Rapid screening techniques for selecting salt-tolerant plants are heretofore untried, untested, or unproven. Theoretically, we know it is possible to screen plants for this trait. Halophytes and salt-tolerant ecotypes exist in nature and variability in tolerance has been demonstrated in a number of agronomic species (48). However, the complexities of salt tolerance and the multitude of ways in which plants adjust and adapt to it have caused much confusion. The effect of salinity on a plant may depend on ontogeny (3, 11), humidity (21, 22, 34), temperature (21, 35), light (14, 35), irrigation management (8, 9), cultural practices (6, 11), soil fertility (10, 32), air pollution (20, 26), and the particular growth or yield parameter measured (3, 49). If all environmental conditions are optimal it is possible to grow some agricultural crops at seawater salinity concentrations. Barley, wheat, millet, and various other crops have been grown on sandy beach areas using seawater for irrigation (4, 5, 16, 24). The use of sand facilitates leaching and minimizes salinity accumulation. Additionally, coastal areas may be cool and humid, and, if fog is common, have low light intensities. These factors create a favorable environment and decrease salinity damage. Recently, Epstein and colleagues used such an environment to screen a barley composite for salt tolerance (16). Several lines were selected which seemed to produce higher yields than the test cultivars. It is possible that such research will result in the selection of traits that will enhance salt tolerance in barley cultivars adapted to other environments.

Screening for salt tolerance based on physiological criteria can only be successful when incorporated into a sound plant breeding program. Conventional plant breeding techniques must be used to combine salt tolerance with other acceptable characteristics such as yield, market quality, disease and pest resistance, and tolerance to other environmental factors. In this manner, a highly salt-tolerant tomato ecotype of Lycopersicon cheesmanii is being back-crossed to a commercial cultivar of L. esculentum (16, 45). The objectives are to improve the salt tolerance of the commercial type without decreasing nutrition, yield, or quality.

The tolerance of a plant to salinity is a measure of its ability to withstand the effects of soluble salts concentrated in its root zone. The simplicity of this definition is deceiving; however, soil salinity includes a wide variety of ions in a range of different proportions. The soluble salt concentration is a dynamic function dependent upon soil composition and structure, and its equilibrium with the ever-fluctuating soil moisture content. Variation among these parameters within a plant's root zone may be quite extensive and difficult to duplicate or quantify in the laboratory. Additionally, little is known about how the plant integrates the heterogeneity within its root zone with its shoot environment and its own genetic potential.

Salt ions may have both general and specifc effects on plants. When ion imbalances affect the plant, the situation can often be diagnosed and ameliorated. In some plants, high concentrations of CI may induce succulence or high SO4 may reduce stomate numbers, but usually growth reduction is very similar at iso-osmotic concentrations of most salt solutions. Probably the most obvious symptom of salinity damage is leaf burn, but often the symptoms are more subtle and impaired plant growth and yield may be the only visible indications.

The relationship between soluble salt in the plant root zone and the effects on metabolism that slow growth and cause death is still fundamentally unknown (27, 36). Physiologists have shown that growing cells are basically undamaged by salinity and that development, although slower, follows the normal pattern. Specific enzymes, total protein, and nucleic acids are reduced in balance with the slower growth (31, 33, 54). Some processes, such as cell enlargement and respiration, may actually be stimulated (30, 38); others, such as polyribosome content, may initially decrease, in relation to fluctuations in relative water content (44). However, plants adjust osmotically to saline solutions without a concomitant increase in growth. To date no single physiological factor has been correlated with salt tolerance.

Despite what is unknown regarding the physiological mechanisms of salt tolerance, there is a growing body of information that may prove applicable to the development of rapid screening techniques. In a recent review, Maas and Nieman (27) described several mechanisms of salt tolerance that can be induced by salinity during a single generation. Adaptations that have been incorporated and genetically fixed in halophytes and salt-tolerant ecotypes have been reviewed by others (17, 53). In general, plants avoid toxic salt effects either by restricting ion uptake into the shoots and then making necessary osmotic adjustments or by allowing osmotic regulation through ion uptake and then adjusting to high salt concentrations in the green tissues. Actually, most plants are probably between these extremes and are restrictive accumulators of salts (Fig. 1) (47). In any case, a certain proportion of photosynthate normally directed toward growth must be diverted to salinity responses. Possibly, the higher respiration rate noted for salt-affected plants is a result of the increased energy needed to maintain homeostasis.

Mechanisms of tolerance at the root

The plant is usually first exposed to salinity through its root membranes (Fig. 1). Salts may enter these membranes either passively or by active transport against concentration gradients. Ion passage has been shown to be selectively regulated across plasma membranes, tonoplast, or into specialized cells, e.g., salt glands or specialized cells along the xylem parenchyma (29, 53). Certain ion-specific ATPases that regulate this ion movement are affected by concentrations of other ions (25). Thus, species and even cultivars may differ in their capacity to regulate ions. Under conditions of high salinity, the integrated effects of several ion transport mechanisms will dictate the efficiency, capacity, and direction of net salt movement. For instance, salt-tolerant sugarbeet translocates Na much faster than corn (28). Whereas corn translocates Na only from root to shoot, beet and most halophytes translocate it in both directions.

Rapid screening for root membrane ATPases of specific ion transport capacities is beyond present technology, but procedures that measure the net result of root transport mechanisms (i.e., salt movement into the shoot) have been used. For example, lines can be selected that have high leaf K/Na ratios or high K concentrations in the presence of salinity. Some success with this latter technique has been reported for cultivars of sorghum (41). The time involved in quantifying ions is a major drawback and restricts the use of such criteria to genotype or family screening. Rapid screening of individuals is not feasible with such time-consuming techniques.

In some instances, visual symptoms (e.g., leaf burn) suffice as ion uptake indicators. Since salt injury is reversible to some extent, rather severe stresses can be imposed upon a population and tolerant individuals can be selected.

The ability of plant to withstand high salt concentrations in the root zone without foliar injury has been used as a test for salt tolerance for citrus, grape, avocado, almonds, pecans, and stonefruits (11). Cooper (12, 13) demonstrated that leafburn in citrus was directly related to Cl uptake and found that rootstocks differed with cultivar in their capacities to exclude this anion. This work has been applied to a breeding and evaluation program for citrus seedlings (18, 42). In a recent study, 52 lines of tall wheatgrass were evaluated for salt tolerance based upon visual observations for leaf burn that were found to be related to Cl uptake (Fig. 2) (47). Restricted uptake of Cl into leaves and stems of salt-tolerant soybean cultivars is controlled by a single dominant gene (1). However, in citrus, the inheritance of salt tolerance associated with restricted Cl movement into leaves was quantitative (18). It seems that this screening technique could have broader applicability of salt tolerance work and could also prove useful for detecting plants that accumulate salt without foliar damage.

A minor aspect of salt effects on roots is the disruption of normal ion transport mechanisms. Active phosphate uptake by carrot root discs and excised barley roots was reversely inhibited by NaCl (27, 37). Loss of uptake capability was correlated with a loss of proteins from the root tissue and recovery was dependent upon protein syn-

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Mechanisms of tolerance in the shoot compounds such as choline and betaine (51) have been investigated. Organic acids such as malate (40) and oxalate (39, 53), and other to drought and salinity stresses. The amino acid proline (23, 50), protein can be used in a rapid screening technique as an indicator of salt sensitivity.

Fig. 1. A schematic representation of salinity effects and plant responses.

Summary

Techniques for selecting plants for salt tolerance are well established. These usually involve screening at a particular growth stage, e.g., germination, seedling development, or maturation. Some particularly salt-tolerant plants, such as barley, may be screened from seed to seed (16). Provided that precautions are taken to control and regulate salinity, such techniques can be very useful (16, 36, 48).

Ideally, selections should be made at one or more predetermined critical salt levels and applied salts should not be deficient in Ca. However, selections made for tolerance at early growth may not prove salt tolerant during later growth, or even at other salinity concentrations or compositions. Furthermore, screening mature plants not only takes more time, energy, and space than screening at earlier growth stages, but also requires more sophisticated control or measurement of salinity. The development of rapid screening techniques based upon the physiological factors that confer salt tolerance could circumvent many of the problems.

Our lack of knowledge about the physiological mechanisms of salt tolerance has hampered the development of reliable and rapid screening procedures. Nevertheless, several techniques have been proposed. Resistance to osmotic shock (46), reaction to dye reduction techniques (52), cyclosis and plasmolysis (43), respiration rate, solute uptake (41), rooting, and survival have all been proposed as possible criteria for selecting salt tolerant lines. As yet, none of these methods has proven wholly reliable or been widely accepted.

In this capsule review I have attempted to present a few additional and perhaps some novel approaches to screening and selection based on what is presently known about the physiological and morphological mechanisms of salt tolerance. Success depends upon one's ability to identify plants that have heritable characters that enable them to withstand high salt concentrations. One of the biggest choices that must be made concerns the mechanisms of salt exclusion. Should selections be made for ion exclusion or ion accumulation? While many salt-tolerant glycophytic lines exclude Na or Cl, the efficiencies and thresholds in such systems may be inferior to halophytic systems which accumulate salt. Conversely, the effect of ion accumulation on nutritional quality of food crops will require additional investigation. Finally, salt tolerance adaptations fall into two categories: 1) those that are induced by the presence of salt, and 2) those that are phenotypically fixed with or without salinity. The salt-tolerant ideotype would have a large number of inducible traits so that it would not be maladjusted in nonsaline environments.

Literature Cited


