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Salt-tolerant crops: origins, development, and prospects of the concept

EMANUEL EPSTEIN
Department of Land, Air and Water Resources, University of California, Davis, CA 95616, USA

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Summary The genetic approach to the problems posed by salt-affected soils and water, *i.e.*, breeding crops resistant to salinity stress, is traced to two principal origins: the European ecological interest in halophytes, and the exigencies of growing crops in the arid and semi-arid lands of the American West. The point is made that breeding for resistance to salinity stress cannot be divorced from breeding for various other desirable traits of mineral plant nutrition and metabolism. A survey is conducted of the existing body of information on breeding for desiderata of mineral nutrition in general and salt tolerance in particular. The prospects of breeding crops for salt tolerance are discussed, with emphasis on a) its relation to breeding for resistance to other mineral stresses; b) field trials; c) collaboration between plant physiologists and geneticist-breeders; and d) extensive exploration of germplasm.

Introduction: the origins

The organizers of this symposium have asked me to present not so much an account of recent advances as a review of the origin and evolution of the concept that salt-tolerant crops can and should be developed, and some preview of what might reasonably be expected. There are two main intellectual traditions that have joined and contributed to the worldwide enterprise that this Biosalinity Workshop was a part of. The first is the European interest in the ecology and physiology of halophytes. Europe, being an amply watered continent (except for some of its southern regions), and the British Isles have well leached soils, so that there was little agricultural impetus for an interest in saline conditions. But around the turn of the century Schimper[42] in Germany and Tansley[46] in Britain became impressed by the different types of vegetation in various environments and soils. Plants in saline environments did not escape their attention, and thus the foundation was laid for the study of halophytes, Schimper stressing physiological approaches and Tansley, genetic differentiation and competition. Neither these nor other investigators at that time confined their attention to halophytes. They were interested in all geographical factors in plant distribution, including edaphic ones such as salinity.

American interest in the interplay between plants and saline soils had an altogether different origin. The early settlers on the eastern coast of the continent found climatic and soil conditions not radically different from those they were used to in Europe. That changed when the inexorable expansion brought settlers into the arid west, and places with names such as Salt River Valley, Bitter Lake, and Alkaline Flat appeared upon the maps.

The saline and alkali soils of the West were troublesome because the early settlers were farmers for the most part, not adventurers and gold miners as the mythology has it. To farm in the arid west was a novel challenge, and indeed a challenge that even knowledgeable persons did not believe possible to meet. William H. Brewer was a member of the first California State Geological Survey. He recorded his observations in letters subsequently published under the title, Up and Down California in 1860–1864[2]. Here is what he had to say about the San Joaquin Valley, today the foremost agricultural region of California (pp 202–204):

'The San Joaquin (pronounced San Waugh-keen') plain lies between the Mount Diablo Range and the Sierra Nevada – a great plain here, as much as forty to fifty miles broad, desolate, without trees save along the river, without water during nine or ten months of the year, and practically a desert. The soil is fertile enough, but destitute of water, save the marshes near the river and near the Tulare Lake . . . Barren, very barren, few trees – often one will have a prospect of a dozen or even twice that number of square miles without a tree or shrub large enough to be seen, the ground either entirely bare or with a very scanty vegetation of stunted grass and low weeds . . . The streams that form in these hills in the spring all sink when they enter the plain, and as summer advances they dry up farther and farther until they all disappear. Such is an immense region, such it must ever remain, supporting a scanty population.'

Competent observer that he was, Brewer failed to visualize the potential for irrigation that lay in the snowpack of the Sierra Nevada to the east.

E. W. Hilgard was Professor of Agriculture at the University of California from 1875 to 1906[23]. He studied another aspect of arid lands: the salinity and alkalinity of their soils[21]. He knew that by reclamation procedures including drainage and the use of amendments, such soils could be rendered suitable for agriculture, and indeed he was the foremost developer and proponent of such procedures.

Hilgard was very broadly informed and had wide-ranging interests and vision. He was aware of the reclamation of polder lands from the sea in northern Europe and expressed the hope that the lands of the Near East could once again become fertile. He would have relished seeing what has since been accomplished in reclamation in many parts of the world, our host country, Israel, prominent among them.

Finally, he had what now seem prophetic words to say about plant life and agricultural crops on such soils. He commented favorably on the use of Australian saltbushes, *Atriplex* spp., as fodder for stock in California (21, p. 469). As for crops, two of his collaborators, J. B. Davy and R. H. Loughridge, conducted a survey of the responses to salinity and alkalinity of about a hundred field crops, vegetables, and fruit trees (pp 466–484). Hilgard's conclusion from this survey was not overly optimistic: 'it may be said generally that the search for widely acceptable kinds has not been very successful' (p. 468). This is among the earliest scientific estimates of the feasibility of crop production on salt-affected soils. 'It will require more extended experience and experiments before any of these plants will be definitely adopted for propagation by farmers and stockmen' (p. 468).

During and after Hilgard's tenure at Berkeley the enterprise of irrigation agriculture expanded in California, and many scientists kept struggling with the problems posed by salt-affected soils, poor quality, saline irrigation water, and inadequate drainage. These problems were considered to be primarily in the domain of the soil scientist, the irrigation specialist, and the grower. When, in 1937, the United States Regional Salinity Laboratory, now the United States Salinity Laboratory, was established in Riverside, California, this focus was maintained, but crop evaluation of the kind already initiated in Hilgard's day was also pursued.

Development: the genetic approach

The key to existence in arid and semi-arid environments is water of good quality. The ever-growing demand for water for urban and industrial uses and for agriculture was the impetus for a conference that met in 1961 at Woods Hole, Massachusetts, under the auspices of the National Academy of Sciences-National Research Council to consider the problem of desalination. If efficient, cheap ways could be devised for getting nonsaline from saline water, many of the problems besetting arid regions could be overcome. The participants in this conference were for the most part chemists, physicists, and engineers. But James Bonner of the California Institute of Technology reminded the organizers that living cells very effectively concentrate ions from their aqueous media and maintain steep diffusion gradients across their membranes. Perhaps an opportunity could be made for someone to present evidence on this biological salt transport and 'desalination.' He was kind enough to recommend me for the job. He was aware of my interest in ion transport in plants in general and in the selectivity between sodium and potassium in saline environments in particular[9,13].

I chose to use the opportunity to assemble what evidence I could find on the genetic control of ion transport in plants, with a view to determining the feasibility of projects for selecting and breeding for salt tolerance: 'It is axiomatic in present-day physiology and biochemistry that specific physiological and biochemical performances depend ultimately on the synthesis of appropriate enzymes, and that the synthesis of enzymes in turn is gene-controlled. This should apply to those physiological performances, notably selective ion transport, involved in the ability of plants to thrive in saline substrates'[10]. Because my colleagues in the plant sciences were unlikely to read the proceedings of a desalination research conference, I was fortunate to be able to expand and update that paper for publication in the Annual Review of Plant Physiology. This I did in collaboration with R. L. Jefferies, then a visiting scientist and now at the University of Toronto[14]. 'The large varietal differences in salt transport and toleration that have been encountered make it likely that much is to be gained by an energetic pursuit of the possibilities of breeding for salt tolerance.' We noted that hardly anything had yet been done along this line.

Up to that time there existed only a few reviews on genotypic differences among plants on any aspect of mineral nutrition and metabolism, none with salt tolerance as their focus or impetus. There were, however, some prescient individual research papers. A notable one was by Lyon[29], published in 1941. He used cultivars of two tomato species, *Lycopersion esculentum* and *L. pimpinellifolium* and the F_1 generation from their cross. He observed differences in some characters in response to salinization of the nutrient solution, none in others. He wrote that to 'accompany proper soil management practices and more detailed studies of salt antagonisms and toxicity effects, it may be possible and desirable to select and breed plants for tolerance to saline conditions. Such a program should eventually involve not only the production of strains with the characteristic of general tolerance to high salt concentrations but the actual selection and breeding of strains for specific concentrations of two or more ions.'

It is from these diverse and scattered beginnings that the enterprise on which we are now engaged has grown. Our present thinking, as reflected by the contributions to this conference, is to the effect that a genetic dimension of selection and breeding has been added to the traditional approach of reclamation and drainage, essential as these measures will continue to be.

Selection and breeding for salt tolerance should not, indeed cannot, be separated from selection and breeding for other aspects of mineral metabolism and nutrition of plants. On the contrary, from the beginning it has been considered in that broader context. There are four reasons for continuing that connection. (a) The first is that salinity-tolerance breeders will have their scientific intellectual horizons broadened and their competence enhanced by contact with geneticist-breeders concerned with other aspects of mineral plant metabolism. (b) A more specific reason for such collaboration is that plants on salt-affected soils often are exposed to a number of adverse conditions which, strictly speaking, do not fall in the category of salinity or sodicity. Iron deficiency chlorosis is a prime example[3]. It has been shown that this and other difficulties can be tackled by means of selection and breeding. (c) In breeding for a given trait it is not uncommon to introduce inadvertently genes that have unexpected and, more often than not, deleterious effects on the organism. Salinity-tolerance breeders may therefore find themselves dealing willy-nilly with matters other than salt tolerance *per se.* (d) Finally, comparative physiological and biochemical studies of genotypes contrasting in salt tolerance (or sensitivity) are of both intrinsic and potentially practical importance, and such studies are likely to be more fruitful if done in the wide framework of mineral plant metabolism than within the confines of the more narrow context of salt tolerance alone.

With this in mind, I have compiled in Table 1 reviews, chapters, and volumes dealing with the genetic control of mineral nutrition and metabolism in plants. Additional references from Eastern Europe and the U.S.S.R. not available to me are given by Sarić in the volumes edited by him (Sarić[41a]) and Sarić and Loughman[41b]. (The two volumes are almost identical – the proceedings of the same symposium held in 1982 in Beograd.) No original research papers are included, nor are reviews dealing specifically with salt tolerance. That topic is amply covered in the proceedings of several conferences that preceded the present one. The principal ones are listed in Table 2. Further reviews appearing in other publications are listed in Table 3.

The still broader matters of plant resources for arid (and hence salinity-prone) lands and the direct use of halophytes have been discussed at various conferences; see for example Goodin and Northington[19], Manassah and Briskey[31], and contributions to the present volume. Another conference on plant resources was held at the Royal Botanic Gardens at Kew later in 1984. It would, however, be beyond the scope of the present paper to do more than make mention of the many activities, including publishing ventures, dealing comprehensively with the manifold problems of arid lands. Paylore[34] recently has forcefully drawn attention to the need to devise means not just for generating

Table 1. Reviews, chapters, and volumes dealing with the genetic control of the mineral nutrition and ion relations of plants[a]

Author(s) or Editor	Year	Title	Reference
Kruckeberg, A. R.	1959	Ecological and genetic aspects of metallic ion uptake by plants and their possible relation to wood preservation	27
Myers, W. M.	1960	Genetic control of physiological processes: consideration of differential ion uptake by plants	33
Millikan, C. R.	1961	Plant varieties and species in relation to the occurrence of deficiencies and excesses of certain nutrient elements	32
Epstein, E.	1963	Selective ion transport in plants and its genetic control	10
Gerloff, G. C.	1963	Comparative mineral nutrition of plants	17
Vose, P.B.	1963	Varietal differences in plant nutrition	47
Epstein, E. and R.L. Jefferies	1964	The genetic basis of selective ion transport in plants	14
Epstein, E.	1972	Physiological genetics of plant nutrition	11
Klimashevsky, E.L., Ed.	1974	Variety and nutrition	25
Läuchli, A.	1976	Genotypic variation in transport	28
Wright, M. J., Ed.	1977	Plant adaptation to mineral stress in problem soils	51
Jung, G. A., Ed.	1978	Crop tolerance to suboptimal land conditions	24
Brown, J. C.	1979	Genetic improvement and nutrient uptake in plants	3
Clark, R. B. and J. C. Brown	1980	Role of the plant in mineral nutrition as related to breeding and genetics	5
Wegrzyn, V. A., R.R. Hill, Jr. and D. E. Baker	1980	Soil fertility – crop genotype assocations and interactions	49
Duvick, D. N., R.A. Kleese and N. M. Frey	1981	Breeding for tolerance of nutrient imbalances and constraints to growth in acid, alkaline and saline soils	8
Klimashevsky, E. L.	1981	Physiological genetics of plant mineral nutrition	26
Sarić, M. R.	1981	Genetic specificity in relation to plant nutrition	40
Clark, R. B.	1982	Plant response to mineral element toxicity and deficiency	4
Devine, T. E.	1982	Genetic fitting of crops to problem soils	6
Sarić, M. R.	1982	Genetic specificity of mineral nutrition of plants	41a
Sarić, M. R. and B. C. Loughman	1983	Genetic aspects of plant nutrition	41b

Table 1 (*continued*)

Author(s) or Editor	Year	Title	Reference
Epstein, E. and A. Läuchli	1983	Mineral deficiencies and excesses	15
Gerloff, G. C. and W. H. Gabelman	1983	Genetic basis of inorganic plant nutrition	18
Vose, P. B.	1984	Effects of genetic factors on nutritional requirements of plants	48

[a] Publications dealing exclusively with particular types of inorganic ions or compounds such as heavy metals or salt are not included, nor are in-house items and reports for government agencies which are of such limited distribution as to be virtually unavailable. Publications dealing with salt tolerance are listed in Tables 2 and 3.

Table 2. Proceedings and volumes dealing with the development of salt-tolerant crops[a]

Editor(s)	Year	Title	Reference
Hollaender, A., J. C. Aller, E. Epstein, A. San Pietro and O. R. Zaborsky	1979	The biosaline concept: An approach to the utilization of underexploited resources	22
Rains, D.W., R. C. Valentine and A. Hollaender	1980	Genetic engineering of osmoregulation: impact on plant productivity for food, chemicals, and energy	37
Qureshi, R. H., S. Muhammed, and M. Aslam	1981	Proceedings of the workshop/ seminar on membrane biophysics and development of salt tolerance in plants	35
Rains, D. W.	1981	A conference on biosalinity: The problem of salinity in agriculture	36
San Pietro, A.	1982	Biosaline research: A look to the future	39
Staples, R. C. and G. H. Toenniessen	1984	Salinity tolerance in plants: strategies for crop improvement	45

[a]Proceedings and volumes of limited distribution or mainly local scope and those dealing with particular crops are not included.

information but for disseminating it in useful ways. What was said there applies to our more specialized subject as well.

Take-home lessons and prospects

What can we gain from a survey such as this? First, the task in which we are engaged is to learn how to grow food, fodder, and fiber in those large parts of the world where soils and water are affected by salt. The development of plants tolerant of these conditions is a new challenge to plant breeders, and it is useful therefore to provide for them a survey

Table 3. Reviews on the development of salt-tolerant crops not appearing in the volumes listed in Table 2[a]

Author(s)	Year	Title	Reference
Gupta, V. S.	1978	Genetic and breeding aspects of salt tolerance in plants	20
Shannon, M. C.	1979	In quest of rapid screening techniques for plant salt tolerance	43
Epstein, E., J. D. Norlyn, D. W. Rush, R. W. Kingsbury, D. B. Kelley, G. A. Cunningham and A. F. Wrona	1980	Saline culture of crops: a genetic approach	16
Epstein, E.	1983	Crops tolerant of salinity and other mineral stresses	12
Downton, W. J. S.	1984	Salt tolerance of food crops: prospectives for improvements	7

[a] Specialized reviews and those devoted mainly to particular methodologies or crops are not included.

of what has been thought and done about it so far. The present review should give them ready access to the available literature on genetic aspects of mineral metabolism and salt relations of plants. (When, for a 1976 workshop[51], I compiled a list like those of Tables 1–3, it contained only eight items, all individual review papers. Tables 1–3 contain 35 items, 10 of them multi-authored volumes. Clearly we have come a long way in a short time.)

The other important benefit we may get from such a survey is an assessment of the needs and the opportunities that we are facing in this endeavour. Such an assessment is of course a matter of judgment, and I do not expect unanimous agreement with the points I shall make.

(a) Salt-affected soils and saline water represent mineral stresses. In programs devoted to the development of plants resistant to these stresses we should view our task in the broad context of breeding for resistance to all manner of other mineral stresses, for many of them have a bearing on and occur in conjunction with salinity stress.

(b) We have for the most part explored feasibilities, conducted experimental studies, and done screening for salt tolerance on a modest scale, often under greenhouse conditions. We shall have to expand the scale of our operations and include more work under field conditions, on salt-affected soils, and even experimentally salinized ones, using irrigation water of the kind available in the areas for which the crops are being developed.

(c) With regard to the point just made about field experimentation, the refractory problem of spatial and temporal variability of salinity and sodicity must be given close attention. Experience so far is too limited to permit us to devise breeding strategies for these patchy situations. It is thus not easy to agree that selection should be done on nonsaline soils[38]. What is needed are careful analyses of field conditions on an extensive scale, statistical evaluations of the results, and the development of breeding strategies based on the results of these analyses and evaluations.

(d) We shall have to convince more plant breeders to include salt tolerance among their breeding objectives. Plant breeders have been highly successful in breeding for numerous traits such as yield, quality, and disease resistance[44]. There is no reason why breeding for salinity tolerance should be an exception. There were only three geneticist-breeders at this workshop. I for one hope that there will be many more at our next meeting.

(e) We shall have to search more extensively than we have done for sources of suitable germplasm. There are, to be sure, limits to genetic variability and limits to the degree of any stress to which plants may become adapted[1]. On the other hand, physiological traits are under genetic control, and much genetic variability is available to the breeder[11,30]. Salt tolerance is such a trait. The quest for salt-tolerance germplasm is a very recent development. There is every indication that salt tolerance exists, and in forms that breeders can exploit. Wide crosses are likely to play an increasingly large role.

(f) We should not be deluded by facile claims that genetic engineering, specifically recombinant DNA techniques, will solve our problems quickly and cheaply, but we must be alert to these and a whole range of relatively new technologies and the potentials they offer. Selection at the cell level, somaclonal variation, protoplasmic fusion, and also such older methods as mutation breeding and still other techniques may all contribute to the development of salt-tolerant crops.

(g) We shall continue doing what we have already done with some measure of success, *i.e.*, study the mechanisms of salt tolerance as a guide to further progress. We should, however, resist the temptation to make large claims for the utility of such studies for the enterprise of selection and breeding for this trait; *cf.* Woolhouse[50]. To make such mechanistic studies as useful as possible for this purpose, plant physiologists and biochemists will have to learn to make their studies meaningful to plant breeders. A much closer symbiosis than now exists between the two groups will have to evolve.

(h) Finally, we shall have to make decisions about the kind of salt-tolerant crops to aim for. I have argued elsewhere[12] for development of halophytic crops, the consumable part of which is botanically fruit (grains, tomatoes, *etc.*). Most halophytes, in contrast to more or less salt-tolerant non-halophytes, use salt itself as the major osmoticum; I enumerated the reasons why that is an energetically advantageous mechanism[12]. But as a result of salt absorption, the foliage of these halophytes has a high salt content – a disadvantage if the foliage is to be used as feed or food. Fruit, on the other hand, receives most of its solutes via the phloem, which tends to screen out much of the salt. Finally, in halophytes the adaptation to saline conditions is mainly at the cellular level rather than at higher levels of organization (tissue, organ). Therefore, the new technologies mentioned above (f) lend themselves most readily to application in the development of crops with truly halophytic adaptation to salinity[12]. All these considerations lead me to favor the development of crops with truly halophytic response to salinity, the consumable part of the plant being botanically fruit (grains, seeds, berries, pomes, *etc.*). This emphasis on fruit does not, however, apply to crops grown for fiber, chemical feedstocks, medicinals, or biomass for generating energy.

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