Proc. Workshop on Adaptation of Plants to Soil Stresses. p. 117-132.
In: J.W. Maranville, B.V. Baligar, R.R. Duncan & J.M. Yohe (eds.)
INTSORMIL. Pub. No. 94-2, Univ. of NE, Lincoln, NE, August 1-4, 1993.

Development of Salt Stress Tolerance - Screening and Selection Systems for Genetic Improvement

Michael C. Shannon
U. S. Salinity Laboratory, USDA-AIRS
Riverside, CA

ABSTRACT

Selection for high-yielding, salt-tolerant cultivars has proven to be an elusive target for plant breeders, and the identification of reliable genetic markers for salt tolerance has been even more elusive for plant physiologists, and cellular and molecular biologists. The plant is an integrated system that is adapted to a specific environment on which salinity has become an intrusion. A comprehensive program to develop a salt tolerant cultivar should be composed of seven essential elements. Preliminary assessments for salinity, genotypic variability, and economic considerations are crucial to the definition of the problem situation. Close cooperation with growers or farmers is necessary to establish specific requirements and preferences for the crop and its management in the saline environment. An evaluation of management options are necessary to assess the current technology available and to simplify solution possibilities. A conceptual model should be developed that will fulfill the essential requirements of the problem situation. This model should match needed inputs with farming objectives for yield, quality, and production sustainability. Based on the conceptualized model, several desirable ideotypes should be considered and a number of these., depending on resources, can be selected for the breeding program At this point appropriate screening methods can be developed for segregating populations derived from crosses of the selected parental lines. An integral part of the program should consist of a plan to maintain and improve the cultivar during development. This may require specific knowledge of and cooperation with the social infrastructure that maintains, improves, and distributes seed to farmers.

INTRODUCTION

Salinity is a serious environmental constraint to crop production in many parts of the world. It is especially prevalent in irrigated agriculture and in marginal lands associated with poor drainage or high water tables. Estimates for the extent of salinity damage vary from 25 to 50 percent of the world's irrigated land (Postel, 1989; Adams and Hughes, 1990)). Recent interests in maintenance of the environment, encompassing preservation of natural resources and conscience toward human health and nutrition have put new **impetus** on the importance of preserving water quality. These issues, and the occurrence of cyclic drought conditions throughout the world have increased the need to use recycled water, drainage water, or poor-quality water on crops. The development of crops with improved salt tolerance is proposed as part of the solution to some of these problems.

At least five basic strategies exist for the development of salt tolerant plants (Table 1). One strategy is to use conventional breeding and selection among existing cultivars; another is to introgress genes from wild progenitors into crops that have retained many of their salt tolerance traits. Another strategy is to develop new crops from some of the wild species that currently inhabit saline environments (halophytes) by breeding and selection for agronomic characteristics. The use of tissue cultures to select single salt tolerant cells for plant regeneration or to produce salt tolerance through somaclonal variation is a strategy that has been developed within the last two decades. The boldest strategies have suggested that individual genes for salt tolerance can be identified, isolated and manipulated across conventional geneticbarriers through molecular **biological** techniques. The greatest portion of the efforts to improve salt tolerance using these **strategies have** not been highly successful (Shannon and Noble, 1990).

Too little progress has been madeinimproving salt tolerance of crops. One reason is that, despite significant progress in the development of an understanding of the effects of salt stress, there are still many unanswered questions concerning the primary stress signals and the morphological and physiological changes that ensue. Recently, physiologists have been subjected to constructive critiques for their short-comings and encouraged to develop better hypotheses for their research efforts (Munns, 1993). At present, development of a new direction and a cohesive approach in the area of salt tolerant crop development is needed. Realistic short and long range research goals should be established that will provide the continuity to

Table 1. Examples of strategies for the selection, breeding and development of salt tolerant plants.

Approach	Crops	Examples
Conventional breeding	Barley. lettuce	Ramage, 1980
		Shannon, 1980
Wide crosses	Tomato	Rush and Epstein, 1981
		Tal and Shannon. 1983
Domestication of wild salt-tolerant species	Salicomia	Glenn et.al., 1991
Tissue cultures	Tobacco, chickpea	Nabors et.al., 1980
		Pandey and Ganapathy, 1984
Molecular biology	Wheat	Gulick and Dvorak, 1987

deliver salt-tolerant cultivars to the farmer. The purpose of this chapter is to outline some of the foremost issues and strategies concerning selection and breeding for plant salt tolerance, to identify some of the fundamental gaps in our present understanding, and to suggest a more comprehensive approach to selection and breeding for salt tolerance.

BREEDING PROGRAM FOR SALT TOLERANCE

The development of a breeding program for salt tolerance should consist of the same basic steps, regardless of which previous approach was used to enhance the germplasm base for the desired character. The steps that are proposed include: Preliminary assessments, Management requirements, Crop requirements, Development of a functional model, Development of ideotype, Establishment of the screening procedures, and Cultivar development and maintenance (Fig. 1).

Preliminary Assessments

Preliminary assessments must be made for the Salinity Situation, Genetic Variability, and Economic Constraints. These are interactive elements that describe the problem situation that is being addressed by the breeder.[1]

The breeder should initially consider the Salinity Situation that is causing the problem (it is assumed that a specific crop of interest has been targeted). An estimate of the cropping area that is affected should be developed. Is more than one location, basin or watershed affected? How are farming practices and environmental factors in these areas similar or different? The origin and composition of the salt should be identified. Is salt indigenous to the soil or the result of improper management? Is it arising from a high water table or is it a constituent of the irrigation water for whatever reason? What is the composition of the salt in the water and its probable composition when it is in the soil water solution? Are specific ions a particular problem in this species or is the problem the result of a general salinity phenomenon? Are interactions between salinity and other nutrients (e.g. calcium, phosphate) part of the problem? Such interactions have been described for a number of nutrients and crop species (Grattan and Grieve, 1991). What are the high

[1] The term 'Breeder' will be used throughout the rest of the paper as the subject that should perform the functions and fulfill the objectives that are described. The breeder should, in fact, be a member of an interdisciplinary team that may include geneticists, agronomists, physiologists, morphologists, pathologists, soil scientists, chemists, economists, and other disciplines.

and low limits of soil water salinity concentrations between irrigation (or rain) cycles? The distribution of the salt within the root and vadose zones should be measured or predicted,, based on management criteria. This assessment should quantify, for future reference, as many of the potential interacting variables of the environment as possible to include soil types, drainage conditions and ranges of various climate factors. Extemporary factors, such as air pollution, that are known to interact with salinity, should also be considered (Maas et al., 1973).

An assessment of the Genetic Variability should be conducted through literature surveys and, possibly, experimental testing. Information should be obtained concerning the parameters of salt tolerance related to crop yield, e.g., threshold and slope (Maas, 1986; 1990). Although considerable research has been devoted to quantifying the salt tolerance of the various crop species (Francois and Maas, 1978, 1985), data are usually based on comparisons among only a few cultivars for many species. Some studies that have examined a range of cultivars have revealed wide intraspecific variation for salt tolerance; whereas other studies have shown limited differences. In many cases, only a relatively small portion of the existing germplasm base has been adequately tested. Many wild progenitors of cultivated species have not been examined or exploited at all.

If information is not sufficient, variability among cultivars and other feasible germplasm sources should be determined for tolerance to both

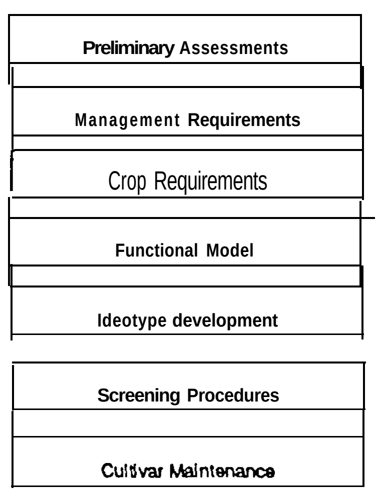

Fig. 1. **Steps necessary for the systematic and comprehensive development of a breeding program for tolerance to salinity stress.**

general and specific salt stresses applied at various concentrations, and as they relate to the final product yield and quality. Only a complete understanding of the problem situation will enable the breeder to develop the insight needed to decide whether to proceed with the development of the program. In some cases, sufficient genetic variability may not exist to warrant initiation of the breeding program. Management options may be the only alternative, or perhaps, additional research may be needed concerning the effects of specific salts or the effects of salts on growth and development.

An integral part of the decision to further develop a breeding program is dependent on an Economic Assessment of the situation from the viewpoint of the eventual user of the technology, i.e., the grower. The breeder should have a general knowledge of what the 'average' grower is spending for seed, water, fertilizer, chemicals, field operations, fuel, labor, transportation, and overhead. Other useful information should be gathered concerning allotments and supports that might be available for the grower. Potential costs should be considered, especially those that may be uniquely associated with the salinity and/or drainage problem (Letey et al., 1990). Market considerations are also important. Incentives for early harvest or product quality are important to farming objectives and should be recognized by the breeder. Some potential or intangible benefits are impossible to derive without direct contact with the grower. Good breeders do not undertake programs without direct and frequent contact with farmers and farm advisors.

Management Requirements

Management requirements are also developed as a result of grower contact. These include the operational goals of the growers in the area that is affected by the observed salinity condition. Many growers focus on profit as it may be derived from particular combinations of high yield and quality, but recently sustainability has become a growing concern of both farmers and society. With salinity, the aspect of sustainability may have particular importance. Yields of fruit tree crops may be maintained or even increased using significant quantities of saline water for a few years at the risk of subsequent loss of the trees (Hoffman et al., 1989). Minimum leaching can save water costs but increase salinity risk. The management practices being used to grow the crop should be known to the breeder; in addition, potential management practices that can be implemented either with or without additional costs should be explored. Is irrigation being practiced? Are amendments used, or can they be? What are the tradeoffs between potential costs and potential benefits?

Crop Requirements

Crop requirements are determined in the context of the specific salinity problem in the target environment. This is an elaboration of the information that was obtained during the assessment for Genetic Variability. At this point, information should be assembled through literature and research concerning the effects of salinity during the most critical growth stage(s), the effects of specific salts on growth during the most sensitive stages of growth and development, and the exacerbating or ameliorating impact of anticipated factors of the environment with salinity stress. Ranges of genetic variability should be inspected in relation to the management requirements and the crop growth stage that may bc affected.

The probability of success for the total breeding program will be determined to a great extent by the thoroughness with which these three initial steps have been conducted. Reiteration and integration of the first three steps is recommended. For example, if stand establishment was determined to be a limiting factor in the Salinity Situation, once. an assessment of Genetic Variability for germination and emergence has been conducted, it is necessary to decide whether the limitation can be overcome by breeding, management (e.g. better bed preparation to move dissolved salts away from the seed; a timely irrigation of high or medium quality water; more dense seeding or plant spacing) or a combination of strategies based on economic factors.

Development of a Functional Model

Development of a functional model can proceed at this stage. The model should encompass the crop as it relates to the whole farming system. The model should include farming and environmental inputs and yield, quality, or any other factor that has been determined to be critical to the farming system, as outputs (Fig. **2).** Labor, seed, water, chemicals and equipment are designated as inputs that might be supplied by the grower. Biotic and abiotic stresses, **including salinity,** are inputs supplied by the environment. Outputs may be yield, crop residue, and drainage. This model should include possible threats of specific diseases, pests and adverse environments, weed competition, yield and harvest quality factors. At this stage, boundaries need to become fixed around the system that is to be designed through the breeding process. For example, if germination and stand establishment are the major causes contributing to yield loss due to salinity, then considerations of other growth stages can be reduced and the breeder might establish a screening system in the greenhouse to select material that has vigorous stand establishment under saline conditions. Applicability of the materials selected by screening to the total agricultural system must be maintained, however.

Vigorous growth may make the plant more susceptible to the type of midseason drought that is typical to the target area (see discussions by Ball et al., 1993). Alternately, the screening system could identify segregants of a cross that have high salt tolerance, but also have more susceptibility than the parental lines to disease or acid soil conditions prevalent in the target area. The model allows some reductionism of the problem based on the perceived goals of the breeding program, but keeps the integrated system in context for which the plant cultivar is being developed

Development of Plant Ideotype

Development of plant ideotype is a concept that was established by Donald (1968). He contended that most plant breeding was based on attempts to eliminate defects or improve yield and suggested an alternative approach based on the breeding of plants that would conform to some ideal concept or model. He noted that the success of this novel approach was dependent on three resources: adequate genetic diversity, suitable techniques, and sufficient knowledge. Perhaps the lack of sufficient knowledge is one of the main reasons that his ideas have not caught on to a large extent. Twenty-five years

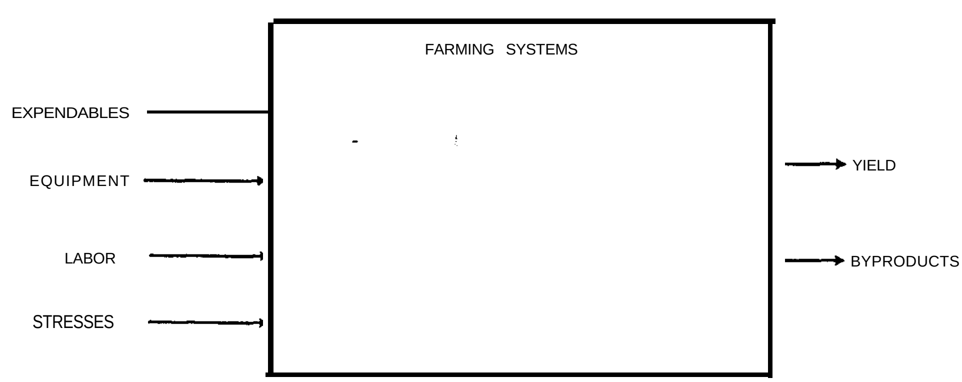

Fig. 2. A general functional model of a farming system that should be validated and quantified for specific crops.

ago, many adversaries of Donald's concept contended that sufficient physiological knowledge necessary to devise a model with confidence did not exist. Other arguments were that the definition of the model would narrow the breeding program and that high yields could be achieved with a number of radically diverse ideotypes.

A number of significant advancements have occurred since the proposal of crop ideotypes. New insights into the physiological connections between growth, yield, and development that contributes to it are being unraveled daily. An entirely new discipline, crop modelling, is serving both as an integrator of the new findings, and also as the basis for identifying the critical lesions in our present understanding of plant physiology. Crop models are also useful in conceptually testing unwieldy numbers of radically diverse ideotypes without the requirement that they be physically synthesized through laborious plant breeding techniques. Opponents would argue that process models are still very crude, but it is obvious that progress is being made in this area, and it would be unfortunate if breeders were not alert enough to take advantage of the progress that has occurred over the last quarter century. Present models do not incorporate algorithms that account for salinity stress, but the modular nature of some of the current plant growth models could be adapted with sufficient effort (Fig. 3).

Donald (1968) made two points related to the environment. One was that the ideotype should be designed for the most simple environmental situation (i.e., nonstress), and that the production of the crop ideotype could require the concurrent creation, through changes in management practices, of a new environment. He may have been half right. The greatest potential of crop ideotypes may be in specific stress situations - situations in which the concurrent meshing of new management practices can act in concert with the beneficial attributes of the crop ideotype to reduce the effect of overall yield. For example, salinity stress drastically reduces tiller number in wheat (Triticum *aestivum* L. em Thell), and tillering capacity is a main component of yield; whereas; mainstem yield is very resistant to salinity stresses across a wide range of concentrations (Maas et al., 1993). Uniculm wheat was proposed by Donald as a possible character for his wheat ideotype, but this has not been found to be an ideal character; under nonstress conditions, multiple tillers contribute substantially to high yield in many modern cultivars. Under salinity conditions, smaller plants with the uniculm character can be planted at higher densities to maintain crop yield and offset the losses due to tiller reduction (Francois, et al., 1993). Uniculm cultivars that have larger mainstem headsize, thicker and stronger stems, and the ability to grow under high population densities might be developed that will further improve yields under saline conditions.

Richards (1983) has noted that high yielding wheat cultivars generally out-yield more salt-tolerant or more environmentally stable lines in situations in which salinity is spatially variable across the field. Spatial salinity variability is a common occurrence, but the concept of crop ideotype allows the conceptual development of at least two possible solutions to the problem. First, an ideotype can be developed that has expressed salt tolerance characters and/or characters inducible by saline stress that will enable the plant

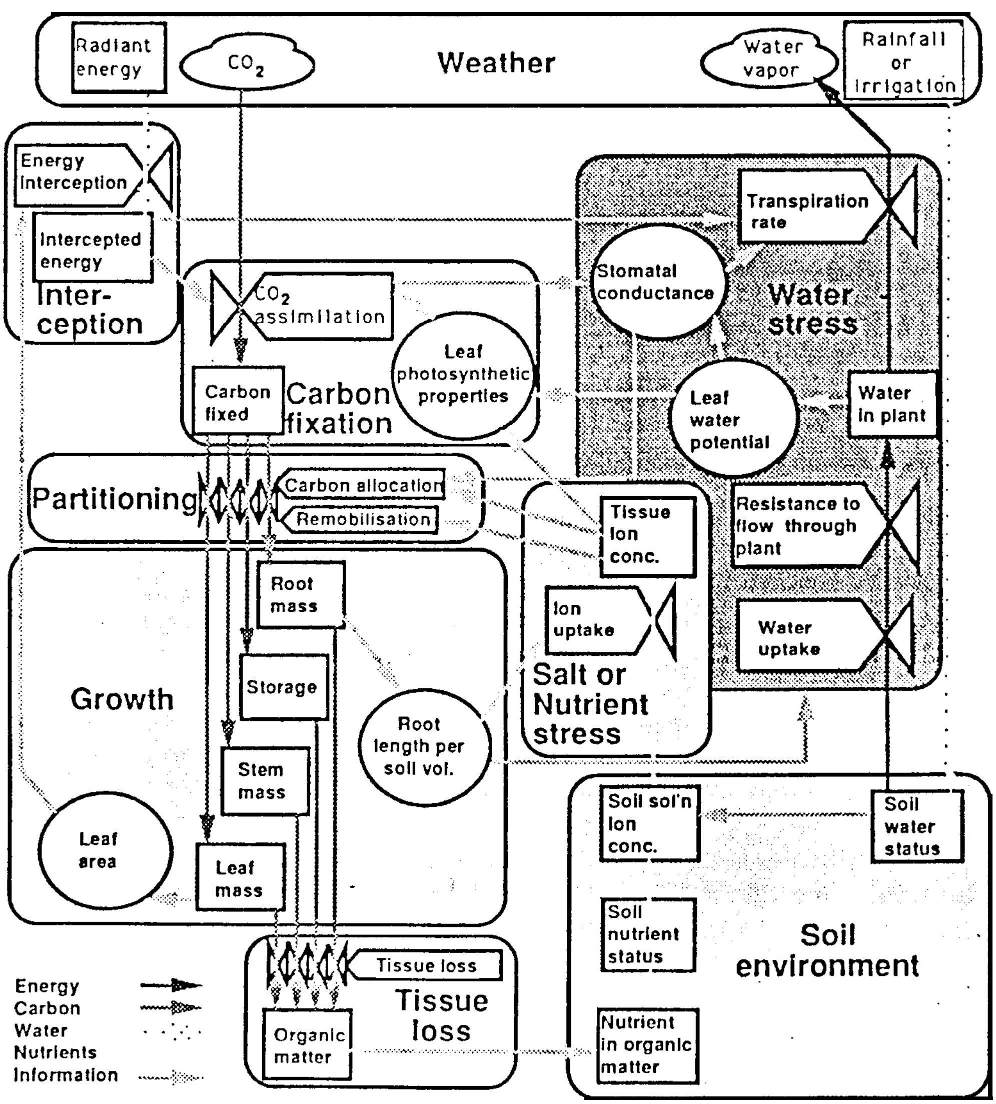

Fig. 3. A possible modular design for a process-based plant growth model that would include salinity effects.

to survive and produce seed better than the strictly high yielding line; or, second, different cultivars can be planted in specific parts of the field based on the predicted salinity stress. Both of these strategies are technologically feasible. Prescription farming has become a common term used to describe the technology for site-specific application of fertilizers and herbicides. Recent advances in rapid surveys for salinity assessment open the way for prescription planting in saline fields (Rhoades, 1993; Rhoades and Carter, 1993). In support of the first solution, both yield and tolerance can be theoretically improved if enough information is available to define the stress situation (Rosielle and Hamblin, 1981; Shannon, 1985). Acultivar developed under a specific salinity condition for both high yield and tolerance should be more productive than its counterpart that has been developed for high yield alone. The phenomena that Richards (1983) has described may derive from the fact that most salt tolerant lines are not developed for the specific climatic environment in which they are being tested. Environmentally stable lines suited to a wide range of climatic and stress environments cannot be expected to compete with high-yielding lines developed for the target environment.

Establishment of the Screening Procedures

Establishment of the screening procedures should be initiated at this point in the described program. The available information on crop salt tolerance, potential variability among cultivars and closely related species, and sensitivities to specific ions and environmental interactions has been collected. The precise growth stage that is limiting to productivity has been determined and the economical management techniques that can be used to overcome the limitation has been explored. A clear idea has been formulated of the crop requirements and management needs. It is now time to develop a screening procedure for the sensitive growth stage(s). 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. This might be accomplished simply by breeding **for** improved stands through germination and/or emergence tests (Beatty and Ehlig, 1973, for example). Usually it is more complicated.

Sometimes an indirect selection approach may be necessary to save time or effort (Shannon, 1979). Several investigators have demonstrated salt tolerance mechanisms that they thought were limiting to growth under saline conditions, and based on some of these reports, screening methods to improve plant salt tolerance have been proposed. These mechanisms include ion selectivity (Shannon, 1978; Sykes, 1985), ion exclusion (Noble et al., 1984), ion accumulation (Tal and Shannon, 1983), compatible solute production (Grumet and Hanson, 1986; Wyn Jones et al., 1977), osmoregulation (Morgan, 1977), late maturation (Bernal et al., 1974)) pollen sterility (Akbar and Yabuno, 1977), and pyramiding characters. Pyramiding characters refers to the concept of building salt tolerance in an additive manner based on strengthening tolerance within lines that already have a high degree of salt tolerance (Yeo and Flowers, 1983; Pasternak, 1987). This technique could be employed with or without knowledge of the physiological basis of salt tolerance (Ramage, 1980). Several investigators have proposed breeding programs for salt tolerance based on more direct methods (Dewey, 1962; Shannon et al., 1983). Many of the suggestions for both direct and indirect selection methods have been reviewed previously (Shannon, 1982, 1985, 1990), but it is worthwhile to summarize the rationale for some of the indirect methods.

Ion selectivity is a character for which screening procedures have been developed (Abel, 1969; Shannon, 1978, Noble et al., 1984; Sykes 1985). 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, cytoplasm of the aerial parts (Flowers, et al, 1977; Harvey, 1985). 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. Tolerant accessions of tall wheatgrass (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).

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 cultivars of some species. This also may be accomplished by finding tolerance to the toxicity of a specific ion associated with salt stress. 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).

Ion accumulation may be important in some species for osmotic adjustment ifphysiological mechanisms have co-evolved to sequester the salt away from metabolic sites and synthesize compatible solutes for osmotic balance. Halophytes take up high concentrations of ions as an adaptation mechanism to saline environments (Flowers et al., 1977). The accumulation of salt is thought to reduce the requirements for increased wall extensibility, leaf thickness and water permeability that might otherwise be required to maintain positive growth and turgor at low soil water potentials. The wild tomato species, *Lycopersicon cheesmunii,* is thought to be more salt tolerant than the cultivated species as a result of its halophytic nature, or its capacity to accumulate ions (Rush and Epstein, 1981). More recently, a salt-tolerant tomato *L. esculentum* Mill, cv. 'Edkawy', has also been shown to accumulate higher concentrations of Na' in leaf tissues than does more sensitive cultivars (Hashim et al., 1986). As with salt restriction, salt accumulation within tissues is thought to be well-regulated, and generally sequestered away from cytosolic compartments containing the salt-sensitive metabolic machinery of the cell. Few crop species are true halophytes and it probably would be difficult to transfer halophytism into glycophytic crop species. However, several investigations have shown interest in developing the agronomic potential of wild halophytes into new and useful salt-tolerant crops (Glenn and O'Leary, 1985; Glenn et al., 1991).

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. Morgan (1977) has noted substantial differences among wheat genotypes in their capacity for -osmotic adjustment. However, whether osmoregulation occurs in higher plants is controversial (Munns and Termaat, 1986). High humidities improve the tolerance of corn, bean, onion, 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). This may indicate that certain crops may benefit from selection pressures that improve their capacity to adjust osmotically or maintain more favorable water relations under salt stress (Tal and Gardi, 1976; Shannon et al., 1987).

Organic solutes (sugars, proline, glycinebetaine, and other compounds compatible with metabolism) may 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). High betaine genotypes of barley *(Hordeum vulgare* L.) maintained lower solute potentials than near-isoline, low-betaine genotypes grown at the same salinities (Grumet and Hanson, 1986). This suggests that betaine and other solutes could be used as a selection index for improved salt tolerance.

Water-use efficiency could be useful selection criteria as **a** mechanism that slows the process of salt accumulation in the root zone. Unfortunately, most water relation measurements are not accurate or reliable enough to be useful as screening techniques for salt tolerance. Future advances in instrumentation and better understanding of water relation mechanisms may some day improve the breeder's ability to select genotypes based on the maintenance of optimum water relations during salt stress. Increased leaf resistance, fewer stomata, increased mesophyll resistance, increased cuticle thickness, and an increased root-shoot ratio might be useful selection criteria in the interim.

Whatever selection criteria are chosen or are devised, the initial step should be to evaluate a range of cultivars and introductions to determine genetic variance for the desired character. 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 ifintracultivar selection will be effective. If genetic variance is low or if a greater degree of tolerance is required, wild-related species and lines developed from hybridizations can be evaluated. Field experiments should be conducted at an early stage after screening to verify the relationship of the criteria selected to the desired field characteristics.

Cultivar Development And Maintenance

Cultivar development and maintenance must be a continuing step in the breeding program. Salt tolerance is a difficult character to maintain under present commercial systems of seed production and breeding. Given that a germplasm line with high salt tolerance is produced by the breeder, successive crosses to improve quality, yield or resistance must be followed by selection in saline environments to assure that the characters associated with tolerance are not lost (Rosielle and Hamblin, 1981). The requirement to continue breeding and selection under saline conditions is difficult to meet for most seed producers. If breeding and selection for salt tolerance remains completely dependent on high yield as an index, seed producers will need to have access to saline water, methods for uniform salinity application, and more intensive and disciplined agronomic management techniques. This dependency could be replaced by physiological or morphological markers as more information is obtained on the mechanisms of salt tolerance and the inheritance of associated characters.

CONCLUSIONS

Salt tolerance is a character that is determined by a complex array of genes and genetic mechanisms, many of which are influenced in their expression by other environmental interactions. As a consequence, yield under saline conditions is influenced by both tolerance and agricultural management. The tendency for tolerance to be lost when selection for yield alone is conducted under nonsaline conditions makes breeding for salt tolerance a multiobjective task. Efforts to improve tolerance, yield and other characters for quality and resistances should be considered in a holistic program for seed production and improvement. The development and testing of functional models and ideotypes will make screening and selection more effective.

REFERENCES

Abel, G.H. 1969. Inheritance of the capacity for chloride inclusion and exclusion in soybeans. Crop Sci. 9,697-699.

Adams, W.M., and FM.R Hughes. 1990. Irrigation development in desert environments. In: Techniques for Desert Reclamation. AS. Goudie (ed.). John Wiley, New York. pp. 135-160.

Akbar, M. and T. Yabuno. 1977. Breeding for saline resistant varieties of rice. IV. Inheritance of delayed-type panicle sterility induced by salinity." Japan J. Breed. 27,237-240.

Ball, D.M., J.F. Pedersen, and G.D. Lacefield. 1993. The tall-fescue endophyte. Amer. Sci. 81:370-379.

Beatty, K.D. and Ehlig, C.F. 1973. A technique for testing and selecting for salt tolerance in sugarbeet. J. Amer. Soc. Sugar Beet Technol. 17:295-299.

Bernal, C.T., F.T. Bingham, and J. Oertli. 1974. Salt tolerance of Mexican wheat: II. Relation to variable sodium chloride and length of growing season. Soil Sci. Soc. Am. Proc. 38:777-780.

Bliss, RD., K.A. Platt-Aloia, and W.W. Thompson. 1984. Changes in plasmalemma organization in cowpea radicle during imbibition in water and NaCl solutions. Plant Cell Environ. 7:606-606.

Dewey, DR 1962. Breeding crested wheatgrass for salt tolerance. Crop Sci. 2:403-407.

Donald, C.M. 1968. The breeding of crop ideotypes. Euphytica 17:385-403.

Epstein, E., J.D. Norlyn, D.W. Rush, RW. Kingsbury, D.B. Kelley, and GA. Cunningham, 1986. Saline culture of crops; a genetic approach. Science 210:399-404.

Flowers, T.J., P.F. Troke, and AR Yeo. 1977. The mechanism of salt tolerance in halophytes. Annu. Rev. Plant Physiol. 28:89-121.

Francois, L.E. and E.V. Maas. 1978. Plant responses to salinity: An indexed bibliography. USDA, ARM-W-6, October 1978.291 pp.

Francois, L.E. and E.V. Maas. 1985. Plant responses to salinity: A supplement to an indexed bibliography. USDA, ARS-24,174 pp.

Francois, L.E., E.V. Maas, and C.M. Grieve. 1993. Effect of planting density and salinity stress on wheat yield. (Submitted to Agron. J.)

Gale, J., H.C. Kohl, and RM. Hagan. 1967. changes in the water balance and photosynthesis of onion, bean and cotton plants under saline conditions. Physiol. Plant. 20:408-420.

Glenn, E.P., nnd J.W. O'Leary. 1985. Productivity and irrigation requirements of halophytes grown with seawater in the Sonoran Desert. J. Arid Environ. 9:81-91

Glenn, E.P., J.W. O'Leary, M.C. Watson, L.T. Thompson, and RO. Kuehl. 1991. Salicomia bigelovii Torr.: An oilseed halophyte for seawater. Amer. Assoc. Adv. Sci. 251:1065-1067.

Gorham, J., C. Hardy, RG. Wyn Jones, L.R Joppa, and C.N. Law. 1987. Chromceomal location of the K/Na discrimination character in the D genome of wheat. Theor. Appl. Genet. 74:584-588.

Grattan, SR and CM. Grieve. 1992. Mineral element acquisition and growth response of plants grown in saline environments. Agric. Ecosystems Environ. 38:275-300.

Greenway, H. and W.D. Andrew. 1962. A screening technique to predict field behavior of medics in saline soil. Aust. J. Exp. Agric. Anim. Husb. 2:234-235.

Grumet, R and AD. Hanson. 1986. Genetic evidence for an osmoregulator function of glycinebetaine accumulation in barley. Aust. J. Plant Physiol. 13:353-364.

Grumet, R, T.G. Ialeib, and AD. Hanson. 1985. Genetic control of glycinebetaine level in barley. Crop Sci. 25:618-622.

Gulick, P. and J. Dvorak. 1987. Gene induction and repression by salt treatment in roots of the salinity-sensitive Chinese Spring wheat and the salinity-tolerant Chinese Spring x Elytrigia elongatum amphiploid. Proc. Natl. Acad. Sci. USA 84:99-103.

Harvey, D.M.R 1985. The effects of salinity on ion concentrations within the root cells of Zea mays L Planta 165:242-248.

Hashim, M., R.A. Jones, and A.S. El-Beltagy. 1986. Comparative responses to high salinity between salt-sensitive and salt-tolerant genotypes of the tomato. Acta Hortic. 190:533-543.

Hoffman, G.J., PB. Catlin, RM. Mead, RS. Johnson, L.E. Francois, and D. Goldhamer. 1989. Yield and foliar injury responses of mature plum trees fo salinity. Irrig. Sci. 10:215-229.

Hoffman, GJ., and J.A. Jobea. 1978. Growth and water relations of cereal crops as influenced by salinity and relative humidity. Agmn. J. 20:765-769.

Hoffman, GJ., and S.L. Rawlins. 1971. Growth and water potential of root crops as influenced by salinity and relative humidity. Agron. J. 63:877-880.

Hoffman, G.J., S.L. Rawlins, MJ. Garber, and EM. Cullen. 1971. Water relations and growth of coton as influenced by salinity and relative humidity. Agron. J. 63:822-826.

Kuiper, PJ.C. 1968. Lipids in g-rape roots in relation to chloride transport. Plant Physiol. 43:1367-1371.

Letey J., K. Knapp, and K. Solomon. 1990. Crop production functions. In: Agricultural Salinity Assessment and Management Manual. K.K. Tanji (ed.) ASCE, New York. pp. 305-326.

Maas, E.V. 1986. Salt tolerance of plants. Applied Agricultural Research. 1:12-26.

Maas, E.V. 1990. Crop salt tolerance. In: Agricultural **Salinity** Assessment and Management Manual. K.K. Tanji (ed.) ASCE, New York. pp. 262-304.

Maas, E.V., GJ. Hoffman, S.L. Rawlins, and G. Ogata. 1973. Salinity-ozone interactions on pinto bean: Integrated response to ozone concentration and duration. J. Environ. Qual. 2:400-404.

Maas, E.V., SM. Lesche, L.E. Francois, and C.M. Grieve. 1993. Tiller development in salt-stressed wheat. (Submitted to Cmp Sci.)

Morgan, J.M. 1977. Differences in osmoregulation between wheat genotypes. Nature 270:234-235.

Munns, R 1993. Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. Plant Cell Environ. 16:15-24.

Munns, R, and A. Termaat. 1986. Whole-plant responses to salinity. Aust. J. Plant Phyeiol. 13:143-160.

Nabors, M.W., S.E. Gibbs, C.S. Bernstein, and M.E. Meis. 1980. NaCl-tolerant tobacco plants from cultured calls. Z. Pflanzenphysiol. 97:13-17.

Noble. C.L., G.M. Holloran, and D.W. West. 1984. Identification and selection for salt tolerance in lucerne (Medicago sativa L.). Aust. J. Agric. Res. 35:239-252.

Pandey, R, nnd P.S. Gnnnpnthy. 1984. Isolation of sodium-tolerant callus line of Cicer arietinum L. cv BG-203. Plant Cell Reports 3:45-47.

Pasternak, D. 1987. Salt tolerance and crop production-a comprehensive approach. Ann. Rev. Phytopathol. 25:271-291.
Postel, S. 1989. Water for agriculture: Facing the limits. Worldwatch Paper 93. Worldwatch Institute, Washington DC.
Prisco, J.T., and J.W. O'Leary. 1973. The effects of humidity and cytokinin on growth and water relations of salt-stressed bean plants.
Ramage, RT. 1980. Genetics methods to breed salt tolerance in plants. In: Genetic *Engineering of Osmoregulation: Impact on Plant Productivity for Food, Chemicals and Energy* (D. W. Rains, R C. Valentine and A. Hollaender, eds.) pp. 311-318. Basic Life Sci., Vol. 14. Plenum Press, NY.
Rhoades, J.D. 1993. Electrical conductivity methods for measuring and mapping soil salinity. Adv. Agron. 49:201-251.
Rhoades, J.D. and L.M. Carter. 1993. New soil salinity mapping techniques. In: Utilization of Soil Survey Information for Sustainable Land Use. (in press).
Richards, RA. 1983. Should selection for yield in saline regions be made on saline or non-saline soils? Euphytica 32:431-438.
Rosielle, AA. and J. Hamblin. 1981, Theoretical aspects of selection for yield in stress and non-stress environments. Crop Sci. 21:943-946.
Rush, D. W. and E. Epstein. 1981. Breeding and selection for salt tolerance by the incorporation of wild germplasm into a domesticated tomato. J. Amer. Soc. Hort. Sci. 106: 669-670.
Shannon, M.C. 1978. Testing salt tolerance variability among tall wheatgrass populations." Agron. J. 70, 719-722.
Shannon, M.C. 1979. In quest of rapid screening techniques. HortScience 14:587-589.
Shannon, MC, 1980. Differences in salt tolerance within 'Empire'lettuce. J. Amer. Soc. Hort. sci. 105:944-947.
Shannon, M.C. 1982. Genetics of salt tolerance: New challenges. In: *Biosaline Research: A Look Into the Future. (A. San Pietro,* ed.) pp. 271-282. Plenum Press, NY.
Shannon, M.C. 1985. Principles and strategies in breeding for higher salt tolerance. Plant and Soil 89:227-241.
Shannon, M.C., and C.L. Noble. 1990. Genetic approaches for developing economic salt-tolerant crops. In: Agricultural Salinity Assessment and Management Manual. RK. Tanji (ed.) ASCE, New York. pp. 127-130.
Shannon, M.C., and L.E. Francois. 1978. Salt tolerance of three muskmelon cultivars. J. Amer. Soc. Hort. Sci. 103:l27-130.
Shannon, MC., M. McCreight, and J.H. Draper. 1983. Screening tests for salt tolerance in lettuce. J. Amer. Soc. Hort. Sci. 108:225-230.
Shannon, M.C., J.W. Gronwald, and M. Tal. 1987. Effects of salinity on growth and accumulation of organic and inorganic ions in cultivated and wild tomato species. J. Amer. Soc. Hort. Sci. 112:416-423.
Sykes, S. R 1965. A glasshouse screening procedure for identifying citrus hybrids which restrict chloride accumulation in shoot tissues. Aust. J. Agric. Res. *36:779-789.*
Tal, M., and I. Gardi. 1976. Physiology of polyploid plants: Water balance in autotetraploid and diploid tomato under low and high salinity. Physiol. Plant. 38:257-261.
Tal, M., and M.C. Shannon, **M. C.** 1983. Salt tolerance in the wild relatives of the cultivated tomato: Responses of *Lycopersicon esculentum L. cheesmanii, L. peruvianum, Solanum pennellii* and F1 hybrids to high salinity. Aust. J. Plant Physiol. 10:109-117.
Weimberg, R, and M.C. Shannon. 1988. Vigor and salt tolerance in 3 lines of tall wheatgrass. Physiol. Plant. 73:232-237.
Wyn Jones, R G.. R Storey, R.A. Leigh, N. Ahmad, and A Pollard. 1977. A hypothesis on cytoplasmic osmoregulation. In: *Regulation of Cell Membrane Activities in Plants* (E. Marre and 0. Ciferri, eds.) pp 121-136. Elsevier Press, Amsterdam.
Yoo, AR, and T..J. Flowers. 1983. Varietal differences in tho toxicity of sodium ions in rice leaves. Physiol. Plant. 59, 189-195.