# Saline Culture of Crops: A Genetic Approach

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*Summary.* Increasing salinity of soil and water threatens agriculture in arid and semiarid regions. By itself, the traditional engineering approach to the problem is no longer adequate. Genetic science offers the possibility of developing salt-tolerant crops, which, in conjunction with environmental manipulation, could improve agricultural production in saline regions and extend agriculture to previously unsuited regions.

Agriculture in those large areas of the world that depend on irrigation faces a serious challenge: it must improve upon or at least maintain crop productivity while coping with ever more saline soils and waters. The problem is an ancient one, but it demands contemporary and innovative approaches. We advocate the development of crops tolerant of salinity as a strategy for meeting this challenge.

In arid and semiarid regions, insufficient precipitation results in extensive reliance on irrigation and a concentration of (mainly sodium) salts in soils and water supplies that is high enough to impair the growth of plants. High salt concentrations in the soil solution create high osmotic pressures, reducing the availability of soil water to the plants, and specific ions such as sodium or chloride may prove toxic at high concentrations. Only the latter effect operates in sodic soils, soils in which the negatively charged soil particles bear a high proportion of exchangeable sodium ions. In this article the sodic condition is included when the terms salt and salinity are used.

The threat posed by progressive salt buildup has led to the implementation of large schemes of reclamation, drainage, and irrigation with high-quality water often conveyed long distances. Such measures minimize the salinity to which crops are exposed. These activities should be continued and even expanded in regions where irrigation is meant to provide food, fiber, and other usable biomass on a permanent basis. The cost, however, is high in terms of dollars, energy, and water.

We refer to the engineering approach to the salinity problem as a technological fix (*1*)—manipulating the environment to benefit the plants. We believe that this should be supplemented by a biological fix—genetically adapting plants to saline conditions. Economically feasible engineering schemes cannot eliminate salt from saline environments; they can only minimize it. Development of salt-tolerant plants would make possible improved utilization of saline soils and water.

At salt concentrations injurious to conventional strains, salt-tolerant crops can perform well, although probably not as well as plants not subjected to salt stress. Regions now ruled out for culture of certain species might be usable for selected salt-tolerant strains of those species. With such strains, the quasi-steady-state salinity of the soil of a given area could be maintained at a higher level than otherwise, reducing the frequency of irrigation and reclamation cycles and thus saving both water and the energy for pumping or conveying it. Use of saline water for irrigating salt-tolerant strains would free high-quality water for irrigating species that absolutely require it and for nonagricultural uses. Pumping of groundwater in coastal areas may cause the intrusion of seawater into the subsurface water supply. In those locations, planting salt-tolerant strains would reduce the economic and aesthetic losses that tend to accompany such intrusion. Where water has become saline from being used domestically, in industries such as petroleum production and strip mining, and for agriculture or aquaculture, the availability of salt-tolerant plants might render these effluents useful for applications ranging from food production to the generation of biomass for energy. Finally, systems of crop production based on seawater might be established along sandy coasts, allowing exploitation of the water itself, mineral nutrients dissolved in it, sandy land, and solar energy.

Thus a single new strategy, the development of salt-tolerant crops, may lead to a great variety of benefits.

## Agriculture and Salinity

The existence in arid lands of unleached, often fertile soils but limited water supplies makes those lands both potentially productive and highly susceptible to the vagaries of water availability and quality. The soil must remain fertile and free of excessive concentrations of salts, but supplying water (of whatever quality) to it makes its salt-free maintenance difficult and expensive. Nearly all aspects of agricultural technology in arid lands seem to work against the maintenance of systems unencumbered by excess salt: evaporation of water from canals, reservoirs, and fields concentrates the salt; soil amendments and fertilizers add to it; and cultural practices may compact the soil and impede the downward percolation of water, causing retention of salts in the root zone (Fig. 1).

The problem exists even in some of the world's subhumid regions, but is most widespread, severe, and threatening in arid and semiarid lands. Estimates of the extent of saline soils range from nearly $400 \times 10^6$ (*2*) to $950 \times 10^6$ hectares (*3*). The wide range is due to the difficulty of mapping the soils by uniform standards and methodology. An estimated $230 \times 10^6$ ha are irrigated worldwide (*4*); of this area, about one-third is affected by excess salinity (*5-7*). Even highly sophisticated agricultural systems like those of the western United States have salt problems. Citing American in-

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stances, H. E. Dregne (Texas Tech University) wrote, "The most pervasive problem [of irrigated agricultural lands] is the increase in soil salinity—sometimes slow, sometimes more rapid—that threatens many thousands of hectares" (8). In California, the situation is critical in the Imperial, Coachella, and Sacramento-San Joaquin valleys (9). As more land is put into production and the demands for water from agricultural, mining, recreational, domestic, and industrial interests increase, the problem grows. The issue is vital to that half of the world's nations having part or all of their territory in arid or semiarid zones (3, 5, 7, 10, 11).

Dealing with salinity has become a highly sophisticated science in recent years. Institutions such as the U.S. Salinity Laboratory, the Food and Agriculture Organization of the United Nations, the United Nations Educational, Scientific, and Cultural Organization, Ben Gurion University of the Negev, and several organizations in India have been leaders in developing and applying new methods and equipment for irrigation management in areas where salinity and waterlogging threaten.

Much of what we know of such technology derives from lessons learned over thousands of years of irrigation. The same problems are still with us: waterlogged soils; silted-in canals, reservoirs, and drainage ditches; saline soils and groundwater; overdrafts and wasteful application of available water; and the use of inappropriate crops for the agricultural conditions prevailing. The persistence of these troubles is evidence that they are not dealt with easily or cheaply. There is no substitute for wise management of water resources, nor is the approach we advocate feasible unless it is used in conjunction with appropriate irrigation technology.

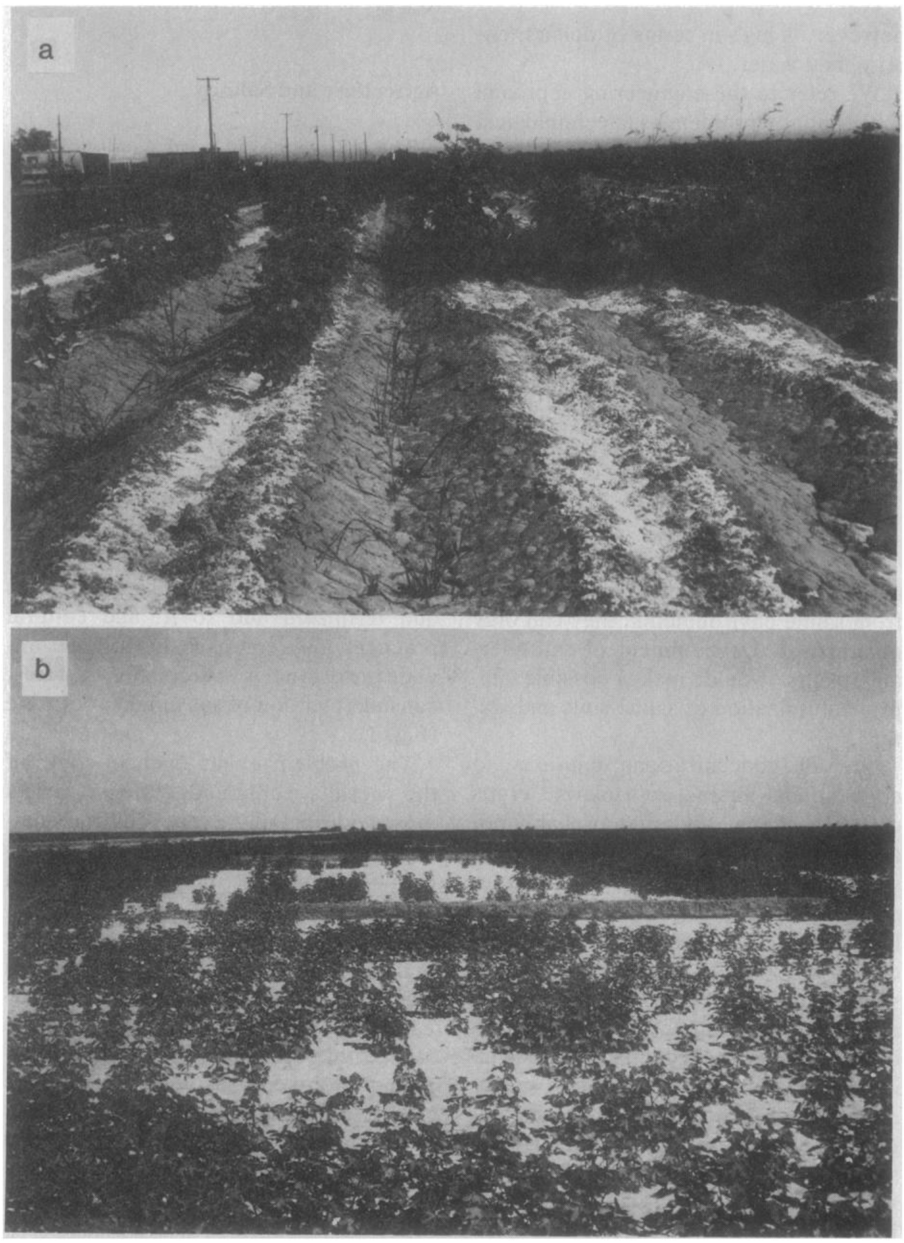


Fig. 1. Salt-affected agricultural land in the southern portion of San Joaquin Valley, California. This land, the edge of an interior drainage basin and dry lake bed (Tulare Lake), is afflicted by native salts and those introduced by irrigation water. The gaps in these rows of cotton were caused by salt accumulation in the seedbed [note the salt crusting in the foreground of (a)] and by waterlogged clays with high salt concentrations (b). High water tables bring salt to the surface, compounding the problem. As much as 25 percent of some fields in this region are severely affected by salt.

## Adaptation of Plants to Saline Conditions

*Development of the concept.* Until recently, land, water, and energy were so abundant, at least in agriculturally advanced countries, that there was little pressure to develop crop plants tolerant of salinity. Furthermore, some scientists felt little confidence that salt-tolerant crops could be developed.

In the past two decades, however, the genetic approach to the salinity problem has slowly gained ground. This is due in part to a growing awareness among agricultural plant scientists of the halophytes—wild species that live and reproduce in oceans, seashores, estuaries, deltas, salt marshes, and saline desert soils. They provide evidence that plant life can flourish under highly saline conditions. Some crops, the beet and the date palm among them, have halophytic characteristics.

As early as 1941, Lyon wrote (in a paper on tomato tolerance of sodium sulfate) that "it may be possible and desirable to select and breed plants for tolerance to saline conditions" (12). However, his prescient paper was overlooked. At a 1961 conference, Epstein discussed the genetic control of mineral ion transport and salt tolerance in plants with special reference to "breeding economic plants more tolerant of salt than present-day crop species" (13). At about the same time, Dewey (14) reported investigations on the salt tolerance of species and varieties of *Agropyron* (a range grass). He was the first to conduct a systematic study of the salt tolerance of a considerable number (60) of strains of a given species (*A. desertorum*) and to outline a breeding program for salt tolerance. He noted that "nothing conclusive can be said about the extent of intraspecific variability for salt tolerance since no species has been adequately surveyed for this characteristic" (*14*). This statement is still true today. Epstein and Jeffries (*15*) recognized the importance of varietal differences in tolerance of salt and elaborated on Epstein's earlier comments.

The volumes edited by Boyko (*16*) in 1966 and 1968 drew attention to the possibility of using highly saline water for producing usable biomass ranging from conventional crops to forest trees. In 1968, Wadleigh wrote: "As economic pressures on water supplies force agriculture to use more and more water of impaired quality with respect to salt loading, salt-tolerant crops will increase in importance" (*17*).

In 1972, Mudie *et al.* (*18*) examined the possibility of irrigating with highly saline water, including seawater, and Mudie later discussed the economic potential of halophytes (*19*) and the use of their "particularly knowledgeable DNA" in breeding salt tolerance into crop species (*20*). Epstein reiterated his conviction that "breeding for salt tolerance emerges as the greatest challenge to plant breeding aimed at problems of mineral metabolism" (*21*). Greenway expressed similar sentiments: "Breeding of salt-tolerant varieties should be a prerequisite for areas with saline waters, i.e., in the same way as in most cereals tolerance to rust has become a prerequisite before further selection for other characteristics" (*22*). Thus by the early 1970's the stage was set for a considerable expansion of the sporadic activities dealing with the introduction of genetics into applied research on salinity.

This expansion is now under way. A recent survey (*23*) revealed that at least 61 researchers around the world are interested in genetic aspects of plants resistant to the damaging effects of salts. Two workshops have dealt with the "biosaline concept" (*11, 24*) and the "genetic engineering of osmoregulation" (*25*), the latter phrase referring to "the application of the science of genetics toward osmotically tolerant microbes and plants" (*25*). A second workshop on biosalinity is to be held in November 1980 (*26*). In addition, other recent publications attest to the growing recognition of the potential of salt-tolerant crops (*2, 27*).

*Work at Davis.* Our work in the Agricultural Experiment Station at Davis on this problem is distinguished by the following features. (i) Thousands of genotypes of barley and wheat have been screened. (ii) In the case of the tomato, exotic germ plasm has been used to transfer salt tolerance from an economically useless species to a commercial one. (iii) All initial screening has been done by means of culture in salinized solution media of known composition. (iv) Successful selections have been field-tested under saline conditions.

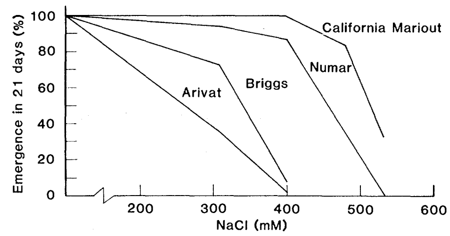


Fig. 2. Performance of four barley cultivars under salt stress. The criteria for emergence were satisfied when the first true leaf appeared through the coleoptile sheath and the plant was subtended by viable roots.

Screening among the relatively few cultivars in use today appears to have only limited potential. These genotypes are themselves the products of breeding for various desirable traits (yield, disease resistance, and so forth), and much of their original variability may have been lost in the process. For many important crops, however, there exist collections of seeds representing a great diversity of germ plasm: varieties, lines, land races, primitive cultivars, and other genotypes from all over the world (*28*). Breeders draw on these banks of germ plasm in their quest for desirable traits. We believe that these collections must be screened if the genetic limits to tolerance of salt by crop species are to be determined.

In some important species the variability in salt tolerance may be inadequate for a successful breeding program. In such cases it may be possible to find salt-tolerant wild relatives and use them as sources of germ plasm (*29*).

The use of salinized solution media for screening ensures that the chemical features of the root environment—concentrations of individual ions, total salinity, and *p*H—are defined. The entire root system is uniformly exposed to the saline medium; such ill-defined phenomena as "partial root contact" and "subterranean dew" (*16*) are thus avoided. The salt concentration can be changed at will and root growth can be observed and measured. The plant can be recovered, without injury to the roots, for measurement, chemical analysis, or transfer to another medium.

Finally, field testing provides reliable information concerning the performance of the plants.

We shall briefly summarize our experience with barley, wheat, and tomato.

*Barley. Hordeum vulgare* is the most salt-tolerant grain grown on a large scale. The native salt tolerance of this species has been recognized for centuries; *H. vulgare* is widely used in fields newly reclaimed from saline wasteland and in fields salted-out by previous irrigation practices (*5, 7, 30*). Furthermore, barley genetics and physiology have been extensively studied (*31*), variability of salt tolerance within the species is great (*32*), and there is enormous diversity in the world collection of genotypes available for selection and breeding (more than 20,000 entries are banked by the U.S. Department of Agriculture).

An indication of the genetically controlled variability in salt tolerance among just a few barley cultivars is given in Fig. 2 (*33*). Seeds of four barley cultivars were subjected to various concentrations of sodium chloride, the highest being roughly equivalent to that found in seawater. Emergence was determined at the end of 21 days. California Mariout was the most tolerant and Arivat the least tolerant entry under the test conditions. Briggs and Numar are the results of a breeding program at the University of California at Davis (*34*). Numar, with California Mariout four times in its pedigree, outperformed Briggs, which has California Mariout twice in its pedigree. It is evident that California Mariout contributes to the salt tolerance of these two cultivars at this stage of the life cycle; an additive genetic effect is suggested (*35*).

In order to screen a large spectrum of barley germ plasm for salt tolerance, we made selections from Composite Cross XXI, which was derived from the American World Collection and is very heterogeneous genetically, having been synthesized from 6200 lines (*36*). Selection was done by culturing the plants in solution media salinized with synthetic sea salt (the purpose of this particular project was selection for seawater culture). The selection procedure and eventual field testing among the dunes at Bodega Marine Laboratory, 80 kilometers north of San Francisco, have been described (*37*).

The best selections, grown under irrigation with undiluted seawater supplemented by nitrogen and phosphorus, had an average yield of 1082 kilograms per hectare, 23 percent more than the 833 kg/ha obtained from several standard cultivars entered into the test. For comparison, the average annual world yield of barley is under 2000 kg/ha (*38*), a yield approached in a subsequent trial at Bodega (about 1500 kg/ha). Table 1 gives an indication of the salinity at which these results were obtained. The specific electrical conductance of the Pacific Ocean water used averaged 45.8 millimhos per centimeter during the growing season (1975–1976) of this experiment. Modern guidelines for irrigation water quality state that "severe problems" are to be expected when water having electrical conductivity greater than 3 mmho/cm is applied to agricultural soils (*39*).

It should be kept in mind, however, that the seawater was applied to dune sand with excellent permeability and drainage characteristics—quite different from conventional agricultural soils. Also, what few rains fell during those drought years, though always followed immediately by extra saline irrigations to minimize the dilution, probably (to judge from subsequent experiments) played an important role in the survival of the plants at the early seedling stage.

*Wheat. Triticum aestivum* is probably the most economically important grain, but it does not have as good a reputation for salt tolerance as barley (*39*). Tests of cultivars have shown, however, that this species does have intraspecific variability in salt tolerance (*40*). Using methods similar to those successful with barley, we have screened over 5000 accessions from the collection of the Department of Agriculture. Thirty-four lines of spring wheat are capable of producing grain at a salinity 50 percent that of seawater, a level of stress lethal to commercial wheat. Further improvement seems likely. Some of these lines have been crossed with high-yielding varieties, and the progeny will soon be tested.

The extent of variability uncovered in the screening operation is illustrated in Fig. 3. Relative survival rates of the more sensitive and the more tolerant accessions are shown. Plants of the sensitive populations died within 7 weeks of germination (before they were much larger than seedlings). The tolerant lines survived much longer and grew more vigorously, and 17.3 percent of the plants produced viable seeds.

Table 2 presents preliminary data on total biomass production of plants grown

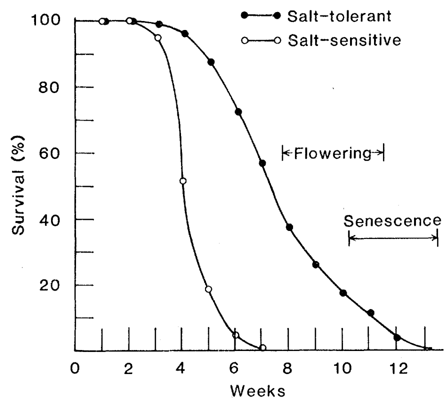


Fig. 3. Survival of 34 salt-tolerant and 30 salt-sensitive selections of wheat grown in solution media salinized to 50 percent the salinity of seawater.

to maturity in salinized solution media. Salt-sensitive and salt-tolerant selections were compared with a high-yielding California cultivar (Anza) and with one of the most salt-tolerant Indian varieties (Kharchia). After only a single selection cycle, strains were obtained that outperformed Kharchia. With further selection over several generations, substantial improvement seems likely.

*Tomato*. Preliminary screenings of lines of *Lycopersicon esculentum* showed little promise; we therefore turned to a wild, economically useless, but salt-tolerant species, *L. cheesmanii*. Seeds of this species had been collected by Rick (*41*) on Isla Isabella in the Galápagos Islands from a plant growing a few meters above the high-tide line and presumably much exposed to salt. This genotype was found to be quite salt-tolerant (*42*). Individuals grown from the seed of this plant survived in medium equal in salinity to seawater, although their growth was impaired under the stress. The fruit from this species is, however, very small and commercially useless. Physiological studies comparing the Galápagos tomato with a commercial salt-sensitive cultivar revealed marked differences in ion transport, salt accumulation or exclusion, and several other features (*42*).

These two species proved useful not only for comparative studies of the mechanisms of salt tolerance but also for a program of breeding for this trait. Crosses were made and the progeny were selected for salt tolerance by culturing them in medium containing sea salt at 50 percent the salinity of seawater. Several successive backcrosses to the commercial cultivar (to incorporate desirable characteristics such as size and color) have been completed.

Selection under salt stress after each cross has maintained a promising degree of salt tolerance. After each series of crosses and selections for salt tolerance at germination and seedling establishment, vigorous survivors were planted in plastic greenhouse shelters on dune sand at Bodega Marine Laboratory and irrigated with seawater dilutions up to 70 percent. The commercial parent cultivar did not even survive at 70 percent seawater, while the selected crosses survived, flowered, and set fruit about the size of large cherry tomatoes, with flavor components much more intense than those of the commercial parent. Table 3 gives survival and yield data of domestic and selected salt-tolerant lines under conditions ranging from fresh water to 70 percent seawater. The experiment demonstrates the feasibility of transferring salt tolerance from wild species to commercial ones (*29*).

Table 1. Concentrations of salts in and electrical conductivities of selected water supplies. These numbers are broad guidelines only, since the effect of a given water supply on plants depends on many other factors as well.

| Salinity measurement | Water supply | | | | |
|---|---|---|---|---|---|
| | Irrigation water, good quality | Irrigation water, marginal quality | Sacramento River | Colorado River | Pacific Ocean |
| Electrical conductivity (mmho/cm) | 0 to 2 | 2 to 5 | 0.2 | 1.3 | 46 |
| Concentration of dissolved salts (parts per million) | 0 to 1,000 | 1,000 to 3,000 | 300 | 850 | 35,000 |

## Other Methodologies

The methods of selection and breeding used in our project are not the only ones that can be brought to bear on the task of developing salt-tolerant genotypes. Several teams have used cell and tissue culture techniques for selection of lines tolerant of high salt concentrations (*43*). There is evidence that the salt tolerance of crops may be enhanced by inoculating their roots with appropriate mycorrhizal fungi (*44*). In legumes that symbiotically fix atmospheric nitrogen, selection of appropriate rhizobial strains may enhance the salt tolerance of the host-symbiont system (*45*). Less intimate associations between nitrogen-fixing microbes and roots in saline media may also prove useful (*46*). For woody plants like grapevines and fruit trees, graftage (*47*) has possibilities. Mutation breeding, recombinant DNA techniques, and somatic hybridization have not yet been used to develop salt-tolerant crops, but may be avenues for future progress.

## Basic Research

Plant scientists know little of the mechanisms that enable salt-tolerant plants to survive and even thrive and reproduce in saline environments that are fatal or severely inhibitory to salt-sensitive ones. In general, research interest in this subject has been confined to three disciplines. First, as already mentioned, agricultural scientists have had to cope with salinity problems worldwide. They have done so mainly by minimizing the salinity of soils and water so that conventional salt-sensitive lines could be grown. Second, ecologists have studied the halophytic flora of naturally saline settings. Finally, plant physiologists have performed experiments on salt-sensitive plants (almost invariably crops) and halophytic species. The reviews by Maas and Nieman (*48*) and Greenway and Munns (*49*) treat mainly the former; that by Flowers *et al.* (*50*), the latter.

This historic concentration of interest in plant groups at the extremes of the range in response to salinity has had the result that an appreciable area of potentially useful research has not received the attention it merits. There has been only sporadic research on the comparative physiology of the salt relations of plants. In particular, only a few investigations have been conducted on closely related plants, especially genotypes within a species, that differ markedly in their tolerance of salinity. Yet comparative studies have commonly shed light on other kinds of plant responses. The research of Clausen *et al.* (*51*) on environmental responses of climatic races of *Achillea* is a classic instance of the usefulness of this comparative method. It seems unlikely that mineral metabolism, including the salt relations of plants, should be an exception and not amenable to this approach. There is evidence that this aspect of plant physiology can yield to a comparative attack (*21*, *52*).

The selection of plants belonging to the same species or genus but contrasting markedly in their degree of salt tolerance will make available experimental material ideally suited for comparative studies of salt tolerance. Chances are good that contrasting features of structure and physiological function may bear a causal relation to the differential responses of the plants to salt.

Selection of highly salt-tolerant genotypes within a species can therefore be expected to provide useful material for experimental comparisons with ordinary, relatively salt-sensitive lines or even, to magnify the contrast, with lines selected for salt sensitivity. Interspecific comparisons within a genus can also be enlightening. This basic research into the structural and functional features associated with salt tolerance can in turn be expected to advance the applied work discussed in this article. It may, for example, lead to the discovery of structural or biochemical features consistently associated with salt tolerance.

Table 2. Biomass production of selected wheat lines cultured at various salinities. Values are percentages of the control value (culture with fresh water) for each line. [Data from (*54*)]

| Line | Salinity (% of seawater salinity) | | |
|---|---|---|---|
| | 20 | 40 | 60 |
| Sensitive selections (mean of two lines) | 30.7 | 2.3 | 1.6 |
| Anza | 28.5 | 5.3 | 3.7 |
| Kharchia (mean of two lines) | 26.3 | 7.3 | 5.9 |
| Tolerant selections (mean of three lines) | 33.0 | 9.4 | 6.4 |

Table 3. Survival and fruit yield (fresh weight) of a domestic tomato and of salt-tolerant genotypes grown at various salinities. Values are percentages of the control value (culture with fresh water). [Data from (*42*)]

| Irrigation water salinity (% of seawater salinity) | Domestic cultivar | | Tolerant genotypes | |
|---|---|---|---|---|
| | Survival | Yield | Survival | Yield |
| 30 | 100 | 24 | 100 | 48 |
| 50 | 41 | 7 | 81 | 28 |
| 70 | 0 | 0 | 57 | 19 |

## Research Needs

Environmental manipulation has been the traditional approach to salinity problems in agriculture. What is now needed most is the addition and vigorous application of a new genetic dimension to research and development dealing with salinity. This new approach is beginning to yield results, but it is indeed only a beginning. Researchers in this area have available to them a minuscule fraction of the resources that are devoted to R & D in the traditional areas of reclamation, drainage, and irrigation with high-quality water.

Selection and breeding for resistance to any environmental stress ultimately depend on two factors: genetic variability with respect to resistance to the stress, and exposure of genetically variable populations to the stress. The latter factor facilitates identification of individuals approaching or possessing the desired phenotype. There are large collections of germ plasm that can be screened for salt tolerance (*28*, *29*). In addition, salt-tolerant wild relatives of crop species can be drawn on. Exploitation of the available genetic diversity in crops (and related species) for the purpose of selection and breeding for desirable traits is a method of proven effectiveness (*53*). In principle, there is nothing new in applying the same approach to the development of salt-tolerant crops.

The imposition of an appropriate stress is another matter. Saline soils and water supplies are exceedingly variable in both the kinds of salts present and their concentrations. The cation exchange properties of soils add more complexity, as do spatial and temporal variations in all these features. It will therefore be necessary to test whether selections made under one set of saline conditions are equally effective under a different saline regime. The solution media used in our studies have the advantage that they can be made to exact specifications in terms of salts and their concentrations and can be accurately monitored thereafter. They represent, however, media quite different from soils in many chemical and physical characteristics. Research is therefore needed to test salt tolerance selection media ranging from solutions to saline soils in the field. Even broadly successful selections will have to be further developed in "adaptability research" to fit them for particular local conditions.

Basic research on mechanisms of salt tolerance should not be confined to crop species. The wild halophytes possess the competence we are interested in. They should not be neglected in R & D aimed at combining that competence with the economic utility of a crop plant.

Finally, there is need for geographic, economic, and social studies to identify regions where saline crop culture can have the most beneficial effect. Mechanisms for international collaboration and technology transfer need to be established.

Excessive salinity is one of the facts of plant life, and hence of all life, in the arid and semiarid parts of the world. Of the possible strategies for coping with it, only that of ameliorating the soil and water has been extensively applied. It should be complemented by genetic manipulation of crops to adapt them to saline conditions.

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