feigin et al., 1987; Martinez and Cerdá, 1989). Many attributed this reduction to Cl^- antagonism of NO_3^- uptake (Bar et al., 1997; Feigin et al., 1987; Kafkafi et al., 1982) while others attributed the response to salinity's effect on reduced water uptake (Lea-Cox and Syvertsen, 1993).

Apparently the counter-cation may influence Cl^- antagonism of NO_3^- uptake. Kafkafi et al. (1992) found that Cl^- from $CaCl_2$ and not KCl, inhibited NO_3^- uptake in melon and tomato in a range to which the plants would likely be exposed in field conditions (i.e. up to 60 mol/m^3). It was only in the high concentration range (100–200 mol/m^3) that KCl inhibited NO_3^- uptake. The authors concluded that the effects of NaCl and KCl are similar, but that nitrate inhibition by Cl^- is much more pronounced at the lower salinity range if the counter ion were Ca^{2+} rather than a monovalent cation.

Another interesting observation is that the nitrate influx rate (Kafkafi et al., 1992) or even the interaction between NO_3^- and Cl^- (Pérez-Alfocea et al., 1993) may be related to the salt tolerance of the cultivar under investigation. Kafkafi et al. (1992) found that the more salt-tolerant tomato and melon cultivars had higher NO_3^- influx rates than the more sensitive cultivars. More convincing are data by Pérez-Alfocea et al. (1993) that showed a negative correlation between shoot NO_3^- and shoot Cl^- concentration but the slopes from linear regressions increased (i.e. became more negative) with increasing genotypic sensitivity to salinity.

In contrast to the effect of Cl^- on NO_3^- uptake, others have reported that increased NO_3^- in the substrate decreased Cl^- uptake and accumulation in numerous annual horticultural crops (Bernstein et al., 1974; Kafkafi et al., 1982; Feigin et al., 1987; Martinez and Cerdá, 1989). This effect is particularly relevant in tree or vine crops that are prone to Cl-toxicity. One study demonstrated that addition to the growth media of NO_3^- above what would be considered sufficient for optimal growth in the absence of salinity, decreased Cl^- concentrations in avocado (*Persea* spp.) and citrus (*Citrus* spp.) leaves to the extent that foliar injury was reduced, thereby lessening growth inhibition (Bar et al., 1997). In this study the NO_3^- concentration in the soil solution that was needed to be effective was high and molar ratios of NO_3^-/Cl^- needed to be 0.5 or higher. The authors cautioned that although this study may have practical implications in reducing Cl-toxicity in field-grown citrus and avocado, this practice could put the environment at risk particularly in relation to NO_3^- contamination of the groundwater.

The form in which N is supplied to salt-stressed plants can influence salinity–N relations as well as affect salinity's relation with other nutrients (Lewis et al., 1989; Martinez and Cerdá, 1989). NH_4^+-fed maize (Lewis et al., 1989), melon

(Feigin, 1990) and pea, *Pisum sativum* L. (Speer et al., 1994) plants were more sensitive to salinity than NO_3^--fed plants when grown in solution cultures. Addition of Ca^{2+} to the media improved the growth rate of the plants in the NO_3^- treatment, but not those treated with NH_4^+ (Lewis et al., 1989). In addition, Martinez and Cerdá (1989) found that Cl^- uptake was reduced in cucumber when only NO_3^- was added to the solution but when half the NO_3^- in the solution was replaced by NH_4^+, Cl^- accumulation was enhanced. These investigators further noted that when NO_3^- was the only N-source, accumulation of K^+ in the plant was increased under saline conditions. When the media contained both NO_3^- and NH_4^+, K^+ was reduced. Similar effects were found in salt-stressed melon (Adler and Wilcox, 1995; Feigin, 1990). As the NH_4^+/NO_3^- ratio was increased, plants accumulated more Na^+ and Cl^- and less Ca^{2+} and K^+ in their leaves.

The results of salinity and N-source studies conducted in hydroponic or sand cultures contrast markedly with studies where plants were grown in soil. For example, wheat (*Triticum aestivum* L.) was more sensitive to salinity as the ratio of $NH_4{}^+/NO_3{}^-$ increased, when grown in solution and sand culture (Leidi et al., 1991; Silberbush and Lips, 1991a, b). However when wheat was grown in soil salinised with NaCl, Shaviv et al. (1990) found the crop more salt-tolerant in terms of grain yield under a combination of NH_4^+ and NO_3^-, than NO_3^- alone. This was also found for peanut, *Arachis hypogaea* L., in a N-salinity study comparing plant response in solution cultures vs. soil (Silberbush et al., 1991). In these soil studies, it is likely that the NH_4^+ concentrations in the soil solution are reduced rapidly due to interaction with the solid phase. Although we find no references to studies that show this effect for horticultural crops, this is a classic example of how plant-nutritional experiments conducted in solution cultures alone may lead to inappropriate fertiliser recommendations for the field.

The salinity–N relations of horticultural crops are obviously complex. The bulk of the studies indicate the N uptake or accumulation in the shoot may be reduced under saline conditions, although there are studies that found the opposite or no effect (Feigin, 1985). Nevertheless in those studies where NaCl-treated plants contained less N than non-stressed plants, there is no strong evidence to support the fact that this effect is growth-limiting (Munns and Termaat, 1986).

5. Phosphorus

The interaction between salinity and phosphorus (P) nutrition of plants is equally as complex as that between salinity and N. The interaction is highly dependent upon the plant species (or cultivar), plant developmental age, the composition and level of salinity and the concentration of P in the substrate. Therefore, depending upon plants selected and conditions of the experiment, different results can be obtained.

Champagnol (1979) reviewed 17 publications and found that P, added to saline soils, increased crop growth and yield in 34 of the 37 crops studied. Similar to the effect of added N, added P did not necessarily increase crop salt tolerance. After analysing studies including horticultural crops such as carrot, maize, sugar beet, *Beta vulgaris* L. and tomato, he concluded that added P increased, had no effect on, or decreased salt tolerance as salinity increased from low, to moderate, to high levels, respectively. This demonstrates the complexity of interpreting horticultural studies regarding whether or not the addition of N or P to deficient soils or media increase crop salt-tolerance.

We found only one study where additions of P increased crop salt-tolerance over a fairly wide range of salinity (10–100 mM NaCl: Awad et al., 1990). Although this was a greenhouse study on tomato using flow-through solution cultures, the researchers maintained low levels of phosphate and a beneficial response was observed as phosphate concentrations increased from 0.1 to 10 μM.

In most cases, salinity decreases the concentration of P in plant tissue (Sharpley et al., 1992), but the results of some studies indicate salinity either increased or had no effect on P uptake. Plant-growing conditions, plant type and even cultivar play a large role in P accumulation (Grattan and Grieve, 1994). It is not surprising that these differences among studies occur since P concentrations vary widely in different experiments and other nutrient interactions could be occurring simultaneously.

Most of the studies that show salinity-reduced P concentrations in plant tissues were conducted in soils. Phosphate availability is reduced in saline soils not only because of ionic strength effects that reduce the activity of phosphate but also because phosphate concentrations in soil solution are tightly controlled by sorption processes and by the low-solubility of Ca–P minerals. Therefore, it is understandable that phosphate concentrations in field-grown agronomic crops decreased as salinity ($NaCl + CaCl_2$) increased (Sharpley et al., 1992). In many cases, tissue P concentration was reduced between 20% to 50%, yet there was no evidence of P deficiency in the crops.

Champagnol (1979) concluded that it is unlikely that Cl^- and $H_2P0_4^-$ ions are competitive in terms of plant uptake but Papadopoulos and Rendig (1983) concluded that Cl^- may have suppressed phosphate uptake and accumulation in tomato shoots. In most cases, however, reduction in plant P concentration by salinity results from reduced activity of P in the soil solution due to the high ionic strength of the media and low solubility of Ca–P minerals.

Some research indicates that salinity stress may increase the P requirement of certain crops. For example, Awad et al. (1990) found that when NaCl increased in the substrate from 10 to 50 to 100 mM, the P concentrations in the youngest mature tomato leaf necessary to obtain 50% yield increased from 58 to 77 to 97 mmol/kg dry weight, respectively. Their conclusion was also supported by appearance of P-deficiency symptoms that were evident on plants grown at high

NaCl but were not evident on others at lower salinity with equal leaf-P concentrations.

Most studies that demonstrated that salinity increased tissue-P concentration were conducted in sand or solution cultures (Grattan and Grieve, 1994), not soils. Phosphate concentration in solution cultures are often orders of magnitude higher than that in soil solutions (e.g. 2 mM vs. 2 μM). Several studies conducted in solution cultures have shown that P concentrations that are optimal in non-saline solutions may adversely affect growth or be toxic to corn (Bernstein et al., 1974; Nieman and Clark, 1976) as well as other agronomic crops grown under saline conditions. In these cases salinity by some unknown mechanism causes the plant to lose control of phosphate uptake (Roberts et al., 1984) and transport to the shoot. The increased P accumulation in the shoot is presumably controlled at the root level and is independent of the salt composition (Grattan and Maas, 1985). It should be emphasised, however, these adverse interactions observed with corn and other agronomic crops would rarely occur under field conditions, since phosphate concentrations in soil solutions are usually orders of magnitude less than those used in these studies (Grattan and Grieve, 1994).

6. Potassium

Maintenance of adequate levels of K^+ is essential for plant survival in saline habitats. Potassium is the most prominent inorganic plant solute, and as such makes a major contribution to the low osmotic potential in the stele of the roots that is a prerequisite for turgor-pressure-driven solute transport in the xylem and the water balance of plants (Marschner, 1995). Under saline-sodic or sodic conditions, high levels of external Na^+ not only interfere with K^+ acquisition by the roots, but also may disrupt the integrity of root membranes and alter their selectivity. The selectivity of the root system for K^+ over Na^+ must be sufficient to meet the levels of K^+ required for metabolic processes, for the regulation of ion transport, and for osmotic adjustment.

Numerous studies with a wide variety of horticultural crops have shown that K^+ concentration in plant tissue, expressed on a dry mass basis, declines as the Na-salinity or as the Na^+/Ca^{2+} in the root media is increased (e.g. Francois, 1984; Subbarao et al., 1990; Izzo et al., 1991; Graifenberg et al., 1995; Pérez-Alfocea et al., 1996). In contrast, other research has demonstrated that K^+ may be preferentially acquired and transported against a strong Na^+ concentration gradient. As a result, K^+ levels in the cell sap of bean leaves increased with increasing NaCl-salinity (Meiri et al., 1971; Cachorro et al., 1993). Often, however, leaf-Na^+ accumulation increases in concert with leaf-K^+ and both K^+/Na^+ ratio and K^+:Na^+ selectivity coefficient decrease with increases in salinity (Salim, 1989; Akhavan-Kharazian et al., 1991; Cachorro et al., 1993). Ruiz et al.

(1997) examined K^+ uptake and transport by citrus rootstocks. Of the four species that were tested, only *Citrus macrophylla* leaves, but not the roots showed an increase in K^+ level as salinity increased. These and other authors (Walker, 1986) have attributed leaf-K^+ increases in some citrus rootstock/scion combinations to an exchange between Na^+ and K^+ in the basal stem and proximal root whereby K^+ was released from the root to the xylem for transport to the leaf.

Sodium-induced K^+ deficiency has been implicated in growth and yield reductions of various crops, including tomato (Song and Fujiyama, 1996; Lopez and Satti, 1996), spinach (Chow et al., 1990), fennel, *Foeniculum vulgare* Mill. (Graifenberg et al., 1996), and maize (Botella et al., 1997).

Reduction in K^+ uptake in plants by Na^+ is a competitive process and occurs regardless of whether the solution is dominated by Na^+ salts of Cl^- or SO_4^{2-}. However, plant species may differ in response to each of these salinising systems. Although the K^+ content of chickpea, *Cicer arietinum* L. (Manchanda and Sharma, 1989; Manchanda et al., 1991) and pea (Mor and Manchanda, 1992) decreased significantly regardless of salinity type, shoots grown in the SO_4^{2-} system contained more K^+ than in the Cl^- system. These investigators observed that Ca^{2+} uptake was greater from a Cl-dominated substrate compared to the sulphate system, and speculated that enhanced Ca^{2+} levels had adverse effects on K^+ absorption. Meiri et al. (1971) observed that K^+ concentrations in bean leaf-sap increased with increasing salinity and that the increase was more marked with sulphate-salinity than chloride-salinity. In other Na-stressed crops, the nature of the salinising anion has little influence on the magnitude of K^+ reduction, e.g. apple shoots (Schreiner and Lüdders, 1992), blueberry, *Vaccinium* spp. (Muralitharan et al., 1992).

At the same time that K^+ uptake is impaired by salinity, higher K^+ levels in tissue are required for shoot growth. While increases in leaf-Na^+ concentrations may help to maintain plant turgor, Na^+ cannot completely substitute for K^+ which is specifically required for protein synthesis and enzyme activation (Marschner, 1995). High K^+ concentrations in the stroma are necessary for the maintenance of optimum photosynthetic capacity under stress conditions (Chow et al., 1990). These investigators determined that K^+ demand in spinach leaves grown in solution cultures containing 250 mM NaCl was twice as high as in non-saline substrates.

The presence of adequate Ca^{2+} in the substrate influences the K^+/Na^+ selectivity by shifting the uptake ratio in favour of K^+ at the expense of Na^+. Improvement in Ca^{2+}-mediated membrane integrity invariably leads to reduction of K^+ leakage from root cells and a more favourable root-K^+ status (Alberico and Cramer, 1993; Cachorro et al., 1994). As a result, the beneficial effects of supplemental Ca^{2+} on the K^+ status of salt-stressed plants are often more evident in root tissue rather than the shoots e.g. maize (Izzo et al., 1993), tomato (Lopez and Satti, 1996). Likewise, K^+ levels increased and Na^+ decreased in Troyer citrange roots with the addition of Ca^{2+} to the saline substrate (Bañuls et al., 1991). Depending on genotype, supplemental Ca^{2+}, added to saline solution cultures containing basal levels of K^+ (3 mM) was as effective in improving the K^+ levels in salt-stressed tomato roots (Lopez and Satti, 1996) and shoots (Satti and Lopez, 1994) as were increases in substrate K^+.

Potassium concentrations in salt-stressed plants depend on whether the source of nitrogen fertilisation is NH_4^+ or NO_3^-. K^+ uptake by cucumber seedlings salinised with NaCl was inhibited by the combination of both NH_4^+ and NO_3^- but stimulated by NO_3^- alone. While this response may be primarily associated with the well-documented competition between K^+ and NH_4^+, Martinez and Cerdá (1989) point out that the lower K^+ influx from substrates containing NH_4^+ may be due to changes in membrane potential and pH differentials.

Results from solution culture experiments show the deleterious effects associated with reduced uptake and translocation of K^+ by plants grown in high-Na^+ can frequently be alleviated by the addition of K^+ to the substrate. Growth of Na^+-stressed tomato (Satti and Lopez, 1994; Song and Fujiyama, 1996), maize (Botella et al., 1997), bean and sunflower (*Helianthus annuus* L.) (Benlloch et al., 1994) improved with increases in external K^+/Na^+ ratio. Other studies, however, have shown that addition of K^+ to Na^+-dominated substrates has little effect on plant growth or yield. Differences in growth between maize plants grown with and without salinity at different K^+ concentrations were not reduced by increasing K^+ in solution cultures containing 50 mM NaCl. (Cerdá et al., 1995). Likewise, Bernstein et al. (1974) found that increasing solution K^+ from 0.4 to 2 mM did not improve leaf K^+ or yield of corn grown in sand cultures. Bar-Tal et al. (1991) reported an increase in the yield of corn grown in sandy soil, but the response was proportional at all salinity levels. These investigators concluded that despite its beneficial effects on increasing K^+/Na^+ within the plant, K fertilisation did not reduce the deleterious effects of salinity.

In field conditions, soil solution K^+ remains relatively low even after fertiliser additions of K^+. Therefore, it is difficult to imagine many situations where reasonable amounts of K^+ added to the soil would completely correct Na^+-induced K^+ deficiencies in plants suffering from this disorder.

7. Calcium

Even under non-saline conditions, significant economic losses of horticultural crops have been linked to inadequate calcium nutrition. Factors which influence the availability of Ca^{2+} to plants include the total Ca^{2+} supply, the nature of counter-ions, substrate pH, and the ratio of Ca^{2+} to other cations in the substrate solution. Thus, calcium-related disorders may occur in plants grown on substrates where the calcium concentration appears to be adequate as well as where the calcium content is low (Geraldson, 1957; Bernstein, 1975). Deficiency symptoms generally arise from differences in calcium allocation to the growing regions of the plant. In addition, competitive sinks, e.g. leaves, fruits and meristems, exert their influence on calcium movement independently (Clarkson, 1984). Although foliar symptoms are easily induced in non-saline hydroponic or sand cultures, they are seldom seen in mature leaves of field grown crops (Millaway and Wiersholm, 1979). Instead, they may appear as physiological disorders of young tissue enclosed within older leaves, e.g. blackheart of celery (*Apium graveolens* L.), internal browning of Brussel sprouts (*Brassica oleracea* L., gemmifera group), cabbage (*B. oleracea*, capitata group) and cauliflower (*B. oleracea*, botrytis group). Calcium deficiency in reproductive tissues has also been implicated in degradation of fruit quality: blossom-end rot of tomato, melon and pepper (*Capsicum annuum* L.); bitter pit, cracking and storage disorders of apple, pear (*Pyrus communis* L.), and stone fruit, as well as 'soft nose' of mango (*Mangifera indica* L.) and avocado. Shear (1975) described over 40 disorders that result from inadequate levels of calcium in fruits, storage roots, tubers, and leafy vegetables and this list continues to expand as research in this area progresses.

The hazard to these crops, which are susceptible to Ca^{2+}-related disorders even in the absence of salinity, becomes greater under saline conditions. As the salt concentration in the root zone increases, plant requirement for Ca^{2+} also increases (Gerard, 1971; Bernstein, 1975). At the same time, the uptake of Ca^{2+} from the substrate may be depressed because of ion interactions, precipitation, and increases in ionic strength. These factors reduce the activity of Ca^{2+} in solution thereby decreasing Ca^{2+} availability to the plant (Cramer et al., 1986; Suarez and Grieve, 1988). Severity of the calcium disorder depends on the kinds of ions that contribute to salinity and environmental conditions.

7.1. Effects of salinity on calcium-related disorders in vegetative tissues

In those plants whose marketable product consists primarily of large heads enveloped by outer leaves, [e.g. cabbage, lettuce (*Lactuca sativa* L.), escarole or endive (*Cichorum endiva* L.)] excessive transpiration by the outer leaves diverts calcium from the rapidly-growing meristematic tissue (Bangerth, 1979). Problems of nutrient transport to the shoot meristem arise because this tissue has only rudimentary vascular traces and is supplied with plant resources (mineral nutrients, assimilates) via diffusion. Furthermore, meristems generally lack a transpirational driving force and must compete with cells through which plant resources are serially transported (Lazof and Läuchli, 1991).

Increased incidence and severity of calcium deficiency of artichoke (*Cynara scolymus L.*) buds were directly related to increased levels of salinity (supplied by NaCl and $CaCl_2$). The disorder was characterised by necrosis of the inner bracts.

The number of marketable artichokes was reduced 20% when irrigation water salinity exceeded 2 dS/m, and up to 50% at 10 dS/m (Francois et al., 1991; Francois, 1995). In this field trial, substrate Na^+/Ca^{2+} remained low. An abundance of calcium was taken up, but was translocated to the leaves and outer bracts, rather than to the inner bracts. Root pressure, the process that would normally provide Ca^{2+} movement to the inner bracts, was severely reduced as soil salinity increased. In contrast, Graifenberg et al. (1993, 1995) observed no visible damage to artichoke buds in response to NaCl-salinity. These investigators reported only small reductions in calcium allocation to bud tissue as salt stress increased. Differences in artichoke response reported by the two research teams were undoubtedly the result of disparate environmental conditions. In contrast to the greenhouse pot culture experiments described by Graifenberg et al., 1993, 1995, the field trial described by Francois et al. (1991) and Francois (1995) was conducted in a desert area under conditions of low humidity, desiccating winds, and high temperatures which increased transpiration and undoubtedly reduced root pressure. As a result, calcium distribution to shoot organs may have been strongly affected, and calcium requirement of the inner bracts was not met.

'Blackheart' of celery, which occurred in plants stressed with NaCl-salinity, was controlled by adding calcium to the substrate (Sonneveld, 1988) or by the application of calcium-containing sprays to the young leaves (Osawa, 1963). Other investigators found no evidence of the disorder in salt-stressed plants (Francois and West, 1982), particularly those adapted to NaCl-salinity (Aloni and Pressman, 1987).

Calcium-deficiency disorders have been observed in salt-stressed Chinese cabbage (*Brassica rapa* L., Pekinensis group) grown in solution cultures at high Na^+/Ca^{2+} ratio. Symptoms were more severe when nitrogen was supplied as NH_4^+-salts rather than as NO_3^- (Osawa, 1962). In a field experiment conducted in the Negev Desert of Israel, the frequency of internal tipburn of Chinese cabbage increased with increasing salinity supplied by irrigation waters containing NaCl and $CaCl_2$ (3:1 molar ratio: Mizrahi and Pasternak, 1985). This finding provides another example of the negative effect of salinity on root pressure-driven calcium transport to meristematic tissue. Although relative salt tolerance of other *Brassica* species appeared to be correlated with calcium status (He and Cramer, 1992), subsequent research demonstrated that growth was not improved by increasing Ca^{2+} supply (Schmidt et al., 1993). Likewise, addition of supplemental calcium had no effect on the salt tolerance of certain lettuce genotypes (Cramer and Spurr, 1986b).

7.2. *Effects of salinity on calcium-related disorders in reproductive tissues/ organs*

Low to moderate levels of NaCl-salinity are sometimes used to improve sugar and dry matter content and physical appearance of tomato fruit. This practice often increases the incidence of blossom-end rot (Adams and Ho, 1989). The primary causes of the disorder have been identified as decreased uptake of calcium by roots and increased resistance to transport inside the fruit (Ehret and Ho, 1986a, b; Ho et al., 1993). Symptoms have been associated with calcium deficiency and include retardation of xylem development and localised degradation of distal fruit tissues (Adams and Ho, 1992; Belda and Ho, 1993). Tomato genotypes may also differ in their susceptibility to calcium-related disorders (Adams and Ho, 1992; Martinez et al., 1987). Growth and yield reductions of Na-salinized tomato are generally ameliorated by increases in substrate calcium (Al-Harbi, 1995). Song and Fujiyama (1996) attributed this result to the suppression of sodium transport to the shoot rather than to the antagonism between Ca^{2+} and Na^{+} at the root surface.

The incidence of internal fruit rot of pepper and eggplant grown in salinised hydroponic cultures also increased in concert with increases in external Na^{+}/Ca^{2+} ratio (Sonneveld and van der Burg, 1991; Savvas and Lenz, 1994, 1996). For both species, reduced calcium translocation to the fruit resulted in calcium deficiency which was confirmed by tissue ion analysis.

Fruits of salt-stressed cucumber are rarely affected by calcium-related disorders (Jones et al., 1989; Sonneveld and van der Burg, 1991). However, under high levels of NaCl-salinity, calcium uptake and transport to all organs was significantly reduced. Calcium was preferentially distributed to and accumulated by the fruit at the expense of the calcium balance in young shoot tissue (Ho and Adams, 1994a, b).

Increases in pegging-zone NaCl-salinity produced calcium deficient peanut pods. Symptoms included unfilled pods or small, wrinkled, discoloured seed (Lauter and Meiri, 1990).

Calcium plays an essential role in processes that preserve the structural and functional integrity of plant membranes, stabilise cell wall structures, regulate ion transport and selectivity, and control ion-exchange behaviour as well as cell wall enzyme activities (Rengel, 1992; Marschner, 1995). Because calcium appears to be readily displaced from its membrane binding sites by other cations, these functions may become seriously impaired by reduced calcium availability. Increasing the external concentration of calcium largely counteracted this displacement (Lynch et al., 1987; Lynch and Läuchli, 1988). Maize has proved to be a suitable test plant for investigating the effects of salinity on the whole plant, as well as on the organ and cellular levels of organisation, and for defining plant response to the competitive interactions between Na^{+} and Ca^{2+} (Zidan et al., 1991). In high Na^{+}/Ca^{2+} substrates, maize is particularly sensitive to growth inhibition and exhibits significant changes in morphology and anatomy (Maas and Grieve, 1987; Evlagon et al., 1990; Cramer, 1992). Inhibition of maize root cell production and elongation appear to underlie the regulation of root growth by NaCl-salinity and these processes may be partially restored by addition of substrate-calcium (Cramer et al., 1988; Zidan et al., 1991). Water transport properties of maize primary roots are adversely affected by NaCl-induced morphological and anatomical changes (Evlagon et al., 1990; Neumann et al., 1994). Supplemental calcium tended to reverse or prevent these changes and mitigated reductions in root hydraulic conductivity (Evlagon et al., 1990, 1992; Azaizeh and Steudle, 1991; Azaizeh et al., 1992; Neumann et al., 1994).

Maintaining an adequate supply of calcium in saline soil solutions is an important factor in controlling the severity of specific ion toxicities, particularly in crops which are susceptible to sodium and chloride injury (Maas, 1993). In citrus grown under saline conditions, calcium was found to be effective at reducing the transport of both sodium and chloride from roots to leaves, thereby alleviating foliar injury and/or defoliation (Bañuls et al., 1991; Zekri, 1993a, b; Zekri and Parsons, 1990; Bañuls et al., 1997; Zid and Grignon, 1985; Zekri and Parsons, 1992). Increases in salt tolerance of a variety of horticultural crops have been associated with increases in substrate calcium. Addition of gypsum to saline soils markedly increased yields of potato (*Solanum tuberosum* L.) tubers (Abdullah and Ahmad, 1982). Supplemental calcium led to enhanced germination and growth of salt-stressed bean(Awada et al., 1995; Akhavan-Kharazian et al., 1991) and pigeonpea (*Cajanus cajan* (L.) Huth: Subbarao et al., 1990) primarily through decreases in sodium and/or chloride uptake and accumulation. Cachorro et al. (1994) reported that addition of calcium to the saline media increased root membrane integrity of bean and minimised leakage of $N0_3^-$ and $H_2PO_4^-$. The extent to which supplemental calcium is effective in alleviating the adverse effects of Na^+-salinity depends on the crop, the calcium concentration, and on the Na^+ source. Calcium appeared to offset damage to blueberry shoots salinised with Na_2SO_4, but not with NaCl (Wright et al., 1992, 1993, 1994). For blueberry, low levels of Ca^{2+} (1 mM) were more effective than higher Ca^{2+} concentrations (10 mM) in alleviating salinity damage. These investigators point out that blueberry is a calcifuge and is adapted to sandy, acidic soils that are low in Ca^{2+}. Calcifuges are efficient in Ca^{2+} uptake and their calcium requirements are low. However, in the presence of high substrate Ca^{2+}, they cannot regulate Ca^{2+} influx and accumulate excessive amounts. Wright et al. (1995) found that high levels of supplemental Ca^{2+} led to greater uptake of Na^+ and concluded that, in the calcifuge, blueberry, high Ca^{2+} accentuates the detrimental effects of Na^+ on cell metabolism.

The importance of maintaining a balanced nutrient solution composition to optimise plant performance of horticultural crops under saline conditions has been well-documented in both the horticultural and agronomic literature. This discussion of Ca^{2+} related disorders in salt-stressed crops places further emphasis on the need for using mixed-salt solutions in future salinity studies.

8. Magnesium

Although salinity studies have analysed plant tissue for magnesium, most of the salinity–nutrition studies have directed little attention to magnesium nutrition as affected by salinity.

Calcium is strongly competitive with Mg^{2+} and the binding sites on the root plasma membrane appear to have less affinity for the highly hydrated Mg^{2+} than for Ca^{2+} (Marschner, 1995). Thus, high concentrations of substrate Ca^{2+} often result in increased leaf-Ca along with a marked reduction in leaf-Mg (Bernstein and Hayward, 1958). A more recent example is from a study by Ruiz et al. (1997) where they found that NaCl salinity reduced leaf Mg^{2+} concentrations in citrus. However increases in salinity are not always associated with decreases in leaf Mg^{2+}. Bernstein et al. (1974) found that increases in salinity ($NaCl + CaCl_2$) only reduced leaf Mg^{2+} concentration in beet and had little or no effect in leaves from five other vegetable crops that they examined.

It has been known for several decades that solutions with a Mg^{2+}/Ca^{2+} ratio greater than one, such as those that result by diluting sea-water, reduces the growth of maize (Key et al., 1962). In eucalyptus, Mg-salts were found to reduce root growth more than Na-salts (Marcar and Termaat, 1990) and this effect was associated with low concentrations of calcium in the root. Calcium-induced Mg^{2+} deficiency has been observed in sesame (Nassery et al., 1979) but little work has focused on horticultural crops.

9. Sulphur

Most salinity studies that included sulphur as an external variable have not examined the influence of salinity on sulphur nutrition in the plant. Rather these studies were directed more towards how the plant responds to sulphate-salinity as compared to chloride-salinity. Differences in crop response to chloride and sulphate salinity have measured in terms of identical electrical conductivities (Manchanda and Sharma, 1989; Mor and Manchanda, 1992; Awada et al., 1995) molar or equivalent basis (Bilski et al., 1988a, b; Blom-Zandstra and Lampe, 1983; Muralitharan et al., 1992; Wright et al., 1992; Walker et al., 1993) or isoosmotic potentials (Abd El-Samad and Shaddad, 1996; Cramer and Spurr, 1986a; Lauter and Munns, 1986; Meiri et al., 1971). Whether or not differences in plant response are found between chloride and sulphate salinity may depend on the salinity indices chosen (Kafkafi, 1984).

Very little attention is given to salinity's influence on sulphur uptake and accumulation in crops. In one study that compared the effects of both chloride and sulphate salinity effect on pea, Mor and Manchanda (1992) found that chloride-salinity reduced the sulphur content in the straw. Sulphur accumulation in the roots, however, was enhanced by Cl-salinity.

Many crops are very sensitive to high internal chloride levels, and species are generally more tolerant of sulphate-salinity than chloride-salinity. Consequently Bernstein (1962) suggested that for most vegetable crops the salt-tolerance would be 2 dS/m greater in a sulphate system as opposed to chloride system.

Other sulphate-salinity studies were directed towards sulphate's effect on selenium accumulation in edible plant parts (Tanji et al., 1988). There is strong evidence indicating that sulphate or sulphate-salinity reduces selenate uptake and accumulation in crops (Läuchli, 1993). The inhibition of selenate uptake and accumulation in edible tissue by sulphate reduces the health risk to the consumer when horticultural crops are irrigated with sulphate-dominated saline drainage water that contains high levels of this potentially toxic trace element (Tanji et al., 1988). Similarly, sulphate has been found to reduce another potentially toxic oxyanion, molybdate (Läuchli and Grattan, 1993). These investigators found that Na_2SO_4 salinity substantially reduced Mo accumulation in alfalfa, *Medicago sativa* L. shoots.

10. Micronutrients

The availability of most micronutrients depends on the pH and pE of the soil solution as well as the nature of binding sites on organic and inorganic particle surfaces. In saline and sodic soils, the solubility of micronutrients (e.g. Cu, Fe, Mn, Mo and Zn) is particularly low, and plants grown in these soils often experience deficiencies in these elements (Page et al., 1990), but not in all cases. Differences can be attributed to plant type, plant tissue, salinity level and composition, micronutrient concentration, growing conditions and the duration of study. Consequently, the relationship between salinity and trace element nutrition is complex and salinity may increase, decrease, or have no effect on the micronutrient concentration in plant shoots.

Salinity-induced Mn deficiency has been observed in barley (*Hordeum vulgare* L.) shoots and Mn additions to solution cultures increased barley's salt-tolerance (Cramer and Nowak, 1992).

Most studies on horticultural crops, regardless of whether they were conducted in soils or in solution cultures, indicate that salinity reduces Mn concentration in shoot tissue. Examples include bean (Doering et al., 1984), corn (Izzo et al., 1991; Rahman et al., 1993) pea (Dahiya and Singh, 1976), squash, *Cucurbita pepo* L. (Maas et al., 1972) and tomato (Alam et al., 1989). However these studies did not test whether Mn additions to salt-stressed plants would enhance growth.

Some studies with tomato, however, indicate that salinity either had no effect (Al-Harbi, 1995) or increased (Maas et al., 1972; Niazi and Ahmed, 1984) Mn in leaf or shoot tissue. Salinity was also found to increase Mn concentration in sugarbeet shoots (Khattak and Jarrell, 1989) but these investigators found that salt

($NaCl + CaCl_2$) additions increased Mn in the saturated soil extract, indicating that salt additions increased plant-available Mn.

Zinc applications have been found to improve growth in salt-stressed plants (El-Sherif et al., 1990) but benefits have been greater in sodic conditions than either saline or saline-sodic environments (Mehrotra et al., 1986; Shukla and Mukhi, 1985). Zinc concentration in shoot tissue has been found to decrease with increasing sodicity (Mehrotra et al., 1986; Shukla and Mukhi, 1985) but not necessarily with increasing salinity. The majority of studies in the literature have shown salinity to increase Zn concentration in shoot tissue such as in bean (Doering et al., 1984), citrus (Ruiz et al., 1997), maize (Rahman et al., 1993) and tomato (Maas et al., 1972; Niazi and Ahmed, 1984; Knight et al., 1992), but in other studies it was not affected (Izzo et al., 1991) or actually decreased Zn concentration as in cucumber leaves (Al-Harbi, 1995).

Reports on the influence of salinity on the iron (Fe) concentration in plants are as inconsistent as those that concern Zn and Mn concentration. Salinity increased the Fe concentration in the shoots of pea (Dahiya and Singh, 1976), tomato, soybean, *Glycine max* (L.) Merrill, squash (Maas et al., 1972) and decreased its concentration in the shoots of barley and corn (Hassan et al., 1970).

Very little attention has been directed towards salinity's effect on Cu and Mo uptake and accumulation in horticultural crops. In studies with maize, one group of investigators found that salinity increased Mo concentrations when the crop was grown in soil (Rahman et al., 1993) while others found that salinity had no effect on Mo uptake from solution cultures (Izzo et al., 1991).

Salinity's influence on Cu accumulation was also variable. Leaf and shoot Cu concentrations were found to decrease in salt-stressed maize grown in both soil (Rahman et al., 1993) and solution cultures (Izzo et al., 1991) but NaCl-salinity substantially increased leaf Cu in hydroponically-grown tomatoes.

11. Boron

The optimal concentration range of plant available-B is very narrow for most crops, and various criteria have been proposed to define those levels that are necessary for adequate B-nutrition but at the same time are not so high as to induce B-toxicity (Eaton, 1944; Gupta et al., 1985; Nable et al., 1997). Although B deficiency is more wide spread than B-toxicity, particularly in humid climates, B-toxicity is more of a concern in arid environments where salinity problems also exist (Nicholaichuk et al., 1988).

Toxicity occurs in horticultural crops when boron concentrations increase in either stem or leaf tissue to lethal levels, but soil and plant tissue analyses can only be used as general guidelines for assessing the risk of B-toxicity (Nable et al., 1997). Although experimental evidence indicates that plants absorb B passively as H_3BO_3, contradictions between experimental results and observations in the field suggest that other factors, yet unknown, may affect B uptake (Hu and Brown, 1997). Once boron has accumulated in a particular organ, it has restricted mobility in most plant species but not all (Brown and Shelp, 1997). In some plant species, particularly those that produce a substantial amount of polyols, B is readily translocated as B-polyol complexes.

Despite the common occurrence of high boron and high salinity in many parts of the world, very little research has been done to study the interaction of the two (Ferreyra et al., 1997). From sand-culture experiments conducted in a greenhouse, researchers found that wheat responded to boron in the soil solution independently of salinity ($NaCl + CaCl_2$) (Bingham et al., 1987). The salinity–B interaction was insignificant with respect to leaf B concentration. On the other hand Yadav et al. (1989) found that a mixed salt solution (i.e. Na^+, Ca^{2+}, Cl^- and SO_4^{2-}) reduced leaf B concentration in chickpea grown in pots filled with loamy sand. Salinity (comprised of mixed salts) was also found to reduce the negative response of many field-grown crops to high levels of boron in the irrigation water (Ferreyra et al., 1997). In other studies using a mixture of chloride and sulphate salts, El-Motaium et al. (1994) found that salinity reduced B uptake and accumulation in the stem of several Prunus rootstocks thereby decreasing B-toxicity symptoms. They also found a negative relationship between B and SO_4^{2-} concentrations in tissue suggesting that SO_4^{2-} could be responsible for the salinity-induced reduction in tissue B. Others have also found that a mixture of chloride and sulphate salinity reduces leaf B accumulation in *Eucalyptus camaldulensis* Dehnh. (Grattan et al., 1997). In neither study were the investigators able to suggest the actual mechanism that supports this phenomenon such as direct ion interactions, reduced transpiration in salt-stressed conditions, or both.

In addition to the potential sulphate–boron interaction, the interaction between B and Ca^{2+} in plant nutrition has long been recognised from field studies (Marsh and Shive, 1941). High concentrations of substrate Ca^{2+}, particularly under calcareous conditions, decreased B absorption and can induce a B deficiency (Gupta et al., 1985). Therefore in reference to experiments with mixtures of salts where salinity reduced B uptake and transport to the shoot (Grattan et al., 1997, El-Motaium et al., 1994; Yadav et al., 1989), it is difficult to distinguish influences of either sulphate or calcium on B uptake since in each case these ions increased in the substrate with increasing salinity.

12. Summary

Salinity is a complex phenomenon and its full understanding requires joint efforts of agronomists, biochemists, geneticists, molecular biologists, plant physiologists, soil scientists among others (Gorham, 1992). The relations between salinity and mineral nutrition of plants are equally complex and a full understanding of these interactions would require a multidisciplinary team of equal strength and diversity. It is no easy task to reconcile results from salinity–nutrition experiments conducted in the field vs. the greenhouse; in soils vs. solution cultures; using single salts vs. mixed salts; under one set of environmental conditions vs. another set; or studies conducted over the short term vs. the long term. Nevertheless by accounting for these differences in experimental conditions, one can begin to see more consistencies in salinity–nutrient interactions and obtain a better understanding of the salinity–nutrient relations in horticultural crops overall.

Plant performance, usually expressed as a crop yield, plant biomass or crop quality, may be adversely affected by salinity-induced nutritional disorders. These disorders may result from the effect of salinity on nutrient availability, competitive uptake, transport or partitioning within the plant. For example salinity reduces phosphate uptake and accumulation in crops grown in soils primarily by reducing phosphate availability. Salinity dominated by Na^+ salts not only reduces Ca^{2+} availability but reduces its transport and mobility to growing regions of the plant, affecting the quality of both vegetative and reproductive organs. These disorders are aggravated in environments with high transpirational demands. Salinity can directly affect nutrient uptake such as Na^+ reducing K^+ uptake or by Cl^- reducing NO_3^- uptake. The occurrence of these disorders and whether they ultimately affect crop yield or quality depends upon the crop species and the experimental conditions where the study was conducted.

Salinity can cause a combination of complex interactions affecting plant metabolism or susceptibility to injury. In several studies it has been shown that salinity increases the internal requirement for a particular nutrient. Examples were given for P in tomato as well as K^+ in spinach. In other studies, salinity can cause plants that are deficient in an element to have a lower cellular tolerance for a specific ion. Moreover there are undoubtedly a multitude of other interactions yet to be found.

Despite a large number of studies that demonstrate that salinity reduces nutrient uptake and accumulation or affects nutrient partitioning within the plant, little evidence exists that adding nutrients at levels above what is considered optimal in non-saline environments, improves crop yield. Nutrient additions, on the other hand, have been more successful in improving crop quality. For example Ca^{2+} additions to soils or as foliar sprays can sometimes correct disorders caused by Na-induced Ca^{2+} deficiencies.

Nutrient additions may also reduce the incidence of injury. An adequate supply of Ca^{2+} maintains membrane integrity and selectivity thereby reducing Na^+ and Cl^- toxicity in tree and vine crops. However benefits from added Ca^{2+} are usually restricted to solution culture studies using NaCl as the sole salinising agent. There are also studies that have shown that increased concentrations of NO_3^- can reduce Cl-toxicity in certain tree crops. While these studies may have practical implications, actual practice may present an environmental hazard by increasing NO_3^- concentrations in the groundwater.

It is reasonable to believe that numerous salinity–nutrient interactions are occurring at the same time but whether they ultimately affect crop yield or quality depends upon the salinity level and composition of salts, the crop species, the nutrient in question and a number of environmental factors.

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