275

Mineral element acquisition and growth response of plants grown in saline environments

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ABSTRACT

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Plants acquire mineral nutrients from their native soil environments. Most crop plants are glycophytes and have evolved under conditions of low soil salinity. Consequently, they have developed mechanisms for absorbing mineral nutrients in non-saline soils. Under saline conditions, which are characterized by low nutrient-ion activities and extreme ratios of Na^+/Ca^{2+}, Na^+/K^+, Ca^{2+}/Mg^{2+} and Cl^-/NO_3^-, nutritional disorders can develop and crop growth may be reduced.

Additions of N and P generally increase the growth of plants grown in N- and P-deficient environments, provided that the plant is not experiencing severe salt stress. When salinity and nutrient deficiency are both factors limiting growth, relief of the most limiting factor will promote growth more than the relief of the less limiting factor. Therefore, addition of a limiting nutrient can either increase, decrease or have no effect on relative plant tolerance to salinity, depending on the level of salt stress. Failure to account for the severity of salt stress when interpreting salinity × nutrient interactions has caused considerable confusion among researchers.

Salinity disrupts mineral nutrient acquisition by plants in two ways. First, the ionic strength of the substrate, regardless of its composition, can influence nutrient uptake and translocation. Evidence for this is salinity-induced phosphate uptake in certain plants and cultivars. The second and more common mechanism by which salinity disrupts the mineral relations of plants is by reduction of nutrient availability by competition with major ions (i.e. Na^+ and Cl^-) in the substrate. These interactions often lead to Na^+-induced Ca^{2+} and/or K^+ deficiencies and Ca^{2+}-induced Mg^{2+} deficiencies.

Halophytes have not received the attention glycophytes have in the area of salinity–mineral nutrient relations. Nevertheless, some halophytes may show symptoms of mineral nutrient imbalances despite their remarkable ability to absorb nutrients selectively from soil solutions dominated by Na^+ and Cl^-.

INTRODUCTION

The mineral nutrition of plants is complex in itself when plants are grown in fertile, non-saline environments. In the presence of salinity, not only are

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the activities of nutrient ions reduced but high concentrations of the major ions in the soil solution, usually Na^+ and Cl^- may exceed nutrient element concentrations by one or two orders of magnitude. In the case of micronutrients, these ratios may be even more extreme. Because salinity reduces the activity of major nutrient ions and produces such large ion ratios in soil solutions, it is understandable that the plant may experience nutritional disorders. Nutrient imbalances may result from the effect of salinity on nutrient availability, uptake or distribution within the plant or may be caused by an increase in the plant requirement for that essential element.

Nutrient availability and uptake by plants is related to: (1) the activity of the nutrient ion in the soil solution which depends upon pH, pe, concentration and composition; (2) the concentration and ratios of accompanying elements that influence the uptake and transport of this nutrient by roots; (3) environmental factors. Plants vary not only in the rate by which they absorb an available nutrient, but also in the manner by which they spatially distribute the element within the plant. These differences occur at all scales (e.g. cellular, organ, whole plant) and at both the intra- and inter-specific levels.

In the absence of salinity, plant response in relation to the concentration of an essential nutrient in the root media is often described by the function illustrated in Fig. 1. This relationship is a modification of the 'generalized dose response curve' illustrated by Berry and Wallace (1981). Plant growth, usually expressed as absolute or relative biomass, is sub-optimal when the concentration or activity of the essential nutrient is less than A and optimal when the concentration is between A and B. Nutrient concentrations that exceed B may inhibit growth.

A substantial body of information in the literature indicates that the 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
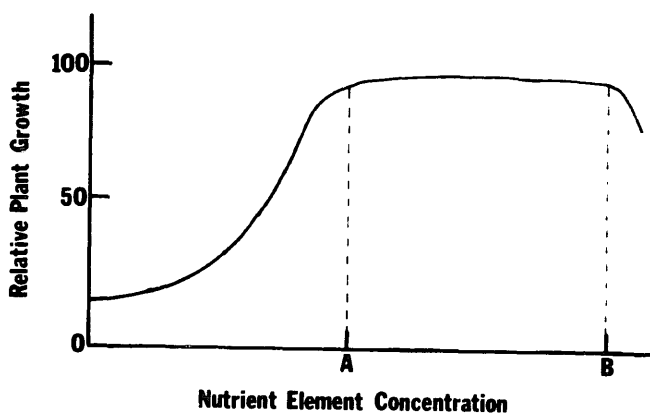

Fig. 1. Relative growth of plants in relation to a wide range of concentrations of an essential nutrient element.

or narrowed or it may shift to the right or left depending upon the plant species (or cultivar), the particular nutrient, the salinity level, or environmental conditions. Unfortunately, too few studies in the literature present sufficient data under saline and non-saline conditions to develop response functions similar to Fig. 1. In most studies, salinity (either concentration or composition) is a major variable and the experiment may only have a few treatments that vary in nutrient concentration. Nevertheless, many studies have shown that an optimal concentration or activity of a particular nutrient in non-saline conditions may be deficient, or in some cases excessive under saline conditions.

INTERPRETATION OF SALINITY × NUTRIENT INTERACTIONS

Regardless of where the experiment may be conducted; in the laboratory, greenhouse, or field, at least two factors can operate simultaneously to limit growth: the presence of salinity and the deficiency (or excess) of a particular nutrient. The 'salt-tolerance' of a crop, as defined by Maas and Hoffman (1977), may vary depending upon whether salinity or nutrition is the factor more limiting to growth. Bernstein et al. (1974) defined three different types of idealized salinity × nutrition interactions that could occur, (a) no effect on salt-tolerance, (b) increased salt-tolerance, and (c) decreased salt-tolerance. In contrast to the definition of Bernstein et al. (1974) as presented by Maas (1990), we prefer to define the interactions based on plant performance at optimal fertility relative to the performance at suboptimal fertility and this interpretation is shown in Figure 2(a)–2(c). Generally, plant growth will be promoted more if the most limiting factor is relieved rather than the less limiting factor. As an example, if nutrient deficiency limits growth more than salinity, a crop may appear more salt-tolerant than it would if the plant were adequately supplied with that nutrient. That is, improving soil fertility to an adequate level would improve plant performance proportionally more in non-saline conditions that under saline conditions. This contribution by Bernstein et al. (1974) is extremely valuable and these salinity × nutrient interaction functions can be useful, if used properly, in interpreting data from experiments conducted by others.

Bernstein et al. (1974) concluded that the effects of salinity and nutrition on grains and several vegetables are independent and additive when nutrient deficiency and salinity are moderate. When either of these factors severely limit growth, the other has little influence on yield. Ten years later, the work of Okusanya and Ungar (1984) with two halophytes and a glycophyte, gave results that support Bernstein's salinity × fertility interaction model. In the study by Okusanya and Ungar (1984), nutrient applications increased the growth of the halophytes in saline conditions, presumably because salinity was moderately growth limiting. On the other hand, nutrient applications did

INCREASED SALT TOLERANCE
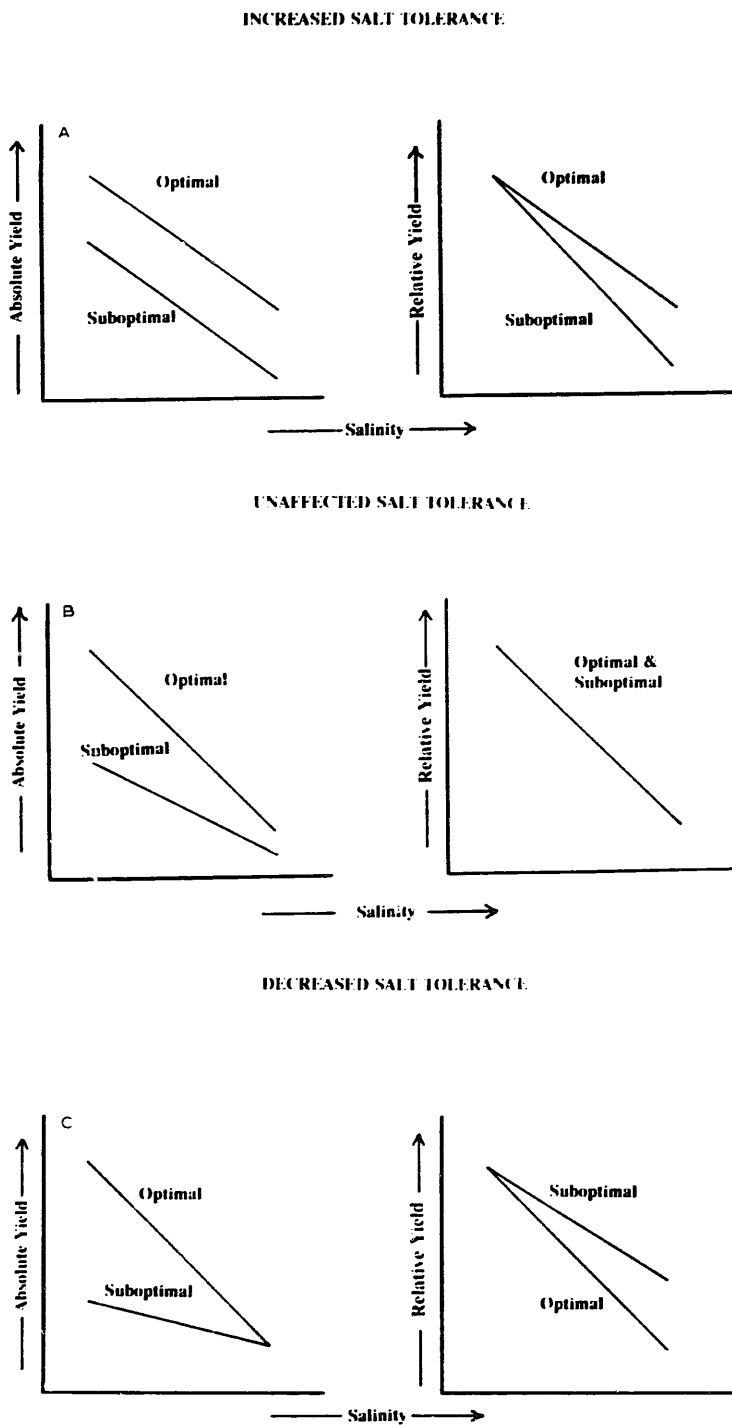
UNAFFECTED SALT TOLERANCE

DECREASED SALT TOLERANCE

Fig. 2. Types of growth responses a plant can exhibit under variable salinity as the nutrient status within the substrate increases from sub-optimal to optimal levels.

not improve plant growth of the glycophyte under saline conditions, presumably because salinity was severely growth-limiting.

It should be made clear, however, that the salinity×fertility interactions described by Bernstein et al. (1974) are idealized and therefore can be misleading if used improperly. They emphasized that growth (or yield) is controlled by the factor (salinity or nutrient deficiency) that is most growth limiting. Yet the interactions are based on plant response to salinity as it increases from non-limiting to severely-limiting levels. In many situations, the nutrient concentration is the most 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 emphasized by Champagnol (1979) in his literature review on the relationship between salinity and phosphorus nutrition of plants. A clear understanding of how this interaction changes from low to high salinity is absolutely essential. Without a clear understanding, it can be concluded by reviewing salinity×nutrition literature that contradictions exist. Much of the data in the literature that describes salinity×N or salinity×P response functions can be re-analyzed by examining the interactions under low, moderate and high salinity levels. In many cases, a response function similar to that illustrated in Fig. 3 will be obtained. Under low salinity stress, nutrient deficiency is limiting plant growth more than salinity and a (+) interaction or increased salt-tolerance response occurs. Under moderate salinity, nutrient deficiency and salinity stress may be equally limiting plant growth and no interaction (0) occurs. Under high
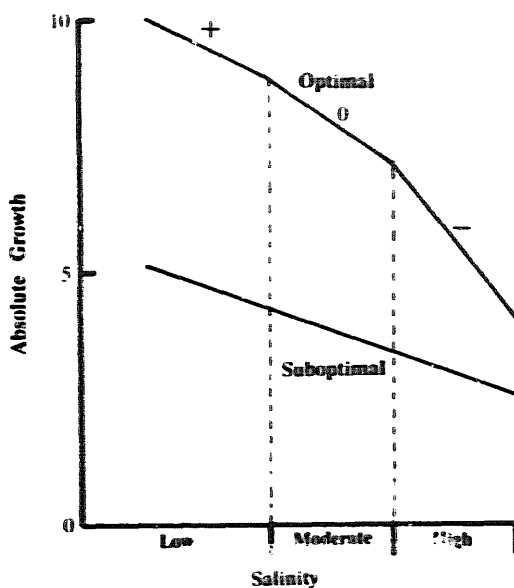

Fig. 3. Influence of low, moderate and high levels of salinity at sub-optimal and optimal levels of nutrient supply on plant growth. (+, 0, and − refer to an increase, no effect, and decrease in plant tolerance to salinity, respectively.)

salinity, salinity limits growth more than nutrient deficiency. In fact, plant performance would always exhibit a (—) interaction or a 'decreased salt-tolerance' (Fig. 2(c)) response if a nutrient was limiting growth under non-saline conditions and the upper salinity treatment was lethal or severely growth-limiting. In this case only plants grown in non-saline environments would respond to a nutrient addition.

In light of the discussion above and the multitude of interactions that could occur, results reported by various scientists on this subject may not be as contradictory as reviewers (e.g. Jurinak and Wagenet, 1981; Kafkafi, 1984; Feigin, 1985; Adams and Doerge, 1987) have suggested.

SOIL AND SOLUTION CULTURE STUDIES

Many of the studies in the area of plant-nutrition $\times$ 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 major nutrients in the soil solution, particularly, P and K^+, are controlled by the solid phase and are difficult to measure or predict. To complicate matters further, salinity and nutrient concentrations vary spatially and temporally. In solution cultures, nutrient ratios differ considerably from those found in soil solutions, and root development is entirely different from that in soils. It is reasonable to assume that plant responses and interactions observed in artificial media may not necessarily occur, at least with the same magnitude, as they would under natural conditions. Nevertheless, solution culture studies are extremely beneficial since the advancement of scientific knowledge is increased by examining plant responses under controlled though often unrealistic, conditions as much as it is by examining the response under normal environmental conditions.

The remaining aim of this paper will be directed towards plant performance and acquisition of the major nutrients, N, P, K^+, and Ca^{2+} in saline environments. This review will include both soil and solution culture studies. Most of the emphasis will be placed on glycophytes since most work has been conducted on this group of plants. Discussion on halophytes will be included where appropriate and where information is available.

NITROGEN

In most soils, saline or non-saline, N is usually the most growth-limiting plant nutrient. Consequently, addition of N usually improves plant growth and yield. In many field studies, researchers set out to test the hypothesis that

N-fertilizer additions alleviate, at least to some extent, the deleterious effect of salinity on plants.

Most salinity $\times$ N studies were conducted on soils deficient in N. Therefore, additions of N improved growth and/or yield of barley (Dregne and Mojallali, 1969), bean (Lunin et al., 1964; Lunin and Gallatin, 1965, Wagenet et al., 1983), carrots, cowpea, tomato, corn, clover, beans, millet and vetch (Ravikovitch and Porath, 1967); coastal bermudagrass (Langdale and Thomas, 1971), corn and cotton (Khalil et al., 1967), corn and millet (Ravikovitch, 1973) tomato (Papadopoulos and Rendig, 1983) spinach (Langdale et al., 1971), and wheat and rice (Ogo and Morikawi, 1965) when the degree of salinity was not severe. In most of these studies, the fact that applied N did not improve the growth under extreme saline conditions suggests that applied N decreased plant salt-tolerance (see response in Fig. 2(c)). On the other hand, only a few studies showed an increase in crop yield under saline conditions where N was applied above a level considered optimal under non-saline conditions (Ravikovitch and Yoles, 1971a,b). In this case, additional N did in fact increase the salt-tolerance of millet and clover. Selassie and Wagenet (1981) also report data that indicate that the salt tolerance of well-watered corn may have been increased with urea additions up to 375 kg ha^{-1} to a soil initially supplied with sufficient N. This practice, however, is not necessarily practical and would most likely be undesirable from both an economical and environmental point of view.

Despite the majority of evidence that indicates that N applied to saline soils above a level considered optimal under non-saline conditions does not improve plant growth or yield, a substantial number of laboratory and greenhouse studies have shown that salinity reduces N accumulation in plants (Cram, 1973; Deane-Drummond and Glass, 1982). This is not surprising since with few exceptions (Gorham et al., 1988), increase in Cl$^-$ uptake and accumulation is accompanied by a decrease in shoot-nitrate concentration. Examples of this effect are also found in barley (Helal et al., 1975; Aslam et al., 1984; Ward et al., 1986; Klobus et al., 1988), cotton (Silberbush and Ben-Asher, 1987), tomato (Kafkafi et al., 1982), tomato and melon (Feigin et al., 1987) and wheat (Torres and Bingham, 1973; Balasubramanian and Sarin, 1975). Aslam et al. (1984) reported that Cl$^-$ inhibited NO$_3^-$ uptake more than SO$_4^{2-}$ when these anions were present on an equal osmolarity basis. Gorham et al. (1986) observed that despite drastic reductions in leaf-NO$_3^-$ concentrations in response to salinity, other nitrogen-containing fractions either increased (e.g. proline, glycine-betaine, total soluble protein) or were not greatly reduced (e.g. total amino acid content). These results argue against nitrogen deficiency per se as a mechanism of salt injury. This conclusion is also supported by Munns and Termaat (1986). In their review, they suggest

that although N-deficiency may occur in NaCl-treated plants, there is no strong evidence to support that this effect is growth limiting.

In contrast to the effect of Cl^- on NO_3^- uptake, others have reported data that demonstrated that increased NO_3^- in the substrate decreased Cl^- uptake and accumulation (Bernstein et al., 1974; Kafkafi et al., 1982; Feigin et al., 1987; Martinez and Cerda, 1989).

Although Cl^- salts were primarily responsible for reduced NO_3^- uptake by plants, NO_3^- reduction in plants was not affected in 12 h studies with barley seedlings (Aslam et al., 1984). The stimulation of nitrate reductase activity promoted NO_3^- reduction, and its subsequent assimilation into protein. However, when NaCl in the substrate was at stressful concentrations, incorporation of labeled NH_4NO_3 into protein was impaired in barley leaves (Helal and Mengel, 1979). In contrast, the decrease in nitrate reductase activity in wheat plants grown for several weeks in saline cultures was attributed to inhibition of NO_3^- uptake by Cl^- (Abdul-Kadir and Paulsen, 1982).

The form in which N is supplied to salt-stressed plants may be important (Lewis et al., 1989; Martinez and Cerda, 1989) although the form of N did not influence the yield of moderately salt-stressed wheat (Leidi and Lips, 1990). Lewis et al. (1989) found that NH_4^+-fed maize and wheat plants were more sensitive to salinity than NO_3^--fed plants when grown in solution cultures. Similar responses were found in melon (Feigin, 1990). 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 Cerda (1989) found that Cl^- uptake was enhanced in cucumber when half the NO_3^- in the solution was replaced by NH_4^+. Martinez and Cerda (1989) further noted that when NO_3^- was the only N-source, accumulation of K^+ in the plant was increased in saline conditions. When the media contained both NO_3^- and NH_4^+, K^+ was reduced. Similar effects were found in salt-stressed melon (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. In experiments with salinized soil, the opposite behavior was found. Shaviv et al. (1990) found wheat to be more tolerant to salinity under a combination of NH_4^+ and NO_3^-, than with NO_3^- alone. Halophytes grown in highly saline, N-deficient environments and glycophytes grown in mildly saline, N-deficient environments, respond similarly to added N (Broome et al., 1975; Smart and Barko, 1980; Okusanya and Ungar, 1984; Skeffington and Jeffrey, 1985; Naidoo, 1987). Skeffington and Jeffrey (1985) found that N additions increased the growth of *Plantago maritima* even when grown in sea water. Furthermore, N additions increased plant ability to survive. Okusanya and Ungar (1984) found that the poor growth of two *Spergularia* species grown in 50% sea water was improved by $Ca(NO_3)_2$ additions. Naidoo (1987) studied the interactive effects of N and NaCl salinity on young mangroves (*Avicennia marina*). The N was supplied as NH_4^+ rather than NO_3^-. This was done

as most mangroves are grown under saturated, and thus anaerobic, environments. Therefore, nitrate reduction is prominent and most plant-available N is in the NH_4^+-form. Naidoo (1987) found that increased salinity decreased N and K^+ in tissues. Furthermore, as NH_4^+-N increased from 1.4 to 14 mg/ L shoot growth increased in the 100 and 300 mM NaCl treatment but not in the 500 mM NaCl treatment. Therefore, in agreement with most of the work with glycophytes, it would be interpreted that added N decreased salt tolerance of these halophytic species.

Some halophytes have salt glands, a unique anatomical feature that allows the plant to selectively excrete salt (particularly NaCl) from its shoot. Not only does this feature allow the plant to reduce its internal salt load, at least to some extent, it improves the nutrient relations within the plant. Waisel et al. (1986) suggested that salt glands, by selective removal of Na^+ and Cl^- from the leaves of *Avicennia marina*, may help this mangrove species metabolize normally by decreasing the ratios of Cl^-/NO_3^-, $Cl^-/H_2PO_4^-$, and Na^+ / K^+ within its leaves.

PHOSPHORUS

The interaction between salinity and phosphate (P) nutrition of plants is perhaps more complex than that between salinity and N. The interaction is highly dependent upon the plant species (or cultivar), plant developmental age (Zhukovskaya, 1973), 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.

It has been more than a decade since Champagnol (1979) reviewed 17 publications and found that P, added to saline soils, increased crop growth and yield in 34 of the 37 crops collectively studied. However, added P did not necessarily increase crop salt tolerance as defined by the nutrient×salinity response model originally developed by Bernstein et al. (1974). After analyzing studies with barley, carrot, clover, maize, millet, sorghum, sugar beet, tomato, vetch and wheat, Champagnol (1979) concluded that added P either increased, had no effect, or decreased salt tolerance as salinity increased from low, to moderate, to high levels, respectively. This is perhaps the most convincing evidence that supports the supposition that the simple application of the model to describe salinity×nutrient interactions introduced by Bernstein et al. (1974), can be extremely misleading. It is important, therefore, that the model be used only when specific salinity levels are identified. This approach was used to a limited extent by Peters (1983). He evaluated the salt-tolerance of barley under control and added-P conditions. Linear regression equations of barley grain yields and soil salinity were compared when average soil salinity was equal to or greater than 0, 4, and 6 dS m^{-1}. Unfortunately, he did not evaluate the effect of added P on crop salt-tolerance separately under low,

moderate and high levels of salinity. The most useful conclusion from studies reviewed by Champagnol (1979) is that P additions to P-deficient soils are beneficial providing that the crop is not experiencing severe salt stress.

Recent evidence indicates that salinity may increase the P requirement of certain plants. Awad et al. (1990) found that when NaCl increased in the substrate from 10 to 50 and 100 mM, the P concentrations in the youngest mature tomato leaf necessary to obtain 50% yield increased from 58 to 77 and 97 mmol kg^{-1} dry wt. Their conclusion was also supported by foliar symptoms of P deficiency that were evident on plants grown at high NaCl concentrations at a given leaf P concentration.

The influence of salinity on P accumulation in crop plants is variable and depends upon the plant and experimental conditions (Champagnol, 1979). In many cases, salinity decreased P concentration in plant tissue (Sharpley et al., 1992) while in others it increased it or had no effect. 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. Champagnol (1979) concluded that it is unlikely that Cl$^-$ and H$_2$PO$_4^-$ ions are competitive in terms of plant uptake. However, Papadopoulos and Rendig (1983) concluded that Cl$^-$ may have suppressed P uptake and accumulation in tomato shoots. Zhukovskaya (1973) found that Cl$^-$ as well as SO$_4^{2-}$ salts reduce P uptake in barley and sunflower. In other cases, reduction in plant P concentration by salinity may result from reduced activity of P in the soil solution due to the high ionic strength of the media (Awad et al., 1990).

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 P but also because P concentrations in soil solution are tightly controlled by sorption processes and by the low-solubility of Ca–P minerals. Therefore, it is understandable that P 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 and 50 percent (Figure 4(a) and (b)) yet there was no evidence of P deficiency in the crops.

Since the solubility of P in the solutions of saline soils containing high levels of Ca^{2+} is controlled by sorption processes on Al-hydroxides and by the solid phase of Ca–P minerals, it is reasonable to question why some plants respond positively to added P. Evidently, the kinetics of sorption and/or precipitation are relatively slow and initial forms of calcium phosphate are thermodynamically unstable (D.L. Suarez, personal communication, 1990). Later, more stable phases are formed, plant availability decreases and repeated P applications to saline/calcareous soils are required.

Unlike studies conducted in the field, most studies that demonstrated that salinity increased tissue P, were conducted in sand or solution cultures. Phos-
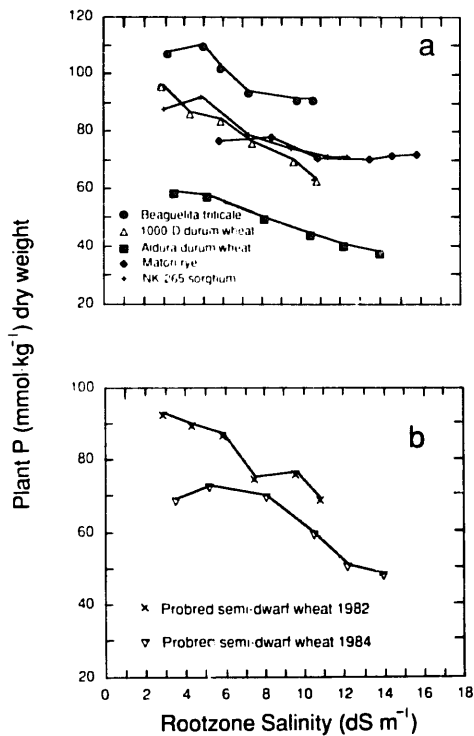
Fig. 4. P concentration in grain crops in relation to soil salinity. Soils were salinized with equal weights on (a) NaCl and (b) CaCl₂ (Sharpley et al., 1992).

phate concentration in solution cultures is often orders of magnitude higher than that in soil solutions (e.g. 2 mM vs. 2 μM) (Sharpley et al., 1992). 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), lupin (Treeby and van Steveninck, 1988), sesame (Cerda et al., 1977) and certain soybean cultivars (Grattan and Maas, 1984) when grown in saline solutions. This is evidence that the optimal P range (A to B in Fig. 1), in these instances, narrows under saline conditions. In all these studies, salinity increased P accumulation in plants at the highest substrate P level. The increased P accumulation in the shoot is presumably controlled at the root level (Grattan and Maas, 1985) and is caused by a salinity-enhanced P uptake rate by roots (Roberts et al., 1984).

Certain soybean cultivars are particularly sensitive to salinity in the presence of 0.2 mM P (Grattan and Maas, 1984) which is only 40% of that in half-strength Hoagland's solution (Hoagland and Arnon, 1950). It is likely that susceptible cultivars would be ranked as 'P-sensitive' as defined by Howell and Bernard (1961). In the experiments conducted by Grattan and Maas (1984), three of the soybeans tested had been ranked for P tolerance. The

two that were ranked P-tolerant did not exhibit the salinity $\times$P interaction whereas the one ranked P-sensitive was extremely sensitive. Phosphorus-susceptible cultivars absorbed and accumulated P at a rate greater than P-tolerant cultivars. Evidently, salinity by some unexplained mechanism, caused the sensitive cultivars to accumulate abnormally large quantities of P in their leaf tissue (i.e. 600–900 mmol kg^{-1} dry wt) and even higher concentrations in their root tissue (i.e. 1000–1400 mmol kg^{-1}) when substrate P was above some threshold concentration (i.e. concentration B in Fig. 1). This threshold concentration varies not only among cultivars of soybean at a given salinity level, but among species as well. The threshold concentrations for the other sensitive species of corn, sesame and lupin are higher than that for sensitive soybean cultivars. For sensitive soybean cultivars, threshold P concentrations were less than 0.12 mM but above 0.02 mM.

The studies with soybean described above demonstrate a unique salinity-induced nutritional disorder. Direct ion interactions play a minor role. Excessive P accumulates in sensitive cultivars regardless of the ratio of Ca^{2+} to Na^+ (Grattan and Maas, 1988a) and is dependent upon the ionic strength or osmotic potential of the solution regardless of the types of salts used (i.e. $NaCl+CaCl_2$, $KCl+CaCl_2$, or $NaNO_3+Ca(NO_3)_2$) (Grattan and Maas, 1988b). Plant mortality, on the other hand, is related to high levels of both P and Cl in the leaf tissues.

It should be emphasized, however, these adverse interactions observed with corn, sesame, lupin and soybean would rarely occur under field conditions since P concentrations in soil solutions are usually orders of magnitude less than those used in these studies. Nevertheless these interactions are important from an academic viewpoint and pose interesting questions regarding the mechanisms of P uptake and transport within the plant. For example, what physical or chemical changes are occurring at the membrane level that cause excessive P uptake despite a decrease in the activity of P resulting from the presence of salinity?

Phosphate additions to halophytes grown in highly saline environments have also resulted in increased plant growth. Okusanya and Fawole (1985) showed that phosphate stimulated the growth of *Lavatera arborea* much more at 40 and 50% strength seawater than under non-saline conditions. The magnitude of this effect may be due partly to the increase in the shoot/root ratio by salinity. When no phosphate was added salinity reduced plant growth. However, when 0.05 and 0.25 mM phosphate was added to the nutrient sand culture, salinity at the concentration of 40% seawater actually increased plant growth. Therefore, addition of phosphate increased the salt tolerance of *Lavatera arborea*.

POTASSIUM

Potassium, like P, is present in relatively low concentrations in the soil solution. Potassium is readily adsorbed onto the surface of soil particles and is

fixed, and thus unavailable, within layers of expandable 2:1 clay minerals. Because of the plant's requirement for an adequate amount of K^+, it is fortunate that the plasma membranes of root cortical cells have a high affinity for K^+ over Na^+. This is particularly important in saline and sodic environments where concentrations of Na^+ in the soil solution are orders of magnitude higher than that of K^+. The high K^+/Na^+ selectivity within plants is maintained, provided that the calcium status in the root is adequate (Carter, 1983; Kent and Läuchli, 1985; Subbarao et al., 1990) and that the roots have a sufficient supply of O_2 (Drew et al., 1988).

Although plants selectively absorb and translocate K^+ in preference to Na^+, the degree of selectivity varies among species as well as among cultivars within a species. Kafkafi (1984) reported the data of Bower and Wadleigh (1948) as the fraction of monovalent cations ($Na(Na+K)$ or $K(Na+K)$) in the exchange complex vs. that within the roots of bean and beet. Kafkafi (1984) then concluded that the roots of the salt-tolerant species (beet) had a higher affinity for K^+, in exchange for Na^+, than the salt-sensitive species (bean). Rathert (1982) found that salinity ($Na^+/K^+ = 9$) reduced the concentration of K^+ in the leaves of the salt-sensitive cotton cultivar ('Dandara') more than that in the salt-tolerant cultivar ('Giza 45').

There is evidence that Na^+ can partially substitute for K^+ in many glycophytic species without affecting growth. Marschner (1986) classified many crop species into four groups, depending upon the extent by which Na^+ can replace K^+. Crop species in Group A can replace a high proportion of K^+ by Na^+ (e.g. beets, turnip, and swiss chard) whereas in crop species in Group D (e.g. maize, bean, and lettuce) no substitution of K^+ is possible. Rice has been classified as a Group C crop where only a minor substitution of K^+ by Na^+ is possible and Na^+ has no specific effect on growth, unlike those crops in Group A and B (Marschner, 1986). However, the addition of 17mM NaCl to solution cultures low in available K^+ improved vegetative growth and increased panicle yield (Tanaka, 1981). Sodium chloride decreased the K^+ content only when the K^+ supply was low. Thus, a relatively high Na^+ content may benefit rice nutrition under saline conditions when the supply of K^+ is low (Tanaka, 1981).

Despite the plant's high affinity for K^+ over Na^+, the K^+ status in plants is related to the ratio of Na^+/K^+ in the saturated-soil extract (Devitt et al., 1981). If it is assumed that the composition of the soil solution is at least close to equilibrium with that on the exchange phase, then it would follow that K^+ accumulation by the root would be reduced if the exchangeable sodium percentage (ESP) on the exchange phase were increased. This effect was observed in bean and beet (Bower and Wadleigh, 1948).

Numerous studies have shown that the K^+ concentration in plant tissue is reduced as Na^+-salinity or the Na^+/Ca^{2+} ratio in the root media is increased (e.g. Okusanya and Ungar, 1984; Cramer et al., 1985; Janzen and Chang,

1987; Subbarao et al., 1990). 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-}. Janzen and Chang (1987) found that barley plants exposed to Na_2SO_4 salinity contained only one-third the concentration of K^+ in their shoots than those grown in non-salinized solutions.

Halophytes, like glycophytes, have also shown a high degree of K^+ selectivity and increasing Na^+ concentrations in the substrate have caused reduced K^+ concentrations in their shoots. Rains and Epstein (1967) found that excized leaf tissue of the mangrove, *Avicennia marina*, was highly selective for K^+ over Na^+. Nevertheless, increased NaCl salinity decreased shoot K^+ in the same mangrove species, even though there was no effect on root K^+ (Naidoo, 1987). In contrast, Clough (1984) found no differences in leaf or stem K^+ in *A. marina* when plants were grown in different dilutions of sea water. The author did note, however, that the K^+ concentration in the media increased 9-fold as the percentage of sea water increased from 0 to 100. Ball et al. (1987) concluded that NaCl salinity produced a salinity-induced K^+ deficiency in *A. marina* by reducing the atrazine binding sites in isolated thylakoids. This caused a loss of functional photosystem II in the leaves of this mangrove species.

Although plants show high selectivity of K^+ over Na^+, excessive amounts of K^+ may be detrimental to some plants. Rush and Epstein (1981) found that the wild tomato species (*Lycopersicon cheesmanii*) could tolerate 200 mM Na^+, but 200 mM K^+ was toxic. On the other hand, the domestic and more salt-sensitive tomato species (*Lycopersicon esculentum*) showed the opposite behavior; it could tolerate K^+ but not Na^+ at the same concentration. With regard to halophytes, the adverse effects of high K^+/Na^+ at high total salt concentration have been observed in *Atriplex amnicola*, *Atriplex inflata*, *Atriplex nummularia*, *Suaeda maritima*, and *Vigna radiata* (Aslam et al., 1988).

Despite the overwhelming amount of data that show reduced uptake and translocation of K^+ by plants grown in high Na^+ substrates, there is little data that shows that the addition of K^+ to sodium-dominated soils improved plant growth or yield. Bernstein et al. (1974) found that increasing solution K^+ from 0.4 to 2 mM did not affect leaf K^+ or yield of corn. Muhammed et al. (1987), on the other hand, found that shoot and root growth of rice plants grown in 100 mM NaCl solutions were increased when substrate K^+ increased from 1 to 7 mM. In other nutrient culture studies, Chow et al. (1990) showed that differences in the shoot growth of spinach between plants grown at low (50 mM NaCl) and high (250 mM NaCl) salinity at a given level of K^+ can be reduced when K^+ is added to the highest salinity treatment. However, plant growth at the low salinity level only doubled when K^+ in the solution was increased from 0.01 to 10.0 mM. In field conditions, soil solution K^+ remains low even after fertilizer 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.

CALCIUM

The presence of Ca^{2+} as the dominant cation in agricultural soils generally insures that the absolute Ca^{2+} level is not a primary growth-limiting factor. As salinity increases, the requirements of plants for Ca^{2+} increases (Gerard, 1971). In saline soils, as contrasted with sodic soils, Ca^{2+} 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 increasing ionic strength that reduce the activity of Ca^{2+}. These combined effects are at least partially responsible for reduced yields under saline or sodic conditions (Bernstein, 1975; Rengasamy, 1987; Janzen and Chang, 1987; Puntamkar et al., 1988). Therefore, in reference to Fig. 1, the optimum range is shifted to the right for most crops grown under saline conditions, particularly if the solution is dominated by Na^+ salts.

The critical Ca^{2+} requirement for plants has been estimated as the ratio of soluble Ca^{2+} to the total cations (Ca^{2+}/TC) rather than to the absolute concentration of Ca^{2+} in the soil solution. Physiological disorders that are related to Ca^{2+} deficiency occur when the Ca^{2+}/TC falls below a critical level (Geraldson 1957, 1970). In the Solonetzic soils of the Canadian prairie, ion imbalances result from high Na^+ and low Ca^{2+} together with predominately sulfate-salinity. Severe Ca^{2+} deficiency in barley occurs in these regions when the Ca^{2+}/Mg^{2+} molar ratio or the Ca^{2+}/TC ratio is less than 0.15 (Carter et al., 1979). The critical Ca^{2+} requirement for the optimum rate of extension of cotton root has been related to the molar Ca^{2+}/TC ratio (Howard and Adams, 1965). Subsequently, the Ca^{2+}/TC ratio, expressed in terms of ion activity, was considered to be a more accurate measure of Ca^{2+} availability (Bennett and Adams, 1970; Khasawneh, 1971; Adams, 1974; Wolt and Adams, 1979). However, it would seem preferable to distinguish specific ion competition e.g. $Ca^{2+}:Na^+$ and $Ca^{2+}:Mg^{2+}$ rather than Ca^{2+}/TC.

The Ca^{2+}/TC in the soil solution has been related to the Ca^{2+}/TC in saturated-paste extracts (Janzen and Chang, 1987). Carter and Webster (1990) used this relationship to predict plant-available Ca^{2+} as well as Ca^{2+} accumulation in plant tissues. Critical levels of Ca^{2+} in barley and wheat (63 mmol kg^{-1} dry wt.) and alfalfa (250 mmol kg^{-1} dry wt.) corresponded to a Ca^{2+}/TC ratio of 0.10 in the soil extract.

Calcium plays a vital nutritional and physiological role in plant metabolism. It is essential in processes that preserve the structural and functional integrity of plant membranes (Hanson 1984), stabilize cell wall structures, regulate ion transport, and control ion exchange behavior as well as cell wall enzyme activities (Demarty et al., 1984). Because Ca^{2+} is readily displaced

from its extracellular binding sites by other cations, these functions may become seriously impaired by reduced Ca^{2+} availability. Root growth and function may be restricted by high Na^+/Ca^{2+} (Kent and Läuchli, 1985, Cramer et al., 1986, 1988; Hansen and Munns, 1988a,b). Solomon et al. (1986) observed abnormal root morphology and anatomy of pea (*Pisum sativum*) 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).

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 (Lynch and Läuchli, 1985). 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^+. Exchange constants, calculated from the relationship between the activities of Ca^{2+} and Na^+ in nutrient cultures and the equivalent fraction of Ca^{2+} and Na^+ in corn shoots, indicated that the cation uptake process is strongly selective for Ca^{2+} against Na^+. As the activity of Na^+ in the substrate increases, however, the system becomes less discriminating and the selectivity for Ca^{2+} is impaired (Suarez and Grieve, 1988).

Nutritional imbalances in salt-stressed cereals have been studied in isosmotic nutrient solutions salinized with various molar ratios of Na^+ and Ca^{2+}. These investigations included corn (Maas and Grieve, 1987), rice (Grieve and Fujiyama, 1987), and sorghum (Grieve and Maas, 1988) as well as wheat, barley, rye and oats (E.V. Maas and C.M. Grieve, unpublished data, 1984). The cereals show striking intergeneric differences in their response to different Na^+/Ca^{2+} molar ratios in cultures of equal osmotic potential (OP). A salt stress of (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 at $Na^+/Ca^{2+} = 5$ than was corn.

Genotypes within a given cereal species may also vary in their susceptibility to Ca^{2+} disorders at high substrate Na^+/Ca^{2+}. Grieve and Maas (1988) compared the response of three sorghum cultivars 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, often necrotic tips. These symptoms have been associated with severe Ca^{2+} deficiency (Kawasaki and Moritsugu, 1979) and this diagnosis was confirmed by mineral analysis. Yeo and Flowers (1985) reported that the elite breeding line (IR 2153) of rice was very unresponsive to external Ca^{2+}. Shoot growth of this line was not

affected over a wide range (5–500) of Na^+/Ca^{2+} ratios and Ca^{2+} concentration had a limited effect on NaCl uptake. In contrast, high Na^+/Ca^{2+} inhibited shoot growth in two rice cultivars (M9 and M201) developed for specific regions of California (Grieve and Fujiyama, 1987). Ca^{2+} deficiency symptoms were observed at an OP of -0.4 MPa and Na^+/Ca^{2+} molar ratios of 198 and 78. Shoot growth improved and the Ca^{2+} disorder was eliminated when the Na^+/Ca^{2+} ratio was reduced to 17.8 (Grieve and Fujiyama, 1987). The shoot and root growth of the rice cultivar KS282 was significantly influenced by external Na^+/Ca^{2+} (Muhammed et al., 1987). Rolling and bleaching of the young leaves occurred when the Na^+/Ca^{2+} ratio exceeded 100. These investigators also attributed differences in root growth to an interaction between Na^+/Ca^{2+} and Na^+/K^+ ratios in the root media. Norlyn and Epstein (1984) observed that triticale lines differed in tolerance to high (500) Na^+/Ca^{2+} during emergence and germination. Emergence of only one line improved when the Na^+/Ca^{2+} was reduced to 37, while other lines showed no effect of added Ca^{2+}. Kingsbury and Epstein (1986) contrasted the response of two wheat genotypes to isosmotic solutions that varied in ionic composition. One line was highly resistant to Na^+ toxicity and, in response to high external Mg^{2+}/Ca^{2+}, showed superior Ca^{2+}-use efficiency.

Several studies (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. Eventually the Ca^{2+} concentration in the older blades of salinized plants was as high as in those in the nonsaline 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 such typical Ca^{2+}-related physiological disorders as blossom-end rot of tomatoes and peppers, black heart of celery and internal browning of lettuce (Geraldson, 1970; Marschner, 1986) and artichokes (Francois et al., 1991).

Increased root permeability, caused by reduction in the availability of external Ca^{2+}, may lead to increased Cl^- uptake. Elevated interval Cl^- concentrations have been associated with decreased shoot growth in several species e.g. cowpea (Imamul Huq and Larher, 1984), pigeonpea (Subbarao et al., 1990) and Leucaena leucocephala (Hansen and Munns, 1988a,b).

The importance of maintaining a balanced nutrient solution to optimize plant performance of glycophytes under saline conditions has been known for over 80 years (see Osterhout, 1906) yet an alarming percentage of salinity studies conducted to date use NaCl as the only salinizing salt. We must therefore emphasize that the use of extreme ratios of Na^+ and Ca^{2+} may introduce unique nutritional problems and result in misleading and erroneous interpretations about plant response to salinity.

MAGNESIUM

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 1986). Thus, high concentrations of substrate Ca^{2+} usually result in increased leaf-Ca along with a marked reduction in leaf-Mg (Bernstein and Hayward, 1958). Increased concentration of $CaSO_4$ in the nutrient solution decreased Mg^{2+} in roots, stems, and leaves of *Leucaena leucocephala* (Hansen and Munns, 1988b). Calcium-induced Mg^{2+} deficiency has been observed in sesame (Nassery et al., 1979). Both photosynthetic rate and water use efficiency declined in salt-stressed corn ($OP = -0.4$ MPa) as the external Ca^{2+}/Mg^{2+} ratio increased (Plaut and Grieve, 1988). Excessive leaf-Ca concentrations may interfere with CO_2 fixation by inhibition of stroma enzymes, particularly those that are Mg^{2+}-activated (Brand and Becker, 1984). In the case of plants grown in sea water or dilutions of sea water, it is possible that nutrient disorders could develop because of the high Mg^{2+}/Ca^{2+} ratio. In most sea water compositions, $Mg^{2+}:Ca^{2+}$ is 5:1 on a molar basis.

MICRONUTRIENTS

The concentrations of micronutrients in soil solutions, with the exception of Cl^-, are low (μM range) and depend on the physical and chemical characteristics of the soil. 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. The solubility of micronutrients usually increases under saline conditions (Sharpley et al., 1992) yet the micronutrient concentration in plant shoots may increase, decrease or have no effect, depending upon the type of plant, tissue, salinity, micronutrient concentration and environmental conditions. Zinc (Zn) concentration has been found to increase in shoots of salt-stressed barley (Hassan et al., 1970a), bean (Doering et al., 1984), soybean, squash, tomato (Maas et al., 1972) and rice grain (Verma and Neue, 1984) but decrease in corn (Hassan et al., 1970b) and mesquite (Jarrell and Virginia, 1990). Salinity increased the manganese (Mn) concentration in the shoots of barley (Hassan et al., 1970a), rice (Verma and Neue, 1984), sugar beet (Khattak and Jarrell, 1989), and tomato (Maas et al., 1972), but decreased its concentration in the shoots of squash (Maas et al., 1972), pea (Dahiya and Singh, 1976) and corn (Hassan et al., 1970b).

The influence of salinity on the iron (Fe) concentration in plants was as inconsistent as it was on Zn and Mn concentration. Salinity increased the Fe concentration in the shoots of pea (Dahiya and Singh, 1972), tomato, soybean, squash (Maas et al.,1972), and rice (Verma and Neue, 1984) and decreased its concentration in the shoots of barley and corn (Hassan et al., 1970a,b).

Although the influence of salinity stress on the micronutrient concentration in plants is highly variable, there is evidence that NaCl salinity may induce an Fe deficiency. In the presence of 100–400 mM NaCl, root epidermal cells of *Atriplex hastata* and *A. hortensis* develop features that are characteristic of transfer cells, e.g. bladder-shaped root hairs and thickened convolutions on the outer peripheral cell wall. Further evaluation of these results showed that alterations were not a specific response to salinity but were a symptom of Na^+-induced iron deficiency (Kramer, 1984).

CONCLUSIONS

Plants acquire mineral nutrients from the root–substrate interface in their native environment. Glycophytes, normally salt-sensitive species that have evolved under conditions of low salinity, have adapted mechanisms for absorbing nutrients from non-saline soils. In contrast, halophytes have evolved mechanisms that permit the selective uptake of nutrie.. .s from saline soils. Saline soils may be characterized by low activity of nutrient ions and by extreme ratios of Na^+/Ca^{2+}, Na^+/K^+, Ca^{2+}/Mg^{2+} and Cl^-/NO_3^- in the soil solution. When glycophytes, which encompass most cultivated crops, are exposed to saline condition, nutritional disorders may develop. These disorders vary in their intensity and can differ among species as well as among cultivars within a species.

Plant performance, usually expressed as a crop yield or plant biomass, may be adversely affected by disorders that result from nutrient deficiencies or imbalances. In the field, additions of nutrients have increased the growth of both glycophytes and halophytes, provided that the plants were not experiencing severe salt stress. Relief of the more growth-limiting stress, salinity or nutrient deficiency, promotes growth more than relief of the less limiting factor. Therefore, addition of a limiting nutrient may increase, decrease or have no effect on plant salt tolerance, depending on the severity of salinity stress. Consequently, interpretation of plant salt tolerance expressed on a relative basis under variable soil fertility can be misleading.

Plants grown in N or P deficient environments, will respond positively to additions of these elements provided the plant is not experiencing severe salt stress. Salinity has been found to reduce N and P accumulation in plants. Although salinity-treated plants may be N- or P-deficient this effect may not be growth limiting. This interaction partly explains why most plants do not respond positively to N or P added above levels considered optimal in non-saline conditions. In fact, P toxicities can develop in certain salt-stressed plants if the P concentration in the substrate is too high.

There is an overwhelming amount of evidence from laboratory studies that indicate that Na^+-dominated soils or solutions reduce K^+ and Ca^{2+} uptake by plants and/or affect the internal distribution of these elements. Neverthe-

less, there are only a few studies that show growth increased by additions of these nutrients to sodic or saline/sodic soils. With regard to K^+, this may be due partly to the large quantity of this nutrient needed to correct the problem. With regard to Ca^{2+}, with the exception of Solonetzic soils, there are not many areas where Ca^{2+} in the soil is deficiently low and Na^+ is high.

Salinity disrupts the mineral nutrient aquisition of glycophytes in two ways. First, the ionic strength of the substrate can have direct effects on nutrient uptake and translocation. Evidence for this is salinity-induced P uptake and accumulation in certain plants and cultivars. This is an osmotic rather than a specific-ion effect and occurs regardless of the type of salts used to reduce the osmotic potential of the root media. These effects have only been observed on plants grown in nutrient solution and sand cultures. The second, and more common mechanism by which salinity disrupts the mineral nutrition of plants is the direct interaction of major ions in the substrate (i.e. Na^{2+} and Cl^-) on nutrient ion acquisition and translocation within the plant. Major ions can influence nutrient absorption by competitive interactions or by affecting ion selectivity of membranes. Examples of these effects are Na^+-induced Ca^{2+} and/or K^+ deficiencies and Ca^{2+}-induced Mg^{2+} deficiencies.

In the area of salinity–mineral nutrition relations, halophytes have received less attention than have glycophytes. Nevertheless some halophytes, despite their remarkable ability to absorb nutrients selectively from solutions dominated by Na^- and Cl^-, may also exhibit symptoms of mineral imbalances and disorders.

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