Mechanisms of Salt Tolerance and their Relevance

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Abstract

The consequences of high levels of salinity in the external medium on growth and metabolism of higher plants are briefly outlined. Mechanisms evolved to cope with saline environments are then discussed. Salt-tolerant plants can be broadly classified as either salt excluders or salt accumulators. The salt accumulators can either tolerate high intracellular salt levels or are able to remove excess salt accumulation from sensitive cellular compartments or tissues. It is suggested that the mechanistic basis of salt tolerance be determined for chickpea and pigeonpea to enhance screening procedures for salt tolerance. The mechanistic approach to screening is to be preferred over relying on empirical methods of screening by growing genotypes at a range of salt levels.

Introduction

This brief discussion paper first considers the range of mechanisms available to higher plants for coping with saline environments and then suggests how this knowledge may be applied to detect salt-tolerant genotypes of chickpea and pigeonpea. In the following paper, Dr N.P. Saxena will more specifically consider how to go about genetically improving salt tolerance in these plants.

In screening and breeding for disease resistance, it is necessary to pinpoint the causal organism and understand how it affects plant growth and function. The pulse pathology work at ICRISAT bears witness to this. Like disease, salinity covers a multitude of causal factors and responses, and, in identifying tolerance, it is necessary to pinpoint causal factors, such as general osmotic effects or specific ion effects, and to understand what possible mechanisms certain plants have of coping with excess salt. This is self-evident, but it is worth emphasizing because many experimenters attempting to identify salt-tolerant genotypes do not seem too concerned about the mechanisms involved. Of course, we could continue to screen genotypes at graded salt levels to pick up differences in response, but knowledge of the mechanisms of salt tolerance operating in our test crops would help streamline the screening process.

The following presentation of salt effects on plants is based largely on the concepts propounded by a former colleague at the University of Western Australia, Dr Henk Greenway (e.g., Greenway 1973; Greenway and Munns 1980; Munns et al. 1983). Further, more detailed discussion of the points raised may be found in the reviews of Levitt (1980, pp. 365–488) and Wainwright (1981).

Major Types of Plant Response to Salinity

Most physiological studies on plant response to salinity have used NaCl as the test salt, and relatively little is known about the physiological consequences of alkalinity/sodicity. Figure 1 indicates a broad classification of higher plants in their response to NaCl in the external medium. Certainly chickpea and possibly pigeonpea would belong to the salt-sensitive group.

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ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1987. Adaptation of chickpea and pigeonpea to abiotic stresses. Proceedings of the Consultants' Workshop, 19-21 December 1984, ICRISAT Center, India. Patancheru, A.P. 502 324, India: ICRISAT.

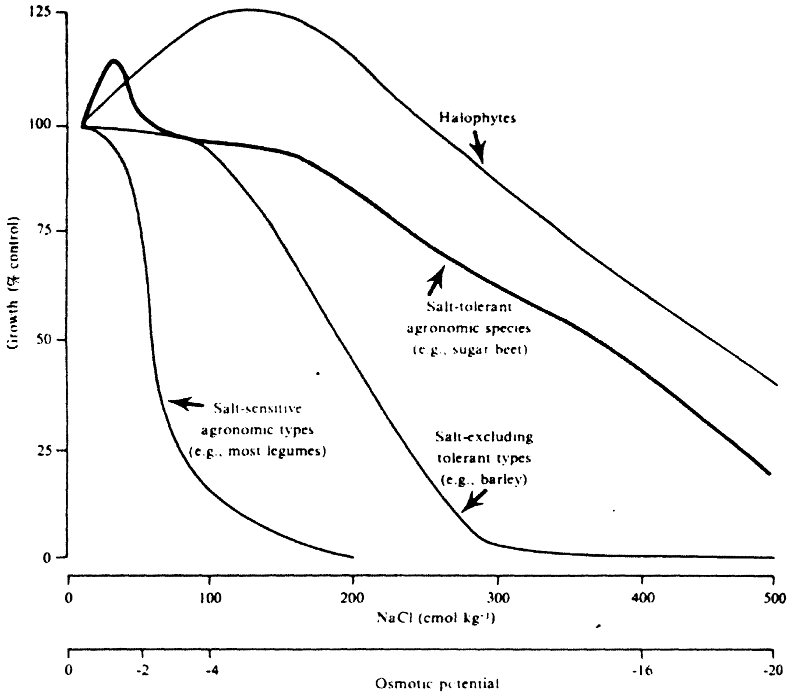

Figure 1. Responses of various categories of higher plants to NaCl salinity. (After Greenway 1973.)

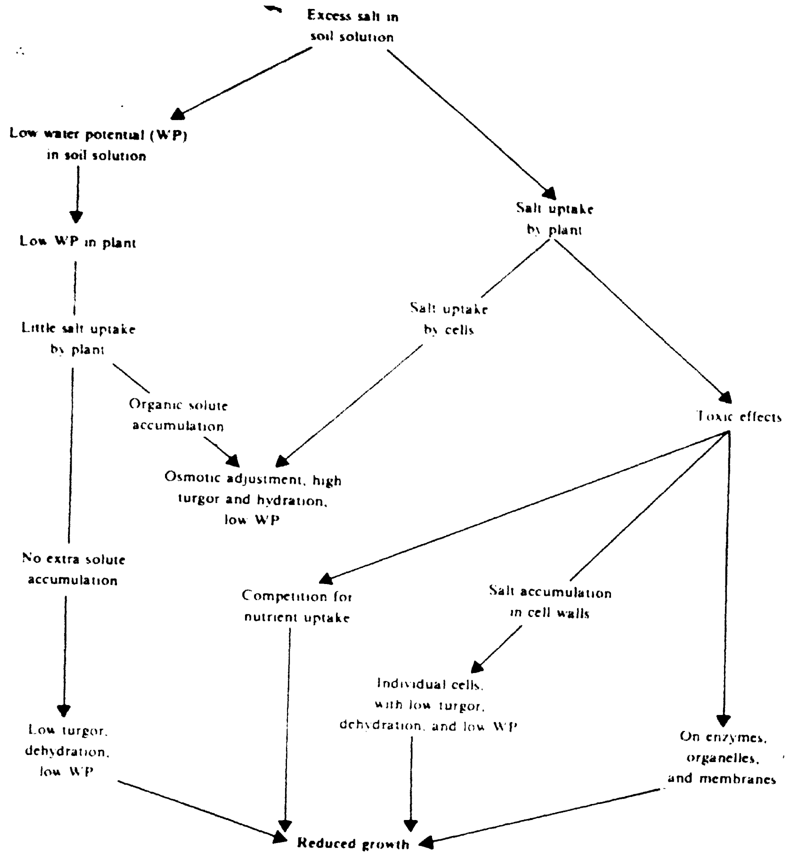

Figure 2. Effects of salinity on various plant physiological processes. (After Greenway 1973.)

Effect of Salinity on Physiological Processes

The consequences of having high salt concentrations in the soil solution are illustrated in Figure 2. Plants growing in a saline environment may be affected by the lower water potential in the environment and plant cells, causing reduced salt uptake, or by increased salt uptake caused by high external ion concentrations. Plants may adjust to this situation by accumulating organic solutes where salt uptake is reduced, or by controlling high levels of salt uptake, so that plant cells osmotically adjust to the external environment and thus maintain high turgor. However, plant growth is reduced where cell turgor cannot be maintained or where internal salt concentrations become toxic to the normal cell metabolism. These toxic effects can manifest themselves as microosmotic effects between adjacent cells or cell organelles, interference with enzyme systems and other metabolic functions, and competition of "salt" ions with nutrient ions in active transport across cell membranes.

Mechanisms of Salt Tolerance

Different higher plants have evolved various mechanisms to cope with a saline environment. These may be summarized as follows.

Salt Excluders

Such plants have an enhanced ability to exclude salt, either from the entire plant or from particular organs. This is accomplished by cell membranes with high ion selectivity, favoring potassium over sodium for example. Examples of such plants include barley, citrus, and soybean. Such plants become particularly prone to moisture deficits under saline conditions, however, and they must rely on organic ion production for osmotic adjustment. This has a high metabolic cost, and overall plant growth rate can be markedly retarded whenever the osmotic imbalance is large. These types of plants are characterized by low sodium and chloride levels in plant tissues.

Salt Accumulators

Such plants are able to cope with a high uptake of salt in several possible ways, some of which are outlined below.

Tolerance of high intracellular salt levels. This includes the group of plants termed "halophytes" and also some plants of agricultural importance, such as sugarbeet. In these plants, cell metabolism is relatively unimpaired by high internal salt concentrations and plant tissues have high Na/K ratios. Indeed, as in sugarbeet and *Atriplex* spp, sodium may substitute for potassium as a plant nutrient. This property allows rapid osmotic adjustment to external saline conditions with a minimal cost of metabolic energy; there is not so much reliance on organic ions for osmotic adjustment. However, this method can lead to specific ion toxicities and mineral imbalances if external salt concentrations become too high.

Removal of excess salt accumulation. By this mechanism plant roots are able to freely take up excess salt, but damaging intracellular accumulation of salt is avoided by:

1. Compartmentation of salts into various plant components, such as vacuoles (as in barley) or stems (as in broad beans).
2. Extrusion of salt from the plant surface by salt glands (as in *Atriplex* spp).
3. Succulence, which is the ability of plants to vastly increase cell volume with water to maintain an appropriate osmotic potential (as in cactus).

Mechanisms Applicable to Chickpea and Pigeonpea

When we consider the salinity response of the entire higher plant kingdom, chickpea and pigeonpea are found comparatively sensitive to saline conditions, with chickpea particularly so. Studies at ICRISAT and elsewhere have indicated, however, genotypic differences in response to salinity within these crop species (Saxena 1984, Y.S. Chauhan, ICRISAT, personal communication). The screening process could be streamlined if we knew the mechanistic basis for these differences. For example, if it is determined that more-tolerant types have an ability to exclude sodium, then chemical analysis of the Na/K ratio of a wide range of genotypes grown and sampled under similar conditions might be a more effective screening procedure than the currently used empirical method of growing plants at graded levels of salinized soil. It should also be noted that chickpea has a particular capacity to produce and exude malic acid from leaf surfaces (Saxena 1984). This process would no doubt have considerable osmotic consequences on leaf cells and may thus be related to the response of chickpea to excess salt accumulation. However, without indulging in any further speculation, I would suggest that a concerted effort be made to identify mechanistic differences between genotypes of chickpea and pigeonpea in coping with excess salt, rather than simply proceeding with the traditional, empirical methods of screening for salt tolerance.

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