

III. How plants adapt to salinity

Some plants survive salty conditions by using metabolic energy to adjust osmotic pressure or by excluding salt from tissues. Recent research links salt sensitivity to specific toxic effects on cellular processes.

Mechanisms of salt tolerance in plants

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Plants may be categorized as halophytes or glycophytes, as far as their responses to salinity are concerned. The distinction is not absolute, because species range from highly tolerant to very sensitive.

Halophytes — salt-tolerant plants native to saline habitats — include two groups that respond differently to increasing soil salinity. In many dicotyledonous halophytes, particularly those belonging to the family Chenopodiaceae, such as the fleshy, jointed-stemmed *Salicornia* of the seashore and other saline habitats, growth is stimulated as salinity increases up to about 15,000 mg/L (250 mM) sodium chloride; higher salinity levels reduce growth, even

in these highly salt-tolerant plants. Most monocotyledonous halophytes are not stimulated by low to medium salinity levels and grow slowly at salt concentrations exceeding about 10,000 mg/L (170 mM) sodium chloride.

The glycophytes, or nonhalophytes, to which most crop species belong, vary in response to salinity from very salt-sensitive to moderately salt-resistant.

Salt tolerance in halophytes

Halophytes belonging to the Chenopodiaceae respond to salinity by taking up sodium and chloride at high rates and then accumulating these ions in their leaves. These plants use the accumulated salt for osmotic adjustment to the low

water potential in the soil. An important feature of this kind of osmotic adjustment is the isolation of the accumulated salt in the vacuoles of the leaf cells, keeping the salt concentration in the cytoplasm and organelles at a low level that does not interfere with the functions of their enzymes and metabolic machinery. This compartmentation has great significance for the performance of halophytes in a saline environment.

As for the cytoplasm, osmotic adjustment in it is accomplished mainly by means of dissolved substances compatible with enzymes and metabolism. These “compatible solutes” are mostly organic compounds such as the nitrogenous compounds glycinebetaine and proline and, in some plants, sugar alcohols, such as sorbitol. In addition, potassium is thought to be maintained in the cytoplasm at a concentration on the order of 4,000 mg/L (100 mM).

For osmotic adjustment to be functional, the solute potentials of cytoplasm and vacuole must be equal, but the particular major solutes are asymmetrically distributed between these two cell compartments, as explained above. Thus, the tonoplast — the membrane separating the cytoplasm and vacuole — must have outstanding transport mechanisms to maintain steep solute gradients. It is likely that the tonoplast of the salt-sensitive glycophytes does not have equally efficient transport mechanisms and therefore may not be able to maintain the solute gradients necessary for osmotic adjustment. Osmotic adjustment in the salt-accumulating halophytes maintains turgor, which is necessary for continued growth.

Responses of glycophytes

Many glycophytes respond to relatively low salt concentrations (below about 6,000 mg/L, or roughly 100 mM) by “salt exclusion,” particularly through low rates of net transport of sodium or chloride, or both, from root to shoot. Most of these salt-excluding glycophytes cannot adjust osmotically to the low external water

Different salts affect plants differently. The growth of grain sorghum was dramatically inhibited by sodium sulfate in nutrient solution (at left) but was much less affected by sodium chloride (at right).



potential by increased synthesis of organic solutes and, therefore, suffer from a decrease in turgor. Hence salinity may induce an osmotic stress in this kind of glycophyte.

Leaf elongation is particularly sensitive to osmotic stress. It is conceivable that, in a saline environment, some relatively salt-resistant glycophytes experience some water deficit in the growing tissues rather than ion-specific effects.

The salt-sensitive glycophytes (for example many legumes, fruit trees, and vines) have inadequate control over ion uptake when exposed to a saline medium. Uncontrolled salt uptake leads to high internal salt concentrations and injury, because the salt-compartmentation mechanisms are not well developed in these plants. This kind of injury is caused not by an osmotic stress but primarily by ion toxicity. The sites of ion toxicity may be at cell membranes, with the possible consequence of impaired ion transport leading to ion imbalances and adverse effects on the mineral nutrition of the plant. High salt concentrations in the cytoplasm may also damage enzymes and organelles.

There are two additional aspects of these responses. First, if a salt-resistant glycophyte can adjust osmotically to a saline medium, the increased rates of ion uptake and transport and, particularly, the synthesis of organic solutes require additional expenditure of energy that would otherwise support growth processes. Although the energy costs of osmotic adjustment are still poorly understood, the drain of energy for ion compartmentation may contribute substantially to the observed growth reduction. The allocation of carbon to the synthesis of organic solutes for osmotic regulation will also involve a cost in terms of reduced growth. Second, salinity stress is first sensed in the root, but osmotic adjustment as well as growth inhibition and ion toxicity are most apparent in the shoot. Thus, in addition to cellular processes, root-shoot interactions and the coordination of the whole plant are an integral part of the responses to salinity.

Ion-specific effects

In recent years, our research has focused on the significance of ion-specific effects as induced by a saline medium, particularly on the interaction between the ionic components of salt stress and the function of cell membranes. E. Epstein, with graduate student D. W. Rush, compared the glycophytic cultivated tomato, *Lycopersicon esculentum* Mill., and its wild, salt-tolerant relative, *Lycopersicon cheesmanii* spp. minor (Hook) C. H.



The salt-sensitive domestic tomato *L. esculentum* (leaves and fruit at right) hybridizes easily with its wild, salt-tolerant relative *L. cheesmanii* (left) from the Galapagos Islands to produce a salt-tolerant fruit (center). Although salt-tolerant, the wild tomato is sensitive to high potassium concentrations; the cultivated tomato tolerates a wide range of concentrations of this ion.

Mull, accession 1401, from the Galapagos Islands of Ecuador. The wild tomato tolerated sodium concentrations up to 5,750 mg/L (250 mM), but survival of the cultivated tomato dropped dramatically at concentrations of 4,600 mg/L (200 mM) or more. In contrast, the wild, salt-tolerant tomato proved extremely sensitive to high potassium concentrations, whereas the cultivated tomato tolerated a wide range of concentrations of this ion. Thus equivalent concentrations of sodium and potassium had diametrically opposed effects on these two tomato species.

Calcium-salinity interactions and the diversity of their mechanisms are another area of interest. Fifteen years ago, LaHaye and Epstein demonstrated that high calcium concentrations (120 to 400 mg/L, or 3 to 10 mM) mitigated the adverse effects of 3,000 mg/L (50 mM) sodium chloride on the growth of bean plants. Sodium uptake was inhibited in the high-calcium treatment. Recently, A. Läubli and graduate student L. M. Kent found that inhibition of the growth of

roots of cotton seedlings at high salinity (11,700 mg/L or 200 mM sodium chloride) was partly overcome by increasing the calcium concentration in the medium to 400 mg/L (10 mM). Unlike the situation in bean plants, however, the calcium-salinity interaction in cotton does not result from inhibition of sodium uptake but is related to the maintenance of potassium/sodium selectivity in the root. In triticale, E. Epstein and Staff Research Associate J. D. Norlyn are finding differences in the calcium response in different lines of this man-made cereal.

Anion effects are also important in plant responses to salinity. Both chloride and sulfate may contribute to salinity in salt-affected soils, but there is great variation in the relative contribution of these two anions to soil salinity. In a study supported by the Kearney Foundation of Soil Science, A. Läubli, E. Epstein, and graduate student P. J. Boursier are investigating the responses of grain sorghum to chloride and sulfate salinity. Plants in the greenhouse were exposed

for three weeks to nutrient solutions containing either sodium chloride or sodium sulfate, as well as to control (no salinity) solutions. The two sodium salts were added at concentrations that reduced the water potential of the solutions to the same extent (0.2 MPa). When compared with control plants in the absence of salinity, growth of grain sorghum was inhibited dramatically by sodium sulfate but much less by sodium chloride. Specifically, sodium chloride reduced the shoot weight to 70 percent of that of the control, whereas sodium sulfate dropped it to 43 percent. Thus, grain sorghum appears to be more sensitive to sulfate than to chloride salinity although, overall, it is considered to be relatively salt-resistant.

The examples described thus far emphasize a variety of ion-specific effects in plant responses to salinity. Additional support for the hypothesis that, in many glycophytes, salinity inhibits growth and performance of the plant mainly through ion effects comes from studies in which the water relations of the plant were also examined. With graduate student R. W. Kingsbury, E. Epstein and R. W. Percy found that two wheat lines differing in salt resistance differed minimally in water relations but substantially in their relative growth rates and photosynthesis. These results suggest that the primary difference was in the response of the two lines to specific ion effects.

A study being conducted by graduate student P. S. C. Curtis, A. Läuchli, and F. E. Robinson indicates a similar response to salinity in the stem-fiber plant kenaf. The plants were grown at the Imperial Valley Field Station (irrigation with Colorado River water, EC=1.7 dS/m, or 1,100 mg/L salt) and in the desert east of the station (irrigation with groundwater, EC=2.8 dS/m, or 1,800 mg/L salt). Growth at the desert site was severely reduced. Leaf water potentials and other measures of water-relations did not differ significantly between the two sites, but irrigation with groundwater greatly increased concentrations of chloride and sodium in the leaves. As in wheat, growth reduction in kenaf does not appear to be caused by salinity-induced water stress but is more likely due to ion effects.

Conclusions

Although our knowledge of the mechanisms of salt tolerance and sensitivity in plants is still scant, we are beginning to understand some of the fundamental differences between halophytes and glycophytes. Crops (mostly glycophytic) are comparatively salt-sensitive, salinity causing osmotic and ion-specific effects

leading to reduction in growth and yield. Much research in the past has put emphasis on the osmotic effects of salinity, whereby the availability of water to the plant is diminished. Our research, however, leads to the conclusion that specific ion effects deserve at least "equal billing" as the cause of salt-induced reduction in the growth of crops.

We need to identify physiological markers related to salt resistance that

may be used in genetic improvement of crops for high productivity in salt-affected soils. Physiological studies with genetic lines differing in salt resistance and investigations comparing cultivated species and wild, salt-tolerant relatives will help in achieving this goal.

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Crop tolerance

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One strategy available to farmers with saline soils is to select salt-tolerant crops. Crop tolerance to salinity ranges widely from the very salt-sensitive bean to the highly tolerant barley and cotton.

The U.S. Salinity Laboratory in Riverside has been testing the salt tolerance of crops since it was established in 1937. It now has data on nearly 70 crops, which will be useful in predicting responses on saline soils (see table). Experiments recently completed or in progress will provide additional data on asparagus, bread wheat, durum wheat, triticale, sorghum, sugarbeet, and guayule. Five or six crops can be tested simultaneously at facilities in Riverside and Brawley, and often more than one crop per year can be tested in a given set of plots. Crops are occasionally tested on field sites, as was done with corn in the Sacramento-San Joaquin Delta (*California Agriculture*, July-August 1983) and as is under way with

plums at the Kearney Agricultural Center, Parlier.

Salt tolerance tests are usually conducted in small experimental plots, where commercial practices are followed as closely as possible, with adequate moisture and fertility. To ensure an acceptable stand, researchers plant seed in a nonsaline seedbed and impose salinity by adding calcium and sodium chloride salts to the irrigation water after the seedlings have emerged. They test several salinity levels to determine both the threshold level that begins to decrease yield and the rate of yield reduction caused by higher levels. Generally, the higher the threshold level, the less yield is decreased as salinity increases.

Because numerous plant, soil, and weather conditions also affect crop growth, yield must be expressed as a percentage of that obtained under similar but nonsaline conditions. Actual yields vary from location to location and year to year, but the relative yield reductions caused by salinity remain reasonably consistent.

Soil salinity in the plant root zone is conveniently measured as electrical conductivity, which is directly proportional to the salt concentration in the soil water. Two commonly used methods pro-

Small plots of wheat are used to determine salt tolerance. Salts are added to irrigation water after seedlings have emerged to determine the point at which salt damage begins to appear and the rate of yield reduction.

