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Principles and strategies in breeding for higher salt tolerance

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Summary Salinity is an environmental component that usually reduces yield. Recent advances in the understanding of salt effects on plants have not revealed a reliable physiological or biochemical marker that can be used to rapidly screen for salt tolerance. The necessity of measuring salt tolerance based upon growth in saline relative to non-saline environments makes salt tolerance measurements and selection for tolerance difficult. Additionally, high variability in soil salinity and environmental interactions makes it questionable whether breeding should be conducted for tolerance or for high yield. Genetic techniques can be used to identify the components of variation attributable to genotype and environment, and the extent of genetic variation in saline and nonsaline environments can be used to estimate the potential for improving salt tolerance. Absolute salt tolerance can be improved best by increasing both absolute yield and relative salt tolerance.

Introduction

The need to develop crops with higher salt tolerance has increased tremendously within the last decade; however, methods and approaches for accomplishing this goal are either not available or not well-defined because of a lack of information required for conducting successful research. The objective of this paper is to describe how some progress may be made toward obtaining plants with enhanced salt tolerance by meshing the theoretical aspects of breeding plants for salt tolerance with the present knowledge concerning the effects and mechanisms of salt stress. For brevity, it will be assumed that the readers are familiar with background information on the physiology and biochemistry of salt effects on plants. If not, there are several recent and thorough reviews on these subjects[6,8,12,15]. Generally, successful breeding requires the existence of variability and a means of stable transfer of a character from one individual to another. A method of recognition or identification of the character is required so that a selection protocol may be devised. The choice of an easily identifiable character, or marker, is highly desirable to simplify the selection procedure. From this point, all approaches basically include selection and breeding, but there is much diversity of selection criteria and philosophies. The actual method of breeding and inducing recombination is dependent upon the breeding system of the crop (*i.e.*, inbreeding, outbreeding, *etc.*).

Variability in plant responses to salinity

Extremely high salt concentrations kill plants through the combined effects of ion toxicity and decreased water potential. More moderate, but still high, concentrations of salt may cause leaf burn and severe growth inhibition. At more moderate to low salinities, differences in growth rate are often the only visual symptom of salt effect, though in some species there is also a slight darkening and/or thickening of the leaf. Although this general description of salt effects applies to all higher plants, there is a great deal of variation among species and even cultivars within a species in the degree of response to any level of salinity.

The subject of genetic variability among plants in responses to salt has been reviewed on several occasions[14,24,25]. Variability in salt response, as with almost any character, increases through the progression from variety to species to genus to family. Although salt-tolerant species are found among a wide range of plant families, some families have greater numbers of tolerant species. For example, the Chenopodiaceae include many salt-tolerant species, ranging from wild species of Salicornia and Atriplex to the cultivated sugarbeet (*Beta vulgaris*). Representative salt-tolerance species in the Gramineae are wild Spartina species, tall wheatgrass (*Elytrigia pontica*), bermudagrass (*Cynodon dactylon*), barley (*Hordeum vulgare*) and sugarcane (*Saccharum officinarum*). Variability in salt tolerance within species has been reported with increasing frequency in recent years; however, the choice of criteria by which tolerance is measured has not been consistent among investigators[14,15,19,23,26].

Tolerant phenotypes

Despite the multitude of comparisons that have been made between salt-tolerant and salt-sensitive species, few distinctive phenotypic markers reliably distinguish sensitive from tolerant individuals. A useful phenotype for plant breeding is an observable or otherwise measurable character. The phenotype (P) of a plant is the expression of the plant's genetic constitution (G), or genotype, modified by the environment (E). This relationship is commonly stated as $P = G + E$. Some traits that investigators have tried to use as markers include the Na^+ exclusion mechanisms in soybean (*Glycine max*)[1], tomato (Lycopersicon species)[20], and wheatgrass (*Elytrigia pontica*)[23], Cl^- exclusion in Citrus[16], and pollen sterility in rice (*Oryza sativa*)[2]. Even these were applicable only within a limited range of salt concentrations and are species- or variety-specific. For example, Rush and Epstein[19,20] found ion accumulation in the wild tomato species *Lycopersicon cheesmanii* to be a reflection of the halophytic nature of that ecotype, whereas Sacher *et al.*[21,22] have found no relationship between ion accumulation and salt tolerance in crosses between *L. peruvianum* and its cultivated descendent *L. esculentum*.

Phenotypic markers have not been used successfully in any concerted breeding effort. One problem is that it is unlikely that salt tolerance is determined by a single gene. Salt tolerance is probably the expression of a number of genes, and the importance of the expression of each is dependent upon its interaction with other salt tolerance genes and the external salt concentration.

The study of the inheritance of any character centers around its variation. Components causing variation (V) must be separated from one another. For example, in a heterogeneous population $Vp = Vg + Ve$, whereas in a genetically homogeneous population $Vg = 0$ and $Vp = Ve$. If both homogeneous and heterogeneous populations can be tested in the same environment, then Ve can be measured with the homogeneous population, and the Vg of the heterogeneous population can thus be determined. Tomato is self-pollinating, and parental and F1 populations can be considered to be highly homogeneous. Leaf Na accumulation in parental and F1 populations of tomato had coefficients of variation (CV) of about 22% (Table 1). The F2 populations, which are heterogeneous, had CV values of 55%, an increase in genetic variance of about 33% for this character as a result of intraspecific crosses.

Measurement of salt tolerance

Maas and Hoffman[11] have proposed that salt tolerance be defined by a simple linear equation, described in general terms as $y = a + b\ (x)$, where y = relative yield and x = salinity of the saturated soil extract of the root zone measured in units of electrical conductivity (dS/m). Actual salt response data are often nonlinear and follow a reverse sigmoid curve with a small but significant increase in yield at low salinities. However, a simple linear equation is applicable to most of the data obtained from salt tolerance studies[11]. Significant parameters of the equation include the slope (b), which is a representation of decline in yield per increment salinity increase, and the threshold, which is the lowest salinity at which a significant yield reduction occurs. Both yield decline and threshold are measured relative to nonsalinized plants. Such measurements are useful for comparing salt tolerance between species with large differences in yield potential, but carefully controlled conditions are necessary to obtain meaningful threshold and slope values.

Table 1. Comparative leaf Na ion contents in small populations of tomato (Lycopersicon) genotypes. Values determined on 6-mm-diameter leaf punches from 6-week-old plants grown in nutrient solutions containing 75 mol m^{-3} salt (5:1 NaCl: $CaCl_2$) (n = population size)

n	Genotype	Na[a]	CV[b]	
	Parental			
40	*L. esculentum* (Le)	288	16.9	
42	*L. cheesmanii* (Lc)	798	22.9	
39	*L. peruvianum* (Lp)	876	21.8	
33	*Solanum pennelli* (Sp)	1822	17.0	
				19.7
	F1			
35	Le × Lc	372	20.7	
36	Le × Lp	286	23.2	
35	Le × Sp	588	28.2	
				24.0
	F2			
84	Le × Lc	268	48.1	
96	Le × Lp	149	62.1	
				55.1

[a] Values given as mmol kg^{-1} dry weight as determined by dry weight measurements made on separate samples.
[b] CV Coefficient of variation.

Threshold values are especially sensitive to interaction with other environmental factors. Additionally, information is lost in comparing high- and low-yielding varieties of the same species on a relative basis. Such loss of information may be avoided if regressions are based on absolute yields in special circumstances in which plant breeding information is required.

Salinity variation within a field and interactions between environmental factors contribute to large standard errors and prohibit comparisons between individuals of segregating generations and between populations with high natural variability or environmental instability. Therefore, other criteria for the determination of salt tolerance are necessary.

Salinity interactions

Salt tolerance is usually expressed in terms of yield, a quantitative character that is also influenced by a wide array of factors other than salinity. For the breeder, yield is a simple phenotypic trait, and salinity is regarded as one component of the environment. There are two types of interaction, however, that may complicate this rather simple relationship. First, other environmental factors can positively or negatively modify the effect of salinity, as has been discussed elsewhere[11,12,24]. Second, genotype-environment interaction means that the 'best genotype' at one salt concentration may not be the 'best' at another. For instance, at a moderate salinity the criterion for selection may be significant yield reduction[26], while at high salinity survival might be the criterion[3,14]. Unfortunately, there is a fundamental gap in our understanding concerning the relationship between tolerance at low and high salinities. This is an important problem in choosing the salt concentration that will be used for screening. While it may be suspected that the physiological mechanisms that prevent damage at low salt concentrations are not the same as those that contribute to tolerance at extremely high concentrations, there is very little experimental evidence on which to base a conclusion. The principles of quantitative genetics could be used to study this problem. It has been demonstrated that a character measured in two different environments may be regarded as two characters rather than one[4]. By regarding tolerance at high and low salinities as different characters, variances of response at low and high salinity can be used to determine the genetic correlation between the characters. A low correlation would mean that different genes are involved and a high correlation would indicate the involvement of the same gene or genes.

Ontogenetic drift is another factor that can modify the relationship between phenotype and environment. Ontogenetic drift is actually a change in genotypic expression with plant development. During plant growth, the form and function of the various organs change. A plant's response and, consequently, its effective salt tolerance are influenced by its ontogenic stage. Thus, salinity effects may vary depending upon the growth stage at the time of stress. Indeed, salt tolerance at germination is not consistently related to tolerance during emergence, vegetative growth, flowering or fruiting[10]. The plant's ability to respond to salt stress depends upon the genes that are functioning at the stage of development during which the stress occurs. Salt-tolerance measurements over a short period of time during the early vegetative growth of muskmelon (*Cucumis melo*) indicated that salt tolerance gradually increases as the seedling matures (Fig. 1) and confirmed data obtained by other methods[11,12].

The effects of and responses to salt stress may also be modified by changes that have occurred due to previous stresses. For example, during rapid vegetative growth, the plant strives to maintain as large a photosynthetic area as possible and to maintain a root system that will support the plant and provide the required water and nutrients. Salinity affects this balance, typically reducing vegetative top growth more

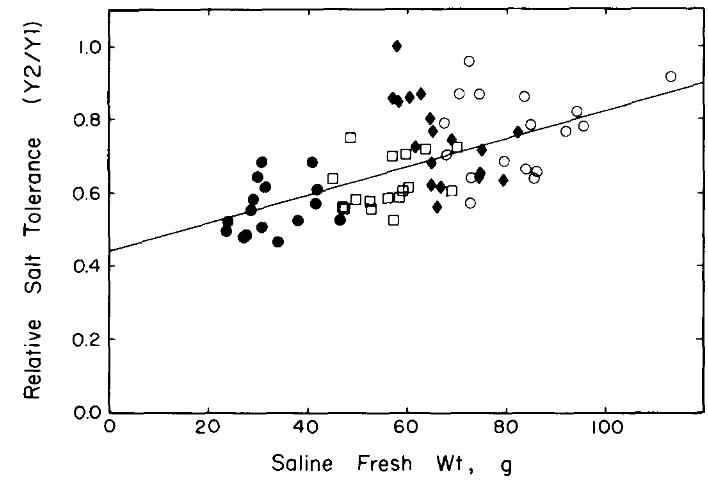


Fig. 1. Salt tolerance of 68 muskmelon (*Cucumis melo*) cultivars in four sand culture experiments in the greenhouse. In each experiment (shown by different symbols) cultivars were irrigated with control (1 dS/m) or saline ($\simeq$ 8 dS/m) nutrient solutions. Time between salination and harvest varied between 2 and 4 weeks with experiment and was directly related to the differences in average fresh weight. Y1 is fresh weight of controls and Y2 is fresh weight of salinized plants.

than root growth[12]. Such changes may affect the severity of and response to subsequent stresses.

Selection criteria

In plant breeding the most widely utilized criteria for selection are (1) mean yield, (2) regression response on site mean yield, and (3) uniformity of regression. Selection for mean yield is fundamentally a selection for the most high-yielding variety. Selection for the latter two criteria are based on stable performances across a range of environments. In the commercial agriculture characteristic of highly developed countries, high yield is the most important objective, whereas stable performance is more important in subsistence agriculture.

Regression response on site mean yield has been employed by breeders to measure yield stability across environments[5] and is similar to the regression method used to measure salt tolerance. A linear regression calculation is made of variety yield against the mean yield of all varieties at each location or environment. The use of mean yield allows a numeric grading of environments across sites and seasons. Because simple variety yields are plotted against the mean of all varieties, the population mean has a slope of 1.0. Slopes greater than unity indicate less stability than slopes smaller than 1.0. A small slope is also an indication of phenotypic stability in the salt tolerance regression. In a range of saline environments there are fundamentally two ways to change this slope. First, increasing the yield at high salinities would effectively reduce the slope, increase environmental stability, and improve salt tolerance, provided that the threshold remains stable. Alternatively, an independent increase in the threshold would make the slope greater and decrease environmental stability. The concept of selection for salt tolerance is actually to select for high yields across a range of saline environments, because salinity is a continuous rather than a discrete variable and is highly variable, even in the same field. These factors make it imperative that varieties are selected that have stable performance at more than a single salt concentration. Recent efforts to study salt tolerance of wheat and barley varieties at field locations have led Richards[17] to conclude that salt tolerance may best be improved by breeding for high yield in nonsaline environments. The main reason for this conclusion was high variability in soil salinity throughout the field. The benefits of high yield versus those of relative salt tolerance have been discussed previously[24]. At low salinities high-yielding varieties may produce better yields than lower-yielding varieties that may have a better degree of salt tolerance. For example, in a 1976 field study the muskmelon cultivar 'Top Mark' was higher-yielding than the cultivars 'Hale's Best' and 'PMR 45' up to saturated soil extract electrical conductivities (EC_e) of about 5 dS/m (Fig. 2). At higher salinities, above an EC_e of 8 dS/m, the lower-yielding varieties had higher yields than 'Top Mark.' Thus, it appears that 'Hale's Best' and 'PMR 45' have more environmental stability, lower yield reductions for corresponding increases in salinity, and higher relative salt tolerance. Although the yields of muskmelon beyond an EC_e of 8 dS/m cannot be considered to be economically important, the genetic characteristics that make melons tolerant to salinity may be a serious consideration to the plant breeder.

The point made by Richards[17] is that high variability in salinity within a field allows anywhere from maximal to zero yields within different portions of the same field. He estimated that fields with high, medium and low salinity problems consist of about 25, 50, and 75 percent, respectively, of nonsaline areas in which 100% yields can be obtained. Thus, high-yielding varieties can contribute substantially to the total yields in these areas. For example, in Table 2 fields similar to those previously reported[17] are classified within salinity ranges and an overall weighted mean salinity is given. The yields of the three muskmelon cultivars from Figure 2 were predicted based on their salt-tolerance thresholds and slope values for each area within these fields

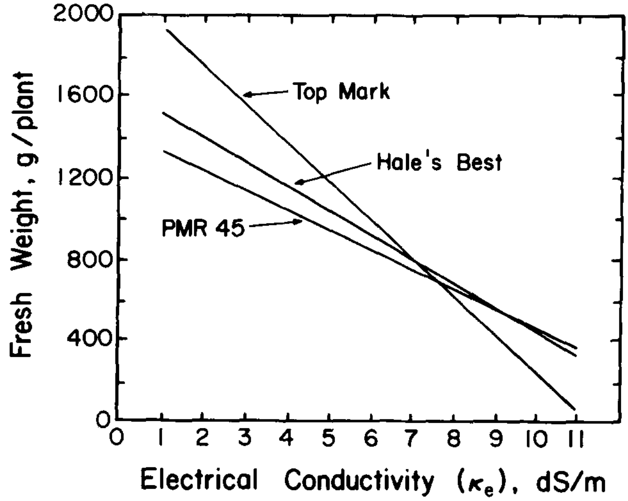


Fig. 2. Variation in absolute salt tolerance of 3 muskmelon (*Cucumis melo*) cultivars. ($\kappa_e = EC_e$).

Table 2. Approximate distributions of saline areas in four model fields as percent of the total field area

	Soil salinity (EC_e) (dS/m)				
Field salinity	0–4	4–8	8–12	> 12	Wt mean EC_e
Nonsaline	100	0	0	0	2.0
Low	75	15	5	5	3.6
Medium	50	20	10	20	6.0
High	25	25	15	35	8.4

(Table 3). It is apparent that 'Top Mark,' because of its high-yielding characteristics, has greater yields up to about 5 dS/m. Based on calculations made according to the Maas and Hoffman convention, 'Top Mark' has the highest threshold value of the three cultivars and the lowest slope value (− 8.8).

Tolerance to stress may be defined in a variety of ways, for example as the difference between yield in a nonsaline (Y1) and in a saline environment (Y2), or Y1 − Y2. This is a measure of tolerance on an absolute scale, since no account is made of differences in normal growth rates. Relative tolerance may be calculated by dividing by Y1. Reducing this equation, we obtain 1 − (Y2/Y1). In both definitions the highest tolerance is indicated by the smallest number. Another definition of tolerance is the mean productivity, which may be mathematically expressed as Y1 + Y2/2.

An example of the results obtained using these tolerance measurements is given for data from greenhouse experiments in which 48 lettuce (*Lactuca sativa*) cultivars were grown under nonsaline (control,

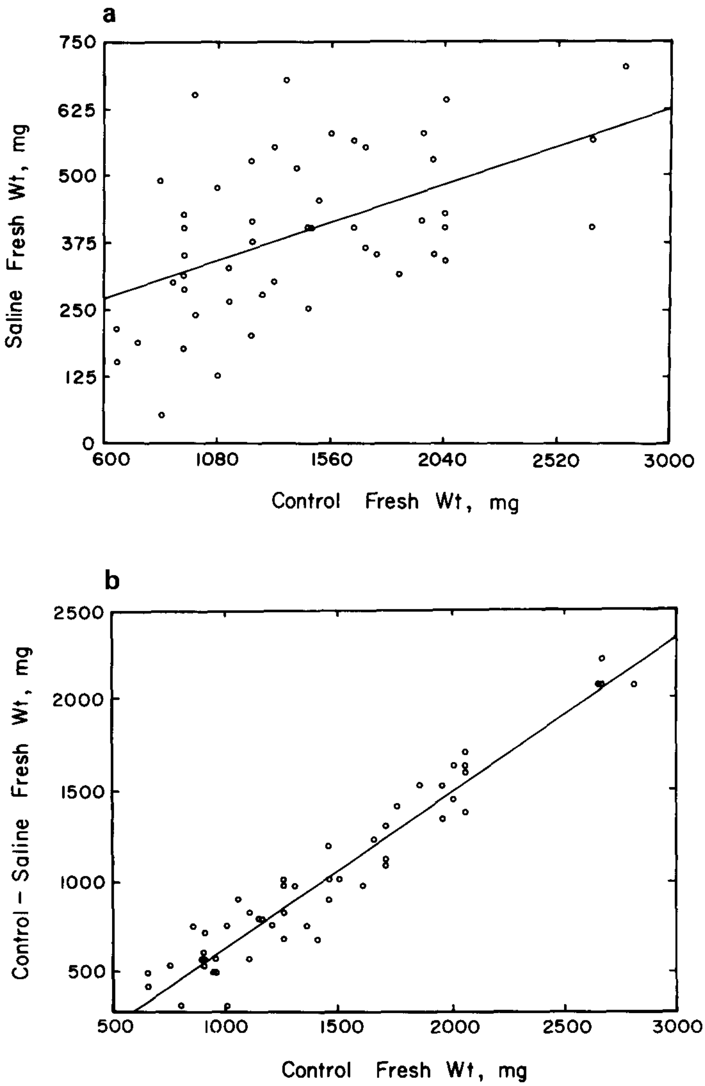
Table 3. Marketable fruit yields of the muskmelon cultivars 'Top Mark,' 'Hale's Best,' and 'PMR 45' in g/plant that would be harvested from fields of variable salinity as described in Table 2

Field salinity	Soil salinity (EC_e)(dS/m) 0–4	4–8	8–12	> 12	Total yield
	'Top Mark'[a]				
Nonsaline	1969	0	0	0	1969
Low	1477	180	22	0	1679
Medium	985	240	44	0	1269
High	492	301	65	0	858
	'Hale's Best'[b]				
Nonsaline	1482	0	0	0	1482
Low	1112	150	26	1	1289
Medium	741	199	51	5	996
High	371	249	77	9	706
	'PMR 45'[c]				
Nonsaline	1317	0	0	0	1317
Low	987	140	27	8	1162
Medium	658	186	55	32	931
High	329	233	82	56	700

[a] Maximum yield = 2178, threshold = 0.91, and slope = − 8.8
[b] Maximum yield = 1662, threshold = 0.52, and slope = − 7.3
[c] Maximum yield = 1439, threshold = 0.73, and slope = − 6.7

1.0 dS/m) and saline (9.3 dS/m) conditions in sand cultures[26]. Fresh leaf weights were compared on the bases of absolute and relative salt tolerance and mean yields. There was high variability in fresh weight in both control and saline environments, but generally variability in nonsaline environments was higher than in saline ones (Fig. 3a). This is a common finding for any environmental stress. It has been found that decreased stress permits a greater range of phenotypic expression and increases variances among lines in 17 out of 20 cases in oats (*Avena* species)[9]. Variation in tolerance as measured by Y1 − Y2 shows less variability in fresh weight than is shown by Y1 alone (Fig. 3b). The correlation between tolerance measured in this manner and control fresh weight shows the direct effect of high-yield potential. Relative salt tolerance is highly variable among low-yielding lines and less variable among high-yielding lines (Fig. 3c). There is a general decrease in relative salt tolerance as the yield potential increases. Conversely, relative salt tolerance is generally higher among lines that have high yields in saline conditions (Fig. 3d). These data indicate that selection for high yield under nonsaline conditions would slightly favor varieties with low relative salt tolerance, and selection for high yield in saline conditions would favor varieties with higher relative salt tolerance.

The question of whether selection for tolerance to stress is even


a
750
625
500
375
250
125
0
600
1080
1560
2040
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Saline Fresh Wt, mg
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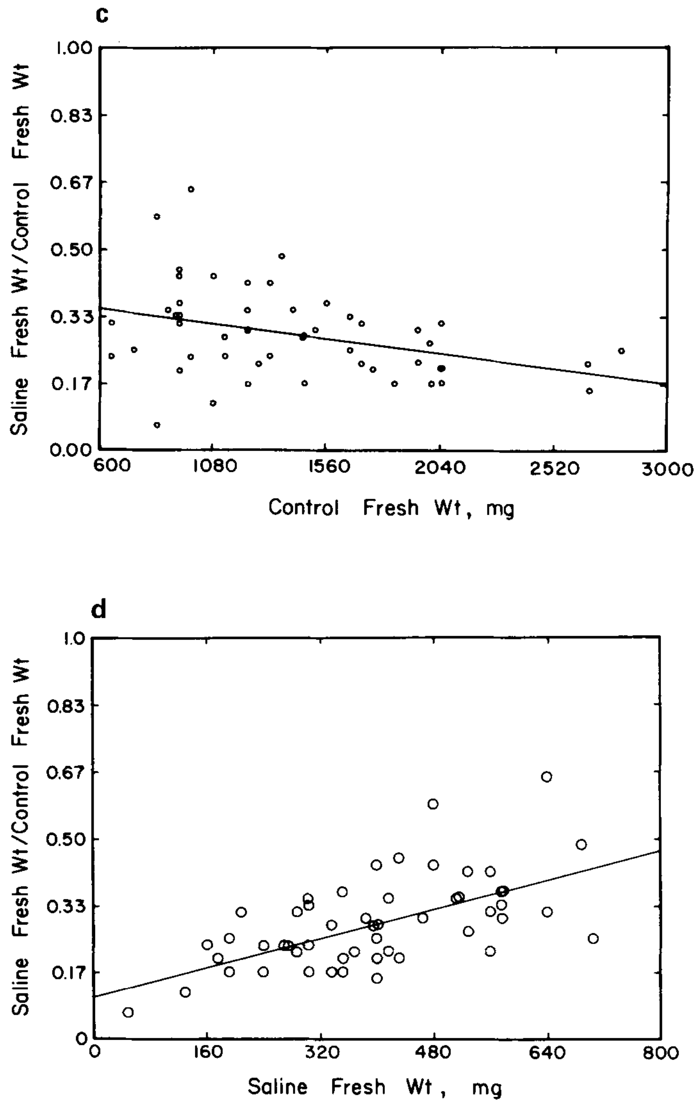

Fig. 3. (a) Correlations between fresh weight yields for 48 lettuce (*Lactuca sativa*) cultivars grown in greenhouse sand cultures and irrigated with either control (1 dS/m) or saline (10dS/m) nutrient solutions.

(b) Correlation between control fresh weights and salt tolerance as measured by the difference between average fresh weight yield under control and saline conditions.

(c) Correlation between control fresh weights and relative salt tolerance (fresh weight of salinized plants/control).

(d) Correlation between saline fresh weights and relative salt tolerance.

worthwhile has recently been proposed[18]. It was shown that selection for mean productivity will normally increase yields in both stress and nonstress environments, provided that genetic variance in the stress environment is less than in the nonstress environment and that the genetic correlation of yields in both environments is highly negative[18]. Alternatively, selection for tolerance under these same conditions would decrease the mean productivity. This implies a negative correlation between mean yield and tolerance. Indeed, the data in Fig. 3c support this contention. For a positive relationship to exist between tolerance and mean productivity the genetic variance in stress environments must be greater than in nonstress environments. This is not common, and it has been pointed out that varieties with high phenotypic stability usually have low mean yields[5,7,13].

Breeding method

Breeding approaches include backcrossing, progeny testing, and pure line selection. The main factor that determines the method of plant breeding, aside from the induction of useful variation, is the breeding system. Two-thirds of the world's food supply is provided by inbred species. Two of the major cereals, rice (*Oryza sativa*), and wheat (*Triticum* species), and most of the important oil and protein crops are inbred species. Outbreeding crops include most of the forages, sugarcane, and most of the tree fruits.

Inbreeding crops are developed by pedigree selection. In this process, one parent is chosen for genetic properties that are useful (*e.g.*, salt tolerance), while the other is chosen for its complementing and desirable agronomic characteristics. Self pollination leads rapidly to homozygous lines which can then be tested for overall improvements. This system is self perpetuating in that it generates some improved lines that can be used as parents in subsequent hybridizations. A disadvantage of this system is that early generations can be expected to be heterogeneous and quite unstable in their response to environmental interaction. This makes early selection difficult, because the individual is the unit of selection and the effects of variation in salinity across a field plot or greenhouse bench can result in some loss of segregates with genes for salt tolerance. Environmental effects during early generations may be reduced by selection under controlled conditions in the laboratory or through the use of saline irrigation water in field selections.

Other practices can be used to reduce environmental effects when screening is conducted in the field. Selection may be delayed until the F6–F8 generation. Bulk generations can be maintained to assure the maximum number of recombinants. The increased homozygousity of these generations will increase the correspondence between genotype and phenotype. However, increases in selection efficiency (in the field) cannot be expected, because environmental interactions may still be rather large. Another method that may be used to reduce environmental effects in inbreeding species is single-seed descent. Individual lines derived through a single unselected seed saved in each generation through F6–F8 may be used to test for a particular character. The advantages of this method are that many populations can be grown through several generations under conditions favoring reduced generation time, and a good correspondence can be expected between genotype and phenotype. Additionally, the F2 population can be used to predict a potential range of variation.

The above systems may be adapted to salt tolerance. Modifications that may improve selection efficiency include the use of saline irrigation water to reduce natural variation in soil salinity and the use of numerous salt concentrations so that regressions against mean yields can be used to determine salt resistance with more reliability.

The production of F1 hybrids takes a prominent place in the improvement of outcrossed species. Genetic advances among hybrids are usually the result of making crosses between selected inbred lines that have been chosen for their individual characters as well as their combining abilities. In species that do not have economical F1 seed production systems, the concept of population improvement is usually adopted. Most forms of population improvement include both mass selection and various types of progeny testing designed to accumulate alleles through recurrent selection over generations. The details of this plan have been the subject of much research and controversy, but the average gain by most of the methods indicates that they are all almost equally effective. The complication of salt tolerance would not seem to make one any more effective than another, but a particular selection procedure for salt tolerance may favor one method over another. For instance, recurrent selection within families includes replicative tests at several locations. This procedure could be developed to minimize the interactions between salinity and environment as well as those between genotype and phenotype. The reconstitution of advanced generations from parents with high scores for salt tolerance at several locations could eventually lead to a quantitative improvement over time.

Tissue culture techniques may eventually improve both of the above mentioned methods if haploid isolation procedures can be developed to allow the single-step creation of homozygous diploids from F1 hybrids. Another possibility is the use of somaclonal variation to induce the needed variability to select for salt tolerance.

Ultimately, the objective should be to increase tolerance by increasing both mean yield and yield stability. An understanding of the basic principles of both salt tolerance and plant breeding will be required to do this.

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