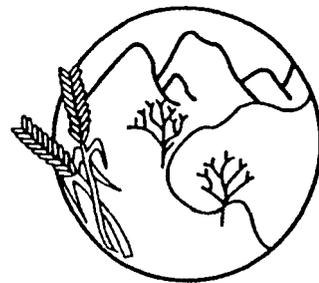


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PLANT RESPONSE TO SOIL SALINITY

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INTRODUCTION

The most common plant response to salt stress is a general reduction in growth and yield. As salt concentrations increase above a threshold level, both the growth rate and ultimate size of crop plants progressively decrease. However, the threshold and the rate of growth reduction vary widely among different crop species. Growth suppression seems to be a nonspecific salt effect that is directly related to the total concentration of soluble salts or osmotic potential of the soil water. Within limits, isosmotic concentrations of different combinations of salts cause nearly equal reductions in growth. On the other hand, single salts or extreme ion ratios are likely to cause specific ion effects, *viz.* ion toxicities or nutritional imbalances which cause even further yield reductions. Since saline soils in the field generally consist of a mixture of different salts, specific ion effects are minimal and osmotic effects predominate, particularly on herbaceous crops. Woody fruit and nut crops, on the other hand, can accumulate Cl^- , Na^+ , or both to toxic levels which cause leaf burn, necrosis, and defoliation. Some herbaceous crops, e.g. soybean, are also susceptible to ion toxicities, but most do not exhibit leaf injury symptoms even though some accumulate levels of Cl^- or Na^+ that cause injury in woody species.

Munns and Termaat (1986) discuss in more detail processes that suppress plant growth and they differentiate between short-term and long-term effects of salt stress. Water deficit is not believed to limit growth of salt-stressed plants (see also Maas and Nieman 1978). More likely, energy becomes limiting for growth because more is expended to accumulate ions and solutes for osmotic adjustment. Nieman found that the adenylate energy charge is lowered in salt-stressed plants and that pools of adenine and uridine nucleotides were

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reduced (Nieman et al. 1988). While toxic concentrations of Na^+ or Cl^- in leaves may limit growth of severely stressed plants, moderate levels of salinity, even for long terms, can cause significant reductions in growth and yield of most crops without evidence of toxicity and foliar injury. Even in tree species, e.g. citrus, yield reductions occur without excessive accumulations of Cl^- or Na^+ and without any apparent toxicity symptoms indicating that the dominant effect is osmotic (see Maas 1993). However, salt accumulation in the woody tissues over several years can reach toxic and lethal concentrations. Bernstein et al. (1956) hypothesised that Na^+ is initially retained in the roots and lower trunk, but after three or four years conversion of sapwood to heartwood releases the accumulated Na^+ which is transported to the leaves causing leaf burn and necrosis. Recent data indicate that injury and even death of stone-fruit trees occurs when the storage capacity of the sapwood is exceeded; *i.e.* conversion of sapwood to heartwood may not be necessary (A-M. Boland and E.V. Maas, unpub. data).

Besides causing specific toxic effects, salinity can induce nutrient deficiencies or imbalances in plants. The specific effects vary among species and even among varieties of a given crop. Excessive salinity can affect 1) nutrient availability, 2) nutrient uptake and/or distribution within the plant, and/or 3) the internal plant requirement for a nutrient element through physiological inactivation (Grattan and Grieve 1992). One example is Na^+ -induced Ca^{2+} deficiencies which occur when the $\text{Na}^+/\text{Ca}^{2+}$ ratio in a saline solution exceeds a certain threshold level. Cereal crops seem especially susceptible to this phenomena (Maas and Grieve 1987; Grieve and Maas 1988) but salinity-induced Ca^{2+} deficiencies have also been observed in crops from other families resulting in blossom-end rot in tomato and bell pepper and black heart in celery (Geraldson 1957) and contributing to bract rot in artichokes (Francois et al. 1991).

TESTING FOR SALT TOLERANCE

Traditionally, salt tolerance data have been obtained in small experimental plots. To the extent possible, crops are grown according to commercial practices with adequate moisture and nutrients. Several salinity treatments (preferably six or more replicated three times) are imposed by irrigating the test crop with

artificially-salinized water. A mixture of NaCl and CaCl₂ (1: 1 by wt.) is added to nonsaline irrigation water to obtain a range of salt concentrations that cause yield reductions of 0 to 50% or more. The soil profiles are leached with the respective treatment waters to presalinize the expected rootzone. However, to ensure an acceptable plant stand, all plots are irrigated with approx. 5 cm of nonsaline water just prior to sowing to provide a nonsaline seedbed. Saline irrigations are imposed after the seedlings have emerged and are continued throughout the growing season. The soil should be sufficiently permeable to allow adequate leaching. Even with the recommended leaching fraction of 50%, salt concentrations roughly double from the top to the bottom of the rootzone.

Having accurate measurements of soil salinity in the rootzone during the growing season is essential to obtain reliable salt tolerance data. This requires monitoring salinity at several depths at various times during the season. These salinity values are averaged to estimate the mean soil salinity encountered by the crop. Soil salinity is conveniently estimated from the electrical conductivity (EC) of water extracted from the soil at some reference water content, e.g. that present in a saturated soil-paste. Although the EC of the saturated-soil extract (EC_s) is approximately half that of the soil water at field capacity, it has commonly been used to express the salinity of the soil. It is a reproducible value that is directly proportional to the salt concentration of the soil water. For further details and a description of other methods that measure EC of the soil water directly or indirectly, the reader is referred to Rhoades and Miyamoto (1990).

GROWTH AND YIELD RESPONSE FUNCTIONS

The salt tolerance of a crop can be described by plotting its relative yield as a continuous function of soil salinity. For most crops this response function follows a sigmoidal relationship. However, some crops die before seed or fruit yields decrease to zero which eliminates the lower part of the sigmoidal curve. However, this response curve has been reduced to a simple “bent stick” model consisting of two line segments, one, a tolerance plateau with a zero slope and the second, a concentration-dependent line whose slope indicates the yield reduction per unit increase in salinity (Maas and Hoffman 1977). The point at

which the two lines intersect designates the “threshold”, i.e. the maximum soil salinity that does not reduce yield below that obtained under nonsaline conditions. This two-piece linear response function provides a reasonably good fit for commercially-acceptable yields plotted against the electrical conductivity of the saturated-soil extract (EC_e). EC_e is the traditional soil salinity measurement with units of decisiemens per meter (dS m⁻¹). For soil salinities exceeding the threshold of any given crop, relative yield (Y_r) can be estimated with the following equation:

$$Y_r = 100 - b(EC_e - a) \quad (1)$$

where a = the salinity threshold expressed in dS m⁻¹; b = the slope expressed in % per dS m⁻¹; EC_e = the mean electrical conductivity of a saturated-soil extract taken from the rootzone.

The threshold and slope concept has its greatest value in providing general salt tolerance guidelines for crop management decisions. Farmers need to know the soil salinity levels that begin to reduce yield and how much yield will be reduced at levels above the threshold. Threshold and slope values in terms of EC_e have been estimated for about 80 different crops (Maas 1990). Data for most crop species are based on the test results of one or two varieties or cultivars. Most commercial cultivars within a species have similar tolerances, perhaps because they were developed under nonsaline conditions and were not selected to endure salt stress. Nevertheless, it must be recognized that significant varietal differences in salt tolerance do occur for some species (Shannon and Noble 1990). Whether the differences reflect differences in salt tolerance or differences in adaptation to the particular climatic or nutritional conditions under which the crops were tested has not been established.

The capability of fruit tree and vine crops to tolerate soil salinity is highly dependent upon the rootstocks. Their tolerance is related primarily to their capability to regulate the uptake of Na⁺ and/or Cl⁻. Fruit yield data on woody fruit and nut trees are scarce, mainly because of the long-term, complex nature of the research (Maas 1993, 1994). Salinity stress imposed one year may have physiological and/or morphological effects on

subsequent years. Furthermore, it is difficult to evaluate tree or vine response to salinity and account for dormant periods, changing climate from year to year, and temporal and spatial changes in the salinity profile. Nevertheless, long-term research is needed to evaluate these factors.

SOIL AND ENVIRONMENTAL FACTORS INFLUENCING CROP SALT TOLERANCE

Soil Factors Although crop yields are a function of salt concentrations within the rootzone, this relationship is influenced by interactions between salinity and various soil, water, and climatic conditions. Except under controlled experimental conditions, soil salinity is seldom constant with time or uniform in space. Depending upon the extent of leaching and drainage, salt distribution may be rather uniform in the soil and change relatively little with depth or it may be highly nonuniform with salinities varying from concentrations approximately that of the irrigation water near the soil surface to concentrations many times higher at the bottom of the rootzone. Since the method of irrigation can affect the distribution of salt in the soil profile (Oster et al. 1984), plants respond differently under different irrigation methods (Bernstein and Francois 1973, 1975; Meiri et al. 1982).

If a saline water table exists within a meter of the surface, salts may be transported upward by capillary flow. In this case, the soil salinity profile may be inverted with the highest concentrations at the soil surface. Salinity also increases between irrigations as the soil water is evaporated. Consequently, the plant must respond to salt concentrations that differ several-fold within its rootzone and that are continually changing. Root growth and distribution are not only affected by soil water content and the type of irrigation, but by variable salinity as well (Bernstein and Francois 1973; Alva and Syvertsen 1991).

Exactly how plants respond to salinity that varies spatially and temporally in the soil profile is still a subject of considerable debate. To relate crop yields to variable levels of soil salinity, Rhoades and Loveday (1990) recommend using a linear, depth- and time-averaged salinity in the rootzone for conventional irrigation, (i.e. where the soil is allowed to dry out between irrigations), and a water-uptake-weighted salinity in the rootzone for high-frequency irrigation.

Salt-affected crops often must contend with water deficits or excess as well. Therefore, actual crop performance during the growing season is related *to* how the plant responds to both salinity and water stress. Water deficit, at least to some degree, is practically unavoidable under field conditions since the soil-water content varies temporally and spatially throughout the season. Exactly how the plant responds to the combination of stresses from salinity and water deficit remains unresolved (Meiri 1984). Although the combined effect is undoubtedly more damaging than either one alone, quantifying the growth-limiting contribution of each is difficult since both change over time and space. Water-deficit stress may predominate in the upper rootzone while salt stress may predominate in the lower rootzone.

In flooded or poorly-drained soils, the overall diffusion of oxygen to roots is reduced, thereby limiting root respiration and plant growth. If the rootzone is saturated with saline water, the combined effects of salinity and waterlogging usually suppress plant growth more than either stress alone (Noble and Rogers 1994). Shallow water tables can also influence the apparent salt tolerance of crops. Plants could extract water directly from this source and, depending on the quality of water, they will likely respond much differently than expected from soil salinity levels *per se*.

Environmental Factors Climatic conditions probably influence plant response to salinity as much if not more than any other factor. In general, crops tolerate higher levels of salinity if the weather is cool and humid than if it is hot and dry. The combined effects of salinity and conditions of high evaporative demand, whether caused by high temperature, low humidity, wind, or drought, are more stressful than salinity alone. Because climate has a pronounced effect on plant response to salinity, the time of year salt tolerance experiments are conducted can affect the outcome. For example, if the salt tolerance of cool-season vegetable crops were assessed in hot, dry climates, results may underestimate their actual salt tolerance in their normal environment which is cooler with a lower evaporative demand.

PLANT FACTORS INFLUENCING CROP SALT TOLERANCE

Stage of growth Crop sensitivity to soil salinity continually changes during the growing season. Most crops are tolerant during germination, but the young developing seedlings are susceptible to injury during emergence from the soil and during early juvenile development. Once established, plants generally become increasingly tolerant during later stages of growth. One of the primary effects of salt stress is that it delays germination and seedling emergence. Delays can be fatal if the emerging seedlings, already weakened by salt stress, encounter additional stresses, such as water stress, extreme temperature fluctuations and/or soil crusting. Because of evaporation at the soil surface, the salt concentration in the seed bed is often greater than at deeper depths. Consequently, the juvenile roots of emerging seedlings are exposed to a greater degree of stress than indicated by the usual measurements of salinity which are made on composite soil samples taken from throughout the soil profile. The loss of plants during this crucial phase can reduce the plant population density to suboptimal levels and significantly reduce yields.

Experiments designed to test the relative effects of salt stress at different stages of growth indicate that sorghum, wheat, and cowpea are most sensitive during the vegetative and early reproductive stages, less sensitive during flowering, and least sensitive during the grain-filling stage (Maas et al., 1986; Maas and Poss, 1989a; 1989b). With cereal crops, it appears that the most serious effect of salt stress during the vegetative and early reproductive stage is the suppression of tiller formation. Results from two wheat cultivars showed that salt stress eliminated most secondary tillers and greatly reduced the number of coleoptilar and primary tillers (Maas et al. 1994). Primary tillers on the first and second leaves were the least susceptible to salt stress. Yield decreases resulted mainly from the reduced number of spike-bearing tillers and less from decreases in seed per spike (Maas and Grieve 1990; Maas et al. 1996). Apparently, most crops become more tolerant at later stages of growth, but there are some exceptions. For example, Akbar and Yabuno (1977) found that salinity caused panicle sterility in some rice varieties but not in others and suggested that resistance to panicle sterility was genetically controlled.

Plant population density Salt tolerance data are generally expressed in terms of yield per plant. If the number of plants per unit land area is constant, the data are valid when expressed on a land area basis as well. Salt

tolerance tests at the U. S. Salinity Laboratory are designed to minimize effects of salinity on plant stands. Salinity treatments are initiated after seedlings are fully established and plant mortality is usually minimal thereafter. An important factor in designing salt tolerance experiments is the plant population density. Usually planting densities similar to commercially accepted practices are used but this may inadvertently bias yield response to saline treatments. If salinity reduces plant growth sufficiently to reduce canopy cover, planting densities appropriate for nonsaline soils may be too low for saline soils and may limit their potential yields per unit area. Higher planting densities would ensure canopy closure and increase the capture of solar energy. Some crops benefit further by the fact that salinity can increase the harvest index by reducing vegetative growth more than it reduces seed yields. However, where the vegetative organ is the marketable product, salinity's effect on size or quality may affect its marketability, e.g. smaller head size in lettuce (Shannon, 1980) or reduced petiole length in celery (Francois and West, 1982).

Experiments on cotton and wheat have shown that yields can be significantly increased on saline soils by increasing the plant population density (Francois 1982, Francois et al. 1996; Keren et al. 1983). The higher planting density in wheat offset the loss of productive tillers and yields were maintained or even increased. Those results clearly show that plant population density can significantly influence salt tolerance data expressed per unit land area. An economic analysis indicates that it could also have a substantial impact on profits and the optimal quantities and qualities of irrigation water (Feinerman, 1983).

EFFORTS TO IMPROVE SALT TOLERANCE

Various approaches have been used to increase the salt tolerance of existing crop species (Shannon and Noble 1990). They involve conventional selection and breeding cell and tissue culture techniques and even attempts at genetic engineering. The results, however, have been limited and disappointing. Flowers and Yeo (1995) have reported that less than a dozen new salt-tolerant varieties have been released and documented in patents and registrations. The reason, in part, is the limited number of breeding programs for salt tolerance compared to those for disease and insect resistance, nutritional and climatic stresses, and yield enhancement. But perhaps

more important is the fact that salt tolerance is a complex trait apparently involving multiple genes that have not yet been identified.

Screening and selection for salt tolerance have been the most successful to date, with improved germplasm reported for alfalfa, avocado, chrysanthemum, maize, meadow cordgrass, muskmelon, red fescue, rice, tomato, saltgrass, and wheatgrass (see Shannon and Noble 1990; Flowers and Yeo 1995). While continued efforts seem worthwhile, particularly with crop species having genetically diverse backgrounds, the salt tolerance of most crops is not likely to improve soon. Because yield itself is a complex parameter affected by numerous environmental variables and their interactions with salinity, Shannon and Noble (1990) and Flowers and Yeo (1995) have advocated using physiological characters rather than yield as the basis of selection and breeding for salt tolerance. Clearly this approach requires a close cooperative effort among plant physiologists, biochemists, geneticists, and breeders.

Other approaches have been less fruitful. Hybridization of crop species with wild relatives, e.g. barley, wheat, rice, and tomato, (see Subbarao and Johansen 1994) has produced progeny with higher tolerance, but so far as is known, no commercial cultivars are available. Regeneration of salt tolerant plants from cultured cells and tissue has rarely been successful. For the period between 1982 and 1993, Flowers and Yeo (1995) found patents for only two crops, alfalfa and flax, where regenerated plants had enhanced salt tolerance, but no evidence that they were more tolerant in the field. Molecular approaches and genetic engineering have made gene identification, isolation and transformation possible in many areas of plant science, but have not, as yet, contributed to the development of salt-tolerant varieties.

Domestication of halophytes provides an alternative to the genetic improvement of traditional crops. They are naturally adapted to saline soils and tolerate salinity levels approximately 10-fold higher than glycophytic crop species. A number of native species are already being used throughout the world as forage and fodder for animals (see Choukr-Allah et al. 1996). The feasibility of growing *Atriplex* species with saline irrigation water and harvesting the forage with conventional farm equipment has been demonstrated (e.g. Watson and O'Leary

1993). Other species, such as *Distichlis palmeri*, *Kosteletzkya virginica*, and *Salicornia bigelovii*, have been evaluated for their potential as seed or oil crops (O'Leary 1994). While these species possess certain desirable nutritional properties, all will require improvement of various agronomic characteristics before becoming accepted as new food crops. While we may be more successful domesticating wild halophytic species than increasing the tolerance of existing crops, as O'Leary (1994) and Flowers and Yeo (1995) believe, problems of productivity, nutritional value, palatability, high salt content, and toxic constituents limited their commercial value. There is reason to be hopeful but whether this approach will produce useful and widely adopted new food sources remains to be seen.

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