

ADAPTATION OF PLANTS TO SALINITY

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I. INTRODUCTION

If life evolved in the sea, and if ancient seas were saline, why then are crop plants sensitive to salt? This somewhat naive rhetorical question is worthy of consideration. Geologic processes contributed to the slow dissolution of the earth's crust and led to the deposition of significant amounts of sodium, calcium, magnesium, chloride, sulfate, carbonate, and numerous other inorganic compounds into the oceans. Thousands of salt-tolerant plant species, ranging from unicellular algae and diatoms to the giant plankton and seaweeds, inhabit the oceans and seas of the earth. As terrestrial environments arose from the abating seas, new niches were provided for plant exploitation-environments in which wetting and drying cycles occurred. Survival and success under such conditions required root and vascular systems to harvest and transport water, mechanisms to sequester and recycle nutrients to aerial shoots, and tolerance to desiccation. Plants colonizing land areas distal to the oceans were dependent on rain. Those species that could rise above the ground to intercept light from their neighbors had a competitive advantage. This kind of competition may have led to the gradual loss of characters contributing to salt tolerance, a loss that has been exacerbated beginning a few hundred thousand years ago following the discovery of agriculture, when early plant breeders based selections on high growth rates.

The art of agriculture eventually led to irrigation. Irrigation practices began about 2500 years ago and have increased dramatically during the past 30 years (Postel, 1989). They have contributed substantially to increases in world agricultural productivity (Rechcigl, 1982; Shannon, 1987). Irrigation has also contributed to increasing salination of agricultural lands and has caused the destruction of agriculture in some areas (Armillas, 1961; Rhoades, 1974; van Schilfhaarde, 1984). It is now estimated that 10% of the world's croplands are affected by salinity. Of the irrigated lands, as much as 20-27% may be salt affected and up to 37% may be saline, sodic, or waterlogged (Ghassemi et al., 1995). In the United States, 23% of irrigated cropland is saline or sodic and, if both irrigated and nonirrigated lands are considered, saline-affected soils cover more than 19.6 Mha. Salination is inevitably associated with irrigation. Typically, irrigation water contains 0.1-4 kg salt m^{-3} and is applied at rates from 1 .0 to 1.5 m annually. Thus, from 1 to 60 metric tons of salt per hectare are applied to croplands annually. In order for agriculture to be sustainable, this salt, minus water used in evapotranspiration, must be removed from the crop root zone by leaching and drainage.

There is evidence that farmers first dealt with salinity by replacing salt-sensitive crops with more salt-tolerant ones; barley (*Hordeum vulgare*) replaced wheat (*Triticum aestivum*) in early Ethiopia (Marr, 1967). Thus, crop substitution was probably used as a method of dealing with salinity long before technologies were developed to leach salts from soils and to avoid salinity problems using various

management strategies. Substitution of salt-tolerant crop species for sensitive species is still practiced in all the saline growing areas of the world. Some crops, such as sugar beet, barley, cotton (*Gossypium* spp.), asparagus, sugarcane, and dates, are very salt tolerant; however, climatic, nutritional, and economic needs often require a greater diversity of salt-tolerant crop species than is now available. The improvement of salt tolerance in cultivated plants has only recently attracted the attention of plant breeders and scientists.

Vast reclamation projects have been implemented to recover some croplands, but strategies have also been proposed to improve the salt tolerance of crop species not as an alternative to reclamation but as an augmentation to it (Shannon, 1982, 1984; Epstein, 1985). Recently, interests in maintenance of the environment, preservation of natural resources, and a consciousness toward human health and nutrition have placed a new impetus on water quality standards (Ghassemi et al., 1995). These issues, and the occurrence of drought conditions in the western United States during a period when urban water requirements are at an all-time high, have forced severe demands on high-quality water resources (McClurg, 1993). The use of recycled water, drainage water, or other poor-quality water on crops with improved salt tolerance has been proposed as part of the solution to some of these problems (van Schilfgaarde and Rhoades, 1979).

Thus, within the past 15 years, interests have gradually increased to improve the salt tolerance of both crop and ornamental plant species. Four major strategies have been proposed; (i) to gradually improve the salt tolerance of crops through conventional breeding and selection; (ii) to introgress crops with their wild progenitors, which may already possess salt tolerance; (iii) to domesticate wild species that currently inhabit saline environments (halophytes) by breeding and selection for improved agronomic characteristics; and (iv) bold strategies have been suggested in which genes for salt tolerance can be identified, cloned, and manipulated across conventional genetic barriers using the advanced techniques of molecular biology.

II. RATIONALE FOR BREEDING FOR SALT TOLERANCE

Crops are generally selected for marketability and how well they fit the environment and rotational system. Specific varieties are selected for resistances and tolerances to local diseases and environmental stresses. Where soil or water salinity is a potential problem, the crop salt tolerance is an important determinant. Conventional selection and breeding can be used to improve salt tolerance in both sensitive and tolerant crops. Increased salt tolerance in sensitive species has great economic potential beyond the improvement of yield in moderately saline areas. It provides the farmer greater flexibility for crop selection when markets for the

limited number of salt-tolerant crops are saturated. Additionally, in areas where reclamation is required through leaching, relatively small increases in salt tolerance may greatly reduce the leaching requirement. Leaching efficiency decreases, as measured by percentage decrease in soil salinity per unit water applied, depending on the soil salinity that can be accepted (Hoffman, 1980). Improved salt tolerance in sensitive and tolerant crops would allow more extensive use of brackish water supplies—an especially important consideration where water costs are high or water availability is low.

The development of new crops that have a high degree of salt tolerance is also a tenable strategy. Jojoba, although not too salt tolerant, is a high cash value crop in areas unsuited to conventional farming practices. Other new crops, such as *Atriplex*, *Salicornia*, and *Distichlis*, have high salt tolerance but have not yet emerged as widely accepted crops (Glenn and O'Leary, 1985; Glenn *et al.*, 1991; Yensen, 1988). New crops could be produced with recycled or reclaimed water that is no longer suited for municipal purposes or irrigation on conventional crops. However, even this strategy faces competition; reclaimed municipal water is now commonly used to irrigate golf courses and parks. Consequently, there is a corresponding interest in maintaining the quality of municipal water, which has led to restrictions on the use of water softeners and general water quality guidelines for sewage. Clearly, water quality has become an important socioeconomic issue and conflicts between water use for agriculture versus municipal and industrial purposes will continue to increase.

All these potential advantages draw attention to the fact that too little progress has been made in improving salt tolerance of crops. However, in a recent review, Flowers and Yeo (1995) conclude that salinity has not yet become a significant agricultural problem to warrant an intensive breeding effort. There is currently a need to develop new direction and cohesive impetus in the area of salt-tolerant crops development. Realistic short- and long-range goals need to be established and continually pursued. The information that we now have is extensive but fragmented. The purpose of this chapter is to outline some of the foremost issues and strategies concerning selection and breeding for plant salt tolerance, to highlight crucial advances in knowledge in recent years, and to identify some of the fundamental gaps in our understanding.

III. SELECTION FOR SALT TOLERANCE

Salt tolerance is a complex, quantitative, genetic character controlled by many genes. A few of these genes have been identified and provide information that can be useful in screening and selection programs (Shannon, 1996; Shannon and Noble, 1990). Information is lacking on how most genes function in concert with other genes that may have influenced the mechanisms of salt tolerance.

A. MEASUREMENT

To be able to improve salt tolerance, we must first be able to measure it in a meaningful way. Plant salt tolerance is generally thought of in terms of the inherent ability of the plant to withstand the effects of high salts in the root zone or on the plant's surfaces without a significant adverse effect. Salt resistance is another term that is often used for this phenomenon, and although some have tried to differentiate the two terms (Levitt, 1972), the terms are used interchangeably. In an agronomic context, salt tolerance is described as a complex function of yield decline across a range of salt concentrations (Maas and Hoffman, 1977; van Genuchten and Hoffman, 1984). Using a simple convention, salt tolerance can be measured on the basis of two parameters: the threshold (EC_e), the salinity that is expected to cause the initial significant reduction in the maximum expected yield (Y_{max}), and the slope (s) (fig. 1). Slope is simply the percentage of yield expected to be reduced for each unit of added salinity above the threshold value. Relative yield (Y) at any salinity exceeding EC_e , can be calculated as

$$Y = 100 - s(EC_y - EC_e), \quad (1)$$

where $EC_y > EC_e$.

Usually, salinity is measured in units of electrical conductivity of a saturated soil paste extract (EC_e), taken from the root zone of the plant as averaged over time and depth. Soil paste extracts are soil samples that are brought up to their water saturation points. Electrical conductivities are measured on the filtered water extracts from these samples in units of deciSemens per meter ($dS\ m^{-1}$), or previ-

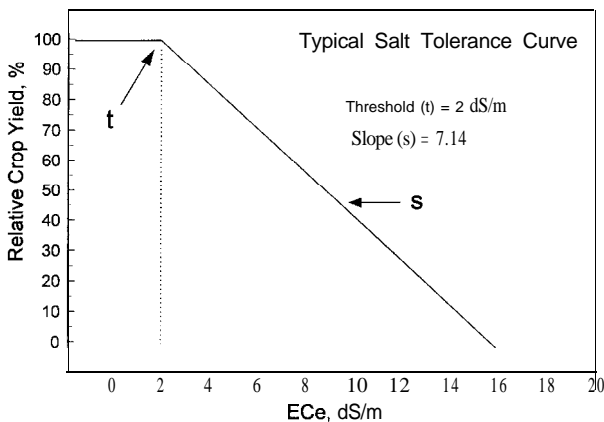


Figure 1 Typical salt tolerance graph depicting the threshold (t) and slope (s) parameters. Threshold is defined as the salinity at which yield decline is significantly reduced relative to nonsaline conditions. Slope is a function of the amount that yield is reduced by salinity beyond the threshold.

ously as millimhos per centimeter. New methods use electronic probes or electromagnetic pulses to calculate EC_e with less time and effort (Rhoades, 1976; 1993a).

Reliable data to describe the salinity functions can only be obtained from carefully controlled and well-replicated experiments conducted across a range of salinity treatments. In order to provide information to growers concerning the potential hazards of a given saline water or soil, data of this type have been compiled for 127 crop species, which include 68 herbaceous crops, 10 woody species, and 49 ornamentals (Mass, 1986, 1990). Thus, crop substitutions can be made if the potential hazards indicate that expected yield reductions may be economically disastrous. A brief examination of the threshold and slope parameters gives an indication of the potential range in variability that is found among the major domesticated plant species. Although the information that comprises this database is considered to be reliable, it is significant that multiple varieties were examined in trials for only 28 of the species. Clearly, the variability for salt tolerance based on yield criterion has not been adequately explored.

B. YIELD AND PRODUCTIVITY

Unfortunately, traditional measurement of salt tolerance as just described is not directly applicable to selection methods. One component of the measurement, the threshold or the salt concentration at which yield decline begins, is highly sensitive to environmental interaction and is dependent on both the accuracy of salinity measurements and the method by which they are integrated over plot area, depth, and time. Because of this, there is a degree of error in evaluating the slope at salt concentrations near the threshold. At the highest salt concentrations, there is a tendency for the slope to "tail-off." This results in added uncertainty at this part of the curve. For agronomic purposes, salt tolerance at high salinities has little economic importance but the merit of selecting for tolerance at these salinities has not been thoroughly evaluated. It has been speculated that the physiological and genetic factors that contribute to the growth of glycophytes at very high salt concentrations may be proportionally related to survival more than to high yields and probably are not of interest to the grower except in cases of subsistence agriculture at the most meager level (Shannon and Noble, 1990). Among glycophytes, genetic variance is usually lower at these high salinities than at lower salinities.

The fundamental selection criteria in plant breeding are mean yield and yield stability across environments. Richards (1983, 1995) indicates that because of the heterogeneity of saline soils it is best to select for productivity rather than salt tolerance. When the genetic correlation for yields across environments is highly negative and genetic variance in the stress environment is less than that in the non-stress environment, selection for productivity will normally increase yields in both environments (Rosielle and Hamblin, 1981). Alternatively, if it can be shown that there is some capacity for selection under a particular stress environment, i.e., ge-

netic variance is high compared to that under nonstress, tolerance might be improved without a concomitant yield decrease in a nonstress environment. These principles were demonstrated by Johnson *et al.* (1992), who found that selection for increased yield in alfalfa (*Medicago sativa*) was effective under low and moderate salinities but not under nonsaline conditions.

Salt tolerance (S) can be described as a reduction in yield at a given salinity (Y_s) with respect to a measured yield under nonsaline conditions (Y_c):

$$S = Y_s/Y_c. \quad (2)$$

This index may change with the degree of the salinity stress that is imposed. Another index for stress was proposed by Fischer and Maurer (1978) that allows comparisons where the mean population relates the ratio of yield under stress and nonstress conditions to the ratio of the means of all genotypes under stress and nonstress conditions (D is the mean of all genotypes under stress/mean of all genotypes in a nonstressed environment):

$$S = \frac{1 - (Y_s/Y_c)}{1 - D}. \quad (3)$$

One of the difficulties in making selections for salt tolerance is that low-yielding varieties seem to be proportionately less sensitive to the effects of salinity than are high-yielding varieties. It has been previously found that there is a negative correlation between high mean yield and phenotypic stability across environments (Finlay and Wilkinson, 1963; Frey, 1964). Selection for salt tolerance under the wrong conditions or using the wrong genetic material can result in low-yielding selections that are not competitive with higher yielding, nontolerant varieties (Richards, 1983).

Thus, salt-tolerant lines selected on the basis of Eqs. (2) or (3) may be lower yielding lines at low to moderate salinities. This almost universal phenomenon may be due to the fact that high-yielding lines are nearing their capacity to divert as much of their assimilated carbon to yield potential as possible, whereas, low-yielding lines may still retain some mechanisms for stress adaptation.

In addition, certain complications are inherent in the measurement of salt tolerance for purposes of screening. As noted, assessments for tolerance as measured in Eqs. (2) and (3) cannot be made on single plants in a segregating population because information must be collected on a relative basis. How well a plant grows under saline conditions depends on both salt tolerance and vigor. Comparisons between performance under control and saline conditions can be made on genetically segregating material only if progeny lines with some degree of homozygosity are established first. This is a time- and labor-consuming process.

Because of the difficulties in accurately measuring salt tolerance, indices other than yield have been suggested for breeding work. These include tolerance during germination; conservation of shoot dry weight, root weight, or shoot number; resistance to leaf damage; maintenance of flowering, seed and fruit set, leaf size,

canopy volume, or quality; and plant survival under salt stress. The selective value of these assessments depends on the agronomic situation and will be discussed more thoroughly in a later section. Other indices of tolerance have been proposed that are based on specific physiological characters; for instance, specific accumulation of an ion in shoots or leaves or the production of a metabolite. No such criteria have been unequivocally correlated with salt tolerance, but some, as will be discussed, have higher degrees of correlation than others. The value of any parameter undeniably depends on species and, in certain cases, varieties.

C. GROWTH STAGE

Another nuance associated with assessment and measurement of salt tolerance is variation with ontogeny or growth stage (Lunin *et al.*, 1963). Rice (*Oryza sativa*), for example, is sensitive during the early seedling stages and at flowering (Akbar and Yabuno, 1977) sugar beet is tolerant during later growth stages but is sensitive during germination (Beatty and Ehlig, 1993), and corn (*Zea mays*) is tolerant at germination but is more sensitive at seedling growth than for ear and grain yield (Maas *et al.*, 1983). Efforts to evaluate salt tolerance in a species on the basis of tolerance during germination and emergence have not generally been successful; tolerance at one growth stage usually is not related to another.

Salinity often affects the timing of development. In wheat, sorghum (Sorghum bicolor), and oats, ear emergence, anthesis, and grain maturity occur earlier under saline conditions, whereas, in barley and rye maturity is unaffected by salinity (see Shannon *et al.*, 1994). In cotton, flowering occurs earlier under salt stress, but salinity delays flowering of tomato, *Lycopersicon esculentum* (Pasternak *et al.*, 1979).

Yield components and growth parameters also show differential responses to salinity stress. Ayers *et al.* (1952) found that in barley and wheat seed production was decreased less than shoot dry weight (wt) by salinity. Likewise, at low salinities root growth is often less affected, or sometimes even stimulated by salinity, compared to shoot growth. In muskmelons, salt tolerance decreased in the following order: total vegetative dry wt > total vine yield > fruit yield > marketable yield (Shannon and Francois, 1978). Consequently, the degree of salt tolerance between and within species is likely to vary according to the criteria used for evaluation. In a review, Jones and Qualset (1984) assert that plant growth attributes must be measured throughout the growth period so that particularly salt-sensitive growth stages can be identified.

Because of the differences in salt tolerance between growth stages, some investigators have resorted to selection for tolerance by imposing salt stress over the entire growth cycle (Epstein *et al.*, 1980). However, if a constant salt concentration is used in this strategy, the degree of selection pressure will vary with growth stage. For some species, independent selection at more than one growth stage may be appropriate. This would permit the development of lines with optimal tolerance

at each specific growth stage followed by a crossing program to combine these tolerances into a single variety.

In some agricultural situations, selection for salt tolerance at only one growth stage may have a significant benefit. For instance, sugar beet is very salt tolerant during vegetative growth stages but is sensitive to salinity during germination (Bernstein and Hayward, 1958) and selection during this stage could remove a limiting step to tolerance throughout its growth. For a large number of crops, adequate information is not available concerning salt sensitivities during development. Sometimes salt tolerance at specific growth stages may be used to advantage. Moderate salinity applied during fruit development can change the partitioning of photosynthates and improve soluble solids in melon and tomato (Shannon and Francois, 1978, Mizrahi and Pasternak, 1985; Mizrahi *et al.*, 1988). Any small yield decrease due to salinity is offset by the higher marketable quality of the fruit.

Some grain crops, such as sorghum, wheat, and barley, are extremely insensitive to relatively high concentrations of saline water applied during or just prior to anthesis (Maas *et al.*, 1986; Maas and Poss, 1988). Such tolerance could be exploited by substituting brackish water for irrigation water during later plant growth stages. This strategy has been used successfully for both field and vegetable crops (Rhoades, 1986; Grattan *et al.*, 1987). Genetic variation for salt tolerance at specific growth stages has not been adequately examined.

D. SPECIFIC ION TOLERANCE

The relative salt responses of various crops is often dependent on soil type and other environmental factors (Levitt, 1972). Saline soils and waters include those with high concentrations of dissolved salts of many kinds, any of which may be critically limiting to plant growth. Saline soils may be sodic or acidic and cover a wide range of soil types and moisture conditions. Genotypes that show similar salt tolerance in one environment may differ in response in a different environment. Rana (1985) has cited the complexity of soils and environmental interactions as major obstacles to successful breeding for salt tolerance. He noted that crops adapted to alkali soils are usually tolerant of nonalkaline saline soils, but the converse was not true.

Most salt tolerance data have been collected based on the effects of saline waters predominated by sodium chloride, sometimes with varying amounts of calcium added as needed to avoid the development of soil permeability problems associated with soil sodicity. However, specific ion sensitivities may be critically limiting to crop growth in some geographic locations. For example, iron, aluminum, boron, selenium, arsenic, manganese, or zinc may be found in toxic or growth-limiting concentrations in certain areas. Drainage waters or waters reused from agricultural processing or manufacturing operations may have high concentrations of boron, selenium, arsenic, or other ions that may pose environmental hazards (Francois and Clark, 1979a; Clark, 1982). Plant species have demonstrat-

ed a wide degree of variation in their abilities to accumulate, exclude, or withstand the toxic effects of individual ions (Shannon *et al.*, 1994; Flowers and Yeo, 1986). Even so, the potential for variability between species and varieties remains as one of the research areas that has not been adequately explored. The genetic variability associated with plant tolerance to these ions has been reviewed in detail (Epstein, 1963; Vose, 1963; Epstein and Jefferies, 1964; Lauchli, 1976; Wright, 1976; Jung, 1978; Christiansen and Lewis, 1982).

E. ENVIRONMENTAL INTERACTIONS

Identification of a quantitative character is difficult at best, and the interactions between salinity and other environmental stresses complicate accurate assessments using yield or growth as an index of tolerance. Important environmental factors that show significant interaction with salinity include temperature, wind, humidity, light, and pollution. High temperatures and low humidities may decrease crop salt tolerance by decreasing the effective value of t in Eq. (1) and increasing the value of s . Thus, significant reductions in yields will be realized at lower salinities, and yields will decrease more rapidly with increasing salinity under hot, dry conditions. Two other environmental factors that can influence the measurable effects of salinity include elevated atmospheric levels of carbon dioxide and ozone. Salinity causes leaf stomata to restrict the volume of air exchanged with the environment. This usually improves plant water use efficiency somewhat but reduces the amount of carbon dioxide that can be fixed by the plant and be used for growth. High carbon dioxide concentrations in the air due to the so-called "greenhouse effect" may, in part, offset the reduction in air exchange. However, if pollutants, such as ozone, are present, reductions in air exchange may also reduce the volume of pollutants that enter the plant, thereby decreasing any adverse effects of salinity (Mass and Hoffman, 1977).

Root zone waterlogging is another environmental hazard that can be exacerbated by salinity. Root zone salinity and waterlogging greatly increase salt uptake compared with nonwaterlogged conditions (West, 1978; West and Taylor, 1984). Salt tolerance in saline, drained conditions can be quite different from that in saline, waterlogged conditions.

IV. SALT TOLERANCE MECHANISMS

Salinity exerts complex effects on the plant as a result of ionic, osmotic, and nutritional interactions, although the exact physiological mechanism of salt stress is unknown. Salt tolerance often depends on the anatomical and physiological complexity of the organized plant. This fact makes it difficult to find ways to increase

salt tolerance to large degrees. However, it does give hope that salt tolerance can be increased by finding the factor that is most limited by salt stress during growth and development.

Several investigators have demonstrated salt tolerance mechanisms based on factors such as ion accumulation (Rush and Epstein, 1976, 1981b; Tal and Shannon, 1983), ion exclusion (Abel, 1969; Noble *et al.*, 1984), compatible solute production (Grumet and Hanson, 1986; Wyn Jones *et al.*, 1977), late maturation (Bernal *et al.*, 1974), and pollen sterility (Akbar and Yabuno, 1977; Akbar *et al.*, 1972). Some investigators have suggested that several of these factors can be selected and combined in a reengineered individual, a process referred to as pyramiding characters (Pasternak, 1987; Yeo and Flowers, 1983).

A. ION SELECTIVITY

Salt sensitivity in some crops has been attributed to the failure of plants to keep Na^+ and Cl^- out of the transpiration stream and, consequently, the cytoplasm of the shoot tissues (Flowers *et al.*, 1977; Harvey, 1985). Under salt stress a plant must absorb nutrients and restrict the uptake of toxic ions at lower water potentials than usual. Munns and Termaat (1986) divided salt stress into short- and long-term effects. Short-term effects occur in a matter of days and involve decreased shoot growth, possibly as a result of the root response to water deficit. Long-term effects occur over weeks and result in maximum salt loads in fully expanded leaves and a reduction in photosynthetic activity. Flowers and Yeo (1986) noted that salt damage in leaves of sensitive species may be the result of excess apoplastic ion concentrations or ion toxicity effects on metabolic processes in the symplast.

Plants that limit uptake of toxic ions and maintain normal ranges of nutrient ions could be more salt tolerant than those that do not restrict ion accumulation and lose nutrient balance. Selective ion uptake mechanisms capable of discrimination between chemically similar ions such as Na^+ and K^+ could have adaptive value. The mechanisms responsible for ion discrimination probably are located in the membranes of tissues and various organelles throughout the plant (Bliss *et al.*, 1984; Kuiper, 1968). Breeding for efficient nutrient uptake or low ion accumulation under salt stress may be among the simplest ways to improve salt tolerance in sensitive varieties of some species. This also may be accomplished by finding tolerance to the toxicity of a specific ion associated with salt stress.

Munns *et al.* (1988) concluded that high salt concentrations in the phloem of the salt-sensitive *Lupinus albus* are not directly related to either growth reduction or leaf injury but are, more important, a symptom of disrupted regulation of ion transport properties in the root. Among plant species, mangroves undoubtedly have the most efficient system of restricting salt uptake through the development of a passive root membrane filtration system. The gray mangrove (*Avicennia marina*) can

exclude 90% of the salt in the medium surrounding its roots (Burchett *et al.*, 1984). It has maximal growth at 25% seawater. Other mangrove species can survive salt concentrations two or three times that of seawater (Clough, 1984). The system in mangrove is unique and, unfortunately, has not been reported in other species; most crop species limit salt uptake into the transpiration stream to some degree through membrane-mediated compartmentation in organelles (vacuoles) or tissues (Shannon, 1997). Some species may be able to rid themselves of ions through ion-sequestering organelles (salt glands) or by storing salt in the root, old leaves, petioles, stems, or tracheids (Jacoby, 1964). Salt restriction from the cytoplasm is not complete; the plant will eventually succumb to salt unless its growth rate is high enough that its salt storage sinks do not become filled, thereby preventing salt overflow into sensitive tissues (Flowers and Yeo, 1986).

Selective ion transport differences among species and varieties are the result of specific gene differences (Vose, 1963; Epstein and Jefferies, 1964). The genetic variations that may occur in each of these systems are numerous and little research has been done to evaluate the extent of that variation.

B. ION ACCUMULATION

Restriction of ions into roots or shoots is one of the most frequently reported differences between salt-tolerant and -sensitive varieties. It is well known that halophytes take up substantially high concentrations of ions as an adaptation to saline environments (Flowers *et al.*, 1977); however, some can sequester toxic ions not only in vacuoles but also in specialized organs such as salt glands and bladders (Levitt, 1972; Schirmer and Breckle, 1982). The accumulation of salt in the plant or its excretion onto leaf surfaces is believed to reduce the requirements for increased wall extensibility that might otherwise be required to maintain positive growth and turgor at low soil water potentials. The wild tomato species (*Lycopersicon cheesmanii*) is considered to be more salt tolerant than the cultivated species due to its capacity to accumulate ions (Rush and Epstein, 1981b), and the salt-tolerant "Edkawy" tomato also accumulates higher concentrations of Na^+ in leaf tissues than does more sensitive cultivars of *L. esculentum* (Hashim *et al.*, 1986). As with salt restriction, salt accumulation within tissues is believed to be well regulated and generally sequestered away from cytosolic compartments containing the salt-sensitive metabolic machinery of the cell. In both glycophytes and halophytes, salt may accumulate preferentially in vacuoles, interstitial compartments, stems, or older leaves. The physical and genetic factors that influence ion compartmentation and distribution within plants are mostly unknown. Only a few crop species, e.g., sugar beet, are halophytes. It may not be practical to attempt to transfer halophytism into glycophytic crop species. However, several investigators have shown an interest in developing the agronomic potential of wild halophytes into new and useful salt-tolerant crops.

C. OSMOTIC ADJUSTMENT

Osmotic adjustment is a decrease in plant osmotic potential through an increase in solute content (or a decrease in water content) in response to a decrease in external water potential to the extent that turgor potential is maintained. There is some controversy whether osmoregulation even occurs in higher plants (see Munns and Termaat, 1986). Nevertheless, substantial differences in their capacity for osmoregulation have been noted among wheat genotypes (Morgan, 1977).

High humidities improve the tolerance of corn, bean, onion (*Allium* spp.), radish, and barley but not of cotton, wheat, and red beet (Gale et al., 1967; Hoffman *et al.*, 1971; Hoffman and Rawlins, 1971; Hoffman and Jobes, 1978; Prisco and O'Leary, 1973). The relative sensitivity of crops to osmotic stress may vary with external salt concentrations. This may indicate that certain crops may benefit from selection pressures, which improve their capacity to adjust osmotically or maintain more favorable water relations under salt stress (Tal and Gardi, 1976; Shannon et al., 1987). Generally, poor osmotic adjustment leads to turgor loss and stomatal closure, which is soon followed by reduced gas exchange and photosynthesis. Turgor loss, in turn, can also have detrimental effects on cell division and elongation.

D. ORGANIC SOLUTES

Sugars, proline, glycinebetaine, and other organic solutes are believed to improve salt tolerance by contributing to osmotic balance and preserving enzyme activity in the presence of toxic ions (Greenway and Munns, 1980; Grumet *et al.*, 1985; Tal *et al.*, 1979). Rathert (1984) noted that salinity causes greater leaf sucrose increases in salt-sensitive species than in tolerant species. He suggested that leaf sucrose and starch concentrations could be used as a selective index in screening for improved salt tolerance. High betaine genotypes of barley maintained lower solute potentials than near-isoline, low-betaine genotypes grown at the same salinities (Grumet and Hanson, 1986). This also suggests that betaine could be used as a selection index for improved salt tolerance, although these characters alone may prove to be inadequate criteria if other salt-tolerant characteristics are not maintained.

E. WATER USE EFFICIENCY

Other mechanisms that could prevent turgor loss and better water efficiency are increased leaf resistance (fewer stomata, increased mesophyll resistance, and increased cuticle thickness) or a higher root-shoot ratio. Plant diversity provides evidence that each of these strategies may be accomplished in various ways. Most of

these strategies, however, are associated with some aspect of growth and metabolism that is detrimental to maximum crop production.

Most measurements of water relations are not accurate or reliable enough to be useful in screening techniques for salt tolerance. Future advances in instrumentation and more thorough understanding of water relations mechanisms may some day improve the breeder's ability to select genotypes based on the maintenance of optimum water relations during salt stress.

V. GENETIC VARIABILITY

One requirement for breeding for salt tolerance is that genetic variation exists for the character in the gene pool. Such variation may be between individuals, varieties, or even species that have some degree of sexual compatibility so that genes may be transferred from one individual to another. Another necessity is that salt tolerance can be identified in segregating generations or that specific information exists concerning its genetic control in terms of numbers of genes involved and their heritability. Although considerable research has been devoted to quantifying the salt tolerance of various crop species (Francois and Maas, 1978, 1985; Maas and Hoffman, 1977; Maas, 1985, 1987), data for many species are usually based on comparisons among only a few varieties. In studies that have examined a range of varieties, some species exhibit wide intraspecific variation of salt tolerance, whereas others have limited variation. Usually, only a relatively small portion of the existing germplasm base has been screened. Many wild progenitors of cultivated species have not been tested.

A. GRAINS

Grain crops include both tolerant (e.g., barley) and sensitive (e.g., rice and corn) species (Fig. 2). There are many examples in which salt tolerance has been indirectly developed in varieties selected for high yield in naturally saline environments. Some wheat, barley, cotton, and rice varieties developed primarily for high yield in saline regions of Pakistan, India, Egypt, and the United States have better salt tolerance than varieties developed in nonsaline areas (Akbar *et al.*, 1972; Bernal *et al.*, 1974; Kingsbury and Epstein, 1986). For example, individual plants selected directly from fields in the Kharchi-Pali area of Rajasthan led to the development of the salt-tolerant Kharchi-Rata wheat line (Rana, 1986). Other wheat varieties in which salt tolerance has been demonstrated include Sakha-8 (Egypt), LU-26S (Pakistan), and SARC-1 (Pakistan). Measurement of salt tolerance in wheat varies with growth stage (Srivastava and Jana, 1984; Ashraf and McNeilly, 1988).

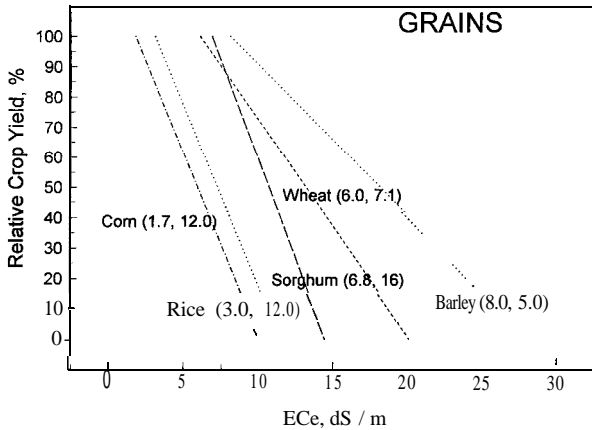


Figure 2 Comparative differences in salt tolerance among a number of grain crops. Values in parentheses represent the threshold and slope values for each species (t , s). Data serve only as a guideline to relative tolerances and may vary depending on climate, soil conditions, and cultural practices.

Barley is one of the most salt-tolerant grain and forage crops. Salt tolerance in varieties such as CM67 and Albacete have been correlated with their abilities to exclude Na^+ from the shoot (Royo and Aragues, 1993; Wyn Jones and Storey, 1978). Extensive screening for salt tolerance in wheat and barley has been conducted among thousands of accessions of the world collections (Kingsbury and Epstein, 1984).

Breeding and selection efforts in wheat involve crossing the cultivated hexaploid species with diploid wheat or closely related wild relatives in an effort to improve the variability for salt tolerance (Dvořák et al., 1985; Dvořák and Gorham, 1992; Dubcovsky *et al.*, 1996; King et al., 1996). Wheat collections have been extensively screened for salt tolerance. Approximately 9% of 5000 hexaploid, tetraploid, and diploid accessions of wheat and triticale survived to the seedling stage in pots irrigated with the equivalent of 50% seawater (Sayed, 1985). In solution cultures, 29 accessions from more than 5000 entries of spring wheats grew to seed set at 50% seawater concentrations (Kingsbury and Epstein, 1984). Among 400 Iranian tetraploid and hexaploid accessions, high grain yield under salinity stress (see Eq. (3)) was found to be a better criterion for salt tolerance than biomass, harvest index, or relative salt tolerance (Jafari-Shabestari et al., 1995). With respect to yield parameters, tolerance has shown a high coefficient of correlation with grain number per ear (Singh and Rana, 1985), but Maas *et al.* (1996) reported that the loss of spike-bearing tillers accounts for most of the yield reduction with salinity. Water use efficiency or photosynthetic capacity as measured by carbon assimilation rate are only two of the parameters in wheat that have not been

shown to be reliable measures of discrimination for salt tolerance. However, a relationship has been shown between tolerance and high K^+/Na^+ in grain and straw (Ashraf and O'Leary, 1996; Chhipa and Lal, 1995), and salt-tolerant varieties such as Kharchia and Sakha-8 were found to have lower concentrations of leaf Na^+ than sensitive varieties (Salama *et al.*, 1994).

Sorghum has intermediate salt tolerance and is more tolerant at germination than during later growth stages, and vegetative growth is less affected by salinity than yield (Francois *et al.*, 1984). Seedling response in two studies, one with 48 cultivars and another with 51 accessions, indicated that significant variation in salt tolerance as measured by dry weight increase exists and that improvement through recurrent selection should be possible (Taylor *et al.*, 1975; Azhar and McNeilly, 1987). Varieties that were most tolerant included Desert Maize, Shallow, and Hegari in one study, and Double-TX, INRA 383, PAK SS 11, and Red Jampur in the other. Previously, Double-TX was selected for salt tolerance (Francois *et al.*, 1984). Genetic variation for osmotic adjustment was found among 10 inbred lines (Basnayake *et al.*, 1994). Variation was attributed to more than a single gene and both GCA and SCA were found to be significant. It has been shown that higher levels of salt tolerance can be induced in sorghum by certain pretreatments. Pretreatment of seedlings with 75-150 mol m^{-3} NaCl for 20 days resulted in plants that could withstand 300 mol m^{-3} NaCl, whereas controls without pretreatment did not survive (Amzallag *et al.*, 1990).

Corn is more sensitive to salinity during the seedling stage than during germination or later growth stages, although genetic variation exists at all stages (Maas *et al.*, 1983). No clear relationship has been found between salt tolerance at different growth stages. Maize responds primarily to osmotic, rather than ionic, effects (Kumar and Singh, 1982; Cramer *et al.*, 1994). A natural recurrent selection program using saline irrigation water (2000-4000 mg liter⁻¹ total soluble salts) over a period of 20 years was used to develop Arizona 8601 maize (Day, 1987). This maize outyielded Pioneer 3 183 in both silage (+38%) and grain (+26%) production under the conditions in which it was selected.

In salt-sensitive rice (*O. sativa*), injury is directly related to the toxic effects of NaCl in the shoot tissues that cause leaf burn. Salt-tolerant genotypes regulate both the absorption and the translocation of ions better than sensitive genotypes (Yan *et al.*, 1992). Interactive factors that influence salt tolerance include the sensitivity of the variety to Na^+ -induced Ca^{2+} deficiency and the capability of the variety to maintain shoot K^+ levels against high concentrations of Na^+ in the root zone (Grieve and Fujiyama, 1987). Transpirational bypass flow has been found to be a major contributing factor in sodium transport and is a heritable trait (Yadav *et al.*, 1996). In plot and field trials based on yield, Giza-159 rice was selected for salt tolerance in Egypt from a cross between the salt-tolerant Agami 1 and the locally adapted Giza 14 (Gad El-Hak, 1966). In subsequent efforts to further improve tolerance, Giza 159 was crossed with the salt-tolerant variety Reiho. Recently, a good correlation among varieties was reported between high paddy yield and shoot

weight after 15-day-old seedlings were grown for 15 days in solution cultures containing 100 mM NaCl (Aslam *et al.*, 1993). Most studies report that salt tolerance at different growth stages in rice is not well correlated to yield under saline conditions.

Despite the limited number of released varieties specifically bred for improved salt tolerance, breeding efforts to produce such varieties are rapidly expanding. There are many studies under way that may result in more salt-tolerant crops in the near future. The International Rice Research Institute (IRRI) has screened more than 10,000 accessions of rice for salt tolerance in greenhouse tests and has identified many promising varieties (IRRI, 1977).

B. FIELD CROPS

This category of crops covers a wide range of salt tolerance, from the salt-tolerant cotton and sugar beet to the sensitive bean and peas (Fig. 3). Cotton is very salt tolerant, although it is more sensitive during germination and emergence (Francois and Bernstein, 1964; Ghorashy *et al.*, 1972). Screening for tolerance at germination and selection was conducted on a number of Egyptian cotton cultivars and Bahtim 110, Menoufi, Ashmouni, and Bahtim 108 were shown to be most tolerant (Ashour and Abd. El-Hamid, 1970). *Gossypium barbadense*, *G. herbaceum*, and *G. neglectum* are generally more tolerant than *G. hirsutum*; of 37 American cotton varieties (*G. hirsutum*), only 7 were tolerant (Novikov, 1943).

Sugar beet (*Beta vulgaris*) is very salt tolerant. Iyengar and Pandya (1977) stud-

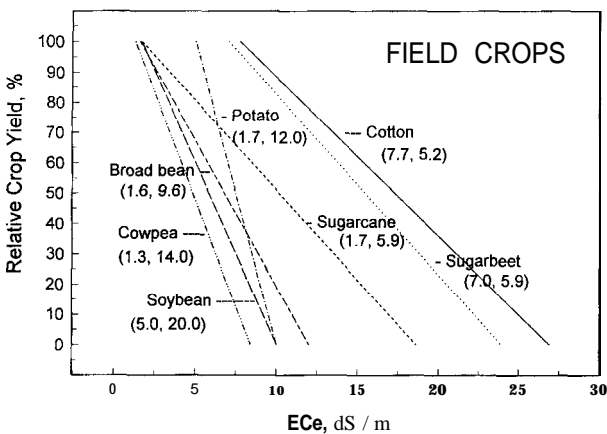


Figure 3 Comparative differences in salt tolerance among a number of field crops. Values in parentheses represent the threshold and slope values for each species (*t, s*). Data serve only as a guideline to relative tolerances and may vary depending on climate, soil conditions, and cultural practices.

ied salt tolerance among 20 varieties representing a range of germplasm. Irrigation with seawater dilutions equivalent to 22,000 mg liter⁻¹ in sand reduced tuber yield in only half of the entries. Sugar content was only slightly reduced in the tolerant entries. The varieties U.S.H.9, Maribo Magnapoly, and Kawep Precopoly were the most tolerant.

Potato (*Solanum tuberosum*) is moderately sensitive to salinity (Ahmad and Abdullah, 1979). Variability for tolerance exists among varieties and wild relatives (Arslan *et al.*, 1987; Bilski *et al.*, 1987) but little effort has been made to improve tolerance in this species. A close correlation has been observed between salt stress response of cultured roots and that of whole plants (Naik and Widholm, 1993).

In field screening trials ion sites in which poor leaching had failed to remove excessive KCl fertilizer, Parker *et al.* (1986) evaluated chloride-induced leaf scorch in 65 varieties of soybean (*Glycine max*) in four maturity groups. As noted, susceptibility to Cl⁻ damage is the result of a single gene. However, it has been shown that an interaction exists between Cl⁻-induced injury and high inorganic phosphate concentrations above 0.12 mol m⁻³ in solution culture (Grattan and Maas, 1984, 1988). In addition, a mixture of NaCl:CaCl₂ was found to be more toxic than NaCl salts at the same osmotic potential because of the added proportion of Cl⁻. These observations are critical in designing screening studies with soybean, especially under controlled conditions in hydroponics and sand cultures. Interactions between phosphate and Cl⁻ also have been reported in sesame (*Sesamium indicum*) and corn (Bernstein *et al.*, 1974; Cerda *et al.*, 1977).

Salt tolerance comparisons among a number of salt-sensitive, cool-season food legumes has shown that faba bean is more tolerant than lentil and chickpea, rated in both germination and yield tests (Saxena *et al.*, 1994). Lentil and faba bean are more sensitive at germination than at later growth stages, but the converse is true for chickpea. Screening for tolerant genotypes had been done in both field and controlled conditions based on yield and visual symptoms.

C. OIL SEED CROPS

Canola (*Brassicu* spp.) is a derivative of rapeseed (*Brassica napus*) that has low saturated fat and, hence, has increased in importance among the oil seeds (Fig. 4). This species is very salt tolerant and in salt-tolerance trials did not exhibit yield decline until soil salinity exceeded 10 dS m⁻¹ in the saturated soil extract. Yield declined at a rate of only 11.2% per unit increase in salinity above this threshold (Francois, 1994). Oil content and protein content in the oil-free seed meal were not affected by salinity.

Safflower (*Curthumus tinctorius*) is less tolerant than sugar beet but more tolerant than the legumes. Like cotton, it is more sensitive during germination and seedling growth than during later growth stages (Abul-Naas and Omran, 1974). In

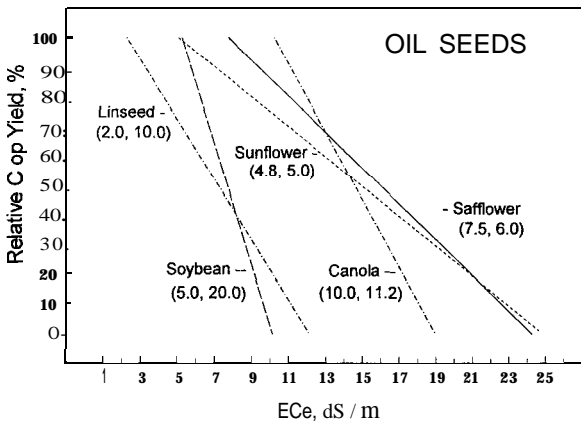


Figure 4 Comparative differences in salt tolerance among a number of oil seed crops. Values in parentheses represent the threshold and slope values for each species (t, s). Data serve only as a guideline to relative tolerances and may vary depending on climate, soil conditions, and cultural practices.

safflower, high salinity does not affect the fatty acid composition of the oil in standard varieties but does decrease oleic acid in a high-oleate variety (Yermanos *et al.*, 1964; Irving *et al.*, 1988). Safflower has a high threshold salinity (approximately 7.5 dS m^{-1}) and a yield decline of approximately 6 dS m^{-1} (Francois and Bernstein, 1964). Little variation was noted among 11 cultivars (Irving *et al.*, 1988).

Sunflower (*Helianthus annuus*) is moderately tolerant to salinity; yield is unaffected by salinities up to 4.8 dS m^{-1} (t) in the saturation soil extract and declines by approximately 5% per unit increase in salinity thereafter (Francois, 1996). Yield decreases were attributed to reductions in the number of seeds per head, but no significant genetic differences were found among four varieties. In a more extensive study for varietal differences, 45 accessions were evaluated for seedling growth in salinity trials, and HO- 1, Predovik, and Euroflor were found to be the most tolerant (Ashraf and Tufail, 1995). A wild relative of sunflower, *H. paradoxus*, has been found to be more tolerant at the seedling stage by virtue of a single dominant gene, Sa_7 , but a modifier gene may also be involved (Miller, 1995). This work could lead to an increase in salt tolerance in progeny derived from interspecific crosses.

Another oil seed crop, linseed (*Linum usitatissimum*), by comparison, is more sensitive to salinity. Based on screening tests conducted on 36 accessions, threshold values for two sensitive genotypes (P-70 and Aver-Ret-Seic) and two tolerant genotypes [T-5(69-S9)B and LS-2] were calculated to be 0 and 2 dS m^{-1} , respectively (Ashraf and Fatima, 1994). Above the threshold, yield declined at a rate of approximately 10 dS m^{-1} .

D. GRASSES AND FORAGES

Some grasses are sensitive to salinity, but many, such as Bermuda grasses and wheatgrasses, have high tolerance (Fig. 5). Growth rate, leaf chlorosis, and recovery rates were found to be useful indices for screening 33 accessions of wheatgrass (Shannon, 1978). Hybridization of two salt-tolerant lines indicated that tolerance was an additive character (Weimberg and Shannon, 1988). The desert wheatgrass (*Agropyron desertorum*) variety Nebraska 10 was selected as a salt-tolerant strain in artificially salinized field trials (Dewey, 1962). Variation for salt tolerance

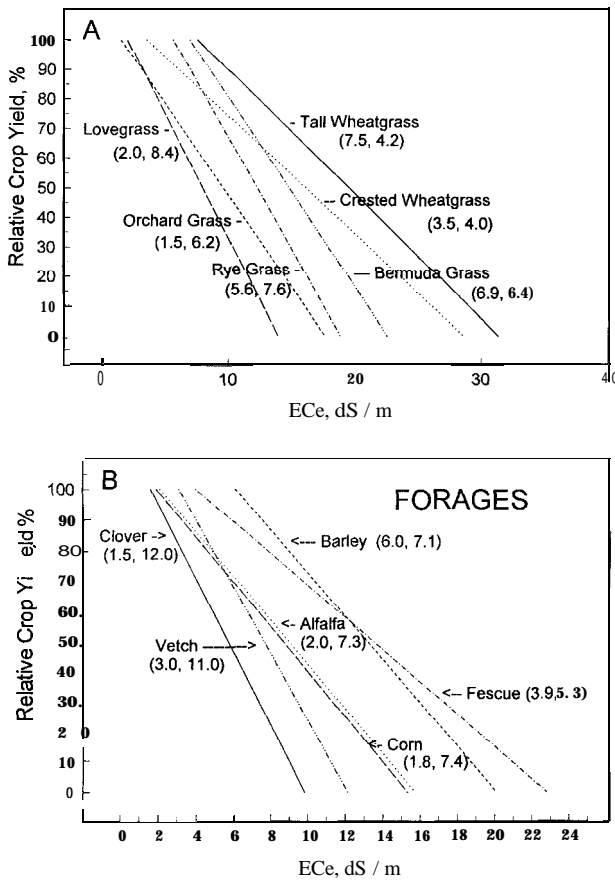


Figure 5 Comparative differences in salt tolerance among a number of grass (A) and forage (B) crops. Values in parentheses represent the threshold and slope values for each species (*t, s*). Data serve only as a guideline to relative tolerances and may vary depending on climate, soil conditions, and cultural practices.

among Bermuda grasses (*Cynodon* spp.) has been demonstrated (Dudeck et al., 1983; Francois, 1988). At high salinities Na^+ increased in shoots and K^+ decreased, despite the fact that Bermuda grasses have salt glands (Breckle, 1992).

Among five Kentucky bluegrasses (*Poa pratensis*), Adelphi and Ram I were shown to be significantly more tolerant to NaCl than other cultivars tested (Torelle and Symington, 1984). Seedling root length in NaCl solution cultures was used as an indicator to determine heritability estimates and demonstrate that improvement in salt tolerance could be made in several grasses including *Lolium perenne*, *Dactylis glomerata*, *Agrostis stolonifera*, *A. castellana*, *Puccinellia distans*, and *Festuca rubra* (Ashraf et al., 1986a,b). An ecotype of red fescue (*Festuca rubra*), selected from a tidal marsh, has been developed into the variety Saltol for use in the revegetation of roadsides that are affected by deicing salts (Cordukes, 1981).

Alfalfa is intermediate in tolerance among the forages (Fig. 5). There are a number of alfalfa varieties that have been selected for salt tolerance. The alfalfa varieties AZ-Germ Salt 1, AZ-Germ Salt 2, and AZ-90NDC-ST were selected for high germination rates and superior forage production from Mesa-Sirsa using recurrent selection under pressures as high as 99% in laboratory and greenhouse salt-tolerance tests (Dobrenz et al., 1983; Johnson et al., 1991). Al-Khatib et al. (1994) used seedling tests to identify salt tolerance in Cargo, Punjab Selection, and Local Syria. Indirect selection at germination and seedling growth, however, has not been found to confer significantly higher tolerance in the field (Johnson et al., 1992). Screening salt-sensitive and -tolerant lines based on leaf damage under saline conditions has shown some utility. Tolerant and sensitive selections have been made from the variety CUF-101 (Noble et al., 1984). High shoot dry weights under saline conditions were highly correlated with low shoot Cl^- (Noble and Shannon, 1988).

Plot trials in Australia have demonstrated significantly superior salt tolerance in Haifa and Irrigation white clover (*Trifolium repens*) (Rogers et al., 1994). Clover selections also have been made based on the ability of plants to exclude NaCl from the shoot. It was found that Cl^- exclusion had high heritability and was the result of a different gene action than Na^+ exclusion, but neither criterion resulted in an improvement in salt tolerance based on yield (Noble and Shannon, 1988). Among six varieties of subterranean clover (*Trifolium subterraneum*), high yield under saline conditions was found to be related to low shoot Na^+ and the maintenance of leaf K^+ (Shannon and Noble, 1995). Salt-tolerance rankings among varieties differed with growth stage for tests conducted during germination, emergence, and vegetative growth.

E. VEGETABLE CROPS

Vegetable crops are generally more salt sensitive than grains and forages; notable exceptions are asparagus, red beet, and zucchini squash (Fig. 6). Salt affects the growth of vegetables predominantly through osmotic effects, but

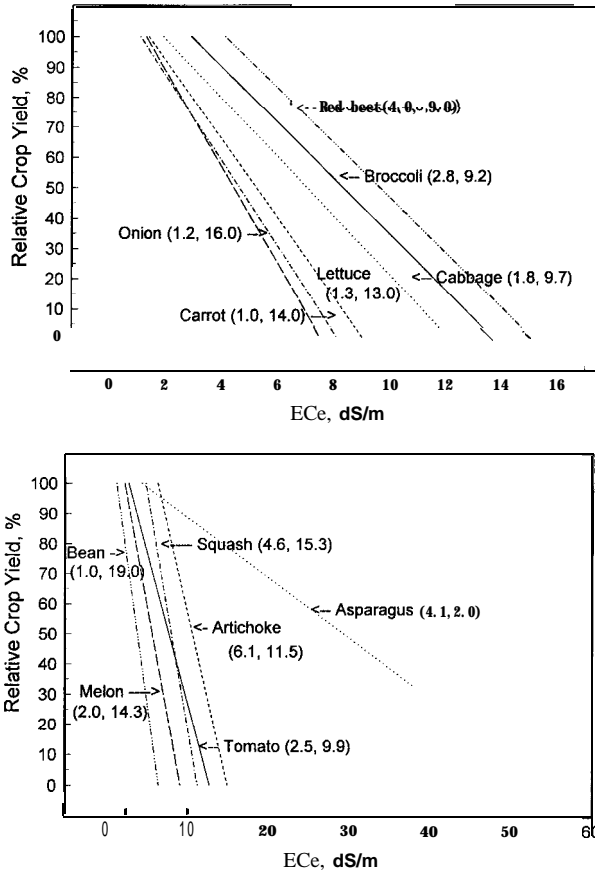


Figure 6 Comparative differences in salt tolerance among a number of vegetable crops. Values in parentheses represent the threshold and slope values for each species (t, s). Data serve only as a guideline to relative tolerances and may vary depending on climate, soil conditions, and cultural practices.

specific ion effects and salinity-nutrient interactions have significant influences on vegetable quality (Bernstein, 1959). In addition, some lettuce cultivars often develop Ca^{2+} -deficiency symptoms when sulfate levels in the soil are too high, and high $\text{Na}^+/\text{Ca}^{2+}$ ratios can cause heart rot in artichoke (Francois, 1995). Excessive Ca^{2+} may restrict the uptake of K^+ , which may be a factor in reduced yields of bean and carrot (Bernstein, 1959).

Under marginal conditions of salinity many vegetables are stunted and exhibit a reduction in growth rate without showing other visible injury symptoms (Hayward, 1955). At high salinity levels, some vegetables exhibit pronounced injury symptoms at the later stages of growth. Bean leaves develop a marginal chloro-

sis-necrosis with an upward cupping of the leaves (Bernstein and Ayers, 1951). Onions have also been shown to develop leaf necrosis (Bernstein and Ayers, 1953a); the growth parameter, other than root weight, that shows the highest correlation coefficient (0.50-0.65) to bulb yield was leaf number (Malik et al., 1981).

High levels of exchangeable sodium frequently restrict vegetative growth because of the unfavorable physical conditions associated with sodic soils. Most vegetable crops appear to be at least moderately tolerant to exchangeable sodium. Bean plants, however, are sensitive to nutritional factors in sodic soils and may be severely affected, even before the physical condition of the soil is impaired.

Most vegetable crops produced on saline soils are not of prime market quality. This is seen in such diverse ways as smaller fruit size of tomatoes and peppers (Bernstein, 1959) reduced petiole length of celery (Francois and West, 1982), and misshapen potatoes (Blodgett and Snyder, 1946). However, not all quality effects are detrimental. The flavor of carrots (Bernstein and Ayers, 1953b) and asparagus (Francois, 1987) is enhanced by a measurable increase in sugar content when grown under saline conditions. Likewise, several studies have shown that total soluble solids in tomatoes are significantly increased as salt stress is increased (Adams and Ho, 1989; Jobs *et al.*, 1981; Shalhevet and Yaron, 1973; Rush and Epstein, 1981a). Unfortunately, this gain in quality is more than offset by lower yields.

A tomato variety with very high salt tolerance has been developed by growers along the northern coast of Egypt (Hassan and Desouki, 1982). The variety Edkway is believed to have been selected from the variety Marmande by regional farmers who grow their crops on sand dunes using drainage water of $4-6 \text{ dS m}^{-1}$ for irrigation. Even though tomato is highly self-pollinated and therefore has limited genetic variability within a variety, enough variation evidently was present for the selection of salt tolerance under high selection pressure.

The cultivated tomato species has been hybridized with several salt-tolerant wild species in an effort to improve its tolerance. A salt-tolerant line was developed through backcrossing *L. cheesmanii* to the cultivated parent (Fredrickson and Epstein, 1975; Rush and Epstein, 1976, 1981a). Another wild tomato species, *L. pennellii*, has been hybridized and backcrossed to the variety New Yorker for nine generations and selected for cold tolerance and earliness. Many breeding lines from this cross had salt tolerance higher than that of the cultivated parent (Sacher *et al.*, 1982). In Israel, a processing tomato variety with improved salt tolerance was selected from an interspecific backcross between a cultivated processing variety and a closely related wild tomato, *L. pennellii*. Four cycles of recurrent selection have produced a line that has high salt tolerance and superior quality characteristics (see Shannon and Noble, 1990).

Differences between varieties have been shown in a number of melon (*Cucumis melo*) varieties screened for salt tolerance at germination and seedling stages and at maturity (Shannon and Francois, 1978; Mendlinger et al., 1983; Shannon *et al.*, 1984). Tolerance at one growth stage is not correlated to tolerance at another stage

nor is there a consistent correlation between tolerance and the accumulation or exclusion of ions in the shoot. An F, muskmelon hybrid has been produced from selected parents of salt-tolerant and locally adapted melon varieties in Israel (see Shannon and Noble, 1990). The selected hybrid, BG84-3, had improved productivity and salt tolerance in preliminary yield trials. In Egypt, a muskmelon variety, Shad El-Dokki, has been selected for superior yields under saline conditions.

Screening tests conducted on 85 lettuce (*Lactuca sativa*) varieties and breeding lines indicated a high degree of variability among entries (Shannon et al., 1983). Lettuce was found to respond primarily to osmotic effects at low salinities and shoot growth was affected more than root growth. Salinity decreases both growth and head-to-frame ratio in crisp head lettuce, but both characters can be improved through selection (Shannon, 1980). Screening tests showed that 115 lettuce introductions had a higher degree of salt tolerance and had a greater degree of variability for the character than the cultivated varieties and breeding lines (Shannon and McCreight, 1984). In field trials, Romaine varieties were more salt tolerant than iceberg varieties (Pasternak et al., 1986).

F. FRUITS, NUTS, AND BERRIES

Most fruit trees are relatively sensitive to salinity with the exception of date palm (*Phoenix dactylifera*), pomegranate (*Punica granatum*), and a few other species believed to be moderately tolerant (Fig. 7). Stone fruits, citrus, and avocado (*Persea americana*) have all shown specific sensitivity to foliar accumulations of NaCl. The accumulation of these ions to harmful levels, as well as the general osmotic growth inhibition, contributes to the reduction in tree growth and fruit yield. Different cultivars and rootstocks absorb chloride and sodium at different rates, so tolerance can vary considerably within a species.

Injury by sodium can occur at concentrations as low as 5 mol m^{-3} in the soil solution (Maas, 1990). However, injury symptoms, which are characterized as tip, marginal, and/or interveinal necrosis, may not appear for a considerable time after exposure to salinity. Some of the more sensitive fruit crops may accumulate toxic levels of sodium or chloride or both over a period of years from soils that would be classified as nonsaline and nonsodic (Ayers et al., 1951; Bernstein, 1980). Initially, the sodium is thought to be retained in the sapwood of the tree; most fruit trees are relatively sensitive to salinity. This may partly explain why stone fruits and grapes appear to be more sensitive to salinity as the plants grow older. With succeeding years, the chloride and sodium accumulate more rapidly in the leaves, causing leaf burn to develop earlier and with increasing severity (Hoffman et al., 1989).

Chloride toxicity in woody species is generally more severe and observed in a wider range of species than is sodium toxicity. Differences in susceptibility to chloride among species, varieties, or rootstocks usually reflect the capability of the plant to prevent or retard chloride accumulation in the plant tops. Recent studies

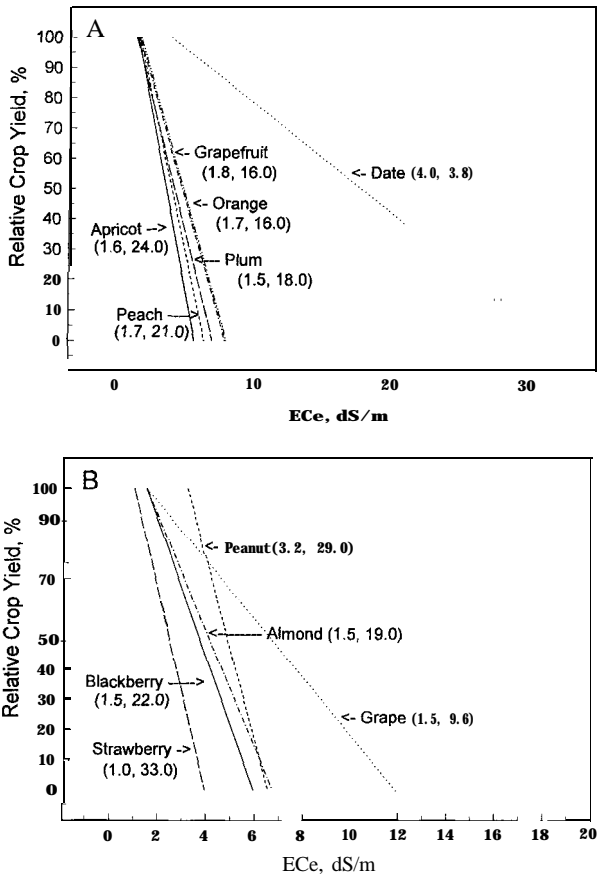


Figure 7 Comparative differences in salt tolerance among a number of fruit (A) and nut and berry (B) crops. Values in parentheses represent the threshold and slope values for each species (t, s). Data serve only as a guideline to relative tolerances and may vary depending on climate, soil conditions, and cultural practices.

have shown that sodium accumulation in plum leaves did not significantly increase until the leaves were already severely damaged by chloride accumulation (Hoffman *et al.*, 1989; Mead *et al.*, 1990). These studies indicate that, when chloride and sodium are present in the soil solution, chloride is the primary damaging ion on stone fruits. Sodium accumulation only occurs after the leaf membranes have already been damaged.

The initial symptom of excess chloride accumulation in fruit crops is leaf tip necrosis developing into marginal necrosis. With citrus, a chlorosis and bronzing of the leaves occur without a well-defined necrosis. As chloride continues to accumulate, the effects become more severe with premature leaf drop, complete de-

foliation, twig dieback, and, in extreme cases, death of the tree or vine (Hayward *et al.*, 1946; Bernstein, 1980).

Growth and yield reduction may occur with woody fruit species in the absence of specific ion toxicity. Francois and Clark (1980), working with Valencia orange, reported a 50% reduction in fruit yield from salinity with no visible leaf injury symptoms. However, it is generally believed that growth and yield of most woody fruit crops suffer from both osmotic effects and toxicities caused by chloride or sodium accumulation (Bernstein, 1980).

The tolerance of many fruit tree and vine crops can be significantly improved by selecting rootstocks that restrict Cl and/or Na accumulation. Crosses between the salt-tolerant Rangpur citrus line and Rubidoux trifoliate orange have been used to produce progeny with a range of salt tolerance (Furr *et al.*, 1963; Furr and Ream, 1968). Although citrus is not considered to be very salt tolerant, there are differences in salt tolerance among the various rootstocks (Cooper *et al.*, 1951; Shalhevet *et al.*, 1974). These differences are attributed to salt exclusion and particularly to chloride exclusion (Cooper, 1961; Walker and Douglas, 1983). Citrus apparently excludes chloride from shoots not by sequestering it in the root but rather by restricting its entry into and/or movement within the roots. The chloride concentration differences found in leaves and to a lesser extent in stems emphasize pronounced rootstock differences in root to shoot transport of chloride and have led to the development of screening procedures based on this characteristic (Walker and Douglas, 1983; Sykes, 1985). The scion appears to have no major influence on chloride transport from the roots to the shoot (Behboudian *et al.*, 1986).

Differences among rootstocks are much greater for chloride accumulation than for sodium and there appears to be no correlation between chloride tolerance and sodium tolerance (Cooper, 1961). These differences are due to the existence of apparent separate mechanisms that operate to limit or regulate the transport of sodium or chloride to the leaves (Grieve and Walker, 1983). The chloride tolerance range for avocado rootstocks is much narrower than for citrus. In addition, because of the wide variation among varieties of the same rootstock, the rootstock tolerances tend to overlap (Embleton *et al.*, 1962). However, the average ranking of chloride tolerance is generally West Indian > Guatemalan > Mexican (Cooper, 1951; Embleton *et al.*, 1962; Haas, 1950a). The general pattern for sodium accumulation with avocado rootstocks tends to follow that for chloride accumulation, and, like chloride, it shows differences among varieties on the same rootstock (Haas, 1950b, 1952).

Cold hardiness has been implicated in the salt tolerance of citrus and avocado rootstocks. Wutscher (1979) reported that citrus rootstocks with good chloride-excluding characteristics were relatively cold hardy. For some citrus species, a short-term, moderate salt stress enhanced cold hardiness in seedlings by modifying growth, water relations, and mineral nutrition (Syvertsen and Yelenosky, 1988). In contrast, the salt-tolerant avocado rootstocks, such as West Indian and West Indian-Guatemalan hybrids, are the least cold tolerant. Likewise, the salt-sensitive Mexican is the most cold-tolerant rootstock (Cooper *et al.*, 1957). The salt-toler-

ant variety, Arsola 1-18, was developed from a cross between a salt-tolerant West Indian variety and a cold-hardy Mexican variety (Cooper, 1951).

Chloride toxicity has been the principal limiting factor for grapevines grown on their own root. However, a significant reduction in chloride accumulation has been shown to occur in chloride-sensitive scions when grown on Dog Ridge or 1613-3 rootstocks (Bernstein et al., 1969). The salt tolerance of these two rootstocks would probably be limited by soil osmotic effects long before chloride reached toxic levels.

G. ORNAMENTALS

The salt tolerance of ornamental trees and flowers is determined by the aesthetic value of the plant species. Bernstein et al. (1972) determined salt tolerance of 25 shrub and ground cover species. Injury or loss of leaves or flowers due to salt stress is unacceptable even though growth may be unaffected. A significant growth reduction might be acceptable and possibly desirable for some species, as long as they appear healthy and attractive.

The type of injury seen on woody ornamentals and trees is similar to damage recorded for fruit trees and vines. Although some woody ornamentals and trees accumulate sodium, the salt tolerance of these species is closely associated with the ability to limit chloride uptake and accumulation (Dirr, 1976; Francois, 1982b; Townsend, 1980).

In northern climates, where NaCl and/or CaCl₂ are used as deicing salts, typical salt injury symptoms occur on roadside trees. These trees are subjected to both soil salinity from runoff and saline spray from passing automobiles. Although salt spray is thought to be the more detrimental of the two modes of deposition (Hall et al., 1972; Lumis et al., 1973), the soil salinity effects may be accumulative and, over a period of years, may result in a slow but progressive decline of the trees.

A limited number of floricultural plants have been tested for salt tolerance. Although chrysanthemum, carnation, and stock (*Matthiola* sp) are considered to be moderately tolerant to salt stress, aster, poinsettia, gladiolus, azalea, gardenia, gerbera, amaryllis, and African violet are somewhat sensitive (Hayward and Bernstein, 1958; Sonneveld and Voogt, 1983; Devitt and Morris, 1987). The aesthetic value of floral plants is the determining factor for salt tolerance.

VI. BREEDING METHODS

A. GENES FOR TOLERANCE

Salt sensitivities in barley (Greenway, 1965), soybean (Abel and Mackenzie, 1964), citrus (Cooper et al., 1951, Cooper and Gorton, 1952), and grape (Bern-

stein *et al.*, 1969; Downton, 1977; Francois and Clark, 1979b) have been found to be related to the inability of the plant to adequately regulate Cl^- transport from the root to the shoot. In some cases (e.g., soybean), a single gene may be responsible, but in other cases multiple genes are involved, making the response quantitative (e.g., citrus). Sometimes it is difficult to distinguish whether toxic effects are due to Na^+ or Cl^- because the concentrations of both increase concomitantly. Woody species seem to be sensitive to Cl^- , whereas beans and corn varieties that better regulate accumulation of Na^+ in the shoot can tolerate low salinity better than those that cannot (Richter and Marschner, 1973; Jacoby and Ratner, 1974). It is important that each species be examined without bias for variability in ion toxicity thresholds, ion restriction ability, and the capacity for ion selectivity.

Hannon and Barber (1972) found that salt-tolerant clones of *Festuca rubra* and *Agrostis stolonifera* restricted shoot uptake of both Na^+ and Cl^- . Populations of *A. stolonifera* collected from maritime habitats had lower Na^+ and higher K^+ concentrations in the shoots than inland populations grown at the same salinity. Often, specific ecotypes have been found to be tolerant to salinity. Another closely related species, *A. tenuis* Sibth., was sensitive to high Mg^{2+} concentrations in seawater. Tolerant accessions of tall wheat grass (*Elytrigia pontica*) limited Na^+ and Cl^- uptake into shoots more effectively than sensitive accessions (Shannon, 1978). Hybridization between tolerant lines yielded progeny with improved tolerance; however, improvement in salt tolerance at this level was not correlated with differences in ion uptake or osmotic regulation (Weimberg and Shannon, 1988).

Dvořák and co-workers (Dvořák and Ross, 1986; Dvořák *et al.*, 1985) have been successful in transferring salt tolerance from *E. pontica* and *E. elongata* to wheat by hybridizing the two grasses to wheat. Some of the derivatives, which varied in chromosome composition, had improved salt tolerance compared to wheat; furthermore, amphidiploids showed tolerance to a wide range of ions (Na^+ , K^+ , Mg^{2+} , Cl^- , and SO_4^{2-}) as well as to seawater. Genes that control K/Na discrimination in wheat have been located on the long arm of chromosome 4D through the use of conventional genetic manipulation of chromosomes and chromosome fragments (Gorham *et al.*, 1987). These investigators made use of disomic D-substitution lines of tetraploid wheat previously developed from crosses between tetraploid and hexaploid wheats with unbalanced A, B, and D genome sets (Sears, 1966).

The distinction of a line as salt sensitive or salt tolerant should depend on its relationship to the average response of the breeding population. Certain gene differences may result in changes that increase sensitivity to a specific ion or salt effect. These genotypes should be differentiated from those that confer greater salt tolerance than is found in the mean population. An example of salt sensitivity is the soybean variety Jackson (Abel and MacKenzie, 1964; Abel, 1969). Similarly, an introduction of wheat PI 94341 was found to be more sensitive to Na^+ than PI 178704 (Kingsbury *et al.*, 1984; Kingsbury and Epstein, 1986).

B. HERITABILITY

Breeding procedure depends on the pattern of inheritance (qualitative or quantitative), the number of genes with major effects, and the nature of gene action. Knowledge of the heritability and inheritance of salt tolerance in a species will determine the selection intensity and number of selection cycles necessary to effectively improve tolerance. Breeding for improved salt tolerance has been discussed for several decades and has been reviewed on numerous occasions (Nieman and Shannon, 1976; Gupta, 1978; Pasternak et al., 1979; Norlyn, 1980; Ramage, 1980; Duvick et al., 1981; Shannon, 1982, 1984, 1985; Noble, 1983; Blum, 1984, 1988; Downton, 1984; Jones and Qualset, 1984; Rana, 1985; Tal, 1985; Epstein and Rains, 1987; Jones, 1987).

Salt tolerance in *Agropyron intermedium* was found to be a heritable characteristic that could be selected based on growth in mature plants (Hunt, 1965). Norlyn (1980) found that salt tolerance in barley was heritable, but that genetic control was complex.

The lack of genetic variation and a poor understanding of genetic control are most often the greatest barriers to improvement of salt tolerance. The nature of salt tolerance as a multigenic, quantitative character imposes several constraints on the type of breeding approach that might be successful. Ramage (1980) emphasized that a favorable background genotype is needed on which to improve the salt-tolerance characteristics. He suggested the use of recurrent selection for both cross-pollinated species and those self-pollinated species that have male sterility systems that can be genetically manipulated. Use of male sterility systems would reduce the work involved in hybrid production during the recombination phase of the recurrent selection procedure with self-pollinators.

C. FIELD SCREENING TECHNIQUES

Selection for tolerance under held conditions is inaccurate because of the difficulty in assessing the physical and temporal variability in salinity in soil solutions proximal to the root zone. The ability of plants to extract preferentially water from the most nonsaline portions of their root zones further complicates this assessment. It may be possible to compensate for these problems to some extent by using very large populations, making a judicious selection of breeding strategy and experimental design, and precisely controlling irrigation in artificially salinized plots. Nevertheless, a low selection efficiency can be expected even under ideal conditions and the efforts will be very expensive. The advantages of field screening are that space is not a major limiting factor to replication and population sizes, and that the environmental conditions are more nearly what will be encountered under real field conditions.

D. SELECTION METHODS

Several screening and selection schemes have been proposed for salt tolerance (Greenway and Andrew, 1962; Dewey, 1962; Beatty and Ehlig, 1973; Epstein *et al.*, 1980; Shannon *et al.*, 1983; Sykes, 1985). Because of the many interactions of salinity with environmental variables and specific ions, a target environment is important to a screening program for salt tolerance. Initial considerations should be made concerning the balance of major and minor ions that could prove toxic or have detrimental effects on nutrients. Recent advances in soil physics and chemistry allow the prediction of soil water compositions in the plant root zone based on applied water quality and soil chemistry (Suarez and Šimůnek, 1995).

Many examples have been cited to support the generalization that salt tolerance varies with ontogeny and development. Salt tolerance measured at one growth stage usually does not correlate well with salt tolerance at other growth stages. Intervarietal variation in salt tolerance during germination has been found, in a number of cases, to differ with tolerance at other growth stages. Germination rates as measured in saline filter paper or gels have very little relationship to emergence potential. Many seeds that germinate on salinized filter papers or in gels may be too weak to break a soil crust and establish as viable plants. Emergence rate might be a more practical screening criterion than germination rate, and seedling vigor may also be an additional useful screening factor for conditions in which saline soils form hard crusts.

Germination or emergence trials under saline conditions should always be conducted using healthy and viable seed lots. Hard or damaged seed should be discarded; however, too much selection may also be a problem. Large seed size has been shown to have greater salt tolerance than small seed selected from the same lot in wheat and sorghum (Amthor, 1983; Grieve and Francois, 1992).

Available information on the salt tolerance of the crop should be collected. Such information should include relative salt tolerance range, potential variability among cultivated varieties and closely related species, and sensitivities to specific ions and environmental interactions.

The process of developing salt-tolerant varieties should begin with the identification of the precise growth stage that is limiting to productivity. It should be determined if economical management techniques can be used to overcome the limitation. For example, if stand establishment is a limiting factor, this limitation could be overcome by better bed preparation to move dissolved salts away from the seed, by applying a timely irrigation of high- or medium-quality water; or by more dense seeding or plant spacing. Seed priming has also been proposed as a method to enhance seed germination and emergence under conditions of salinity and low temperatures (Nerson and Govers, 1986; Shannon and Francois, 1977).

Determine whether other locally adapted varieties are more tolerant at this growth stage. Develop a screening procedure for the sensitive growth stage. The procedure must be based on information concerning average salt concentration and

composition of the soil water during sensitive growth periods and the environmental conditions during the period of salt damage in the field. A selection criterion needs to be one that is related to mean yield response in the field.

Field experiments should be conducted at an early stage to prove the relationship of the criteria selected to the desired field characteristics.

Evaluate a range of varieties and introductions to determine genetic variance for the desired characteristics. Proper controls must be included to separate genetic from environmental effects under both nonsaline and saline conditions. Information from the collected data can be used to determine if intravarietal selection will be effective. If genetic variance is low or if a greater degree of tolerance is required, wild relatives and lines developed from hybridizations can be evaluated.

A point of interest is that a newly selected rice variety, Giza 160, was found to be sensitive to two new blast races prior to its release, and germplasm derived from the salt-tolerant Kharchi wheat line was been found to be susceptible to both rusts and powdery mildew (Rana, 1985). Research has not been conducted to determine whether there is a mechanistic link between salt tolerance and susceptibility to rusts and mildews. It has been speculated that a weaker cell wall structure could favor easier expansion growth under saline conditions. Weaker cell walls could also decrease resistance to rusts and mildews.

VII. NOVEL CONCEPTS

There are a number of new methods and techniques that promise to overcome the barriers that have prevented rapid development of salt-tolerant crops. Among these, and in approximate chronological order of their application to salt tolerance, are tissue culture, molecular biology, and crop modeling. None of these technologies has yet led to breakthroughs in the realm of salt tolerance. However, if applied integratively, they will make valuable contributions in the future.

A. TISSUE CULTURE

The use of undifferentiated cells in tissue culture to improve salt tolerance has been explored in many crops (Dix and Street, 1975; Nabors *et al.*, 1975, 1980; Croughan *et al.*, 1978; Ben-Hayyim and Kochba, 1982; Rangan and Vasil, 1983, Pandey and Ganapathy, 1984; Winicov, 1991). Large populations of cells in cultures can be maintained under precisely controlled environmental conditions and easily manipulated. Mutagenesis, haploid production, somatic hybridization, and transformation are relatively easy in tissue cultures. The major limitation of tissue cultures with respect to salt tolerance is that the selected character cannot be maintained during the regeneration process. In addition, there is still insufficient under-

standing of the relationship between cellular and whole plant response (Petolino and Collins, 1984). An additional limitation is the possibility that epigenetic change, or physiological adaptation, may occur. Tolerance mechanisms that depend on the integrated function of differentiated tissues cannot be readily identified in cell cultures, but it is hoped that some intracellular tolerance characteristics can be improved. Potential characteristics that may be selected from cell cultures include the ability to regulate or partition ions more efficiently, the production of organic solutes to improve osmoregulation under salt stress, and improved metabolic efficiency (Hasegawa *et al.*, 1980; Ben-Hayyim and Kochba, 1983; Ben-Hayyim *et al.*, 1985; Binzel *et al.*, 1983; Watad *et al.*, 1983; Stavarek and Rains, 1984).

Recently, some unconfirmed successes in using tissue cultures to improve salt tolerance have been reported in alfalfa (Winicov, 1991) and bentgrass (Kuo *et al.*, 1994). In potato, cultured stem segments and cell suspensions differed in their response to salinity to that expressed by whole plants, but the response of cultured roots was more closely related (Naik and Widholm, 1993).

B. MOLECULAR BIOLOGY

Recent advances in molecular biology have broadened the possibilities for gene manipulation at the level of cell cultures and higher units of organization. The development of new or improved technologies for monoclonal antibodies, endonuclease digestion, cDNA libraries, purified protein isolation, and rapid amino acid sequencing now make gene identification, isolation, and transformation realities. The major problems that prohibit the use of these techniques to develop salt-tolerant crops are that salt tolerance is a complex, multigenic trait and is often a composite response of the integrated biological system. At its current level of technology, molecular biology is not able to engineer traits that involve whole plant responses. However, the power of molecular biology goes beyond the ability to manipulate genes: It is also useful as a method to monitor environmental effects at the level of the genome.

As new and improved technologies are developed, it can be expected that the molecular approach will contribute significantly to our knowledge of both genetic and physiological events associated with salt stress. Perhaps salt-tolerant genes will someday be transferred to salt-sensitive species by direct integration of DNA or through bacterial or viral plasmid vectors. However, because the number and location of specific genes affecting salt tolerance are unknown, molecular biology techniques that transfer substantial portions of genetic material from one species to another may prove most useful, particularly for somatic hybridization of related species. Electrofusion, for example, can overcome natural interspecific barriers to hybridization by fusing cells from species in different families. Complete transfer of genetic material between species is possible. However, fused cells need to

be cultured, plants regenerated, and the interaction of genes from different species studied. Certainly, we are on the threshold of a new and exciting era.

C. MODELING

Under saline conditions plants respond to increased osmotic potential in the root zone. The initial effects of salinity are a consequence of stomate closure and the resultant decrease in assimilated carbon. In addition, the plant is forced to divert some of the energy normally expended for growth into increased maintenance. Thus, the efficiency with which the plant utilizes its energy resources may be an important aspect of salt tolerance. Salination of the rooting medium initially increases respiration rates in many species (Nieman, 1962; Livne and Levin, 1967), but total respiration then decreases concomitant with decreased photosynthesis, with the latter directly related to stomata closure induced by water stress effects (Schwartz and Gale, 1981, 1983, 1984). Energy costs for cell maintenance increase with salinity. Active transport processes that maintain ion compartmentation and fuel protein synthesis are two of the most costly energy sinks in the plants (Penning de Vries, 1975). Increased maintenance costs during salinity stress, no doubt, are directed toward ion regulation (compartmentation and transport of toxic ions), osmotic adjustment, and maintenance of membrane integrity (Yeo, 1983).

It is almost impossible to conceptualize all these facets in a quantitative manner to determine the given effect of salinity in a given environment. The outcome of subtle genetic modifications on the biochemistry and physiology is modified by the complexities of the aerial environment as well as the physics and chemistry of the root environment. Physiological or process-based crop growth models provide powerful tools for this type of integration. Simultaneous efforts are being made to develop the necessary soil chemistry, physics, and plant water use models that will provide a more comprehensive conceptual framework to describe the processes that influence plant salt tolerance (Grant, 1995; Suarez and Šimůnek, 1995). The development and accessibility of powerful computers and object-oriented languages provide a tool that has not been available so far.

VIII. SUMMARY AND CONCLUSIONS

There is a wide range of salt tolerance in vascular plants. Several genera include species that are extreme halophytes and are ecologically competitive only under saline conditions. Crop species primarily are glycophytes, salt-sensitive, and grow well only under cultivated conditions. Domesticated species typically are provided optimum conditions in order to obtain high yields. In effect, this has constituted

a negative selection pressure for those characteristics that influence adaptation to extreme environments (Rosielle and Hamblin, 1981). Thus, a great many crops are moderately to highly sensitive to salinity and there is a relatively narrow range of variation for salt tolerance and other environmental stresses among crop species. Alternatively, many wild species are moderately to extremely salt tolerant, and although it may be possible to develop the agronomic potential of some halophytes into new and useful salt-tolerant crops, much additional effort is needed to improve agronomic characteristics of new crops.

The subject of salt tolerance has received a tremendous amount of attention during the past two decades and many reviews have been published that describe the mechanisms of salt tolerance, the possibility of breeding for salt tolerance, and the potential of new technical advances in the development of salt tolerant varieties. The concept of developing salt-tolerant plants, even to the degree that they can be grown with seawater, is an interesting one that captures the imagination of both the scientific and the public sector (Boyko, 1966; Epstein and Norlyn, 1977). However, based on the progress that science has made within the past half a century, it would be safe to conclude that the task is not a simple one. Because of its complexity, the elusive goal of routinely developing salt tolerance has not been realized. It is more likely that progress in developing salt tolerance will evolve slowly until a number of technological breakthroughs develop. There is a need for an increased understanding of the mechanisms of salt tolerance, the development of methods to comprehensively integrate and predict the effects of environmental factors on plant response throughout all stages of growth and development, and the development of improved methods to identify and manipulate genes and gene groups between species.

A C K N O W L E D G M E N T S

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