CHAPTER 2

LITERATURE SURVEY

This chapter deals with plant response to salinity in the root growth zone. A brief introduction is followed by the general literature which pertains mostly to the influences of NaCl-dominated salinity on plant growth. The influence of salinity on the morphological aspects of growth is first discussed, followed by the physiological responses of the possible sensitivity and tolerance mechanisms.

The general effects of SO_4-salinity are then presented, followed by sections dealing respectively with Na_2SO_4- and $CaSO_4$-salinity.

Apart from salt concentration and composition, the salt tolerance/sensitivity of plants is dependent on many other factors; these are discussed under the section dealing with environmental and plant factors.

Crop salt tolerance has been of commercial importance for many decades, but with the increasing use of marginal soil and poor quality water for agriculture, it has gained importance. The following section thus deals with the evaluation of the salt tolerance of crops, the criteria and parameters used and some yield response functions available to predict growth and yield of crops under saline conditions.

The chapter concludes with the general trends of salt tolerance found for the agronomic groups investigated in this study, namely cereal and forage crops.

2.1 INTRODUCTION

The agricultural productivity of a crop can be limited by excessive concentrations of soluble salts in the growth medium; this is more pronounced in arid and semi-arid regions or where low quality water is used for irrigation. One of the primary options available to ensure agricultural productivity under such conditions is the choice of suitably tolerant crops or

cultivars. It must, however, be emphasized that using such crops will have only a temporary beneficial effect, economically, and will not prevent the further degradation of the soil. The only proven way to overcome salinity is by appropriate water management and drainage (Richards, 1995).

'Salt tolerance' has generally been defined as a plant's capacity to endure the effects of excess salts in the root growth medium (Maas, 1990). Agriculturally these 'effects' are caused by some property or properties of a saline soil solution on the physiological processes in the plant which in turn affects growth and yield. A study of the salt tolerance of crops thus requires a knowledge of the composition of a specific saline water as well as the property or properties of this water that are mainly responsible for limiting the growth of a specific crop and/or cultivar.

In most investigations 'salinity' is equated with NaCl, with or without $CaCl_2$, as the sole salinizing agent. Soil and irrigation waters are made up of diverse amounts of various salts. The major ions present are chloride, sulphate and bicarbonate salts of sodium, calcium and magnesium (Bernstein, 1964, 1974). The proportions can vary widely but the concentration of some ions, for example of Na and Cl, can exceed those of essential nutrients by many orders (Epstein & Rains, 1987). The most common type of salinities are nevertheless that of NaCl and Na_2SO_4 sometimes together with Mg salts (Poljakoff-Mayber & Lerner, 1994). As a result studies have tended to concentrate on these types of salinities.

The current investigation is concerned mainly with the use of $CaSO_4$ waters for the irrigation of crops. Salinity studies with sulphates have mostly focussed on the effect of Na_2SO_4 compared to the effect of NaCl. Very little has, however, been published on the tolerance of plants to $CaSO_4$-dominated saline irrigation waters.

The following discussion will first focus on the general literature of salinity effects in plants. This information is based mostly on studies where NaCl was the main salinizing agent. This will be followed by a discussion of sulphate salinity.

2.2 GENERAL EFFECTS OF SALINITY ON PLANT GROWTH (MOSTLY NACL)

2.2.1 GROWTH RESPONSES

Plants differ in their ability to grow under saline conditions. Greenway & Munns (1980) suggested four groups of plant species according to their growth under saline conditions. They are halophytes, where growth is optimal under sodic and/or saline conditions; a few crop species termed halophylics, where growth is slightly stimulated by low salinity levels and two groups which are non-halophytes (glycophytes) that range from moderately salt-tolerant to salt-sensitive. Most crop species fall under the last two groups which are, however, not clearly defined.

Although salinity affects plants physiologically in many different ways, injury is not readily seen morphologically, except at extreme salt concentrations. The most general effect is a reduction in growth and growth rate. Plants that are salt-sensitive or moderately tolerant show a progressive decline in growth and yield as salinity levels increase (Bernstein, 1964, 1974).

Plant parts are not all equally affected: shoot growth is usually influenced more than root growth with a concomitant decrease in the shoot to root ratio. The leaf to stem ratio is also often affected, which could be important when crops are used for forage (Maas & Hoffman, 1977).

Leaf growth

The initial growth response of a non-halophyte to salinity is that its leaves grow more slowly (Munns & Thermaat, 1986). With low or moderate salinity levels leaves do not necessarily show specific symptoms such as scorching or chlorosis but can be smaller and of a darker green or bluish-green colour when compared to those of plants growing under optimal conditions. Marginal chlorosis, necrosis (leaf burn) and defoliation occur mostly in woody and in some herbaceous species with NaCl salinity; this is mostly due to toxic accumulation of Na and/or Cl (if Na > 0,25 and Cl > 0,5 % dry mass) (Bernstein, 1964). Leaf analyses have shown Cl-toxicity to be the major cause. These effects start at the tips or margins of the leaves due to death of the tissues. The affected parts become brownish and are sharply distinguished from the healthy part of the leaf, which usually retains its normal colour. The more salt

accumulated, the bigger the leaf area affected. In citrus and some shrubs a general bronzing of the leaves, followed by leaf drop, may also occur, without leaf burn developing. Leaf burn can, however, also be caused by excess boron which sometimes occurs in saline waters (Bernstein, 1964; Maas, 1986).

Most herbaceous plants do not develop such leaf injury symptoms, even though Na and Cl accumulation can be as high as that which causes injury to woody species. Vegetable, forage and field crops often accumulate these elements up to 5 % and sometimes 10 % of their leaf dry mass without showing leaf injury symptoms (Bernstein, 1974). Leaf injury under saline conditions can also be caused by nutritional imbalances leading to specific nutrient-deficiency symptoms.

In glycophytes *leaf area* is usually decreased by any significant increase in salinity, while for halophytes this will depend on the relationship between the external salinity and the growth optimum; above this optimum halophytes can be expected to respond similarly to glycophytes. In the case of natrophylic species, Na can stimulate growth mainly by its positive effect on cell expansion and water balance. With halophytes the leaf area may be increased, but not necessarily transpiration as the number of stomata per unit also decreases with succulence (Marschner, 1986). In sugar-beet, a tolerant crop, Na increased the leaf area, succulence and the number of stomata per unit leaf area but the chlorophyll content was less (Marschner, 1986).

Changes in leaf area can influence the overall water loss of the plant. The rate of water loss may also be decreased by anatomical and morphological properties or changes in the plant. Leaf surface properties such as hairs (which impede vapour exchange), succulence (which generally reduces the number of stomata per unit area) and the properties of the cuticle, may all contribute in reducing the rate of water movement through the plant and consequently also the accumulation of salts (Ahmad & Wainwright, 1976; Hajibagheri, Hall & Flowers, 1983).

Leaf thickness and succulence (water content per unit leaf area) have been observed as a typical morphological response to high substrate salinity and water stress and is usually observed in salt-tolerant species growing in saline substrates (Jennings, 1968). It is also found in most dicotyledons as an adaptation to high substrate salinity both in salt ‘excluders’ and

'includers' (Longstreth & Nobel, 1979). Succulence can be caused by a decrease in surface area and/or an increase in tissue water content. Apart from salinity, succulence can also be induced by a water deficit and hormone related changes (Marschner, 1986).

Root growth

Generally root growth is affected less by salinity than is shoot growth. At low salinity it may not be influenced or may even show an increase. These observations are, however, mostly based on root dry mass; root length, which is important for nutrient and water uptake, has been shown to be a more sensitive parameter than root dry mass for the influence of salinity on root growth (Shalhevet, Huck & Schroeder, 1995).

At higher concentrations root growth can be inhibited and thus also the capacity for uptake of water and nutrients (Neumann, 1995b). Calcium stimulates and Na inhibits root cell elongation in cotton (Kurth, Cramer, Läuchli & Epstein, 1986). Addition of Ca to the root medium ameliorated salt stress on maize root growth (Cramer, Epstein & Läuchli, 1988), and on peas (Solomon, Gedalovich, Mayer & Poljakoff-Mayber, 1986). The yields of storage roots may, however, be decreased much more than those of fibrous roots (Maas & Hoffman, 1977). The yield and quality of potatoes, however, improved with gypsum amendment under NaCl or Na_2SO_4 saline conditions and the total glycoalkaloids, which are associated with a bitter taste, were decreased (Abdullah & Ahmad, 1982; Bilski, Nelson & Conlon, 1988).

2.2.2 PHYSIOLOGICAL RESPONSES

Physiological responses are twofold: firstly they include mechanisms by which growth is adversely affected (adverse or sensitivity mechanisms); and secondly responses by plants to adapt to saline conditions (mechanisms for salt tolerance).

2.2.2.1 Sensitivity or adverse mechanisms

Sensitivity of plants is due to several properties of salinity that include ionic and osmotic effects as well as nutritional imbalances of which the precise physiological mechanisms are not yet quite clear. The main properties of a saline soil solution that have been found to affect growth adversely are:

- water deficit arising from *the lowered osmotic potential* caused by the high concentration of soluble ions.

- specific ion effects, which include :
  - *toxicity* of mainly Cl and also of Na (especially in Graminaceous species) when taken up in excessive quantities. Sodium toxicity is not as widespread as that of Cl, but unfavourable ratios of Na/Ca, Na/K may disturb inorganic nutrition. High Na can furthermore disturb the Ca-homeostasis of root and leaf cells and therefore the uptake of essential nutrients (Rengel, 1992b). It can also indirectly affect growth by its influence on soil structure and fertility, and the formation of a dense natric B-horizon which can obstruct downward percolation and root growth. A high percentage of exchangeable Mg may also affect soil structure in a similar way as a high exchangeable sodium percentage (ESP) (Driessen & Dudal, 1991); and
  - *nutrient imbalances* where uptake and/or shoot transport is depressed by the lowered activity of nutrient ions, and internal distribution of nutrients and especially Ca is disturbed. This also includes unfavourable ratios of Ca/Mg in the external growth medium.

The earlier belief that it was the actual lack of water that limited growth with a saline root medium, has generally been rejected because plants have been shown to adjust osmotically (Maas & Nieman, 1978). More recent literature suggests that in short-term responses of whole plants to salinity, shoot growth is regulated by the water status of the root, through some "messenger system" to the shoots which could include hormonal substances, for example abscisic acid or other anti-transpirants (Rengel, 1992b).

Osmotic potential or specific ion effects?

From the literature it seems that there are two schools of thought on the relative importance of osmotic potential and/or specific ion effects on growth. Although the toxic influences and nutritional imbalances are recognised, some authors maintain that it is mainly the total salt concentration of the soil solution that causes growth reduction (e.g., Bernstein, 1964, 1974; Maas & Hoffman, 1977; Maas & Nieman, 1978). Evidence connected to the direct toxic influence of some ions or the accumulation of toxic amounts of salts in the leaf tissues, leads

others to attach more importance to growth inhibition through ion toxicity or accumulation (e.g., Maas, 1990; Munns, 1993). It is generally recognized that these adverse effects could simultaneously be responsible for growth reduction, but the relative contribution of the three major constraints to growth inhibition at high substrate salinity is difficult to assess (Marschner, 1995; Jacoby, 1994). However, the opinion that growth reduction is primarily due to the osmotic potential is being reviewed as many nutritional and also membrane related studies indicate other possibilities (Reinhold, Braun, Hassidim & Lerner, 1989; Läuchli & Epstein, 1990; Grattan & Grieve, 1992; Rengel, 1992b). Lowered osmotic potential may also influence cell wall hardening and eventually growth (Neumann, 1995a).

Much effort has been made to understand the primary physiological causes of growth reduction in saline environments. These effects are complex and not fully understood (Shannon, 1997). Munns (1993) reviewed work on turgor, photosynthesis and effects on particular metabolites which directly influence growth and concluded:

- "Although turgor is essential for growth...it does not control growth; the rate of cell wall expansion is controlled by the rheological properties of the cell wall and not directly by turgor." This was confirmed by Neumann (1995a). The decrease in turgor is sensed by a "turgor sensor", probably in the plasma membrane. The sensor emits an error signal that activates biochemical processes necessary for solute accumulation or synthesis. This results in osmotic adaptation and the recovery of the turgor pressure. Neumann (1995a) however, examined many related studies and found that complete osmotic adjustment and turgor maintenance do not sufficiently prevent stress-induced inhibition of growth.

- "Salinity affects carbon assimilation per plant via a smaller leaf area rather than a reduced rate of photosynthesis. Concentrations of sugars often increase with exposure to salinity indicating a blockage in utilization".

- Growth reduction and death are mainly due to eventual accumulation of salts in the vacuole above a concentration that the specific specie or cultivar can tolerate and "the cell dies of salt poisoning or dehydration depending on whether salts build up in the cytoplasm or cell wall."

Furthermore, Neumann (1995a), reviewing the effect of cell wall-hardening on growth, suggests that the long-term growth inhibition of roots, stems and leaves under water stress conditions may involve stress-induced hardening of cell walls which is associated with smaller mature cells. In moderately saline situations cell-wall hardening may negatively affect growth and yield but in terminal survival situations it could be advantageous.

Munns & Termaat (1986) suggested a hypothesis of a biphasic model where the external osmotic potential could be the main growth inhibitory factor for *seedlings* in the first weeks of growth: "This phase of growth reduction is a water stress effect and is regulated by inhibitory signals from the roots." In *the vegetative growth stage* accumulation and/or specific ion effects are increasingly important in the leaves and can eventually lead to the death of the older leaves when the vacuoles can no longer isolate incoming salts. They suggest that varietal differences would only appear in the more mature growth stage because the growth of these varieties reacted similarly to osmotic effects in the early growth stages. Neumann (1997), however, presents evidence for varietal differences to osmotic stress in early growth stages.

This two-stage process bears similarities to the "short" and "long-term" effects suggested by other authors (e.g., Cramer & Bowman, 1991). The duration of the "short-term" differs for the different authors, but there seems to be agreement that later growth stages are affected more by the specific ion effects of salt accumulation and toxicity than by the osmotic potential of the external solution (Munns, 1993). Plant species and cultivars differ in their ability to compartmentalise salts at the cell, tissue and whole plant level and thus in their salt tolerance or sensitivity to accumulation.

Other reviews stress the nutritional effects of salinity (Grattan & Grieve, 1992, 1994) and the almost immediate effect of excess Na on the Ca-homeostasis of root and leaf cells (Rengel, 1992b). Rengel (1992b p.629) suggested that "the Na-related changes of the normal pattern of Ca fluxes at the plasma membrane is the primary signal of salt stress perceived by roots and translated into almost immediate changes of the leaf cell environment, at least together, if not preceding, the osmotic changes". With this in mind the hypothesis of Munns & Termaat (1993) of osmotic potential being the main or only growth inhibitor for seedling growth, and of others on "short-term" effects, needs further investigation.

Nutritional disorders

Salinity disrupts nutrition by (i) decreased activity of nutrient ions (decreased availability), due to the ionic strength of the substrate, regardless of its composition (the optimum concentration of most nutrients in a non-saline growth medium could be deficient in saline conditions) (Grattan & Grieve, 1994), and (ii) interactions due to extreme ratios, of for example, Na/Ca, Na/K, Mg/Ca and Cl/NO_3 that can lead to reduced uptake and disrupted translocation of essential nutrients.

As mentioned above, Na-related salinity can also affect the membrane selectivity and efficiency, and the Ca-homeostasis of root and leaf cells (Reinhold, Braun, Hassidim & Lerner, 1989; Rengel, 1992b; Neumann, 1995a; Yermiyahu, Nir, Ben-Hayyim, Kafkafi & Kinraide, 1997).

Nutritional disorders most commonly found with saline soils are reduced uptake or disturbed internal distribution of K and Ca and Mg/Ca interactions (Marschner, 1995).

The influence of salinity on **K** content pertains mainly to the competitive effects of Na on K uptake, regardless of the anion being Cl or SO_4 (Grattan & Grieve, 1994). Cortical root cells have the selective ability to absorb K in preference to Na but the degree of this selectivity varies among species and cultivars (Grattan & Grieve, 1994). Salt tolerance has in some cases been connected to the selective uptake of K over Na by different species. The correlation between the Na/K ratio in plant tissue and salt tolerance has been found significant enough to be used for selection of salt-tolerant wheat cultivars (Suhayda, Redmann, Harvey & Cipywnyk, 1992; Chippa & Lal, 1995).

Ca and **Mg** deficiency can be caused by competition with other cations simultaneously present in excess concentrations, especially by Na. Ca availability can be estimated more accurately as the molar ratio of Ca to the sum of the major cations, rather than the Ca concentration of the soil solution per se. Generally reduced growth is likely to occur when this ratio falls below 0.10-0.15 but this value could be higher, especially if high Na concentrations are present (Grattan & Grieve, 1992).

Salt tolerance of plants is also related to the ability to maintain adequate tissue levels of Ca during salt stress (Suhayda et al., 1992). This was illustrated with kochia and barley where the greater salt tolerance of kochia was related to the degree of selectivity for Ca uptake (Curtin, Steppuhn & Selles, 1993).

Many studies have shown that the addition of Ca (ranging from 5-20 mmol L^{-1}) to NaCl saline growth mediums can ameliorate salt stress and reverse Ca deficiency effects (e.g., Solomon et al., 1986; Fernandez-Ballester, Cerdá & Martinez, 1997). In an investigation of the role of the anion in Ca amelioration of NaCl-stress it was found that $CaSO_4$ was more effective than $CaCl_2$ for *Phaseolus vulgaris* L (Awada, Campbell, Dudley, Jurinak & Khan, 1995). Ca deficiency can also be a result of SO_4 salinity (see 2.3).

A hypothesis has been put forth by Läuchli (1990) that the protective role of Ca against Na-related salt stress operates primarily at the root plasma membrane where Na displaces Ca. Yermiyahu et al. (1997) related quantitative values of the percentage of negative sites occupied by Ca on the plasma membrane, to salt tolerance/toxicity. They found that a salt resistant melon cultivar needed less Ca for protection than the salt sensitive one and that each had a critical value for the fraction of negative sites bound to Ca.

High Mg as part of the Ca/total ions ratio can be partly or largely responsible for a decrease in Ca uptake. If the ratio of Mg to Ca in the growth medium exceeds 1.0, growth can be negatively influenced (Key, Kurtz & Tucker, 1962; Claassens, 1973; Carter, Webster & Cairns, 1979). On the other hand Mg uptake can be depressed by other cations, especially by high levels of K, Ca, Mn and also by H^+ (Claassens, 1973; Heenen & Campbell, 1981; Marschner, 1995).

Salinity can also affect the **N** and **P** content of plants. Nitrate absorption was inhibited to a lesser degree with excess SO_4 than Cl when these were present at equal osmotic potentials (Aslam, Huffaker and Rains, 1984). Although salinity reduces N accumulation in plants, additional N above that considered optimal for normal conditions has generally not proved to increase growth or yield under saline conditions (Grattan & Grieve, 1992).

Crop species also vary in their ability for **P** uptake under saline conditions (Champagnol, 1979). Decreases in **P** uptake have mostly been found with soil studies (probably due to a reduced activity of the $H_2PO_4^{-1}$ ions in the saline solution) and increases in sand or solution studies (Grattan & Grieve, 1992). In one investigation both Cl and SO_4 salts reduced P uptake in barley and sunflower (Zhukovskaya, 1973), but in a more recent study on barley, added P and increased P-uptake increased the salt tolerance (Al-Karaki, 1997). In a review on P nutrition and salt toxicity it was concluded that the influence of added P on the salt tolerance of a variety of crops depended on the severity of the salinity: salt tolerance was increased at low, not affected at moderate and decreased at high salinities (Champagnol, 1979). Grattan & Grieve (1992), found that the most useful conclusion of Champagnol's review was that "P additions to P deficient soils are beneficial provided that the crop is not experiencing severe salt stress." However, in a study by Awad, Edwards & Campbell (1990), it was found that the P requirement of tomato was increased as NaCl salinity intensified from 10 to 100 mmol L^{-1}.

The influence of salinity on **Fe**, **Mn** and **Cu** concentrations in plants is inconsistent; it varies with species, increasing in some crops and decreasing in others (Grattan & Grieve, 1992). High SO_4 can, however, reduce **Mo** and **Se** uptake and thus growth via N and S nutrition respectively (Stout, Meagher, Pearson & Johnson, 1951; Läuchli, 1993).

The above nutritional disorders are dependent on genetic variability, as species and cultivars can vary widely in their nutrient requirements and ability to absorb specific nutrients. There are, however, only a few studies where fertilization with these nutrients increased growth in sodic-saline conditions. Growth is determined by the most limiting factor, in this case salinity stress or nutritional deficiencies (see Bernstein, Francois & Clark, 1974). The amounts needed for corrective fertilization would probably be too large and not economical, especially in the case of K (Grattan & Grieve, 1992, 1994).

2.2.2.2 Tolerance or adaptation mechanisms

Much work has been done to understand the mechanisms by which plants adapt to high concentrations of salt in the root growth medium. The salt tolerance of plants includes complex anatomical and physiological features which makes the breeding of tolerant cultivars very difficult. However, if the property most limited by salinity stress could be identified, salt

tolerance could hopefully be improved (Shannon, 1997). Understanding these mechanisms is important for the genetic breeding of salt-tolerant plants, but it will not be discussed here in detail (for reviews see Maas & Nieman, 1978; Greenway & Munns, 1980; Cheeseman, 1988; Jacoby, 1994 and Shannon, 1997).

Mechanisms of salt tolerance have been attributed to:

- selective uptake of ions (salt 'exclusion')

- compartmentation at the cell (vacuoles), tissue or organ levels (ion accumulation - 'includers'), where ions are kept away from the salt sensitive metabolic components of the cytoplasm

- osmotic adjustment (osmoregulation) whereby the osmotic potential in the plant is decreased by an increase of inorganic or organic solutes thus recovering water uptake and turgor; turgor loss, which could lead to stomatal closure, a decrease of gas exchange, photosynthesis and energy for metabolic processes, is therefore prevented.

- morphological characteristics such as a smaller leaf area, fewer stomata and thicker cuticles, but these changes can decrease crop yield and quality. The salt content can also be controlled by excretion and leaf drop.

2.3 SULPHATE SALINITY

Sulphur rich environments cause some plants to die while others survive, but generally plants are tolerant to high sulphate concentrations in the growth medium and are usually only affected when SO_4 is in the order of 50 mmol L^{-1} (4800 mg L^{-1}), with symptoms similar to those of salt affected plants (Mengel & Kirkby, 1987). Toxicity is usually caused by the cation associated with the SO_4 ion, either by ionic effects or disturbed Ca nutrition and root membrane functioning (Tabatabai, 1986).

The effect of excess sulphur on plant growth was reviewed by Rennenberg (1984). He concluded that: "Survival in a sulphur rich environment is seldom achieved through the

avoidance of the intake of sulphur. The presence of excess sulphur in the soil or in the air usually results in an intake of excess sulphur into plants. An immediate injury by the excess sulphur taken up, is however, prevented by a series of metabolic processes. Storage of excess sulphur in ... the vacuole, appears to occur in most plants." Sulphate can be translocated in both the xylem and phloem, and can thus be stored in plant parts not directly exposed to the excess. With increasing accumulation of sulphate, an increase of storage glutathione was found, suggesting that with increasing accumulation the reduction of sulphate also increases. The level of glutathione has also been shown to correlate with the adaptation of plants to different stresses (May, Vernoux, Leaver, Van Montagu & Inze, 1998). Sulphate can also be decreased in plants by emission of volatile sulphur compounds. It is thus improbable that excess sulphate per se would influence growth through ion toxicity (Rennenberg, 1984). In this respect citrus is an exception as growth was retarded and interveinal chlorosis occurred in citrus when leaf S-levels exceeded 0.5 % (Haas & Thomas, 1928).

However, in a study with wheat species, it was suggested that the greater negative effect of SO_4 compared to that of Cl salinity could possibly be attributed to the "less effective sequestration or mobility of this ion towards some innocuous centres of plant tissues" (Datta, Kumar, Varma & Angrish, 1995 p.2199). They also observed an interesting phenomenon whereby the presence of high SO_4 in a NaCl growth medium resulted in an increase of the uptake of Na and Cl into the shoot, above that of an equal concentration of only NaCl. Consequently the salt tolerance of the wheat cultivars was also decreased, as salt tolerance in wheat is associated with the exclusion of Cl and to lesser extent of Na from the shoot (Shannon, 1997).

Calcium and Magnesium

Excess SO_4 in the soil solution may, however, have nutritional implications, for example a Ca deficiency where very high SO_4 concentrations are accompanied by low Ca levels (Curtin et al., 1993). On the solonetzic soils of the Canadian prairie nutrient problems arise from high Na and low Ca together with the high SO_4 content (Curtin et al., 1993). Calcium deficiency is also related to the Mg content of the soil; Ca deficiency was found to be severe for barley on the above mentioned soils if the ratio of Mg to Ca exceeded 1.0 or when the Ca to total cations were below 0.15 (Carter et al., 1979).

Ca availability in Na_2SO_4 systems can be influenced by the formation of the $CaSO_4$ ion pair. When the ratio of Ca to other cations is determined in activities (which is a better criterion for plant availability than concentration), the mole fraction of Ca will be less, due to the formation of ion pairs (also applicable for $MgSO_4$). However, in a study where barley and kochia were subjected to high Na_2SO_4 concentrations, the results indicated that at the electrical conductivities (EC_e values) compatible for most glycophytic crops (< 800 mS m^{-1}), Ca-deficiency by SO_4-salinity should not repress growth, except for a limited number of crop species that are inefficient in absorbing or utilizing Ca (Curtin et al., 1993).

Another mechanism of Ca deficiency is by the precipitation of Ca-oxalate in plants. Curtin et al. (1993), observed that with SO_4-salinized plants the oxalate content was higher than with Cl- salinity. This was attributed to the fact that the uptake of SO_4 is slower than that of Cl and that more oxalate was synthesized to compensate for a greater positive charge. Although Ca can become immobilised as Ca-oxalate in the plant, some species (e.g., kochia) has the ability to control the precipitation of Ca-oxalate. Sensitivity to this kind of Ca deficiency may again be species and cultivar dependent.

Molybdenum

High sulphate can also reduce the Mo uptake and/or transport (Stout et al., 1951). Barnard and Fölscher (unpublished data) found that the Mo content of the top growth of wheat doubled in the absence of SO_4; Mo was also diminished by other anions in the order of S >B >P >Cl >NO_3 (Barnard, 1978).

Molybdenum is an essential part of the enzymes nitrogenase and nitrate reductase which are two major enzymes in N metabolism. Nitrogenase catalyzes the fixation of molecular N_2 by bacteria and symbiotic microorganisms, and nitrate reductase catalyzes the biological reduction of nitrate to nitrite. Molybdenum deficiency symptoms can thus be similar to N deficiency, with the exception of necrotic leaf margins, caused by NO_3 accumulation (Maynard, 1979).

Crop species have varying Mo requirements, but generally legumes need two to three times more Mo than non-legumes for the N-fixing nodules (Johnson, 1966), and are thus more prone to Mo deficiency by high levels of SO_4. S-fertilization has depressed growth in legumes

growing on soil with low available Mo due to competition of SO_4 with MoO_4 (Reisenauer, 1963).

Although an essential element for livestock, Mo can be toxic at higher concentrations, especially to ruminants. The critical amount of Mo that animals can tolerate depends on the Cu and SO_4 level as the toxicity of Mo is essentially a deficiency of Cu. This Mo/Cu interaction is strongly influenced by the surrounding sulphate level (Albasal & Pratt, 1989).

Plants can tolerate higher levels of Mo in the tissues than the usual 2 mg kg^{-1} dry mass. Forage crops with a high Mo content can therefore be unfit as fodder. Plant Mo availability is low on acid soils and increases to a maximum near neutrality, whereas Cu availability decreases with increasing pH. Sulphate can, however, reduce molybdate uptake by competition. Thus, although Mo would be more available in the pH range of lime treated acid mine drainage water, a high sulphate content should help to prevent excessive levels in forage crops.

To protect animals from toxicity, a guideline of 10 µg L^{-1} exists for irrigation water. In irrigation waters with high SO_4 (such as in the San Joaquin Valley of California), this guideline can be increased to 50 µg L^{-1} due to the effect of SO_4 on Mo absorption (Albasal and Pratt, 1989).

Selenium

Toxic amounts of Se are often present in association with SO_4 salinity in saline soils of semi-arid and arid areas. Selenium is chemically similar to S and in aerated soils is mostly present as the plant available SeO_4. Selenate competes with SO_4, not only in uptake at the SO_4 binding sites, but also by being incorporated into proteins where it can interfere with N and S metabolism (Läuchli, 1993).

Selenium is mainly found in sedimentary and volcanic deposits. Plant availability depends on soil factors such as clay content and pH. Owing to its retention on clay minerals and iron oxides, uptake is more effective from sandy soils. Se is least soluble at slightly acid to neutral

pH, and plant availability is low on neutral to acid mineral soils with a high Fe and organic matter content due to fixation.

Selenium is an essential micronutrient for animals and humans but has not been proved essential for higher plants, except for some Se-accumulators. In crop species Se is usually present at concentrations less than 1 mg kg^{-1} dry mass, but as little as 2 mg kg^{-1} has affected growth in sunflower (Shrift, 1969). Selenium can be toxic in animal feeds, causing deformity and death to animals. The desirable level in cereals and forages is 0.05-2 mg kg^{-1} dry mass, the contents differing with species. Selenium is toxic to plants when the content is greater than 50 mg kg^{-1} dry mass.

High concentrations of SO_4 in Se containing soil solutions can reduce the Se content of many plant species by competition and by reduced activity of SeO_4 in the saline water. Growth inhibition and Se uptake in tall fescue at comparable concentrations of Na_2SO_4 and NaCl were reduced with the Na_2SO_4-salinity (Wu & Huang, 1991). In the halophyte, purslane, SO_4-salinity inhibited Se-accumulation to a level where it did not present a dietary hazard to humans, but met the requirement as an essential micronutrient (Grieve & Suarez, 1997). Tall fescue, a moderate Se-accumulator, may also be used as a supplement for livestock feeds with deficient Se content (Wu & Huang, 1991).

Finally, SO_4 in irrigation water could also have a positive effect as a nutrient in areas prone to deficiency, for example in the tropical savannahs, on soils with a low capacity for adsorbing SO_4 where high seasonal rainfall could possibly deplete unbuffered soils of S compounds.

2.3.1 SODIUM-SULPHATE SALINITY

In most studies of SO_4-salinity the associated cation has been Na (Magistad, Ayers, Wadleigh & Gauch, 1943; Curtin et al., 1993; Mayland & Robbins, 1993; Datta et al., 1997; Grieve & Suarez, 1997). Generally the growth-suppressing effect is similar to that of a NaCl salt effect (Mengel & Kirkby, 1986; Curtin et al., 1993). Curtin et al. (1993) compared the effect of a $CaCl_2$/NaCl system with that of $CaSO_4/Na_2SO_4$ in barley and kochia, from which they concluded that "response functions generated by the $CaCl_2$/NaCl salinisation probably provide an acceptable measure of the tolerance of most crops to SO_4-salinity." Thus, although

the response to Na_2SO_4 can be either more or less severe than with NaCl, at isosmotic concentrations, the general linear decrease response is the same as that of Maas & Hoffman (1977). Toxicity and/or nutritional imbalances occurring with Na_2SO_4-salinity are mostly caused by the associated Na ion. As mentioned above, however, the increased uptake of Na and Cl in the presence of SO_4 may possibly be a new adverse mechanism of SO_4-salinity (Datta et al., 1995).

NaCl (or other anions) versus Na_2SO_4 salinity effects have been investigated in a number of nutritional and salinity studies. Some of the effects were mentioned in the above general discussion of SO_4-salinity (2.3). At equal osmotic potentials, SO_4-salinity can often suppress growth more than Cl salinity can (Mengel & Kirkby, 1987); however, even at equal osmotic potentials, plants differ in their responses to the composition of a salinized growth medium. Contrasting results have been reported. Early investigators compared the effect of specific anions on salt tolerance on the basis of equal moles or equivalents with similar cations in the nutrient medium. On this basis SO_4 generally decreased growth to a lesser extent than Cl. Magistad and co-workers (1939-1943) were among the first to compare NaCl and Na_2SO_4 salinity at equal osmotic potentials. They found that "for some crops" (beets, carrots and beans) "chlorides and sulphates at equal osmotic concentrations are equally harmful, while with other crops" (lucerne and peaches) "chlorides are more toxic than sulphate at approximately equal osmotic values."(Magistad et al., 1943 p.157). This is probably a reflection of either an osmotic potential or of Na/Cl ionic effects respectively. They go on to say that more equivalents of sulphate are needed to produce a given osmotic potential value which explains "why plants can withstand far greater amounts of sulphate than chloride when compared on a parts per million basis" (Magistad et al., 1943).

On the other hand, in the studies of Datta et al. (1997), four genetically diverse wheat cultivars were all more sensitive (differentially) to Na_2SO_4- than to the NaCl salinity at equal osmotic potentials. Furthermore, in a mixed Na/Cl/SO_4 growth medium the presence of SO_4 resulted in increased Na and Cl concentrations in the shoots, the contents of which agreed with the differences in sensitivity of the cultivars. The cereals, barley and sorghum, were also more sensitive to Na_2SO_4 than to NaCl (Curtin et al., 1993; Boursier & Läuchli, 1990; Marschner, 1995).

Reports for halophytic crops also differ : Na_2SO_4 depressed growth more than NaCl in Chenopodium (Warne, Guy, Rollins & Reid, 1990), while kochia grew better with SO_4 salinity (Curtin et al., 1993). Purslane, a common salt-tolerant plant often used as a food source for humans and animals, was evaluated as a prospective salt-tolerant crop for use with a high SO_4 drainage water in the San Joachin valley of California (Grieve &Suarez, 1997). It responded in a similar way as previously found with Cl salinity (Kumamoto, Scora, Clerx, Matsumura, Layfield & Grieve, 1990).

Sodium chloride may also have a greater effect on membrane integrity or leakage than Na_2SO_4, but comparisons are made difficult because different concentrations are needed to acquire treatments with equal osmotic potentials (Jacoby, 1994).

The above mentioned effects would, however, depend on the sensitivity of a specific crop to toxic ions and/or nutrient imbalances.

From the above it can be seen that Na_2SO_4 salinity can affect growth by mechanisms other than, or complemental to, a low osmotic potential.

2.3.2 CALCIUM-SULPHATE SALINITY

Not many studies have investigated the use of irrigation waters with high Ca and SO_4 content. Generally it is considered beneficial to plant growth as salt buildup is restricted by the low solubility and precipitation of gypsum. Growth can however be affected either directly - by decreases of the osmotic potential, nutritional or specific ion effects of the SO_4 or Ca - or indirectly, by influencing soil and soil solution properties.

Papadopoulos (1986) investigated the growth of the moderately sensitive tomato, eggplant and bell pepper with two naturally occurring $CaSO_4$ waters, one with, and the other without Na and Cl in its composition. Both waters - with the same EC's - decreased the yield and/or quality of these crops, the effect of the 'mixed' water being greater. For more tolerant crops, however, soil solutions saturated with $CaSO_4$ may not be limiting. MacAdam et al. (1997) determined the growth of tall fescue and lucerne with ground waters from a plume of high $CaSO_4$ water in Utah near Salt Lake City. The top growth of tall fescue tended to increase and

that of lucerne increased significantly at "moderate" SO_4 levels of the soil solution (646 mg L^{-1} SO_4).

The type of soil being irrigated may, however, affect the growth response to a gypsiferous water. Papadopoulos (1984, 1986) stressed the fact that on a *sodic* soil it can actually be harmful by increasing the fraction of Na in the soil solution and consequently also the sodium adsorption rate (SAR); Na is released by cation exchange, and Ca removed by the precipitation of gypsum. It is well known that such an increase can affect the permeability of the soil. [Pore clogging from gypsum precipitation has also been reported (McNeal, 1974; Frankel, Hadas & Jury, 1978)]. Du Plessis (1983), however, found that irrigating with lime-treated acid mine drainage water, did not pose a serious problem to soil physical properties when viewed against "published data on soil hydraulic conductivity as affected by sodium and electrolyte concentration."

Gypsum is used to ameliorate sodic soils for the correction of imbalances on the exchange complex and to promote good permeability of the soil. Numerous studies have shown that Ca also ameliorates Na stress on plant growth (Rengel, 1992b); in an investigation of the role of the anion of the Ca salt used for this amelioration with *Phaseolus vulgaris* L., it was concluded that $CaSO_4$ treatments ameliorated Na induced salinity stress more than $CaCl_2$ treatments did (Awada et al., 1995). But, when growing *moderately sensitive* crops (2.5.2), it should be taken into account that when leaching with gypsiferous water, the salinity of the soil solution may increase due to an inevitable salt buildup (Papadopoulos, 1986).

When Ca and SO_4 are added to a *calcareous* soil, the Ca can decrease by the precipitation of $CaCO_3$, with a concurrent increase of SO_4 concentration in the soil solution. The presence of Mg will further increase the gypsum solubility by the formation of a moderately strong $MgSO_4$ ion pair (MacAdam et al., 1997). Depending on the Mg content of the soil and irrigation water, this could also have implications for growth via the Ca/Mg ratio.

In soils such as the gypsisols, with a gypsum content higher than 25 %, the nutrient balance can be disturbed by a lower availability of PO_4, K and Mg; the cation exchange capacity also decreases with increasing gypsum (Driessen & Dudal, 1991). Cereal crops and lucerne can be grown where the gypsum content of the upper 30cm is less than 25 %. Yields may, however

be depressed due to nutrient imbalances and mechanical hindrances. Soils with more than 25 % gypsum will not be suitable for dry land cultivation, but could possibly be productive with irrigation and effective drainage (Driessen & Dudal, 1991).

In a field trial, conducted simultaneously with the present study, the long-term effects of irrigation with a gypsiferous mine water on inter alia the soil properties were investigated. Using a soil water/salt balance/crop growth model to simulate 30 years of irrigation with gypsiferous mine water, it was concluded that year-round, high frequency irrigation, with a leaching fraction in winter, would not cause irreparable damage to soil resources in this particular summer rainfall climate (Annandale, Jovanovic, Benade & Tanner, 1999).

In conclusion it can be said that the effects of salt stress on growth can be summarised in terms of the energy needed to adapt to saline conditions: “Salt stress essentially increases the energy that must be expended by the plant to extract water from the soil and to make the biochemical adjustments necessary to grow relative to the non-saline condition” (Rhoades & Loveday, 1990 p.1091). Energy is thus diverted from processes needed for normal growth to adaptive mechanisms (Yeo, 1983)

2.4 FACTORS THAT INFLUENCE SALT TOLERANCE

Salt tolerance data in the literature can only be used as a general guideline for crop selection. Such data for a specific crop are mostly average values for different cultivars grown in a variety of environmental conditions (Maas & Hoffman, 1977). Salt tolerance depends not only on salinity but also on many other factors such as edaphic, climatic, plant variety and growth stage, agronomic and irrigation practices. Therefore salt tolerance data in the literature cannot be used for quantitative predictions of crop yield losses from salinity for every situation. It has been found that when the sensitivity is due to some factor, other than the inherent real tolerance of a species or cultivar, the threshold and slope will increase and decrease together, with no change in the salinity of the extrapolated ‘zero yield’; but when the salinity at zero yield is also affected, it indicates a difference in real tolerance (Meiri & Plaut, 1985). The complexity of environmental interactions with salinity has been a major obstacle to the breeding of salt-tolerant varieties (Shannon, 1997).

2.4.1 ENVIRONMENTAL FACTORS

Soil environment

Chemical and *exchange reactions* and *moisture retentivity* can influence growth on saline soils. The physical structure of the soil influences drainage and aeration. Poor soil aeration amplifies the detrimental effects of soil salinity. The application of gypsum under such conditions can increase the salt tolerance by improving soil structure and aeration (Oster & Frenkel, 1980; Frenkel & Meiri, 1985). Salt tolerance in waterlogged conditions can be very different from that in drained conditions. Waterlogged soil conditions increase the uptake of salts from a saline root medium compared to that in aerated conditions (Shannon, 1997; Marschner, 1995). Extraction of water from the underlying water table can also influence the evaluation of salt tolerance of crops in the field, depending on the quality of that water and the rooting pattern of the crops.

The *fertility* and *fertilization* of soil can result in an 'apparent' relative salt tolerance that can be misleading (Bernstein, Francois & Clark, 1974; Grattan & Grieve, 1994). Crops grown at low fertility levels may show an apparently high relative salt tolerance (Feigin, 1985) because yields on non-saline soils can be relatively more affected by infertile conditions than yields on saline soils, resulting in an apparently higher relative salt tolerance. Improving nutrition by fertilization could, on the other hand, improve growth proportionately more under moderate or non-saline conditions than under saline conditions and result in an apparently lower relative salt tolerance. Bernstein et al. (1974) concluded that in the case of cereals at moderate nutrient deficiency and salinity, these effects are independent and additive. At higher stress levels the growth is, however, determined by the more limiting salinity factor. Nutrient/salinity interaction can thus differ substantially as salinity increases from low to high levels (Grattan & Grieve, 1992). This is probably why most plants do not respond positively to N and P fertilization at high salinity. Feigin (1985) reviewed data on fertilization of crops irrigated with saline water and concluded that standard fertilization for non-saline conditions is also suitable for saline conditions.

Salt tolerance also depends on the *combination of specific salts* in the soil solution (the composition). In some regions ions such as Al, B, Mn, Se may be present in toxic or growth limiting concentrations. Different ions have different toxicity levels, and also influence

osmotic potential differently. The influence on osmotic potential depends inter alia on the osmotic coefficient of the specific salt of which NaCl > $MgCl_2$/ $CaCl_2$ > Na_2SO_4 > $MgSO_4$, depending on the concentration of the particular salt (Robinson & Stokes, 1959). The proportion of $Cl/SO_4/HCO_3$ and Na/Ca/Mg is important for the effect on plant growth. Rana (1985) noted that although crops tolerant to alkali soils are usually also tolerant on non-alkaline saline soils, the opposite is not true. Maas (1990), however, concluded that generally plants respond similarly to salinity over a wide range of salt combinations.

Climate and atmosphere

Climate is probably the factor that has the greatest influence on the salt tolerance of crops. *Temperature, radiation, atmospheric humidity* and *pollution* can all influence salt tolerance. Generally, studies show that crops are more tolerant to salinity under cool, humid conditions than in a hot, dry climate (Magistad et al., 1943). The salt tolerance parameters of threshold and slope can be influenced by hot, dry conditions: the threshold lowered (yield can start decreasing at lower salinities), and the slope increased (a more rapid decrease of yields with increasing salinity). Crops and cultivars can, however, vary in their response. Lucerne and dry bean salt tolerance decreased at higher temperatures (Ahi & Powers, 1938); barley, bean and corn were more sensitive to salinity at low than high air humidity (Maas, 1990), while humidity did not greatly affect the salt tolerance of wheat (Hoffman & Jobes, 1978). High humidity causes greater yield increases in salt-sensitive than in salt-tolerant crops (Maas & Hoffman, 1977).

The *gaseous composition* surrounding the aerial plant parts can also have an effect on the relative salt tolerance. Salinity causes stomatal closure which reduces the CO_2 uptake and consequently the C compounds needed for growth. High CO_2 concentrations can partly reduce this effect. The closing of leaf stomata can also reduce the volume of air pollutants entering the plant, thus possibly reducing the toxic effects on growth. Ozone, a major air pollutant, has a greater effect on the growth of oxidant-sensitive (leafy and forage) crops under non-saline than saline conditions. Such crops may thus seem relatively more tolerant to salinity in such areas (Maas, 1990).

Agronomic and irrigation practices

Agronomic and irrigation practices can also cause increased injury with saline water. In raised seedbeds with furrow irrigation, for example, seeds should be planted on the shoulders away from the areas of salt accumulation (Ayers & Westcot, 1985). The frequency of irrigation influences sensitivity as plants are exposed to increased salinity with time between applications. Species also differ in their response to sprinkled irrigation. This depends on leaf characteristics and the rate of foliar absorption of salts. The Solonaceae family, for example potato and tomato, is most sensitive to leaf injury by salts. Greenhouse tests indicated sensitivity in the following order: sugarbeet <cotton and sunflower <cauliflower <safflower <barley and sorghum <alfalfa <tomato <potato (Maas, Grattan & Ogata, 1982). Foliar injury depends more on the rate of absorption by leaves than on the salt tolerance of the crop (Ehlig & Bernstein, 1959). The rate of absorption increases not only with concentrations in irrigation water but also with duration of contact.

2.4.2 PLANT FACTORS

Species, cultivars and rootstocks

Plant species and cultivars differ in their ability to grow under saline conditions (Maas & Hoffman, 1977). With the greater emphasis on the genetic breeding of salt-tolerant and other stress-tolerant cultivars, agronomical varieties now originate from a more diverse genetic base than in the past. There is thus a greater possibility of cultivars differing in salt tolerance than in the past and this is an important basis for screening (Francois & Maas, 1994).

Since the 1970's much effort has been put into the development of salt-tolerant crop cultivars but only a few cultivars have been released (Richards, 1995). Breeding salt-tolerant varieties is hampered by the fact that salt tolerance is a multigenetic trait with a variety of different mechanisms by which plants are affected by and can adapt to salinity. The spatial- and time-related heterogeneity of saline soils also make selection for breeding very difficult. Most studies are thus on salinized nutrient solutions, of which the problems of extrapolation to field conditions are well known.

Yield is an important parameter for the selection of agronomic crop cultivars. In practice it has been found that generally the more salt-tolerant varieties are lower yielding while those

with higher yields are more salt sensitive. Selecting for salt tolerance can thus develop low yielding cultivars that are not competitive with non-tolerant, high yielding ones (Shannon, 1997). Richards (1995), however, also found that selections made for high yield on naturally saline soils have indirectly developed salt-tolerant cultivars. He concludes that even though the tolerant varieties may survive much better under salt stress, normal high yielding cultivars of for example wheat, barley and sunflower may produce higher yields than their salt-tolerant relatives in saline soils; for breeding it is thus better to select from high yielding rather than from salt-tolerant lines.

Growth stage

The sensitivity of species and cultivars can change during their ontological development. It is important to separate the effects of growth stage from those related to duration of exposure to salinity (Lunin, Gallatin & Batchelder, 1961). Salt tolerance measured at one growth stage does not necessarily correlate well with tolerance at other growth stages. There is, however, little data on specific effects of salinity at the different growth stages of crops. In most studies crops are subjected to salinity either from planting or after the early seedling stage (Francois & Maas, 1994).

The timing of development can also be influenced by salinity. This differs according to crops. In some grains maturity is earlier under saline conditions, for instance in wheat, sorghum and oats; in others it is not affected (rye and barley), while in tomato flowering is delayed (Shannon, 1997).

A major question in the selection or screening of salt-tolerant varieties is whether the tolerance in one growth stage is related to that in other stages. Independent selection at different growth stages and subsequent crossing could possibly then combine salt tolerances at different growth stages into one cultivar (Shannon, 1997). However, where sensitivity is typical for a crop at a specific growth stage, salt tolerance at that stage (e.g., at germination for sugar beet, or early vegetative stages for cereals) could remove a major limitation in its growth.

Germination: Germination can be influenced by salinity through a decreased entry of water (lower osmotic potential) and/or the intake of ions to toxic levels. The percentage of

germination is generally not decreased by salinity, but the rate of germination and emergence have been delayed (Francois & Maas, 1994). Exceptions are sugarbeet, lucerne, cotton and sunflower where germination is sensitive to soluble salts (Läuchli & Epstein, 1990). Pearl millet is sensitive to sodicity during germination (Ray, 1988). It is interesting that some halophytes, that grow optimally at relatively high NaCl levels, appear to be salt sensitive during germination (Ungar, 1978). Determining the salt tolerance of a species during germination has generally not been successful for breeding purposes.

Emergence and seedling stages: Plants are usually most sensitive during emergence and early seedling stages and become more tolerant as growth proceeds from the vegetative to the reproductive and grain-filling stages (Francois & Maas, 1994). Leaf and spikelet primordia and tiller buds of cereals are formed during the early vegetative stage. Salinity stress at this stage may significantly affect the eventual seed yield. Sensitivity at these early stages, and thus the crop stand, can be greatly increased because of the exposure of juvenile roots to intensified salt and water stresses by evaporation from the soil surface.

The *vegetative growth stage* of non-halophytes is generally sensitive to salinity.

Anthesis, pollination and fertilization: Although very limited, there are some indications that this could be a sensitive growth stage, for example in the case of rice (Pearson & Bernstein, 1959; Akbar & Yabuno, 1977). In maize, salt sensitivity was found to be particularly high at tasselling (Maas, Hoffman, Chaba, Poss & Shannon, 1983). On the other hand the insensitivity during or just before anthesis in grain crops such as sorghum, wheat and barley has been used successfully as a stage to substitute with more saline waters for irrigation (Maas & Poss, 1988). During *reproductive development* salt tolerance can, however, increase dramatically (e.g., in cotton yields, Rains, 1981).

Comparing the sensitivity of a particular cultivar at different growth stages is complicated by the criteria used at these stages; germination and emergence are usually determined by survival percentage and thereafter salt tolerance is based on relative growth or yield.

When screening for salt tolerance of different cultivars of a species, the most sensitive growth stage would obviously be studied, but within one genotype there could also be shifts in the

relative salt tolerance of cultivars at different development stages, for example "Salt resistance of three barley cultivars changed over time, the cultivar most sensitive to early salinisation proved rather resistant at maturity, and the one that had the greatest initial resistance ... was more sensitive at maturity." (Lynch, Epstein & Läuchli, 1982).

2.4.3 MICROBIOLOGICAL FACTORS

Other biological factors are the sensitivities of Rhizobium species, and also possibly those of mycorrhiza. Soil salinities above the threshold values of legume species may severely affect the

survival and N-fixing abilities of Rhizobium species. Chloride salts of Na, K and Mg appear to have specific ion effects on Rhizobium growth and are more toxic than the SO_4 salts. Magnesium inhibits Rhizobium growth at lower concentrations than Na and K (Francois & Maas, 1994).

2.5 EVALUATION OF CROP SALT TOLERANCE

Salt tolerance can be evaluated in several ways: survival under saline conditions; absolute growth or yield reduction for specific salinity levels; or, growth in saline relative to that in non-saline (control) conditions (Maas, 1990). Survival is important for ecological studies and perhaps also for revegetation of problem soils, but not for commercial production. The absolute yield reduction at specific salt concentrations can be useful for farmers, but is complicated by the fact that these yields are influenced by a multitude of other factors pertaining to the climate, environment, soil and the plant itself (2.4). Furthermore, yields of different crop species cannot be compared on an absolute basis. These problems are largely overcome by expressing yield or growth on a relative basis. *Relative growth* or yield was defined by Maas (1990) as the growth or "yield of a crop grown under saline conditions expressed as a fraction of that achieved under nonsaline, but otherwise comparable, conditions". Relative salt tolerances may, however, also be misleading (Bernstein et al., 1974), giving rise to 'apparent' salt tolerances that can be higher or lower depending on the proportionate influence of other factors on the control (2.4.1).

2.5.1 CRITERIA USED FOR SALT TOLERANCE EVALUATION

Many criteria have been used to evaluate the salt tolerance of crops, of which survival, shoot dry mass and seed or fruit yield are the most common. Depending on the criteria, differing salt tolerance responses can be elicited. Seed production can often be less affected than shoot growth. The most recent salt tolerance lists of Francois & Maas (1994) include data on the specific parameters used, such as grain yield, shoot growth and tuber yield. Vegetative shoot growth has been the most widely used parameter with non-halophytic crops. Experience has shown that increased biomass can result in increased economic yields (Arnon, 1977). Because tolerance can differ at different growth stages selection for salt tolerance has often been evaluated over the entire growth cycle. In many cases, however, salinity is imposed from the late seedling stage to maturity. Another approach is to evaluate for salt tolerance at the most sensitive growth stage. This could, however, lead to erroneous deductions for the salt tolerance of the total growth cycle of a species (Ray, 1988; Munns, 1993). Physiological criteria, for example the K/Na ratio and Na and Cl exclusion in wheat, have also been found to be an indication of salt tolerance for some species.

2.5.2 SALT TOLERANCE DATA AND YIELD RESPONSE FUNCTIONS

In earlier salt tolerance data, crops were listed according to their yield under saline conditions (Magistad & Christiansen, 1943) or subsequently more qualitatively by placing crops in groups from sensitive to tolerant. In a later approach, semi-quantitative data were given by listing crops with the salinity values at which different yield percentage decreases could be expected (e.g., Bernstein, 1964, 1974).

In 1977 there was a breakthrough for quantitative evaluation of salt tolerance when Maas and Hoffman reviewed all available salt tolerance information and it became apparent “that, in general, yield was not decreased significantly until a threshold salinity level was exceeded, and that yield decreased approximately linearly as salinity increased beyond the threshold” (Maas & Hoffman, 1977 p.126). Two important parameters emerged from this conclusion: the “*threshold*” that is “the maximum allowable salinity without yield reduction below that of the nonsaline control treatment” and the “*slope*” - “the percent yield decrease per unit salinity increase beyond the threshold” (Maas & Hoffman, 1977 p.121) (Figure 2.1)

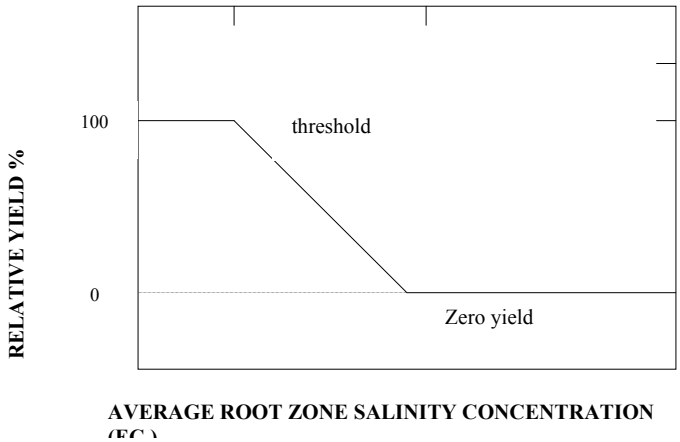

Figure 2.1 Graphic representation of the piecewise linear salt tolerance response function.

The relative yield (Y_r) could now be calculated for any given soil salinity exceeding the threshold, if the threshold and slope values were known, by using the equation

$$Y_r = 100 - B\,(EC_e - A)$$

Where
- A = the salinity threshold expressed in dS m^{-1} ($1\ dS\ m^{-1} = 100\ mS\ m^{-1}$)
- B = the slope expressed in yield decrease % per dS m^{-1} (per 100 mS m^{-1})
- EC_e = the mean electrolytical conductivity of the saturated soil extract of the root zone at 25^0C in dS m^{-1} (over the whole growth period)

The threshold hypothesis of the popular two-section linear, yield/salinity response function was confirmed by Feinerman, Yaron and Bielorai (1982), using a switching regression method instead of the least squares approach used by Maas and Hoffman (1977), to estimate the parameters in the two-section linear response curve.

According to Van Genuchten (1983), salinity can also be expressed as concentration (see Hoffman, Rhoades, Letey and Sheng, 1990, for conversion from EC_e), osmotic potential (see Maas, 1990) and the electrolytical conductivity of the soil water per se (EC_{sw}). Most response

functions for the effect of salinity on crop growth, however, uses the total salt concentration, measured as the electrolytical conductivity of the growth medium or converted to the osmotic potential. The electrolytical conductivity is, however, not a good representation of the osmotic potential in Ca and Mg sulphate waters as these electrically neutral ion pairs, $CaSO_4$ and $MgSO_4$, are not measured in the electrolytical conductivity, but nevertheless contribute to the osmotic potential (Papadopoulos, 1986).

Because salt tolerance functions are mostly based on the assumption that plants actually respond to the osmotic potential of the soil solution (π_{sw}), EC_e is converted to EC_{sw} at field capacity, or at wilting point and then to osmotic potential of the soil solution. Meiri (1994) points out that this conversion must, however, take into account the structure and chemical characteristics of the specific soil involved. He argues that:

- the calculation of the EC_{sw} is based on the ratio of the saturated water content to that at field capacity (θ_e/θ_{fc}) being 2/1 or the wilting point (θ_e/θ_{wp}) being 4/1. These ratios apply to many soils but depend on the soil's structure and water holding capacity; a range of 2.03 to 8.45 for θ_e/θ_{wp} was reported for very fine and coarse soils respectively *(United States Salinity Laboratory Staff*, 1954 as quoted in Meiri, 1994). This can cause an erroneous calculation of EC_{sw} and the osmotic potential of the soil solution, and consequently of salt tolerance;

- the calculation of EC_{sw} as a simple dilution may be true for NaCl, but with gypsiferous soils and those with a high exchangeable sodium percentage, chemical considerations come into play. The threshold EC_e in gypsiferous soils will be about 200 mS m^{-1} higher than indicated by the EC_e, because of the dissolution of gypsum in the preparation of the saturation extract (Maas and Hoffman, 1977). Furthermore, when gypsum is added to soils with a high exchangeable sodium percentage it will further increase the EC_{sw} by the Na released through Ca exchange, and also by increased dissolution of the gypsum.

A comprehensive list of crop salt tolerances with these 'new' parameters was presented in Maas and Hoffman (1977) and these crop salt tolerances have been updated with ongoing research in expanded lists in Maas (1986, 1990) and Francois and Maas (1994). These lists include results from different countries and should thus be applicable as guidelines anywhere.

For quick qualitative rating, Maas and Hoffman (1977) grouped crops according to the salinities where yield starts to decrease (the threshold EC_e):

Sensitive	$EC_e < 130$ mS m^{-1}
Moderately sensitive	EC_e 130 - 300 mS m^{-1}
Moderately tolerant	EC_e 300 - 600 mS m^{-1}
Tolerant	EC_e 600 - 1000 mS m^{-1}
Unsuitable for most glycophytic crops - unless reduced yield accepted	$EC_e > 1000$ mS m^{-1}

(Ayers & Westcot, 1985)

When using values in these lists for yield prediction, the following must be kept in mind:

- These values are averages - not only from different countries but also with different soil types and for different cultivars.

- The listed values are based on data where salinity treatments were often commenced after seedling establishment, and are not representative of sensitivity during germination and seedling stages (although such information is noted when available).

- Soil salinity was mostly maintained at a relatively uniform value throughout the root zone, by irrigating with a high leaching fraction, thus minimizing salinity variations in concentration over time and space (Hoffman et al., 1990).

- Data in these tables mostly apply to soils where Cl is the main anion. Owing to the dissolution of gypsum when preparing saturated soil extracts, the corresponding EC_e values of gypsiferous soils (non-sodic, low Mg) generally range "from 1 to 3 dS m^{-1} (100 to 300 mS m^{-1}) higher than those of the non-gypsiferous soils having the same conductivity in the soil water at field capacity. Therefore plants grown on gypsiferous soils will tolerate" EC_e values "approximately" 200 mS m^{-1} "higher than those indicated in the tables" (Maas, 1986 p.16).

- The lists in 1977 only included crop responses to total soluble salts in the root medium. In subsequent reviews salt tolerance data and limits for specific ion effects of for example B, Cl and Na were also included (e.g., Maas, 1986).

Van Genuchten (1983) developed a computer programme, entitled SALT, which facilitates the calculation of the salt tolerance parameters of the piecewise linear and other nonlinear yield-salinity response functions with limited data points.

The threshold and slope parameters were subsequently implemented in a crop-water production function in which three yield relationships were combined, namely yield and evapotranspiration, yield and average root-zone salinity, and average root-zone salinity and leaching (Letey and Dinar, 1986). Existing models for crop growth response with salinity is reviewed in Castrigano, Katerji & Hamdy (1995).

Currently two kinds of salt tolerance tables are used : (i) tables with the threshold and slope values by which relative growth at a specific salinity can be calculated and (ii) tables that show the maximum level of total salinity or the maximum level of specific ion concentrations permitted in irrigation water or soil solutions (Meiri, 1994).

Meiri (1994) however suggests that the existing tables are too conservative. He argues that these values are mostly based on studies with steady-state soil salinities and that a discrepancy arises from the differences with the temporally and spatially changing salinities under field conditions, and also from the interactions of environmental, edaphic and plant factors with crop response. He stresses the need for a salt tolerance data base with a multi-factor expression that takes the above into account. He stresses that the soil salinity parameter that correlates best with crop response should be found (i.e., the “effective salinity”). He suggests the need for possibly a computer programme that will predict the yield quantities and qualities with temporal and spatial changes in salinity, that will also take into account environmental, edaphic and plant growth factors. Product quality is a parameter of increasing importance that has not yet been included into the available salt tolerance tables (Meiri, 1994).

2.6 SALT TOLERANCE OF AGRONOMIC GROUPS

The general salt tolerance trends for agronomic groups such as cereal, forage, vegetable, fruit and ornamental crops are summarised in Francois and Maas (1994). Most of the crops investigated in the current study fall into the cereal or forage groups.

2.6.1 CEREAL CROPS

With the exception of maize and rice, most cereal crops fall into the moderately salt-tolerant group (2.5.2), for example sorghum, wheat, triticale, rye, oats and barley. Salt tolerance has been indirectly developed in many grain crops by selection for high yield in naturally saline environments (Shannon, 1997).

All cereals seem to follow the same tendencies of sensitivity or tolerance with regard to their growth stage. Seedling and early vegetative stages ('seedling' and 'tillering' stages of Tottman and Makepeace, 1979) are usually the most sensitive, while subsequent stages are increasingly salt-tolerant. This has been shown to be the case for sorghum, wheat, barley, maize and rice and can also be expected with the other cereal crops (Francois & Maas, 1994).

Developmental events during the life cycle of cereals have been separated into three major phases (Francois & Maas, 1994 p.166):

"In the first phase, which encompasses the early vegetative stage, leaf and spikelet primordia are initiated, leaf growth occurs and tiller buds are produced in the axils of the leaves. High soil salinity at this time reduces the number of leaves per culm, the number of spikelets per spike and the number of tillers per plant."

During the second growth phase - which includes 'Stem elongation, booting and inflorescence emergence' of Tottman & Makepeace (1979) -"the tillers grow, mainstem and tiller culms elongate and the final number of florets is set." Tiller survival and the number of functional florets per spikelet can be reduced by salinity stress during this phase which ends at anthesis. In the final phase of fertilization and grain filling, seed number and size can be affected by salinity (Francois & Maas, 1994).

High grain yield of crops such as wheat and sorghum has been found to be a better criterion of salt tolerance than biomass (Shannon, 1997), but Francois & Maas (1994) concluded that through its effect on spikelet and tiller number, salinity has a greater influence on yield in the first phase, than through the yield components of the subsequent two phases.

2.6.2 FORAGE CROPS

Forage crops are mainly from the grass and legume families. Generally the grasses are more tolerant and the legumes more sensitive to saline conditions.

Some grasses are sensitive but there are many salt-tolerant species (e.g., Bermudagrass). As in the case of the cereals, grasses are most sensitive during early seedling growth. Many forage grasses are mostly kept in the vegetative stage by grazing or cutting; when they have passed the early seedling stage and are established, these grasses are less sensitive to soil salinity (Francois & Maas, 1994).

Legumes mostly used for forage or fodder are clovers (*Trifolium* and *Melilotus* species) and lucerne (*Medicago sativa* L.). The salt-tolerance of these crops depends very much on the stage of growth when salinity is imposed. Dark green leaves, decreased leaf area and plant size are typical of the salt effect on these legumes. Owing to the genetic variability of the grass and legume species and cultivars, differences in salt-tolerance do occur (Francois & Maas, 1994).

The salt-tolerance or sensitivity characteristics of the individual crop species will be discussed with the respective results (Chapters 4, 5 and 6).

From this literature survey it should be clear that plant response to salinity must not be over-simplified. Different environmental and plant factors, mechanisms and evaluation methods are involved and should be kept in mind when evaluating and predicting quantitative crop responses to specific saline conditions.