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Mineral Nutrient Acquisition and Response by Plants Grown in Saline Environments

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INTRODUCTION

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 nonsaline 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. This is not surprising since under saline conditions, Na^+ and/or Cl^- often exceeds macronutrient concentrations by one or two orders of magnitude and even more in the case of micronutrients. Halophytes. native to saline environments, may also show symptoms of nutrient imbalance despite their remarkable ability to absorb nutrients selectively from soil solutions dominated by Na^+ and Cl-.

Nutrient imbalance may result from the effect of salinity on nutrient availability, uptake, 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.

Nutrient availability and uptake by plants grown in saline environments 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, and (3) numerous environmental factors. Despite these well-known factors, edaphology remains a relatively unexploited resource among biotechnologists in the development of salt-tolerant crops **(1.2).**

Plants vary not only in the rate at which they absorb an available nutrient element, but also **in the manner by which they spatially distribute the clement within the plant. These**

differences occur on all scales (e.g., cellular, organ, and whole plant) and at both the intra- and inter-specific levels.

In the absence of salinity, plant growth response in relation to the concentration of an essential nutrient element in the root media is often described by the function illustrated in Figure I. This relationship is a modification of the "generalized dose-response curve" illustrated by Berry and Wallace (3). Plant growth, usually expressed as absolute or relative biomass, is suboptimal when the concentration or activity of the essential nutrient element is less than A and optimal when the concentration is between **A** and **B.** Nutrient concentrations that exceed **B** may inhibit growth as a result of either a toxicity or a nutrient-induced deficiency.

A substantial body of information in the literature indicates that the plant may not exhibit the same response function under saline conditions as under nonsaline conditions. In some cases the optimal range may be widened 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 the environmental condition. In most studies, salinity (either concentration or composition) is a major variable and the experiment may have only a few treatments that vary in nutrient concentration. Therefore, most reported studies present insufficient data under saline and nonsaline conditions to develop response functions similar to Figure *1.* *Nevertheless,* many studies demonstrated that an optimal concentration or activity of a particular nutrient element in nonsaline conditions may be deficient, or in some cases excessive, under saline conditions.

INTERPRETATION OF SALINITY AND NUTRIENT INTERACTIONS

Salinity and mineral nutrient interaction studies are conducted in the laboratory, in the greenhouse, and in the field depending upon the agronomic or physiological objectives. In each case, at least two factors can operate simultaneously to limit growth and develop-
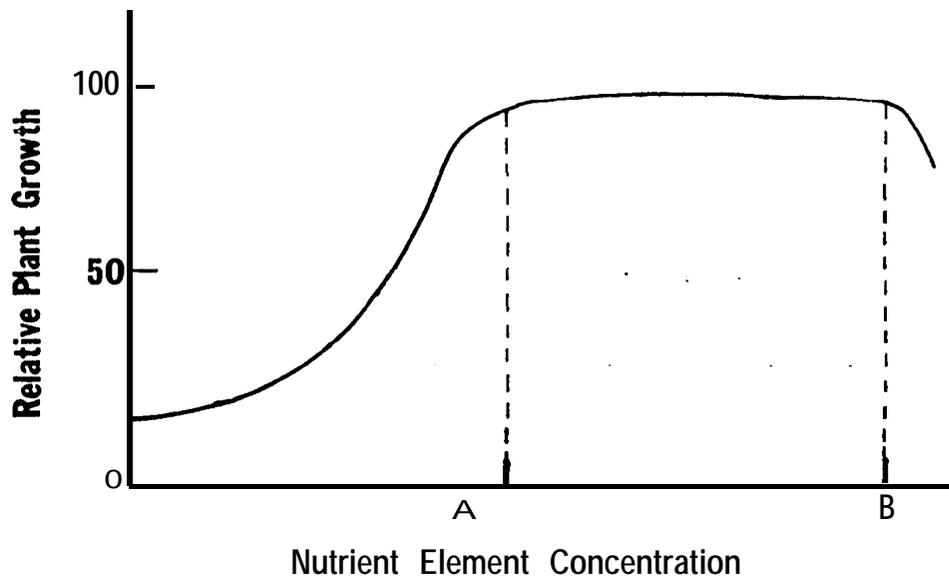

Figure I   **Relative growth of plants in relation to a wide range of concentrations of an essential nutrient element.**

ment: the presence of salinity and the imbalance of a particular nutrient element. The "salt tolerance" of a crop, as defined by Mans and Hoffman (4), may vary depending upon whether salinity or nutrition is the factor more limiting to growth. Bernstein et al. (5) defined three different types of idealized salinity and nutrition interactions that could occur: (I) no effect on salt tolerance, (2) increased salt tolerance, and (3) decreased salt tolerance. In contrast to the definition of Bernstein et al. (5) as presented by Maas (6). 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. Generally. plant growth is promoted more if the most limiting factor is relieved rather than the less limiting factor. For 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 under nonsaline conditions than under saline conditions. This contribution by Bernstein et al. (5) is extremely valuable, and these salinity and nutrient interaction functions can be useful, if used properly. in interpreting data from experiments conducted by others.

Bernstein et al. (5) concluded that the effects of salinity and nutrition on grains and several vegetables are independent and additive when stresses imposed upon them by nutrient deficiency and salinity are moderate When either of these factors severely limits growth, the other has little influence on yield. A decade later, the work of Okusanya and **Ungar** (7) with two halophytcs and a glycophyte gave results that support Bernstein's salinity and fertility interaction model. In the study by Okusanya and Ungar (7), 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 not improve the growth of the glycophyte under saline conditions, presumably because salinity was severely growth limiting.

It should be made clear, however, that the salinity and fertility interactions described by Bernstein et al. (5) are idealized and can therefore be misleading if used improperly. These investigators 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 nonlimiting to severely limiting levels. In many experiments. the nutrient concentration is the most limiting factor in nonsaline or low-salinity conditions, yet when the identical concentration is present in a highly saline environment, salinity is the limiting factor. This point was emphasized by Champagnol (8) 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. Otherwise, it can be concluded by reviewing the salinity and nutrition literature that many more contradictions exist than is in fact the case. Much of the data in the literature that describe salinity $\times$ N or salinity **X** P response functions can be reanalyzed by examining the interactions under low, moderate, and high salinity levels. In many cases, a response function similar to that illustrated in Figure 3 is obtained. Under low-salinity stress, nutrient deficiency limits plant growth more than salinity and a positive (+) interaction or increased salt tolerance response occurs. Under moderate salinity, nutrient deficiency and salinity stress may equally limit plant growth and no interaction (0) occurs. Under high-salinity conditions, salinity limits growth more than nutrient deficiency. In fact, plant performance would always exhibit a negative (-) interaction or a "decreased salt tolerance" (Figure 2c) response if a nutrient element was limiting growth under nonsaline conditions and the upper salinity treatment was lethal or
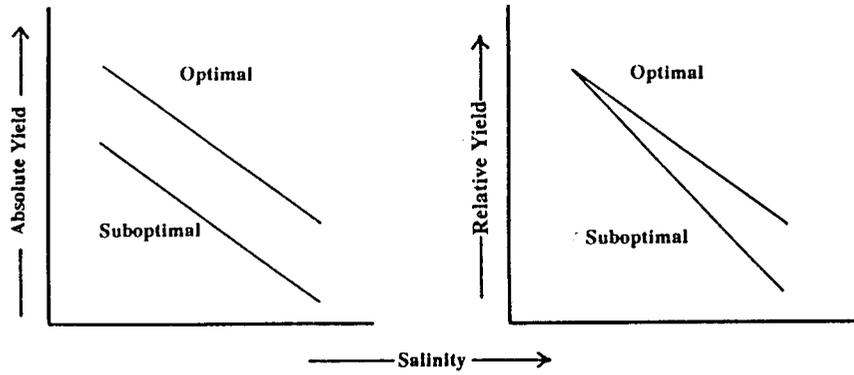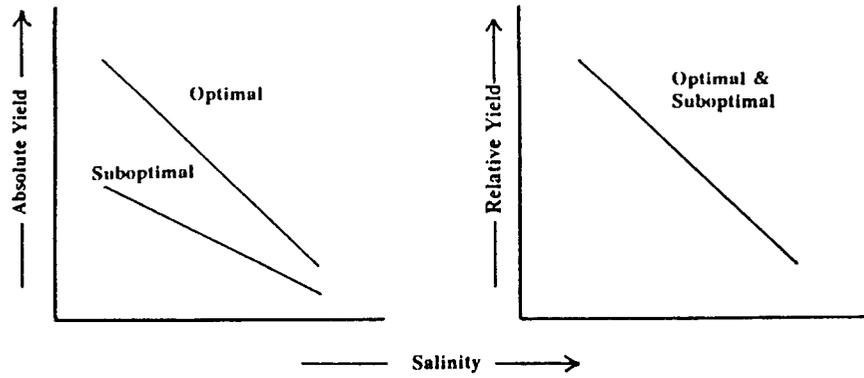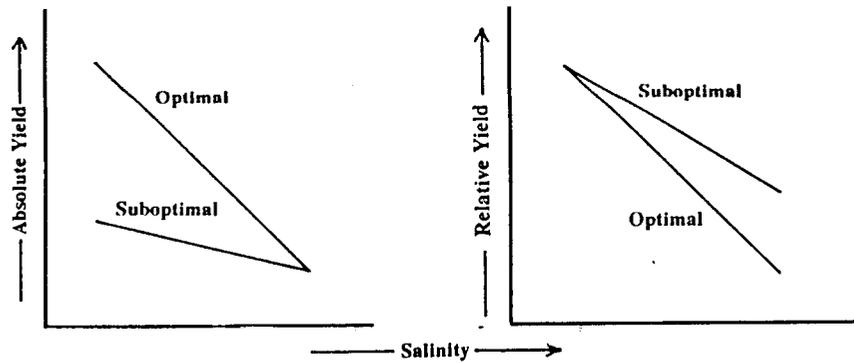
Figure 2 Types of growth responses a plant can exhibit under variable salinity as the nutrient status within the substrate increases from suboptimal to optimal levels. (a) Salt tolerance increased by optimizing plant nutrient status. (b) Salt tolerance unaffected by optimizing plant nutrient status. (c) Salt tolerance decreased by optimizing plant nutrient status.
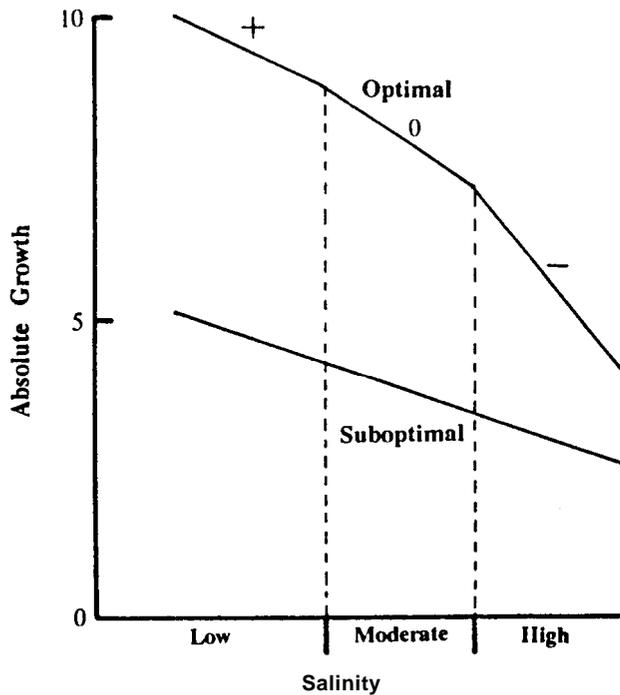
Figure 3 Influence of low, moderate, and high levels of salinity at suboptimal and optimal levels of nutrient supply on plant growth. +, 0, and -: increase, no effect, and decrease in plant tolerance to salinity, respectively.

severely growth limiting. In this case, only plants grown in nonsaline environments would respond to a nutrient addition.

In light of this discussion 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., References 9-1 2) have suggested.

SOIL AND 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 the results obtained in experiments conducted in the field and in solution cultures (9). 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 are very different from those found in soil solutions and root development is entirely different from that in soils. It is obvious 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 they have advanced our understanding of plant salt tolerance and of the physiological mechanisms responsible for nutrient uptake and discrimination.

The remaining portion of this chapter is directed toward plant performance and acquisition of the major nutrient elements (N, P, K^+, Ca^{2+}, and Mg^{2+}) and micronutrient elements in saline environments. This review includes references to both soil and solution culture studies. The emphasis is placed on glycophytes, since most work has been conducted on this group of plants. Discussion on halophytes is included when appropriate and when information is available.

NITROGEN

In most soils, saline or nonsaline, N is usually the most growth-limiting plant nutrient. Consequently, the 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 and N interaction studies were conducted on soils deficient in N. Therefore, additions of N improved growth and/or yield of barley (13). bean (14-16), carrots, cowpea, tomato, corn, clover, beans, millet, and vetch (17), coastal Bermuda grass (18), corn and cotton (19), corn and millet (20), tomato (21), spinach (22), and wheat and rice (23) 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 Figure 2c). On the other hand, only a few studies showed an increase in crop yield under saline conditions when N was applied above a level considered optimal under nonsaline conditions (24,25). In this case, additional N in fact increnscd the salt tolerance of millet and clover. Selassie and Wagenet (26) also reported that the salt tolerance of well-watered corn may have been increased with urea additions up to 375 kg/ha to a soil initially supplied with sufficient N. This practice is not necessarily practical, however, and would most likely be undesirable from both economical and environmental perspectives.

Despite the-majority of evidence indicating that N applied to saline soils above a level considered optimal under nonsaline 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 (27-30). This is not surprising since with few exceptions (31), an increase in Cl- uptake and accumulation is accompanied by a decrease in shoot nitrate concentration. Examples of this effect are also found in barley (32-35), cotton (36), tomato (37), tomato and melon (38), and wheat (39,40). Aslam et al. (32) 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. (41) 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, and total soluble protein) or were not greatly reduced (e.g., total amino acid content). These results argue against N deficiency *per se* as a mechanism of salt injury. This conclusion is also supported by Munns and Termaat (42). In their review, these investigators suggested that although NaCl-treated plants may contain less N than nonstressed plants, there is no strong evidence that this effect is growth limiting.

In contrast to the effect of Cl- on NO_3^- uptake, reported data indicate that increased NO_3^- in the substrate decreased Cl- uptake and accumulation (5,37,38,43).

Although Cl- salts were primarily responsible for reduced NO_3^- uptake by plants, NO_3^- reduction in plants was not affected by salinity in studies with barley seedlings (32). The stimulation of nitrate reductase activity promoted NO_3^- reduction and its

subsequent assimilation into protein. Salinity also stimulated nitrate reductase activity in peanut (44). However, when NaCl in the substrate was at stressful concentrations, incorporation of labeled NH_4NO_3 into protein was impaired in barley leaves (45). Salinity decreased the nitrate reductase activity in tomato and cucumber (46) and sorghum (47). Reduction in nitrate reductase activity in wheat plants grown for several weeks in saline cultures was attributed to inhibition of NO_3^- uptake by Cl^- (48).

The form in which N is supplied to salt-stressed plants may be important (43,49), although the form of N did not influence the yield of moderately salt-stressed wheat (50). Lewis et al. (49) found that NH_4^+-fed maize and wheat plants were more sensitive to salinity than NO_3^--fed plants grown in solution cultures. Similar responses were found in melon (5 1). 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^+ (49). In addition, Martinez and Cerda (43) found that Cl^- uptake was enhanced in cucumber when half the NO_3^- in the solution was replaced by NH_4^+. 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 (51). As the NH_4^+/NO_3^- ratio was increased, plants accumulated more Na^+ and Cl^- and less Ca^{2+} and K^+ in their leaves. Based on the results of their nutrient solution experiments, Leidi et al. (52) suggested that NO_3^- is a better N source than NH_4^+ for wheat grown in salt-affected areas. This conclusion was supported by Silberbush and Lips (53,54), who reported that the mean grain weight of wheat grown in sand cultures was negatively correlated with the NH_4^+/NO_3^- ratio. The results of salinity and N source studies conducted in hydroponic or sand cultures, cited earlier, contrast markedly with those in which plants were grown in soil. Shaviv et al. (55) found that wheat grown in soil salinized with NaCl was more tolerant in terms of grain yield under a combination of NH_4^+ and NO_3^-. This is a classic example of how plant nutritional experiments conducted in solution cultures alone may lead to poor fertilizer recommendations in the field.

Halophytes grown in highly saline, N-deficient environments and glycophytes grown in mildly saline, N-deficient environments respond similarly to added N (7,56-59). Skeffington and Jeffrey (58) found that N additions increased the growth of *Plantago maritima* L. even when grown in seawater. Furthermore, N additions increased plant survivability. Okusanya and Ungar (7) found that the poor growth of two *Spergularia* species grown in 50% seawater was improved by $Ca(NO_3)_2$ additions. Naidoo (57) studied the interactive effects of N and NaCl salinity on young mangroves *[Avicennia marina* (Forsk.) Vierh]. The N was supplied as NH_4^+ rather than NO_3^- to simulate the saturated, and thus anaerobic, environments typical of the natural habitat of mangroves. Therefore, nitrate reduction is prominent and most plant-available N is in the NH_4^+ form. Naidoo (57) found that increased salinity decreased N and K^+ in tissues. The decrease in tissue N is probably caused by NH_4^+/Na^+ competition, since Bradley and Morris (60) found that sea salt salinity reduced the kinetics of NH_4^+ uptake in *Spartinu alterni'oru* Lois. Furthermore, as NH_4^+ N increased from 1.4 to 14 mg L^{-1}, shoot growth increased in the 100 and 300 mM NaCl treatments 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, if the response was characterized over the entire range of salinity.

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. (61) suggested that salt glands, by selective removal of Na^+ and Cl^- from the leaves of *A. marina* (Forsk.) Vierh., 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 phosphorus (P) nutrition of plants is perhaps as complex or more confusing than that between salinity and N. The interaction is highly dependent upon the plant species (or cultivar), plant developmental age (62), 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 (8) 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. (5). After analyzing studies with barley, carrot, clover, maize, millet, sorghum, sugar beet, tomato, vetch, and wheat, Champagnol (8) concluded that added P 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 and nutrient interactions introduced by Bernstein et al. (5) can be extremely misleading. It is therefore important that the model be used only when specific salinity levels are identified. This approach was used to a limited extent by Peters (63). 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, Peters (63) 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 (8) is that P additions to P-deficient soils are beneficial provided 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. (64) 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 weight. 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 (8). In many cases, salinity decreased the P concentration in plant tissue (65); in others salinity increased P 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(8) concluded that it is unlikely that Cl- and $H_2PO_4^-$ ions are competitive in terms of plant uptake. However, Papadopoulos and Rendig (21) concluded that Cl- may have suppressed P uptake and accumulation in tomato shoots. Zhukovskaya (62) 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 (64).

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 P ***con***-centrations 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 (65). In many cases, tissue P concentration was reduced between 20 and 50%, yet there was no evidence of P deficiency in the crops. When plants are P deficient, they may be more sensitive to salinity. Gibson (66) found that P-deficient wheat plants were more sensitive to salinity than those with adequate P and that deficient plants had a lower cellular tolerance for the accumulated ion.

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, U.S. Salinity Laboratory, 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. Phosphate concentrations in solution cultures are often orders of magnitude higher than those in soil solutions (e.g., 2 mM versus *2* μM). Several studies conducted in solution cultures have shown that P concentrations that are optimal in nonsaline solutions may adversely affect growth or be toxic to corn (5,67), lupin (68), sesame (69). and certain soybean cultivars (70) when grown in saline solutions. This is evidence that the optimal P range (A to B in Figure 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 (71) and is caused by a salinity-enhanced uptake rate of P by roots (72).

Certain soybean cultivars are particularly sensitive to salinity in the presence of 0.2 mM P (70), which is only 40% of that in half-strength Hoagland's solution (73). It is likely that susceptible cultivars would be ranked P sensitive as defined by Howell and Bernard (74). In the experiments conducted by Grattan and Maas (70), three of the soybeans tested were ranked for P tolerance. The two that were ranked P tolerant did not exhibit the salinity and 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 the leaf tissue (i.e., 600-900 mmol kg-' dry weight) and even higher concentrations in the root tissue (i.e., 1000-1400 mmol kg-') when substrate P was above some threshold concentration (i.e., concentration B in Figure 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 those for sensitive soybean cultivars. For sensitive soybean cultivars, threshold P concentrations were less than 0.12 mM but above 0.02 mM.

These studies with soybean demonstrate a unique salinity-induced nutritional disorder. Direct **ion interactions play a minor role.** Excessive P accumulates in sensitive cultivars regardless of the Ca^{2+}/Na^+ ratio (75) and is dependent upon the ionic strength or osmotic potential of the solution regardless of the types of salts used. Combinations of

$NaCl + CaCl_2$, $KCl + CaCl_2$, or $NaNO_3 + Ca(NO_3)_2$ all produced similar effects (76). 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, that these adverse interactions observed with corn, sesame, lupin, and soybean 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 or uncontrolled P uptake despite a decrease in the activity of P as a result of the presence of salinity?

Phosphate additions to halophytes grown in highly saline environments have also resulted in increased plant growth. Okusanya and Fawole (77) showed that phosphate stimulated the growth of *Lavatera arborea* L. much more at *40* and 50% strength seawater than under nonsaline conditions. The magnitude of this effect may be partly due 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 were 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 L. *arborea* L.

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. In some vermiculitic soils, applications of K as high as 700 kg ha^{-1} were ineffective at correcting visually obvious symptoms in K-deficient cotton (78). 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^+, even though the degree of selectivity can vary quite drastically among species (79). This is particularly important in saline-sodic and sodic environments, in which concentrations of Na^+ in the soil solution are orders of magnitude higher than those of K^+. The high K^+/Na^+ selectivity within plants is maintained, provided that the calcium status in the root is adequate (80-83) and the roots have a sufficient supply of O_2 (84).

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 (12) reported the data of Bower and Wadleigh (85) as the fraction of monovalent cations [Na(Na + K) or K(Na + K)] in the exchange complex versus that within the roots of bean and beet. Kafkafi (12) 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 (86) 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. Marshner (87) 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 with crop species in group D (e.g., maize, bean, and lettuce) no substitutions of K^+ is possible.

Rice has been classified as a group C crop when only a minor substitution of K^+ by Na^+ is possible and Na^+ has no specific effect on growth, unlike those crops in groups A and B (87). However, the addition of 17 mM NaCl to solution cultures low in available K^+ improved vegetative growth and increased panicle yield (88). 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 (88). 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 (89). 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 follows that K^+ accumulation by the root is reduced if the exchangeable sodium percentage (ESP) on the exchange phase is increased. This effect was observed in bean and beet (85).

Numerous studies have shown that the K^+ concentration in plant tissue is reduced as the Na^+ salinity or the Na^+/Ca^{2+} ratio in the root media is increased (e.g., References 7,82,83,90, and 91). 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 (9 I) found that barley plants exposed to Na_2SO_4 salinity contained only one-third the concentration of K^+ in their shoots compared to those grown in nonsalinized solutions.

Haiophytes, 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. Excised leaf tissue of the mangrove, *A. marina* (Forsk.) Vierh, was highly selective for K^+ over Na^+ (92), and *Hordeum jubatum* L. was found to selectively transport K^+ to the shoot against a strong external concentration gradient of Na^+ (93). Nevertheless, increased NaCl salinity decreased shoot K^+ in the same mangrove species, even though there was no effect on root K^+ (57). In contrast, Clough (94) found no differences in leaf or stem K^+ in *A. marina* when plants were grown in different dilutions of seawater. The author noted, however, that the K^+ concentration in the media increased ninefold as the percentage of seawater increased from 0 to 100. Bail et al. (95) concluded that NaCl salinity produced a salinity-induced K^+ deficiency in *A. marina* (Forsk.) Vierh. by reducing the atrazine binding sites in isolated thyiakoids. 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 (96) found that the wild tomato species *(Lycopersicon cheesmanii* ssp. *minor* (Hook.) C. H. Mull.) 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* Mill.) showed the opposite behavior; it could tolerate K^+ but not Na^+ at the same concentration. In regard to halophytes, the adverse effects of high K^+/Na^+ at high total salt concentrations have been observed in *Atriplex amnicola, Atriplex inflata, Atriplex nummularia* Lindl., *Suaeda maritima* (L.) Dum., and *Vigna radiata (97).*

Despite the overwhelming amount of data that shows reduced uptake and translocation of K^+ by plants grown in high-Na+ substrates, there are few data that show that the addition of K^+ to sodium-dominated soils improved plant growth or yield. Bernstein et al. (5) found that increasing solution K^+ from 0.4 to 2 mM did not affect leaf K^+ or yield of corn. Bar-Tal et al. (98) found 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 fertilization did not reduce the deleterious effects of salinity. Using solution cultures, Muhammed et al. (99) 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. (100) 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. Under field conditions, soil solution K^+ remains relatively low even after fertilizer additions of K^+. Therefore, it is difficult to imagine many situations in which reasonable amounts of K^+ added to the soil would completely correct Na+-induced K^+ deficiencies in plants suffering from this disorder.

CALCIUM

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 (101), stabilize cell wall structures, regulate ion transport, and control ion-exchange behavior as well as cell wall enzyme activities (102). 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+} (81,103-106). Solomon et al. (107) observed abnormal root morphology and anatomy of pea (Pisum *sativum* L.) 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+} (108). Sodium-induced Ca^{2+} deficiencies have notorious growth-distorting effects on developing leaves, as illustrated in several grass species grown in solution cultures (109-l 11).

The presence of Ca^{2+} as the dominant cation in agricultural soils generally ensures that the absolute Ca^{2+} level is not a primary growth-limiting factor. As salinity increases, the requirements of plants for Ca^{2+} increases (I 12). In saline soils, 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 increases in 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 (91,113-l 15). Therefore, in reference to Figure 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 deen 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 (116,117). In the Solonetzic soils of the Canadian prairie, ion imbalances result from high Na^+ and low Ca^{2+} together with predominant 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 (118). The critical Ca^{2+} requirement for the optimum rate of extension of cotton root has been related to the molar Ca^{2+}/TC ratio (119). Later, the Ca^{2+}/TC ratio, expressed in terms of ion activity, was

considered a more accurate measure of Ca^{2+} availability (120-122). However, it seems preferable to distinguish specific ion competition, for example, 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 (91). Carter and Webster (123) 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 mM kg-' dry weight) and alfalfa (250 mM kg^{-1} dry weight) corresponded to a Ca^{2+}/TC ratio of 0.10 in the soil extract.

Although NaCl salinity reduced shoot Ca concentration in barley, this decrease was not due to reduced influx of Ca^{2+} into the roots by the salinizing salts (124). Lynch and Lauchli (124) proposed that sodium may inhibit the radial movement of Ca^{2+} from the external solution to the root xylem by screening of cation-exchange sites in the apoplast. Cramer et al. (90,125) 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 (126).

Nutritional imbalances in salt-stressed cereals have been studied in isosmotic nutrient solutions salinized with various molar ratios of Na^+ and Ca^{2+}. This investigation included corn (1 l1), rice (127), and sorghum (1 l0), 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 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 corn.

In a comparative study of a cultivated barley and a wild barley variety that exhibits higher salt tolerance, the wild species was able to maintain higher tissue concentrations of calcium and was more effective at compartmentalizing Na^+ in the root rather than the shoot (128). This difference between barley species may partly explain why increasing the $Ca^{2+}/(Ca^{2+} + Mg^{2+} + Na^+)$ ratio from 0.02 to 0.09 in the solution culture benefited only the cultivated species. Wild barley (H. *jubatum* L.) populations also differ in their response to salinity. Wang et al. (129) identified three ecotypes, two of which were more tolerant of magnesium-sulfate salinity and high Na^+ than the third. The investigators attributed the enhanced growth of the tolerant ecotypes to their superior Ca^{2+} use efficiency and their ability to restrict Na^+ and Mg^{2+} translocation to the leaves.

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 (110) 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 (130), and this diagnosis was confirmed by mineral analysis. Yeo and Flowers (13 1) reported that the elite breeding line (IR 2 153) 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 (127). Ca^{2+} deficiency symptoms were observed at OP -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 (127). The shoot and root growth of the rice cultivar KS282 was significantly influenced by external Na^+/Ca^{2+} (99). Rolling and bleaching of the young leaves occurred when the Na^+/Ca^{2+} ratio exceeded 100. Muhammed et al. (99) also attributed differences in root growth to an interaction between Na^+/Ca^{2+} and Na^+/K^+ ratios in the root media. Norlyn and Epstein (132) 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; the other lines showed no effect of added Ca^{2+}.Kingsbury and Epstein (133) 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 (99,110) 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, and 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 (87,117) and artichokes (134).

Increased root permeability caused by a reduction in the availability of external Ca^{2+} may lead to increased Cl^- uptake. Elevated internal Cl^- concentrations have been associated with decreased shoot growth in several species, including cowpea (135), tobacco (136), pigeon pea (83), and Leucaena leucocephala (105,106).

Maintaining an adequate supply of Ca^{2+} in the soil solution is an important factor in controlling the severity of specific ion toxicities (137). This is particularly important for tree and vine crops, which are more prone to Na^+ and Cl^- injury than most annual crops. In citrus, calcium was found to be effective at reducing the transport of both Na^+ and Cl^- from the roots to leaves, thereby reducing foliar injury (138-140).

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 Reference 141), 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+} (87). Thus, high concentrations of substrate Ca^{2+} usually result in increased leaf Ca along with a marked reduction in leaf Mg (142). Increased concentration of $CaSO_4$ in the nutrient solution decreased Mg^{2+} in roots, stems, and leaves of L. *leucocephala* (106). Calcium-induced Mg^{2+} deficiency has been observed in sesame (143), and Carter et al. (118)

found that barley growth was reduced as the Mg^{2+}/Ca^{2+} ratio increased above 10. 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 (144). Excessive leaf Ca concentrations may interfere with CO_2 fixation by inhibition of stroma enzymes, particularly those that are Mg^{2+} activated (145).

For plants grown in seawater or dilutions of seawater, it is possible that nutrient disorders could develop because of the high Mg^{2+}/Ca^{2+} ratio. In most seawater compositions, Mg^{2+}/Ca^{2+} is 5:1 on a molar basis. It has been known for over 30 years that solutions with a Mg^{2+}/Ca^{2+} ratio greater than 1 reduce the growth of corn and soybean (146). In a more recent study, Mg salts reduced the root growth of eucalyptus more than Na salts (147). Reduced root growth was associated with low Ca concentrations in the root.

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. Consequently, the relationship between salinity and trace element nutrition is complex (148). In saline and sodic soils, the solubility of micronutrients (e.g., Cu, Fe, Mn, and Zn) is particularly low and plants grown in these soils often experience deficiencies in these elements (149). Nevertheless, 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 (148,150), bean (15 1), soybean, squash, tomato (152), and rice grain (153) but to decrease in corn (154) and mesquite (155). Salinity increased the manganese (Mn) concentration in the shoots of barley (148,150), rice (153), sugar beet (156), and tomato (152) but decreased its concentration in the shoots of barley (cv. CM72)(157), squash (152), pea (158), and corn (154). In the study with sugar beet (156), $NaCl-CaCl_2$ additions increased Mn in the saturated soil extract. Other investigators did not find an effect of salinity on shoot Mn, but found that increasing the sodicity in soil-grown maize had a significant reduction in shoot concentration (159).

Although differences were found in the literature regarding the effect of salinity on shoot Mn concentration in barley, the differences may be explained in part by the composition of the salinizing salts (148). Saline solutions rich in divalent cations increase shoot Mn concentration whereas a saline environment dominated by monovalent cations reduces shoot Mn concentration.

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 (158), tomato, soybean, squash (152), and rice (153) and decreased its concentration in the shoots of barley and corn (150,154). In other investigations with barley, salinity had no effect on shoot Fe concentration, but at low Ca salinity increased root Fe in certain *Hordeum vulgare* L. species (148). This was not observed with foxtail barley *(H. jubatum* L.).

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 L. and *Atriplex*

hortensis L. developed features that are characteristic of transfer ceils, such as bladder-shaped root hairs and thickened convolutions on the outer peripheral cell wall. Further evaluation of these results showed that alternations were not a specific response to salinity but were a symptom of Na^+-induced iron deficiency (160).

SUMMARY

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 nonsaline soils. In contrast, halophytes have evolved mechanisms that permit the selective uptake of nutrients 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 conditions, 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 N and P 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 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 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 nonsaline conditions. In fact, P toxicities can develop in certain salt-stressed plants if the P concentration in the substrate is too high.

An overwhelming amount of evidence from laboratory studies indicates that Na^+-dominated soils or solutions reduce K^+ and Ca^{2+} uptake by plants and/or affect the internal distribution of these elements. Nevertheless, only a few studies show growth increased by additions of these nutrients to sodic or saline-sodic soils. In regard to K^+, this may be partly due to the large quantity of this nutrient element needed to correct the problem. In 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 acquisitions 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 been observed only 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^+ and Cl^-) on nutrient ion acquisition and translocation within the plant. Major ions can influence nutrient absorp-

tion 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.

Salinity can also influence the mineral nutrition of plants by affecting the mobility of a nutrient element within the plant (e.g., sodium's effect on calcium) or by increasing the nutrient requirement for that element in the cells. Furthermore, salinity can cause plants that are deficient in a element to have a lower cellular tolerance for a specific ion.

In the area of salinity-mineral nutrition relations, halophytes have received less attention than 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 imbalance and disorders.

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