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Contents

Potential for Genetic Improvement in Salinity Tolerance in Legumes: Pigeon Pea

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INTRODUCTION

Leguminous crops are cultivated throughout the world because of their importance as a protein source in the diets of humans and livestock. Further, many leguminous species are cultivated as pasture, fodder, or green manure plants. Legumes thereby form essential components of cropping systems, primarily because of their inputs of nitrogen fixed from the atmosphere but also for other benefits they offer, such as improving the soil physical and chemical environment and breaking disease cycles (1). Among various crop plants tested, however, legumes have generally been found to be more sensitive to soil salinity (2). With the emphasis given to increasing cereal production in recent decades, the cultivation of legume crops has generally been forced to more marginal lands, including those prone to salinity problems. Further, legumes grown on residual soil moisture in the season after the rains, such as chickpea and lentil, are particularly prone to salt damage: salts are progressively concentrated in the soil solution and precipitated toward the soil surface as the soil dries out. Thus, legumes generally face a greater threat of salinity than cereals because of their greater salt sensitivity and an increasing likelihood of being exposed to saline environments. Therefore, improvement in the salinity tolerance of legumes is of immediate and increasing concern.

Pigeon pea is a major grain legume crop of the tropics and subtropics and is widely grown in the Indian subcontinent, which accounts for around 90% of the world's crop (3). Traditional, long-duration (180–300 days) pigeon pea is usually grown as a mixed crop or intercropped with cereals (e.g., sorghum, pearl millet, maize, and upland rice), other legumes (e.g., groundnut, soybean, mung bean, and cowpea), or such nonlegumes as castor, cotton, sesame, and sunflower (4). Short-duration pigeon pea (100–150 days), a

relatively new plant type, was recently introduced into India and is normally grown as a sole crop, for example, before the major season crop (after the rains) of wheat in northern India (4).

Pigeon pea is grown throughout India, but the major concentration is in the states of Uttar Pradesh, Gujarat, and Maharashtra, which together contribute about 85% of the total growing area and production of India (3). More than 51% of the saline soils in India are located in these states (5). India's >7 million ha of saline soils (6) coincides with agroclimatic zones otherwise favorable for pigeon pea cultivation. Among cultivated legumes, pigeon pea is classified as moderately sensitive to salinity (7).

With the development of short-duration pigeon pea, its production has spread into nontraditional areas and new cropping systems (4). Short-duration pigeon pea is increasingly grown in irrigated areas, as in the pigeon pea-wheat rotation. Improving salinity tolerance in pigeon pea should allow extension of pigeon pea cultivation to slightly to moderately saline areas. Since secondary salinization is becoming a serious problem in irrigated areas of India, it is important to improve the salinity tolerance in this crop for the long-term survival of pigeon pea-based cropping systems.

In this chapter, pigeon pea is used as a case study for an overview of the current status of information on salinity tolerance in cultivated legumes, with reference to the scope for genetically improving their salinity tolerance.

SALINITY TOLERANCE IN LEGUMES

The *salinity tolerance* of crop plants can be defined as the ability of plants to survive and produce economic yields under adverse conditions caused by soil salinity. Salinity tolerance is normally expressed in terms of the yield decrease associated with a given level of soil salinity or as relative crop yield in saline compared with nonsaline soils (2). A yield decrease or growth reduction of 50% is usually considered a critical level for evaluating the relative salt tolerance of crops (2,8). Various strategies required for improving salinity tolerance in crop plants and the limitations associated with genetic means are covered in Chapter 29. These are largely applicable to the leguminous crops as well, except that additional complications are associated with the general susceptibility of the legume-*Rhizobium* symbiosis to salinity.

Legumes are generally considered either sensitive or only moderately tolerant to salinity (2,9–11). However, considerable variability in salinity tolerance among crop legumes has been reported (Table 1). Among cultivated legumes, *Sesbania cannabina* and *Lupinus luteus* are particularly tolerant to salinity (7,9). *Sesbania grandiflora* has been reported to have a halophytic mode of adaptation (20). Some of the tree legumes, such as *Prosopis* and *Acacia* spp., are highly tolerant to salinity, with their tolerance levels approaching that of seawater (21–23). On the other hand, grain legumes, such as *Phaseolus vulgaris*, *Vigna radiata*, and *Cicer arietenum*, are highly sensitive to salinity, with which 50% growth reduction occurs at 3–4 dSm^{-1} salinity.

SCOPE FOR GENETIC IMPROVEMENT IN SALINITY TOLERANCE IN LEGUMES

Salinity is a complex problem where salt concentration and composition vary temporally and spatially. So, defining the target environment plays a crucial role in directing the

Table 1 Relative Tolerance of Different Legumes to Salinity

Species	EC_e (dSm^{-1}) at 50% yield	Reference
Sesbania cannabina	13.2	7
Lens esculenta	12.8	12
Trifolium subterraneum	11.1	13
Macroptilium atropurpureum	10.6	14
Cyanopsis tetragonoloba	10.1	7
Medicago sativa	10.2	15
Pisum sativum	10.0	16
Macroptilium atropurpureum	9.9	15
Vigna triloba	9.7	14
Indigofera spicata	9.5	14
Macroptilium lathyroides	9.5	15
Permanthus subulatus	9.3	14
Vigna sinensis	9.0	7
Sesbania bipinosa	8.4	17
Trifolium alexandrinum	8.3	15
Vigna aureus	8.3	18
Medicago scutillata	8.2	15
Trifolium hirtum	8.1	15
Desmodium intortum	7.9	15
Arachis pintae	7.9	14
Macrotyloma uniflorum	7.8	15
Medicago truncatula	7.8	15
Medicago littoralis	7.7	15
Vigna unguiculata	7.2	15
Glycine wightii	6.9	15
Vicia faba	6.8	2
Glycine max	6.7	7
Lotonis bainesii	6.6	15
Trifolium fragiferum	6.5	15
Cliteria turnatea	6.4	14
Trifolium repens	6.2	15
Stylosanthus scaraba	5.6	14
Lablab purpureus	5.5	15
Cajanus cajan	5.4	7
Indigofera schimperi	5.4	14
Psolarea tenax	5.3	14
Rynchosia minima	5.1	14
Stylosanthes humilis	5.1	15
Vigna mungo	5.0	7
Arachis hypogea	4.9	2
Desmodium uncinatum	4.9	15
Vigna unguiculata	4.9	2
Trifolium semipilosum	4.2	15
Phaseolus vulgaris	3.6	2
Vigna radiata	3.5	7
Cicer arietinum	3.0	19

genetic improvement in a given crop species (see Chapter 29 for further discussion of this aspect).

Genotypic Variation

Genetic variation is a prerequisite for the improvement in any trait through plant breeding, and this also applies to salinity tolerance. Varietal or genotypic differences in salt tolerance have been reported in several crop legumes (Table 2). In most cases, only a few genotypes or varieties have been examined and the intraspecies variation has not been thoroughly explored. To our knowledge, there have been no concerted attempts to systematically evaluate the world germ plasm collections available in various crop legumes for salinity tolerance.

In alfalfa (lucerne, *Medicago sativa* L.), variation in salinity tolerance within a cultivar, CUF 101, was found (26). Two generations of recurrent selection for tolerance was reported to have significantly increased the mean population tolerance, and heritabilities were estimated as $h^2 = 0.41$. For other forage legumes, such as forage rape (*Brassica napus* L.), berseem clover (*Trifolium alexandrinum* L.), and red clover (*Trifolium pratense* L.), similar variability among plants within a cultivar was reported (44). Based on seedling tolerance to NaCl as a selection criterion, the realized broad sense heritabilities were estimated as 0.62, 0.34, and 0.57 for forage rape, berseem clover, and red clover, respectively; narrow sense heritabilities from parent-progeny regression were 0.74, 0.50 and 0.98, respectively, for these species. This indicates the feasibility of improving salinity tolerance through a population improvement approach in these forage legumes, which are cross pollinated and highly variable genetically.

In pigeon pea, substantial genotypic variation for salinity tolerance at the germination stage has been reported (29–31). However, germination in pigeon pea is less sensitive to salinity than the later stages of growth. All the genotypes tested were able to germinate

Table 2   Legumes for Which Varietal or Genotypic
Differences Have Been Reported

Crop species	References
Lentil (*Lens esculentum*)	12, 24
Alfalfa (*Medicago sativa*)	25, 26
Pea (*Pisum sativum*)	16, 27, 28
Pigeon pea (*Cajanus cajan*)	29–31
Chickpea (*Cicer arietenum*)	19, 32, 33, 35
Groundnut (*Arachis hypogea*)	34
Broad bean (*Vicia faba*)	27, 36
Mung bean (*Vigna radiata*)	37
Urd bean (*Vigna mungo*)	38
Green bean (*Phaseolus vulgaris*)	39
Subterranean clover (*T. subterraneum*)	40, 41
Cowpea (*Vigna cinensis*)	29
Soybean (*Glycine max*)	42, 43
Berseem clover (*T. alexandrinum*)	44
Red clover (*T. pratense*)	44

at salinity levels that are toxic at later stages of growth (31,45). Thus, selection for salinity tolerance at the germination stage is not warranted in pigeon pea (31).

There were large differences among 150 pigeon pea genotypes in their survival (to 60 days after sowing), relative growth rates, and leaf damage symptoms (appearance of leaf necrosis) when grown in a hydroponic system at a critical salinity level of 6 dSm^{-1} (31). These differences in salinity tolerance were confined to a narrow range of salinity, 6–7 dSm^{-1}, however: there were no clear differences among genotypes below 6 dSm^{-1}, and none of the tested genotypes were able to survive above 7dSm^{-1} (31). Thus, the narrow range of genotypic variation for salinity tolerance in cultivated pigeon pea may not be sufficient to allow substantial genetic improvement in salinity tolerance. A large germ plasm collection of over 10,000 accessions (46) is available in this crop species, however, and we have examined only 150 genotypes. Thus, there may still be scope to identify wider genetic variation through systematic testing of pigeon pea germ plasm under a uniform controlled screening system.

To demonstrate genotypic differences under the normally highly variable field conditions, differences between genotypes should persist across a relatively wide range of salinity levels. This is perhaps one of the main reasons we are unable to demonstrate these differences consistently among pigeon pea genotypes under field conditions (8). Thus, the availability of genetic variation over a wider salinity range than identified thus far is necessary if salinity tolerance in pigeon pea is to be exploited under field conditions.

Role of Wild Relatives

Little information is available on the salinity tolerance of wild species related to the major crop legumes. In cereals, substantial sources of higher levels of salinity tolerance have been identified in the wild related species (see Chapter 29 for further discussion on this). In chickpea, limited studies with various wild *Cicer* spp. have indicated that most of these wild relatives are even more sensitive to salinity stress than the already sensitive cultivated chickpea (8). Thus, in this legume crop at least, the role of wild relatives in improving salinity tolerance seems limited, although more comprehensive testing of wild relatives is warranted.

In pigeon pea, the limited variation in salinity response within cultivated pigeon pea prompted us to examine its wild relatives for sources of salinity tolerance. Wild relatives of pigeon pea have proved to be sources of resistance to various diseases and sources of high protein levels (47–50). Various species of *Atylosia*, *Rynchosia*, and *Dunbaria* showed a wide range of variation in salinity tolerance (critical salinity levels between 4 and 12 dSm^{-1}, Table 3) (31). *Atylosia platycarpa* and *Atylosia albicans* were the two most promising species identified; they could provide substantial levels of tolerance (up to 12 dSm^{-1} and possibly higher) for the genetic improvement in cultivated pigeon pea (31). *A. platycarpa* could produce flowers and pods at all salinity levels, including 12 dSm^{-1}. Cultivated pigeon pea is not compatible with this wild species for direct hybridization, however, and bridging techniques are necessary to transfer this higher tolerance level to cultivated pigeon pea; such attempts are currently underway (51). The other tolerant wild species, *A. albicans*, is directly crossable with pigeon pea, however, and this species is thus a readily available source for genetic improvement in salinity tolerance. This species was earlier used as a donor for high seed protein concentration, a trait that was successfully transferred to cultivated pigeon pea through conventional backcross breeding followed by pedigree selection (48, 50).

Further studies showed that the higher level of salinity tolerance in *A. albicans* could

Table 3   Representation of Salinity Tolerance Status (Ability to Survive and Grow) in Pigeon Pea and Its Wild Relatives

| | Resistance up to | | | |
4 dS m^{-1}	6 dS m^{-1}	8 dS m^{-1}	10 dS m^{-1}	12 dS m^{-1}
				A. albicans
				A. platycarpa
			A. sericea	
			A. cajanifolia	
			A. volubilis	
		ICPL 227[a]		
		A. reticulata		
		A. grandifolia		
		A. lineata		
		A. scarabaeoides		
		Dunbaria ferruginea		
	Atylosia goensis			
	A. lanceolata			
	HY 3C[b]			
	A. acutifolia			
Rynchosia albiflora				

[a]Tolerant genotype of cultivated pigeon pea.
[b]Susceptible genotype of cultivated pigeon pea.
Source. From Reference 31.

be expressed as a dominant genetic factor in the F_1 hybrids of reciprocal crosses between this species and a cultivated pigeon pea genotype (ICP 3783) (52). The physiological attributes conferring salinity tolerance in both *A. albicans* and the F_1 hybrids include Na and Cl retention in the roots and limited translocation to the shoots, high K selectivity, and maintenance of the transpiration rate under saline conditions (52,53). This expression of wild-type physiological traits in the F_1 hybrids (52) indicates that these physiological traits are heritable and controlled by dominant genes.

Future Requirements

In pigeon pea, further studies on the segregating F_2 and F_3 generations, including the analysis of the ionic constituents, are needed to establish the inheritance pattern of these physiological traits. If this tolerance is shown to be controlled by a limited number of genes, it seems feasible to improve salinity tolerance in pigeon pea by a simple backcross-ing procedure. However, before undertaking a major program to incorporate this higher level of tolerance into the pigeon pea, we believe it is important to evaluate available accessions in *A. albicans* further, since variation among accessions of the species is likely and thus identification of even higher levels of tolerance in other accessions is possible. For various leguminous crops, we also suggest that the related wild species be thoroughly evaluated for their potential contribution to improving the salinity tolerance of the cultivated legumes.

RESPONSE TO CALCIUM

The calcium level in the growth medium is an important determinant of salinity response in legumes because of the general alleviating effects of supplemental Ca (Chapter 29) (54–56). It is therefore important to understand the interactions between salinity and Ca as they apply to specific legumes. In pigeon pea, positive growth responses were observed in both tolerant and sensitive genotypes to a decreasing Na/Ca ratio under constant salinity at either 6 or 8 dSm^{-1} (57). However, the relative growth differences between tolerant and sensitive genotypes persisted at the different Na/Ca ratios and salinity levels. A decrease in the Na/Ca ratio enhanced K uptake and reduced Na uptake, thus increasing the K/Na ratio (57). The K/Na ratio in shoots of the tolerant genotype was greater than in the sensitive genotype at different Na/Ca ratios at both salinity levels. Tissue chloride levels increased with decreasing Na/Ca ratio at both salinity levels (57). This enhancement is probably a consequence of cation-anion balance. Total cation (Ca + Na + K) con-centrations increase with decreasing Na/Ca ratios, in a manner similar to the increase in Cl concentrations (57). The enhancement of Cl uptake negates to some extent the positive effects of Ca in increasing the K/Na ratio in pigeon pea. Thus, this must be taken into account when recommending the application of gypsum to saline alkali soils as a reclamation measure. The relative growth differences and differences in Na, K, and Cl uptake between tolerant and sensitive genotypes, however, persisted across the range of Na/Ca ratios (57). This shows that the results of screening for genotypic differences at a particular Na/Ca ratio are likely to be applicable to other Na/Ca ratios. Because relative Na/Ca levels vary spatially under field conditions, genotypes selected for salinity toler-ance must perform uniformly across a range of conditions. This seems to be the case, in pigeon pea at least.

CONSIDERATION OF THE LEGUME-*RHIZOBIUM* SYMBIOSIS

The legume-*Rhizobium* symbiosis involves a complex interaction between host root, rhizobial strain, and the environment. Salinity stress may differentially affect any phase of the legume-*Rhizobium* symbiosis: (1) rhizobial survival and growth in the bulk soil or rhizosphere of the host legume; (2) rhizobial infection of host root tissue; (3) nodule initiation and development; (4) nodule function (the nitrogen fixation process), and (5) growth of the host legume. It is difficult to distinguish which phase is primarily affected because of the close interdependence of these phases.

Many *Rhizobium* strains can grow and survive as free-living organisms at salt concentrations that are inhibitory to most agricultural legumes (58). However, there are differences among species and strains of *Rhizobium* with respect to their tolerance of different salts (58–68). For example, *Rhizobium* strains that nodulate berseem clover are inhibited by 0.2–0.4% chlorides and sulfates of Na and K, whereas *sesbania* strains were tolerant up to 1.8%. Chickpea, groundnut, cowpea, and guar rhizobia were found to be stable even at a 3% salt level (59). The rhizobia that form symbioses with pigeon pea showed wide variations in their tolerance to NaCl salinity in YEMA (yeast extract mannitol agar) (Table 4); over a range of 0.25–5.0% NaCl (1% NaCl is equivalent to about 16 dSm^{-1} conductivity). There was a major difference between fast-growing rhizobial strains and slow growers in their level of tolerance to salinity, with fast growers more tolerant than slow growers. The range of variation was from 1 to 5% NaCl among fast growers and from 0.25 to 2% among slow growers. There were no clear trends between rhizobial strains collected from saline and nonsaline soils in tolerance levels (Table 4). The most tolerant rhizobial strain found in this study was IHP 24, a fast grower collected from a nonsaline soil. The study demonstrated that many pigeon pea rhizobial

Table 4 Effect of Salt (NaCl) Stress on the Growth Response of Pigeon Pea *Rhizobium* Cultures[a]

Rhizobium strain	Growth on YEMA	NaCl (%)							
		Control (0)	0.25	0.5	1	2	3	4	5
IHP 24	F	+++	++	++	++	++	++	++	++
IHP 506[b]	F	+++	++	++	++	++	+	+	+
IHP 100[b]	F	+++	++	++	++	++	+	+	+
IHP 70[b]	F	+++	++	++	++	+	+	—	—
BDN-A2	F	+++	++	++	++	+	+	—	—
IHP 494	S	+++	+++	++	++	+	—	—	—
IHP 87[b]	S	+++	++	++	—	—	—	—	—
IHP 213	S	+++	++	+	—	—	—	—	—
CC 1	S	+++	++	+	—	—	—	—	—
IHP 69[b]	S	+++	++	+	—	—	—	—	—
F4	S	+++	++	—	—	—	—	—	—
IHP 35	S	+++	++	+	+	+	—	—	—
KA 1	S	+++	++	+	—	—	—	—	—
IHP 195	S	+++	+++	—	—	—	—	—	—

[a]F, fast grower; S, slow grower; +++, good growth; ++, moderate growth; +, little growth.
[b]Isolated from saline soil.
Source: From Reference 45.

strains can grow normally at NaCl concentrations that are toxic to pigeon pea, that is, 0.5% NaCl (about 8 dSm^{-1}). The minimum tolerance level in most strains tested was more than 0.5% NaCl. Thus, there appears to be little scope for improving the salinity tolerance of free-living rhizobia to improve pigeon pea growth under saline conditions.

Rhizobium colonization of the root surface of Glycine max was not affected by the increasing salinity of the medium, even though nodulation and nitrogen fixation were suppressed more than 90% at 80 mM NaCl (69). Similar observations were made in Pisum sativum (70) and M. sativa (71). The early steps in nodule initiation in G. max, probably the root hair infection process, may be sensitive to salinity (69). Suppression of root hair, mucilaginous layer, and infection thread formation could be responsible for the susceptibility of the symbiosis to salinity in M. sativa (71). On the other hand, in Macroptilium atropurpureum and Neotonia wightii, the early stages of nodule initiation appeared to be less sensitive to salinity (72). Certain tree legumes, such as Prosopis and Acacia spp., can form a symbiosis with Rhizobium and fix nitrogen at salinity levels approaching those of seawater (21–23). This indicates that symbiotic sensitivity to salinity stress is not a universal phenomenon.

In pigeon pea, significant differences among rhizobial strains were observed in their ability to nodulate, fix nitrogen, and support growth under saline conditions (73). For three of the rhizobial strains tested, the number of nodules was decreased with increasing salinity in the medium, and more than 90% reduction was observed in plants inoculated with Rhizobium strain IC 3195 at 8 dSm^{-1} (Figure 1) (73). In contrast, with strain IC 3087, the number of nodules either increased with increasing salinity or was not affected (Figure 1) (73).

When the pigeon pea-Rhizobium symbiosis is established before the imposition of salinity treatments, the salinity response of symbiotic and N-fed plants is similar (74). However, the early stages of establishment of the pigeon pea-IC 3024 symbiotic system were found to be sensitive to salinity (74). Nevertheless, the symbiotic system of IC 3087-A. platycarpa, a wild relative of pigeon pea, was successfully established at up to 12 dSm^{-1}, was efficient in fixing nitrogen, and supported growth comparable to that of N-fed plants, indicating that symbiotic sensitivity to salinity stress varies between symbioses (74).

Mean nodule dry weight and specific nitrogenase activity were not affected by increasing salinity in symbioses with any of the rhizobial strains tested (73,74). This indicates that once nodules are formed, their development and function in general are not sensitive to salinity stress. We believe that there is room for improvement in nitrogen fixation of pigeon pea under saline conditions through the selection of appropriate host-rhizobia combinations.

There are several reasons that the evaluation of salinity tolerance of pigeon pea and its wild relatives is best done using N-fed systems, at least initially. First, symbiotic function seems to be less sensitive than the plant itself to saline conditions, although the infection process in cultivated pigeon pea is more sensitive (74) and may require a separate screening procedure. Second, the interaction between Rhizobium and pigeon pea in the salinity response (73) complicates detection of genotypic differences because differences may be specific to a particular Rhizobium strain. Third, the uptake of sodium and chloride to shoots, which largely accounts for genotypic differences in the salinity response of pigeon pea and its wild relatives, is not greatly modified by the mode of nitrogen acquisition (74).
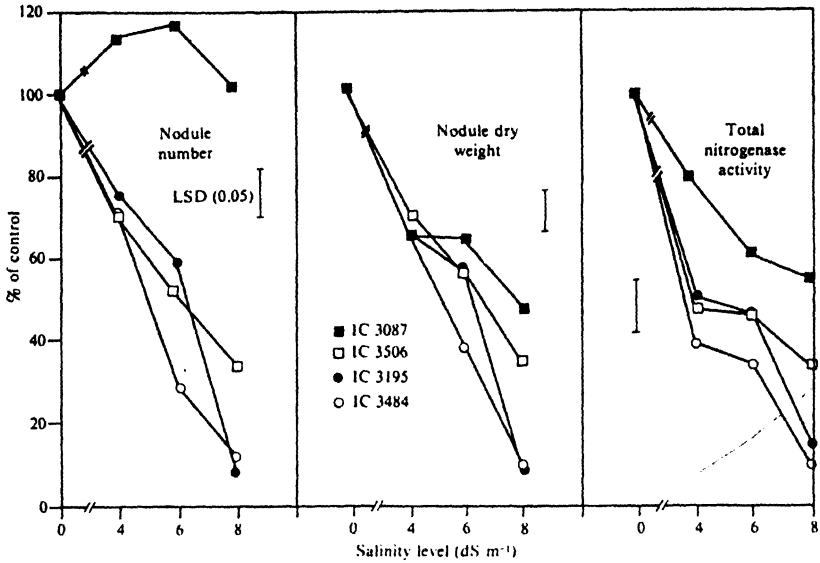
Figure 1   Effect of salinity on (a) nodule number, (b) nodule dry matter, and (c) total nitrogenase activity of pigeon pea genotype ICPL 227 inoculated with four *Rhizobium* strains. Data are means of four replications: 100% nodule number, 460, 135, 202, and 153 (pot^{-1}); nodule dry weight 261, 400, 379, and 419 (mg pot^{-1}); nitrogenase activity 24.0, 45.8, 38.8, and 45.0 (mol C_2H_4 pot^{-1}) for IC 3087 (filled square), IC 3506 (open squares), IC 3195 (filled circles), and IC 3484 (open circles) respectively. (From Reference 73.)

FUTURE OUTLOOK

Worldwide, there is large expenditure on projects aimed at the reclamation of salt-affected areas (75), and these efforts must continue because the problem of salinity is widespread and increasing. Salt-affected areas are found in all parts of the world, and salinity is a gradual soil degradation process (76). Moreover, with the spread of intensive agriculture, most countries are prone to secondary salinity problems. Since legumes are generally less tolerant than other crop species to salinity, secondary salinity tends to disrupt legume-based, sustainable cropping systems in many agroclimatic zones. Lack of appropriate legumes that could be grown in rice fallows affected by secondary salinity is one example. To sustain, let alone increase, current levels of production from irrigated agriculture, genetic improvement in salinity tolerance in legumes should be considered a long-term goal. However, genetic strategies should be seen as only one of the components in the overall management of salinity problems (see Chapter 29 for further discussion of this aspect).

Genetic improvement in salinity tolerance in legumes should receive increased attention at least to maintain the productivity of existing legume-based cropping systems, especially in irrigated areas prone to secondary salinization. Also, salt-tolerant legumes would have a role in being able to enter into the cropping sequence of the reclamation

process at an early stage, after the overall reclamation measures are implemented. Because of the general beneficial effects of legumes on other crops in a rotation, the reclamation process should thus be accelerated. For example, exchangeable sodium percentage (ESP) is reduced more by a rice-berseem cropping system than by a rice-rice-based cropping system (77). Further, crops like pigeon pea (long-duration types) could contribute to the lowering of the water table by transpiration because of its deep rooting charactetistics and to the breaking of hardpans (78) and thus could play a role in the overall approach of managing salinity problems associated with irrigated agriculture.

Systematic efforts should be made to evaluate the world collections of all the major cultivated legumes to assess the viability of the genetic option. This is likely to vary from crop to crop, depending on the extent of variability and the nature of the saline environments for which the crops are actually or potentially destined. Related wild species should also be thoroughly evaluated as potential sources of tolerance to salinity. More studies are needed to understand the physiological mechanisms at the whole-plant level, and also the heritability of specific physiological traits, to enable breeders to devise appropriate breeding methodologies to transfer salinity tolerance into desirable agronomic backgrounds.

For legumes, the symbiotic nitrogen fixation process is particularly sensitive to salinity stress during the *Rhizobium* infection stage. However, there appears to be substantial variation among rhizobial strains in their ability to form a successful symbiosis under saline conditions. This was evident from the present case study with pigeon pea, which indicates that there is scope for improving the nitrogen fixation of legumes through the selection of specific *Rhizobium* strains for use under saline conditions. Criteria for strain selection should be based on symbiotic performance rather than survival and growth of *Rhizobium* alone.

As indicated, the response of legumes to salinity is a complex phenomenon, requiring understanding across a wide spectrum of disciplines (biological to physical). Most reported attempts to enhance salinity tolerance in legumes have been at least initiated from a limited disciplinary viewpoint. It is thus not surprising that there are no clear examples of legume varieties with deliberately improved salinity tolerance growing in farmers' fields. It therefore seems that a genuine interdisciplinary approach, involving a team of scientists, is obligatory if economically important improvements in the salinity tolerance of legumes are to be achieved.

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29
Strategies and Scope for Improving Salinity Tolerance in Crop Plants

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INTRODUCTION

Salinity is a condition of excess salts in the soil, which affects plants by increasing the osmotic pressure of the soil solution, interfering with normal nutrient uptake and inducing ionic toxicity and associated nutrient imbalances. Osmotic stress under saline conditions, termed physiological drought (1), subjects plants to dehydration. Ionic toxicity resulting from the accumulation of specific ions, such as Na and Cl, in the cytoplasm or apoplast interferes with plant metabolic functions (2).

Under low to moderate salinity (actual salinity levels may vary from low to moderate depending on the crop species), plants adjust osmotically by using a portion of their photosynthates to increase internal solute concentrations and thus do not show dehydration symptoms. Also, plants regulate their ionic balance to maintain normal metabolism. For example, uptake and translocation of toxic ions, such as Na and Cl, are restricted, and uptake of metabolically required ions, such as K, is maintained or increased.

Although plants may not show water deficit symptoms and metabolize normally under low to moderate salinity levels, the additional energy requirements for maintaining normal metabolism demand substantial photosynthate diversions from growth (3). This leads to a reduction in leaf area, light interception, light utilization efficiency (due to partial stomatal closure and the resultant decrease in CO_2 fixation), and, ultimately, a reduction in growth and yield. Plants die when salinity levels exceed a certain critical level (which varies from crop to crop). Death is the result of physiological mechanisms breaking down and consequent ionic toxicity. Poor plant stand is one of the factors causing low yields under saline conditions, as salinity is nonuniform in its distribution under field conditions.

The main objective of this chapter is to present an overview of the current status of knowledge and approaches to the genetic improvement of salinity tolerance in crop species. Management aspects that could alleviate salinity problems for crop production are also discussed, however, because genetic improvement cannot be considered in isolation in confronting a salinity problem. The chapter is focused on giving a conceptual framework for the genetic improvement of salinity tolerance. This demands an interdisciplinary team approach; to our knowledge, there is little evidence of this in present-day research efforts.

SALINITY AND CROP PRODUCTION

The expected yield losses under different levels of salinity for various crops are given in Table 1. Data on regional yield losses for various crops due to salinity are not readily available. Irrigated agriculture contributes substantially to crop production in arid and semiarid regions of the world. Secondary salinization, which is associated with irrigated agriculture, is becoming a serious concern in these regions. Nearly 40% of irrigated lands are affected by some degree of salinity (4). Considering that nearly 240 million ha land worldwide is under irrigated crop production (5), the economic impact of secondary salinization on crop production could be astronomical. Rain-fed agriculture can also be affected by salinity through the effects of deforestation and other vegetation changes in altering underground movement patterns of water and salts.

We discuss in this section the various aspects related to the understanding of crop response to salinity, including the growth stage response, the role of environmental factors in modifying the salinity response, and the management options that could alleviate the crop tolerance to soil salinity.

Measurement of Soil Salinity

It is important to quantify and characterize salinity distribution in a production area to make decisions regarding the selection of a crop and the management practices necessary to minimize yield reduction. Appropriate sampling techniques and salinity measurement methods are necessary to assess salinity levels properly and map their distribution in the production area during a cropping season.

Soil Sampling

Generally, major root activity occurs in less saline strata of the soil profile (6), and this should be taken into account when relating plant growth and yield to soil salinity status. Soil samples should be taken from the active root zone and should not be contaminated by surface salt encrustations. Since salt concentrations can vary markedly with soil depth, samples are best collected at several depths, such as 0–15 and 15–20 cm, depending on the root zone (7).

Determination of Salinity

The electrical conductivity of a saturation extract EC_e, expressed in dS m^{-1} at 25°C, is recommended for correlating salinity level with growth (8). The electrical conductivity of the saturation extract is directly related to the soil soluble salt concentration. The relationship between EC_e and osmotic potential Ψ_0 is $\Psi_0 = -0.36\ EC_e$. Use of EC_e is recommended by the U.S. Salinity Laboratory because the saturation percentage is easily determined and is accurate for soils that vary widely in texture (8). For most soils, the

Table 1 EC$_e$ at Which 10, 25, and 50% Yield Reduction Can Be Expected for Various Agricultural Crops

	% Yield reduction		
	10	25	50
Field crops			
Barley	11.9	15.8	17.0
Sugar beet	10.0	13.0	16.0
Cotton	9.9	11.9	16.0
Safflower	7.0	11.0	14.0
Wheat	7.1	10.0	14.0
Sorghum	5.9	9.0	11.9
Soybean	5.2	6.9	9.0
Sesbania	3.8	5.7	9.0
Rice	5.1	5.9	8.0
Corn	5.1	5.9	7.0
Broadbean	3.1	4.2	6.2
Flax	2.9	4.2	6.2
Bean	1.1	2.1	3.0
Vegetable crops			
Beets	8.0	9.7	11.7
Spinach	5.7	6.9	8.0
Tomato	4.0	6.6	8.0
Broccoli	4.0	5.9	8.0
Cabbage	2.5	4.0	7.0
Potato	2.5	4.0	6.0
Corn	2.5	4.0	6.0
Sweet potato	2.5	3.7	6.0
Lettuce	2.0	3.0	4.8
Bell pepper	2.0	3.0	4.8
Onion	2.0	3.4	4.0
Carrot	1.3	2.5	4.2
Bean	1.3	2.0	3.2
Forage crops			
Bermuda grass	13.0	15.9	18.1
Tall wheatgrass	10.9	15.1	18.1
Crested wheatgrass	5.9	11.0	18.1
Tall fescue	6.8	10.4	14.7
Perennial rye	7.9	10.0	13.0
Beardless wild rye	3.9	7.0	10.8
Alfalfa	3.0	4.9	8.2
Orchard grass	2.7	4.6	8.1
Meadow foxtail	2.1	5.5	6.4
Clovers, alsike and red	2.1	2.5	4.2

Source: From Reference 39.

soluble salt concentration in the saturation extract is about one-half the concentration of the soil solution at field capacity and about one-fourth the concentration at permanent wilting point (9).

Crop Tolerance to Salinity

There are different ways of defining crop salinity tolerance, depending on the context in which it is used. Some of these are as follows:

1. "The capacity to persist in the presence of increasing degree of salinity" (10): a given species may make little or no growth at higher salinity levels but does survive. This is the criterion generally used by ecologists in evaluating halophytic environments. Ecologists maintain that the species most capable of persisting in a saline area become the climax vegetation of that area.
2. "The degree to which osmotic adjustment can be made without sacrifice in growth" (11).
3. "The absence of negative effects on growth in plants that accumulate salts in their tissues" (1).
4. "Yield decrease expected for a given level of soluble salts in the root medium as compared with yield under non-saline conditions" (9).
5. "The sustained growth of plants in an environment of excess salts in the growth medium" (12).

In the context of crop production under saline conditions, definitions 4 and 5 are more relevant. Crop salt tolerance has usually been expressed as the yield decrease expected for a given level of salinity in the root medium compared with yield under nonsaline conditions (8). Therefore, salt tolerance is a relative value based upon the growing conditions of the crop.

Growth Stage Response

Information on the growth stage response to salinity within a crop is important in adopting suitable genetic and management strategies for saline soils. For example, if a crop is more sensitive during one stage than another, there is an opportunity to regulate the salinity of irrigation water during the season to minimize salt injury at the sensitive stage.

Ontogenetic drift, a change in genotypic expression with plant development, is one of the factors that can modify the relationship between phenotype and environment. During plant growth, the form and function of various organs change. 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 (13). Thus, salinity effects may vary depending upon the growth stage at the time of stress. One example, often cited, is that salt tolerance at germination is not consistently related to tolerance during emergence, vegetative growth, flowering, or fruiting. Sugar beet, barley, and cotton are among the most salt tolerant agricultural crops, but each is relatively sensitive during germination or early seedling growth (14,15). On the contrary, corn, pea, gram, and beans are more sensitive during later stages of development (15,16).

Relative sensitivity could change from one developmental stage to another. Rice is tolerant during germination (17) and becomes very sensitive during the seedling stage and again somewhat sensitive during fertilization of florets (18). Corn is more salt sensitive during emergence and seedling growth but becomes more salt tolerant by the flowering

stage (19). Salt resistance is low in young tomato plants, becomes much higher by the bud stage, and decreases during flowering (20).

Sensitivity to salinity in durum and bread wheat decreases with age, indicating the importance of keeping soil salinity levels low during germination and seedling emergence (21). Similarly, cowpea becomes increasingly more salt tolerant as plants develop during the growing season (22). One of the reasons for decreasing sensitivity with age could be a gradual acclimation of the crop to salinity. This indicates that if cowpeas or wheat are irrigated with water containing salt levels below the threshold, before the flowering stage, higher levels of saline irrigation water could be used at later growth stages without any deleterious effect on yield (21,22).

Within a species, varietal rankings could change with the growth stage, and this has been observed with rice (23). For barley, varietal differences increased with plant development stage (24). Changing varietal differences (that is, relative tolerance rating) over time were also reported in sugarcane (25). This would complicate the screening and selection process, if it is based on a single growth stage.

Environmental Interactions

Interactions between salinity and soil, water, and climatic conditions change the plant's ability to tolerate salinity. A basic understanding of the interactions between salinity and environment is necessary for an accurate assessment of salt tolerance. In addition to precipitation, temperature and atmospheric humidity can markedly influence salt tolerance. Many crops are less tolerant when grown under hot dry than under cool humid conditions (9). This is mainly due to decreased ion accumulation and/or improved plant water relations (26,27).

Rice suffered more salt injury at 30.7°C and 64% relative humidity (RH) than at 27.2°C and 73% RH (28). High humidity overcame lethal levels of salinity on *Phaseolus vulgaris* L. (26). In wheat, a higher transpiration rate occurred at low RH and high temperatures, thus increasing the mass flow of salts into the transpiration stream and their accumulation to toxic levels in the shoot (29). Further, salts may accumulate in the rhizosphere with increased transpiration (29).

Suboptimal soil conditions can also affect the apparent salt tolerance of crops. For example, plants grown on low-fertility soils may appear more salt tolerant than those grown with adequate fertilization (30). A reason for this could be that soil fertility, not salinity, is the prime limiting factor for crop growth. In this case, proper fertilization would increase yields under saline as well as nonsaline conditions, but proportionally more under nonsaline conditions.

Comparative Effects of Different Salts

Specific ion toxicity is the primary cause of plant mortality at higher levels of salinity (1). Different salts have different threshold osmotic concentrations for injury, and the relative toxicities of specific salts are not constant for all crop plants under all conditions (1). For example, cotton, rice, and wheat are less resistant to NaCl than Na_2SO_4 salinity (31–33), but *Phaseolus*, guayule, flax, and chickpea show the reverse relationship (34,35). Alfalfa is more affected by Na_2SO_4, K_2SO_4, and NaCl salts than $MgCl_2$ and $MgSO_4$ salts (36), whereas the reverse is the case with mung bean and red kidney beans (37,38). Beans and wheat are more affected by $CaCl_2$ compared to NaCl salinity (39,40), whereas the response is the opposite with corn (34). Mung bean and red kidney beans were equally affected by NaCl, Na_2SO_4, KCl, and K_2SO_4 (37,38). For many crops, carbonates are more toxic than Cl and/or SO_4 (34).

Protective Effects of Calcium

The importance of Ca in maintaining membrane stability and for selective ion uptake by plants is well documented (41). Under saline conditions, the ratio between required ions (e.g., K) and unessential ions (e.g., Na) is reduced, and thus selective ion transport by plant roots becomes crucial for survival. Low levels of Ca (<1 mM) in the absence of NaCl salinity support normal growth in most crop plants (2). Under saline (NaCl) conditions, however, such levels of Ca in the medium result in Ca deficiency in many crop plants (42,43). Under NaCl salinity, a decrease in the membrane-associated Ca content due to the displacement of Ca by Na leads to the disruption of membrane integrity (43). This causes an increase in passive Cl and Na transport and results in ion toxicity (44). The NaCl salinity (at low Ca levels) also inhibits Ca transport from roots to shoots by interfering with the active loading and release of Ca into xylem vessels (45).

Several reports indicate that supplemental Ca (usually up to at least 5 mM) may alleviate the reduced growth caused by NaCl salinity. In *P. vulgaris*, dry weights increased with increasing Ca levels up to 3 mM at 50 mM NaCl in the ambient solution, and there was no further improvement at higher Ca levels (46). A positive growth response to increasing Ca under NaCl salinity was also reported for barley (47). The germination and seedling growth of Wimmera ryegrass under NaCl and $MgCl_2$ salinity improved with increasing Ca concentration in the growth medium (48). Some crops, however, including rice and lettuce, do not respond positively to Ca addition under NaCl salinity (49,50).

Supplemental Ca, under NaCl salinity, normally improves Ca absorption of the plants (51). Calcium also protects NO_3 transport under saline conditions (52). In pigeon pea (*Cajanus cajan*), a positive growth response to a decrease in the Na/Ca ratio was observed at a constant salinity of 6 or 8 dS m^{-1} (53). A decrease in the Na/Ca ratio in the medium improved K/Na in the shoot and thus improved plant growth. With a decrease in Na/Ca ratio, however, tissue Cl levels increased and to some extent counteracted the positive effects of improving the K/Na ratio (see Chapter 30).

Management Practices That Minimize Yield Reduction Under Saline Conditions

Although the main objective of this chapter is to document the scope for genetic options to improve salinity tolerance in crop plants, this topic cannot be considered in isolation from various management options that reduce salinity damage. Further, we emphasize that a practical approach to alleviating salinity effects is a close integration of genetic and management options. Management practices that can be used to minimize yield reduction under saline conditions are mostly related to the control of root zone salinity and reduced damage to the crop plants (54). Control of root zone salinity can be achieved by irrigation and leaching. For example, intermittent leaching can be more advantageous than leaching at each irrigation (55,56). Similarly, by increasing the irrigation frequency, the salinity effect on crop growth can be considerably minimized (57). The control of root zone salinity in the initial stages of germination and early seedling growth could play a major role in plant stand establishment.

Several cultural and management practices have been developed to enhance plant stand establishment under saline conditions (54,58):

1. Irrigate lightly each day after seeding with a sprinkler system until the stand is established, and then convert to furrow irrigation.

2. Leach salts from the soil surface before planting to allow stand establishment before salts can accumulate at levels that would interfere with germination or damage seedlings.
3. Prepare seed beds in such a way that salts accumulate at the top of ridges, and then sow seeds in the furrow or on the slope between the furrow bottom and ridge top (54).
4. By applying a mulch to reduce evaporation, increase water uptake by plants and increase leaching of salts (59).

Although soil salinity reduces plant growth potential, this may not necessarily reduce total field yield. Field yield is the product of stand density and yield per plant. Using the crop growth model of Maas and Hoffman (9), the predicted reduction in individual plant growth due to salinity can be estimated. Therefore, plant populations could be adjusted to compensate for reductions in individual plant growth (60).

Salinity and Fertilizer Use

By changing the fertilization regimens (type and quantity of fertilizers and method of application) from those considered appropriate for nonsaline conditions, it is possible to alleviate the effects of salinity on agricultural crops (61). Salinity interfered with P translocation in cotton (62) and the uptake of NO_3 in barley (63). Reduced P translocation is caused by inadequate Ca levels in the roots, and thus the primary response is on Ca uptake (62). This can be corrected by either foliar P fertilization or Ca fertilization. The latter is more desirable because it corrects the primary effect and thus improves the salinity tolerance. Different crops and genotypes are known to have differences in their ability to take up Ca during NaCl salinity (2). Tolerant genotypes are able to maintain Ca uptake, whereas sensitive genotypes are not. Therefore, depending on the crop or genotype used in a particular fertilizer trial, different responses can be expected. Positive growth responses to fertilization under saline conditions are reported in clover (64), wheat (65), tomato (66), bean (67), and pepper (*Capsicum annuum* L.) (68). On the other hand, negative growth responses were reported in cotton (69), rice, barley (70), corn (68–70), and soybean (71).

GENETIC IMPROVEMENT IN SALINITY TOLERANCE

Several points must be considered before initiating a breeding program to improve salinity tolerance. In the first instance, alternative cropping strategies should be evaluated. Selection of a different crop that is more salt tolerant may result in productivity far exceeding the genetic limits of the crop originally targeted for salinity tolerance breeding. For example, by changing the cropping system from wheat to barley, the necessity of genetically improving wheat salinity tolerance can be avoided: considerable genetic improvement in wheat is needed to raise its tolerance to the level already existing in barley.

This strategy of expanding the use of salt-tolerant species without going through selection within a species could be sufficient to circumvent salinity problems to some extent. However, economic considerations, food habits of the region's population, and cropping systems that have evolved based on these crops and that fit well into existing agroecological niches may not allow replacement of existing crops with a more salt tolerant crop. For instance, salinity problems that confront lettuce, tomato, and other vegetable growers in California could be eliminated if these vegetable crops were replaced

by barley. Vegetable production is a highly commercialized system and the economic backbone of California's agriculture, which does not permit such an option (12).

Legumes are very sensitive to salinity in comparison to cereals (see Chapter 30 for detailed discussion) (72). The semiarid regions, which include a large proportion of the world's irrigated agriculture, are now under threat from secondary salinization. Legumes play an important role in these production systems, which are largely based on cereal-legume cropping patterns. Such patterns contribute to maintenance of soil fertility and soil structure and long-term sustainability of these production systems. For example, in rice-based cropping systems, such legumes as green gram and black gram play an important role in this cereal-legume cropping pattern in the Krishna and Godavari delta regions of peninsular India. This production system has recently been threatened by secondary salinization, and the legume component is being affected first because of its higher susceptibility to salinity. Although the long-term sustainability of this production system requires the development of suitable management practices to arrest the further buildup of salts, this process could be enhanced by the use of legume genotypes with higher levels of salinity tolerance than are now available.

For many biotic and abiotic stresses, the feasibility of a genetic approach in improving crop tolerance has been demonstrated convincingly. For certain abiotic stresses, however, such as drought and salinity, genetic improvement remains a challenging task because of the difficulties in defining precisely the target environment, which is a prerequisite to focusing genetic improvement. Further, serious obstacles to genetic improvement of salinity tolerance are the diversity of physiological mechanisms that determine the level of tolerance to salinity or drought, their multigenic nature of inheritance, and the lack of appropriate screening methodology, appropriate selection criteria for evaluation of germ plasm, and segregating material. These points are discussed in detail in this section.

Screening Methodology

Field Environments

Field salinity is inherently variable (levels can vary from <4.0 to >40 dS m^{-1}); variation occurs both horizontally and vertically and changes temporarily within and between growing seasons (depending mainly on the amount of precipitation and evapotranspirational demands) (73). Spatial variation in a saline soil can be enhanced further by irrigation (73); on the other hand, an insufficient moisture supply exacerbates the variability in plant growth by the development of variable moisture stress conditions, in addition to variable salinity effects. Plant roots avoid more saline soil areas and take up water and nutrients from less saline areas (74). Plant growth under such variable saline conditions may be more a result of escape than of genetic differences in tolerance (75).

Because of the natural field variability in salinity levels, it is very difficult to evaluate germ plasm lines under field conditions. Environmental variance effects are likely to exceed those of the genetic component, thereby making selection for genetic improvement difficult.

An alternative approach is field testing under relatively controlled conditions, as done by the U.S. Salinity Laboratory at Riverside, California (9). Using a nonsaline, sandy loam soil and by irrigating with different levels of saline irrigation water (usually by adding NaCl + $CaCl_2$ wt/wt), relatively uniform salinity levels, within a given salinity treatment, can be created. By increasing irrigation frequency and by applying excess

irrigation water, the buildup of salts can be prevented. A nonsaline control treatment for all genotypes is usually used to determine inherent differences in growth and yield potential. Therefore, genotypes can be evaluated at different salinity levels on a relative yield basis (76).

Controlled Environments

Most researchers use controlled environments, such as greenhouses or growth chambers, for the preliminary evaluation of germ plasm lines. This helps to reduce the number of lines to more manageable levels for more rigorous testing at a later stage under controlled environment or field conditions. Also, selection of breeding materials in early generations involves exposure of plants to salinity in a relatively controlled environment to minimize environmental variance and maximize genetic variance. Plants are then grown in containers with a salinized media. Salt concentrations for selection vary with species sensitivity. For most glycophytic crop plants, the concentrations used for screening range between 50 and 300 mM NaCl (representing rice and barley, respectively) (75).

In most large-scale screening of germ plasm lines for salinity tolerance, an aerated and salinized hydroponic system is used. The principles to observe in any hydroponic system are (1) balanced supply of nutrients; (2) proper aeration; (3) control of salt concentration and solution pH over time; and (4) gradual increase in salinity level in several increments over time until the desired treatment salinity level is reached, to avoid osmotic shock to the plants.

Salinity Tolerance Criteria

Genotypes may be evaluated for vigor, leaf damage, survival, and ability to grow under saline conditions. A salinity level is chosen to select about 10% of the material for further evaluation over a range of salinity levels. Sand culture under greenhouse conditions may be used to determine growth response curves at various salinity levels. The parameters that might be used in assessing the effect of salinity on a particular species include survival, leaf damage, and vegetative growth and yield. All are of course interrelated: there can be no yield without survival, although a species may survive vegetatively and yet fail to produce yield. Therefore, knowledge of all these parameters contributes to the assessment of the effects of salinity on a particular crop species.

Based on Germination

Selection on the basis of germination tests shows little promise as a means of improving salinity tolerance in subsequent growth stages (77). However, lack of association does not mean that germination tests are not useful in a salt tolerance breeding program. In many situations, the ability to germinate and establish a good plant stand in saline soils is an important factor in crop production. However, this depends on the crop under consideration and the agronomic practices associated with it. In rice, tolerance at germination and initial seedling growth is not important, because this crop is mostly transplanted. Development of genotypes with tolerance at all growth stages requires selection at several points in the life cycle.

Based on Survival

Plant survival at high salt concentrations, irrespective of their growth rate and productivity under moderate salinity levels, has been proposed as a selection criterion for tomato, barley, and wheat (78–80). The philosophy behind this is to focus on tolerance per se,

thereby separating yielding ability from salinity tolerance; considering that these two are independent attributes. The ability of a genotype to survive and complete its life cycle at very high salinity levels, irrespective of its yield potential at moderate salinity levels, is considered tolerance in the absolute sense. Also, yield is regulated by a number of genetic factors not contributing directly to salinity tolerance. Once sources of very high levels of salinity tolerance are identified, attempts can be made to combine these with high yield potential through standard breeding procedures. This is similar to the approach adopted in disease resistance breeding, in which the initial selection emphasis is on identifying the sources of disease resistance rather than the yield ability in disease environments.

Based on Leaf Damage

Most crop plants are glycophytes and, unlike halophytes, cannot tolerate high salt levels (mainly Na and Cl) in their leaf tissues. Therefore, one important factor in the physiological mechanisms operating in glycophytes is preventing Na and Cl ions from translocation to the shoot. Beyond a certain critical level of salinity stress this regulation breaks down, resulting in the translocation of large amounts of Na and Cl to the shoot, causing ionic toxicity. Critical levels vary among genotypes, varieties, and crops and usually determine differences in the level of tolerance. Leaf damage (bleaching or necrosis) is a symptom of breakdown in ionic regulation. Therefore, selection against leaf damage should lead to the identification of genotypes that have more efficient ionic regulation and other physiological mechanisms that contribute to higher tolerance levels. In alfalfa (lucerne), selection criteria based on leaf damage of less than 10% resulted in rapid improvement in selection for salinity tolerance (81).

Based on Growth and Yield

Salinity tolerance is usually assessed in terms of absolute and/or relative growth or yield. Although absolute yields have an obvious practical application, they often reflect qualities other than tolerance to salinity and can lead to illogical conclusions if considered alone. Inherent differences between genotypes in their growth rates or habits does not permit a valid assessment of their relative salinity tolerances using absolute yield or growth criteria at a particular salinity level. For example, a genotype may suffer severe yield reduction at a given level of salinity and yet yield more than another genotype whose yield is unaffected by salinity (82).

The performance of a genotype under saline conditions in comparison with that under nonsaline conditions provides a measurement of salt tolerance stripped of extraneous influences. Also, this approach provides a means to compare crops whose yields are expressed in different units or that differ widely. However, the reliability of relative salt tolerance data depends upon the degree to which yield reductions are unaffected by extraneous interactions (9). If reductions in relative yield are independent of differences in absolute yield caused by irrigation, climate, fertility, or other variables, the relative yield-salinity relationship permits a useful expression of plant tolerance to salinity (83).

The crop response to salinity is usually described as a decreasing function with an increase in the EC_e of the soil solution. It has been suggested (9,84) that a reduction in crop yield due to salinity can be linearly related to the EC_e of the soil solution after a certain threshold value of EC_e is reached (Figure 1). This can be expressed as
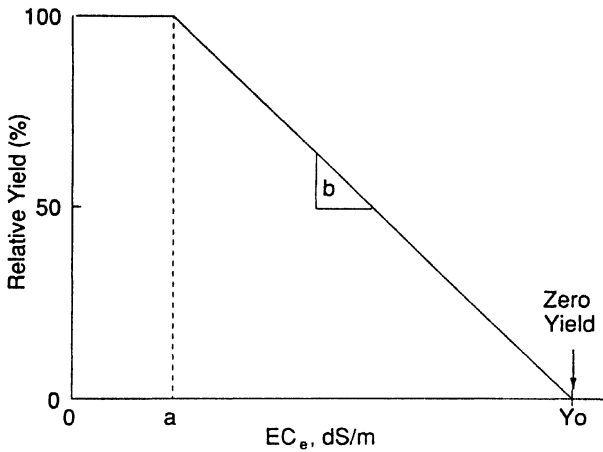
Figure 1   Response curve to salinity. (From Reference 54. Reprinted by permission of Kluwer Academic Publishers.)

$$\frac{Y}{Y_{max}} = 1 - b(EC_e - a) \tag{1}$$

where: Y = yield

Y_{max} = yield of nonsaline control

a = salinity threshold value, EC_e units ($dS\ m^{-1}$), that is, the maximum soil salinity that does not reduce yields below those produced under nonsaline conditions

b = slope, the relative reduction per unit salinity increase from threshold

Based on the salinity threshold level a, slope value b, and salinity level at which yield becomes zero Y_0, Maas and Hoffman (9) grouped most important crops into four categories: (1) sensitive, (2) moderately sensitive, (3) moderately tolerant, and (4) tolerant.

Genotypes or germ plasm lines could be evaluated for their salinity tolerance using this linear growth response model. However, many data points above and below the threshold level are required to define the threshold level accurately and to measure the slope value (85). This kind of evaluation should mainly be used to assess the production capacity of selected, contrasting genotypes in saline environments, not for the initial evaluation in which many germ plasm lines must be screened.

Conceptual Framework for Genetic Improvement Under Salinity Stress

The linear growth model of Maas and Hoffman (9) could be used as a conceptual framework for the genetic improvement in salinity tolerance. To improve crop performance genetically under saline conditions, it is necessary to shift the threshold value a to the maximum extent possible and to reduce the slope value b to give stability in crop performance across a range of salinity levels and an increase in Y_0. Genetic improvement

in these three components would involve screening, selection, and recombination through breeding. This should result in better crop performance under saline conditions.

The three components of the model (a, b, and Y_0) may be considered independent crop attributes, because each component refers to crop response at a given range of salinity (i.e., the a value refers to the crop performance at low salinity levels, the b value to moderate salinity levels, and Y_0 to high salinity levels). Considering the principles of quantitative genetics, Falconer (86) proposed that a characteristic in two different environments may be regarded as two characteristics rather than one.

The criteria for evaluating crop salinity tolerance vary, depending on the level of salinity stress. In a low to moderate salinity range, the production capacity of the genotype is the main criterion, whereas survival ability is the main criterion at higher salinity levels (87). It is likely that the physiological mechanisms that play a major role in maintaining the production capacity of a genotype are not the same as those that contribute to tolerance at extremely high salt concentrations (88).

Assuming that these three components are independent crop attributes, independent genetic improvement should be sought for each component. Once improved sources of genetic materials are identified for each component, these could be combined into a single genotype through breeding. However, the decision to breed for improved salinity tolerance for a given crop should be carefully considered. The plant breeding approach, although remarkably successful in some instances, is very time consuming and labor intensive when conventional breeding methodologies are used. Also, it must be realized that salinity tolerance is a finite attribute, and genetic improvement through selection and recombination can improve tolerance only up to a certain level within a given crop species. The degree of improvement depends upon the availability and extent of variability for salinity tolerance and the existing tolerance level of the species. Also, higher levels of soil salinity could place considerable pressure on the plant's photosynthetic capability, because physiological defense mechanisms that permit survival and production under saline conditions demand a larger portion of available photosynthate (3). This leads to a decline in production potential. If production falls below a certain level, the economics of cultivation of the crop under consideration comes into question.

Potential gains from a breeding program should be realistically estimated. Gains from improving stress resistance may be offset by adverse correlated responses that are inevitable because of the physiological interconnections of plant growth processes. This can result in developing varieties that are salinity resistant and suitable only for saline soils but not for nonsaline soils since their yield ability may be low and unable to compete with existing commercial varieties that can be grown in these nonsaline soils.

The various management options discussed earlier can also improve crop performance to a greater extent than may be realized through breeding. The physiological requirements for a given crop to perform under saline conditions should be evaluated. Careful assessment of energetic and assimilatory requirements for growth under various degrees of stress can reveal whether it is physiologically feasible to expect improvement in production in stress environments. Ideally, fundamental growth processes should be well enough understood that crop growth can be modeled at various degress of salinity stress. The results of such modeling exercises could provide guidance about the extent of physiological improvement required for the known or anticipated level of salinity (89).

The following aspects should be considered in initiating a program for the genetic improvement of salinity tolerance in a given crop:

  1. Define the target environment.
  2. Define the level of improvement necessary.
  3. Define the growth stage response.
  4. Choose the screening methodology to be adopted.
  5. Choose the selection criteria.
  6. Assess the genotypic variation for the various traits under consideration that may have a functional role in improving salinity tolerance.
  7. Identify genetic sources for the various components (traits) of salinity tolerance.
  8. Determine the genetic basis for traits under consideration, and estimate their heritability.
  9. Initiate breeding programs that combine various traits from different sources into a locally adapted variety or genotype for the ultimate development of a salt-tolerant variety.
  10. Test evolved genotypes in multiple locations, in a range of saline soils within a production environment, to assess their potential adaptability as new varieties.

Strategies for Genetic Improvement

Define the Target Environment

This is one of the most crucial requirements for the success of a genetic improvement program: it is unrealistic to attempt to develop a single variety that can be grown universally in all types of saline soils. The type of salinity (i.e., salt composition) in the target environment and the anticipated salt dynamics during the growing season should be assessed. This should help in designing genetic improvement programs specifically aimed at developing varieties that best fit given target environments. Laboratory or greenhouse studies should reflect the specific ion toxicities (and proportions) in the area where the crop is intended to grow. Even in a specific environment, the concentration of soluble salts changes depending on the soil structure and composition and its equilibrium with a variable moisture content. The amount of salt carried by irrigation water may also vary throughout the growing season. Such changes must be monitored and taken into consideration when developing appropriate breeding strategies to alleviate salinity problems.

Screening and Selection

Once a target environment is well defined, appropriate screening methodologies should be adopted to test the available germ plasm for genetic variability in salinity response. Analyses of variability are needed to establish that genetic variability exists and that it can be utilized in breeding. This requires formal studies on the heritability of the stress response and related physiological and morphological characteristics.

Varietal testing for salt tolerance often reveals only small differences among the limited numbers of varieties examined, such as lettuce (90), muskmelon (88,91), and grapevine (92). A greater variation for salt tolerance is more likely to occur among species of halophytic origin, such as sugar beet (93). Based on germination and early seedling growth in barley with 75% seawater, large differences among genotypes were reported (94). Systematic large-scale screening of available gene pools of wheat and barley using hydroponic systems has been attempted with the specific aim of selecting genotypes suitable for seawater culture (80,95,96). Nearly 7200 barley genetic lines synthesized from a composite cross (involving a number of lines) were evaluated (97). Of these, only

22 lines were able to survive, grow, and complete the life cycle by setting seed at 75–90% seawater salinity in a hydroponic system. Tolerance here refers to the ability to germinate, establish seedlings, grow, flower, and set seed at 75–90% seawater supplied throughout the life cycle of the plant (80). Further, these lines were evaluated under field conditions for their yield ability by irrigating with undiluted seawater. Some of these lines could yield up to 1.58 t ha^{-1}. This shows the feasibility of this approach in developing barley lines or varieties that can be grown with seawater-based irrigation (80). Therefore, the basic concept of irrigating barley with seawater is at least a "biological success," and the selection approach based on tolerance throughout the life cycle appears to be feasible in identifying lines capable of producing under saline conditions. Similar attempts have been made in rice (98).

There is scope for the selection and development of rice varieties that are high yielding under saline conditions. The IRRI (International Rice Research Institute) has developed a number of salt-tolerant varieties, such as IR 50. This was reported to yield an average of 3.0 t ha^{-1} in multilocational yield evaluation trials in saline fields, where the traditional high-yielding varieties could not survive (99). It was also demonstrated that, using cumulative crosses involving a number of tolerant cultivars, one could develop varieties with higher levels of tolerance than their parents. Crosses using two of the IRRI most salt tolerant cultivars have demonstrated overdominance for salt tolerance in F_1, and many progeny lines of F_3 are far more tolerant than either of the parents (100).

Screening plants from germination to maturity using large-scale solution culture systems is the best option for identifying genotypes or genetic materials that are tolerant to salinity at all growth stages. If different genotypes respond differently at different growth stages, however, this suggests that salt tolerance is under separate genetic control at each of the developmental stages. If this is so for the crop under improvement, then genetic sources may need to be identified that possess higher levels of tolerance for each of the growth stages, with the assumption that tolerance at each growth stage could be an independent attribute. Jones and Qualset (89) proposed that by reducing tolerance to similar developmental units, the genetic components of this tolerance potentially will also be simpler. Analysis may therefore be facilitated by reducing the number of segregating loci in crosses, thereby simplifying genetic segregation ratios and identifying the underlying physiological basis of adaptation. It might then be possible to integrate differential tolerances at specific stages into a single highly tolerant cultivar with a high yield potential.

Role of Wild Relatives

Wild relatives have been used as sources of disease, insect, and nematode resistance, to widen adaptation, to provide alternative cytoplasms and develop cytoplasmic sterility systems, to improve quality, to alter modes of reproduction, to induce short stature, to increase crossability between species, to improve resistance to stress, and to increase yield (101). The use of wild relatives in crop improvement accelerated after systematic efforts by the CGIAR (Consultative Group for International Agricultural Research) centers to collect, maintain, and make this material available to researchers. Many breeders are reluctant to use wild germ plasm in their breeding programs, however, because it takes a long time and much backcrossing to remove the undesirable traits that are linked with the desirable traits.

Several studies have shown that in many crops wild relatives can offer higher levels of tolerance to salinity that can be transferred to cultivated crops through breeding. In the

tomato, the lack of variation in the cultivated germ plasm prompted Epstein and his colleagues to test various wild relatives of tomato (102–104). *Lycopersicon cheesmani*, a wild tomato collected from the Galapagos Islands, was found to be highly salt tolerant and could survive and produce with 50% seawater, a saline level toxic to the cultivated tomato. Further studies with interspecific hybrids of cultivated tomato demonstrated that the higher level of tolerance is a dominant genetic factor. Recurrent selection for salt tolerance of the hybrids resulting from backcrosses to a domestic cultivar gave plants that survived in up to 70% of the concentration of seawater. Fruit size, quality, and yield increased with successive backcrossing.

In barley, preliminary studies with a limited number of accessions of *Hordeum spontaneum*, an immediate progenitor to cultivated barley and the only wild relative in the primary gene pool, did not show any additional sources of tolerance compared with cultivated barley (G. V. Subbarao and S. Jana, unpublished results). However, a large number of collections are available in this species that could offer higher levels of tolerance than cultivated barley. Other species of *Hordeum*, such as *Hordeum jubatum* and *Hordeum marinum*, have substantially higher levels of tolerance to salinity than that available in cultivated barley (105). Utilization of this tolerance depends on the development of techniques to overcome incompatibility barriers.

Several wild species related to wheat have shown substantially higher levels of salinity tolerance than cultivated wheat (106). *Elytrigia elongata*, a wild wheatgrass, had a higher salinity tolerance than cultivated wheat (*Triticum aestivum*). The salinity tolerance trait was expressed in the amphidiploids of *T. aestivum* $\times$ *E. elongata*, indicating that the tolerance trait is a dominant genetic factor (107). By transferring five chromosomes and a telosome from *E. elongata* to *T. aestivum* in the BC_2F_4 derivative, it was found that the tolerance trait was expressed in these derivatives. These derivatives grew to maturity even at 35 dS m^{-1} salinity, similar to the tolerant parent *E. elongata* (108). *Oryza coarctata*, a wild rice species, tolerates salinity up to 40 dS m^{-1} (109). The cultivated rice (*Oryza sativa*) could tolerate only 5 dS m^{-1}. Some pigeon pea wild relatives were found to have higher levels of tolerance to salinity than the cultivated pigeon pea (see Chapter 30 for more discussion on this aspect) (110).

FUTURE OUTLOOK

The salinization of soil and water is becoming an increasingly serious constraint for crop production, particularly in the arid and semiarid regions of the world. These areas are under immense pressure to produce more food per unit area of land because of ever-increasing human populations and expectations of economic improvement. Increasing areas of land in arid and semiarid regions are being brought into production through the introduction of canal irrigation, without taking into account the salt balance of these production systems or providing suitable drainage (111). Secondary salinization, which is usually associated with irrigated agriculture, is becoming a serious problem in many areas of the world, threatening the long-term sustainability of these production systems. Nearly 1.5 million ha prime farmland in the world is going out of crop production each year because of secondary salinization (112). The long-term survival of present agricultural production systems based largely on irrigation depends on tackling salinity problems in a much more integrated manner. This is suggested to be through a proper balance between the management approach, in containing further salinity buildup in these soils, coupled with the biological option of genetic improvement in salinity tolerance.

The biological option, apart from contributing to the survival of present production systems, also opens the way for the novel concept of using seawater irrigation for food production along coastlines at present lying idle for lack of crops that can be grown in these regions. Early attempts by Epstein and his colleagues with barley demonstrated the feasibility of this approach. However, much more needs to be done to realize this dream. Not all barley germ plasm collections have been systematically evaluated for their potential to grow with seawater irrigation. Apart from this, wild relatives of barley have not been thoroughly explored for their potential to contribute to the genetic improvement in salinity tolerance. The *Hordeum* species, such as *H. spontaneum*, *H. jubatum*, and *H. marinum*, could provide the necessary "genetic means" to develop barley cultivars that could be grown with seawater to give reasonable yield levels. We hope that future efforts will be directed toward realizing this goal.

Improving salinity tolerance in many crops whose production systems are being threatened by secondary salinization is of immediate importance to the continuation of these crops in their present production environments. "Genetic support" should be recruited from wild species should sufficient variation not be found among cultivated germ plasm collections.

Traditional breeding approaches can be used for genetic improvement in salinity tolerance in a target crop species, and these may have a higher level of success if integrated with physiological research. Biotechnological approaches, such as using somaclonal variation in tissue culture for generating salt-tolerant cell lines and, finally, plants, have been projected to have much promise (113). Consistently, however, no salt-tolerant plants have been regenerated from these so-called salt-tolerant cell lines (114). Salt tolerance is much more of a whole-plant phenomenon. It depends on a number of physiological processes that need to coordinate at the whole-plant level to provide the necessary stable ionic environment in the cytoplasm and the required osmotic adjustment for the turgor-driven water uptake under saline conditions. It is thus not surprising that plants regenerated from the tolerant cell lines have not shown the same level of tolerance as the original cell lines (114).

However, other aspects of biotechnology show promise for use in the genetic enhancement of salinity tolerance. For example, RFLP (restriction fragment-length polymorphisms) or RAPD (random amplified polymorphic DNA) markers could be used for tagging the physiological components of salinity tolerance. These methodologies could be effectively integrated into breeding programs for the genetic improvement in salinity tolerance in crop plants (115).

More concerted attempts should be made to integrate physiological research in plant salinity tolerance with genetic aspects so that a combined physiological-genetic approach may be realized. We hope that wild relatives of crops will play a more prominent role than hitherto in the development of salt-tolerant crop varieties.

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To   : ICRISAT Editorial Committee Secretariate   Date: 13 Jan 93

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Please record for SAT News, Annual Reports, etc:

Subbarao, G.V. and Johansen, C. 1993. Strategies and scope for
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Handbook of Plant and Crop Stress (Pessarakli, M., Ed.). New
York, USA: Marcel Dekker Inc. JA 1428.

Subbarao, G.V. and Johansen, C. 1993. Potential for genetic
improvement of salinity tolerance in legumes : Pigeon pea.
Pages 581-595 *in* Handbook of Plant and Crop Stress
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Photocopies of these book chapters are attached.

C. JOHANSEN

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