

Seed-Bearing Halophytes



***Seed-Bearing
Halophytes as Food Plants***
PROCEEDINGS OF A CONFERENCE

G. Fred Somers, Editor

DEL SG 375

This work is the result of research sponsored in part by NOAA Office of Sea Grant, Department of Commerce, under Grant No. 235223

COLLEGE OF MARINE STUDIES • UNIVERSITY OF DELAWARE • NEWARK, DELAWARE 19711

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SEED-BEARING HALOPHYTES AS FOOD PLANTS

Proceedings of a Conference

University of Delaware

June 10-11, 1974

G. Fred Somers, Editor

DEL-SG-3-75

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Preface

The impetus for this conference originated with John C. Woodhouse, a retired chemist, formerly director of research of E. I. du Pont de Nemours & Co., who is currently an adviser to the College of Marine Studies, University of Delaware. He recognized that if seed-bearing plants could be grown, or could be developed to grow, in highly saline water they might make a significant contribution to the food supply for man and/or domesticated animals. His suggestion stimulated a lively discussion among colleagues. One result was a grant from the University of Delaware Research Foundation to support a conference where the desirability and feasibility of a search for potential food plants tolerant to high salinities would be examined. These "Proceedings" report that Conference. It should be recognized that the "Invited Papers" as they are published here are not, in most cases, verbatim accounts of the manuscripts as they were presented. The authors illustrated their talks with a number of slides, most of which they omitted in the final draft. The final draft does, however, accurately reflect the content as presented.

Without the support and cooperation of many people the conference would not have been held and these proceedings assembled for publication. I express my thanks to all those who participated in the Conference and to the University of Delaware Research Foundation for its generous support. Some must be singled out for special mention. These include

John C. Woodhouse, a constant stimulus and a sage adviser; Dean W. S. Gaither and Walter Vincent for guidance and administrative support; my colleagues in the College of Agricultural Sciences, Leroy V. Svec, Allen L. Morehart and Leo J. Cotnoir; and Mary Boyer for her patience and skill in transcribing the rough output of the Conference with a beautiful typescript.

G. Fred Somers

February, 1975

Agenda for
SEED-BEARING HALOPHYTES AS FOOD PLANTS
- A Special Conference -
University of Delaware

June 10, 1974

A.M. Welcome and Opening Remarks
 L. Leon Campbell
 Provost and V.P. for Academic Affairs

Purpose and Format of the Conference
 G. Fred Somers

Wild Rice Domestication as a Model
 Ervin A. Oelke

Sea Grasses as Potential Food Plants
 Richard Felger
 (paper prepared in collaboration
 with C. Peter McRoy)

P.M. Terrestrial Halophytes as Potential Food Plants
 Valentine J. Chapman

Potential of Adapting Present Crops to Saline Habitats
 James W. O'Leary

Problems in Managing Saline Soils
 Leon Bernstein

June 11, 1974

See separate listing of topics and participants

P.M. Workshops cont.

Reports from workshop groups

General discussion of such topics as:

Could the goals of this proposed program be accomplished?

What would it take to accomplish them?

Would it be worthwhile?

OPENING REMARKS

Leon L. Campbell¹

We welcome you to the University of Delaware and wish to express our thanks to you for being willing to take time to join us in an evaluation of a proposal for research into what is, for us, a new area. I will make comments in three general areas:

What brings us here today?

The Advisory Board of the College of Marine Studies was charged by President Trabant to suggest promising new areas for research. In response, a suggestion from Dr. John C. Woodhouse, a member of this Board, led to this conference. The question posed by Dr. Woodhouse and refined by Dr. Somers and others, is as follows:

Are there seed-bearing halophytes which can be grown using water approaching, or equal in salinity to that of the oceans and which could be used for food sources, including protein, for man and domesticated animals, or which could be modified by selection and breeding to serve such use?

This question, while not new, was found so intriguing by President Trabant and other University leaders that support was obtained from the University of Delaware Research Foundation for this Conference today and tomorrow.

¹Provost and Vice President for Academic Affairs, University of Delaware.

During the past few months two things have happened in response to this general question:

1. A proposal has been submitted to Sea Grant for funds to initiate research. We hope we might have some notion of the acceptance of this proposal before this Conference is over.
2. Development of a statement of the problem as a basis for this Conference. All of you have received a copy of this statement.

Why are we here today?

The challenges posed by this statement of the problem are many and complex. Before the University proceeds further we want a candid evaluation of:

- need
- potential
- merit of our concepts
- advice in refining our perception of the problem and procedures for addressing it.

And if this Conference is as successful as we hope it will be, we expect to publish the proceedings of the Conference.

Where do we go from here?

This depends in no small measure upon recommendations which grow out of this Conference. Note particularly the discussion scheduled for 4 p.m. tomorrow afternoon. In essence everything up to that point is prologue. Now there are three questions which you'll be discussing tomorrow afternoon after your workshop is over, and they are:

Could the goals of this proposed program be accomplished?

What would it take to accomplish them? and

Would it be worthwhile?

President Trabant and I look forward to receiving the responses from this Conference to these important questions regarding halophytic plants serving as food.

(excused himself at this point)

A SEARCH FOR ANGIOSPERMOUS FOOD PLANTS WHICH COULD BE GROWN
USING WATER APPROACHING OR EQUAL TO SALINITY OF THE OCEANS

A problem statement for a Conference

June 10-11, 1974

Robinson Hall, University of Delaware

Prepared by: G. Fred Somers

In cooperation with: L. J. Cotnoir, Jr., A. L. Morehart,
L. V. Svec, and John C. Woodhouse

Synopsis

We propose that the conferees discuss the question: Are there seed-bearing halophytes which can be grown using water approaching, or equal in salinity to that of the oceans and which could be used for food sources, including protein, for man and domesticated animals, or which could be modified by selection and breeding to serve such use?

(In framing this question we have deliberately omitted the large marine algae and propose that grasses which are suitable only for hay or pasture receive little or no attention since technologies exist for such use.)

An affirmative answer to this question would be of tremendous importance. Not only would it increase our options in supplying food for man and his domesticated animals but in doing so would conserve a valuable resource for which there is a growing concern - fresh water. If waters of the oceans, or others of high salinity, could be used for irrigation, not only areas subject to tidal inundations, but lands contiguous to saline or brackish tidal streams could have abundant water available for irrigation. Moreover, some plants which are adapted to tidal areas might be expected to grow in vast inland areas for which only saline water is available (see 119,130,135,136 for examples), provided, of course, that associated problems of water and land management could be solved.

Limited attempts have been made to expand the salt tolerance of common food crops. These have the advantage of being accepted in commerce, but they might be expected to suffer from a deficiency with respect to adaptability to salt tolerance. They were derived from gene pools which apparently evolved in recent geological times in nonsaline or only mildly saline habitats.

The proposition of this Conference, on the other hand, is to tap gene pools which have arisen during evolutionary exposure to saline habitats. It proposes a search for plants native to such habitats which show promise as food plants. Could these, by breeding and selection, be improved until they merit serious consideration for commercial cultivation?

Statement of the problem

Ancient man brought into culture essentially all of the food plants now cultivated by man. Certainly those crops which meet the present basic needs for energy and protein came from antiquity. A new need is now being recognized: ". . . the suddenness with which the scarcities of food and energy developed has been a sharp reminder that global resources are finite and that the present phase of shortages and high prices may only be a premonitory tremor of worse upheavals to come," (Wade, 1). Wade says further: "Food has become an important factor in foreign policy," and "Farm policy used to be geared to dealing with the problem of surpluses; overnight, the problem has changed to one of scarcity." Loosli says (2): "The problem is a critical one, since protein-calorie malnutrition is the most serious and common cause of infant mortality and debility in developing countries, and among the poor in the industrialized countries."

It is the central hypothesis of this problem statement that coastal areas to which abundant sea water is available could contribute to meeting this need for food. They are highly productive of dry matter both in the sublittoral (3) and intertidal zones (4,5,7,140). From the sublittoral zone are harvested large brown and red algae (141) which, while important in food technology, provide little useful energy for humans or domesticated animals. Even less direct use has been made of the plant material which grows so abundantly in the intertidal zone. Some areas are grazed; some hay is harvested. Teal and Teal (140) graphically document that, "Estuaries in general and salt marshes in

particular are unusually productive places," exceeding in this regard both cultivated lands and coastal waters. Could intertidal areas or other land to which coastal waters could be applied readily be used to produce high-energy or protein-rich food for use by man or domesticated animals?

The idea may seem farfetched at first, but others have suggested using saline waters for food production. Various aspects of the use of sea water for irrigation were considered by Boyko and others (Boyko, 40, 149), who have limited attention to irrigating food crops. Epstein and his colleagues, Jeffries and Rains, have repeatedly (85,86,87,88) called attention to the potential of using saline waters for crop production. They stress the potential this approach might have for food production. Waisel (5) expressed a similar view:

The increasing use of water of poor quality, the continuous addition of waste salts to our environment, as well as increasing contamination of underground water sources lead to gradual soil salinization. Soberly analyzing the consequences of such a process, one must reach the conclusion that the future of plants lies with some group of halophytes.

Understanding the basic processes of adaptation to salinity and the know how of applying such principles to crop plants would be, in the near future, a matter of 'life and death' to the growing population of a world 95% of whose water sources are saline.

Meinzer (135) noted many years ago the contribution halophytic crops, which could obtain their water from water-saturated soils, could make to millions of acres of arid land.

In a personal communication to Woodhouse, Norman Borlaug, Nobel prize winner for his role in the development of the "green revolution," said:

Why didn't I think of that! I can see no more important development in the critical area of food needs than of food plants tolerant of salt water.

Bronowski (6), British scientist and philosopher wrote:

I guess the single most important biological contribution to world peace will be to produce plants which grow effectively in quite salty water.

While the tidal wetlands in Delaware would provide a convenient site for testing this hypothesis, it is significant that they have attributes in common with a number of other areas: The water supply is highly saline and the soils are waterlogged. ". . . only very few groups of higher plants can withstand such conditions. Most terrestrial species are unable to tolerate even one-tenth of the salt concentration of ocean water . . ." (5).

Kreutzer, after evaluating the prospects of producing irrigation water by desalination using nuclear energy, recommends breeding salt-tolerant plants (9). Kim (10), in Korea, recommends the use of halophytes abundant in tidal lands. The Salinity Laboratory of the U. S. Department of Agriculture has long studied inland salinity problems (8). A similar organization with several substations exists in India. There is thus a widespread recognition of this problem. However, as will be made clear below, almost all of the attention is being directed to inland soils and conventional crops.

It is our hope to use Sea Grant funds to explore this problem in a preliminary way in the context of plants native to tidal wetlands and

other coastal areas. Particularly if it is the consensus of this Conference that the problem merits more substantial investigation, a serious effort will be made to find additional funds. Obviously our findings could be significant for contiguous areas to which sea water or saline water from tidal streams could be applied and may have more widespread applicability as well. That this may be so could be expected from the fact that several genera, and even species, of plants are widespread in tidal areas throughout the temperate zones of the world and in inland saline areas as well (5,7,119,130,138,156,157) and by and large the same salts are involved (5,8), except that in inland areas the relative proportions are frequently different. They may be more alkaline and may contain toxic levels of some salts, especially borates. Moreover, our results should have applicability also to the establishment of plants upon dredge spoils, particularly since we expect to use a recent dredge spoil as a nursery area.

A search of current literature reveals that work is being done on halophytes and various aspects of crop and soil management in saline areas, but we find nothing dealing with a search for new halophytic food crops. A brief review of some relevant literature follows:

The biology and ecology of coastal vegetation and halophytes has been the subject of various reviews (5,7,11-15). Even so Waisel in 1972 writes (5):

Despite the fact that halophytes have attracted scientists for so many years, our knowledge of their biology is extremely limited.

In most cases we are ignorant of the metabolic adaptations and direct physiological processes which enable plants to survive under saline conditions. It is well agreed that sodium chloride is the dominant factor in 'halophytism', yet the mechanisms of uptake of such ions, as well as germination, growth, and flowering of plants under saline conditions are relatively unknown.

Research on biology of halophytism is continuing (16,17,18,19,20).

Populations show adaptability to both marine and inland habitats within a single grass species (19,157). Several years ago serious attention to the problems of saline soils was initiated at the U. S. Salinity Laboratory (8,21,12). Similar research is continuing in various parts of the world (23,24,25). The Salinity Laboratory classified a number of crops with regard to their salt tolerance (8). Their criterion for "high salt tolerance" corresponded to a concentration of NaCl about 1/3 that of ocean water. There is a great deal of testing of various crops for their tolerance of saline habitats in many parts of the world (25-51,117,118,147). Crops getting most attention are rice, sorghum, and barley, though other cereals such as wheat and corn are being tested also. Cotton and tomatoes are getting some attention. Some legumes are included as well, e.g., mung bean and Chinese milk vetch (Astragalus sinensis). Other less common crops include bajra (Pennisetum typhoideum), Rhodes grass (Chloris gayana), and safflower. Such research is being done in Australia, Egypt, India, Israel, Italy, Korea, Kuwait, Pakistan, Philippines, Rumania, Russia, Spain, Taiwan, Tunisia, in addition to the U.S.A. Obviously the concern is worldwide and the crops getting most attention are cereals. Inland areas seem to be getting the greatest attention, though some mention is made of reclaimed tidal lands which have been leached to reduce salt content. The

salinities reported are nearly all somewhat less than marine levels encountered along our coasts and many of them are very much less.

One further comment about the crops being tested seems pertinent. They are all varieties of upland, or in the case of rice, fresh-water-wetland crops. A germ-plasm pool which has evolved under marine- or tidal-wetland salinity levels is not included. Nonetheless, some varieties of some of these crops, e.g. barley, may merit further consideration because they exhibit some adaptability to rather high salinities.

A great deal of work is being done on managing saline soils and irrigation water (24,27,35,36,37,40,48-84,123-125,127,128,132,133). Successful irrigation of barley on light soils with water from the Baltic Sea was reported by Nitsch (74). The soluble salts accumulated during the growing season were leached out by heavy precipitation during the subsequent autumn and winter. Boyko and others (40,149) reported nearly a decade ago the results of using sea water for irrigating various plants. More recently Mudie (153) has conducted similar experiments with beets.

Some attention is being given to finding new specialty crops for saline habitats at the National Botanic Gardens, Lucknow, India (150, 151,154) and in Egypt (155). Particular attention in these selections is being paid to the oil content, including essential oils, and to fibers. Apparently little or no attention has been or is being given to new food plants adapted to saline water sources.

Clearly the question, "Can man expand his horizons for food crops from essentially fresh-water, upland habitats to include new plants adapted to saline waters and soils?" is not being answered. Perhaps there exist reasonable candidate plants in tidal wetlands.

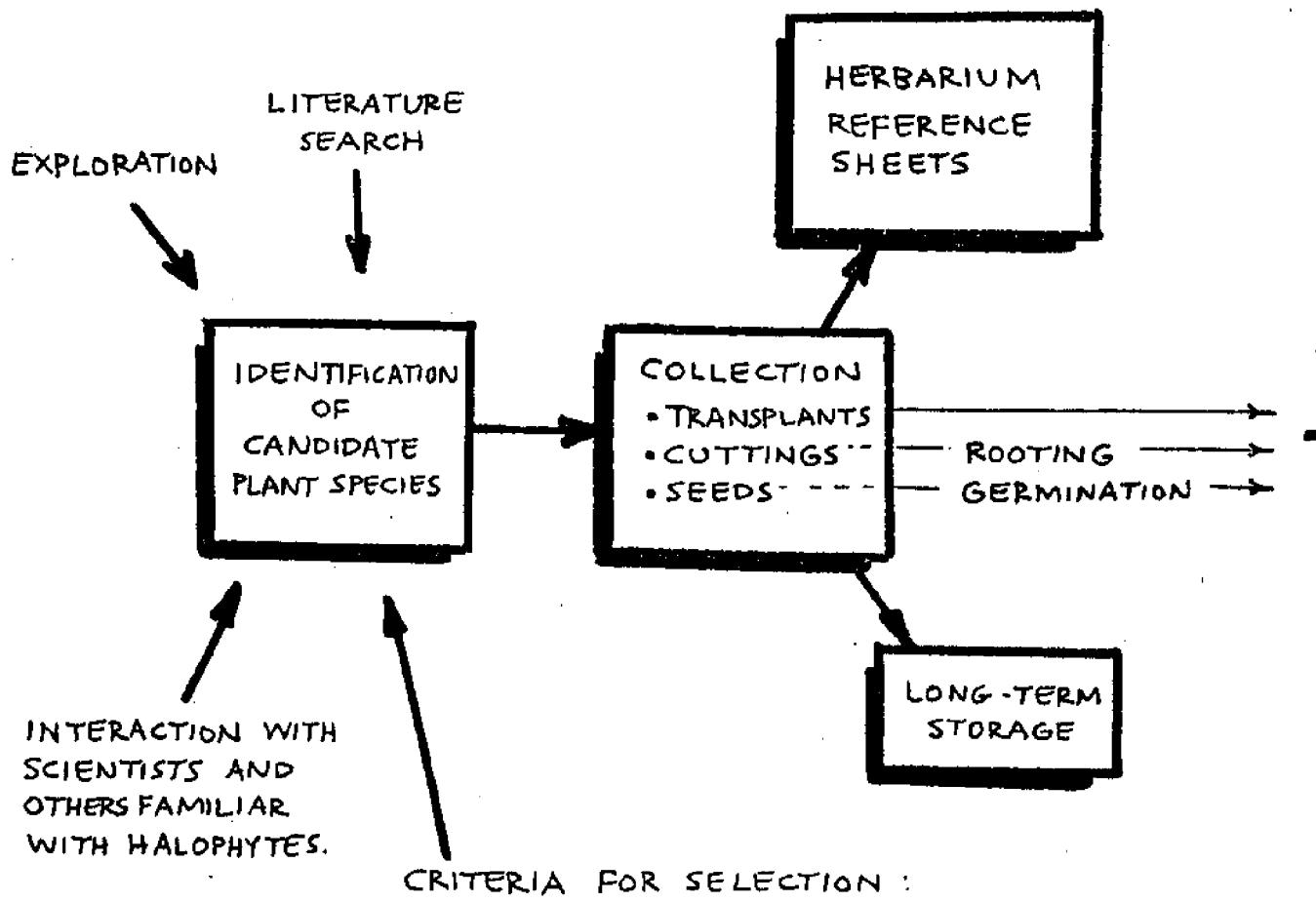
Reclaimed tidal lands have been used since ancient times in western Europe. Reclamation is continuing (77). But can they be used directly, without reclamation? The list of plants which might be tested is long. Some are suggested in the Appendix.

There are various reports, some recent, of ecology, germination, transplanting, etc. of tidal wetland plants (7,105-115). The recent success of Seneca and his colleagues (105,106,107,158) and of Garbisch (Environmental Concern, Inc.) in this regard is striking. These observations will be useful to us. But even with this, and discounting for the moment problems of technological acceptance, the breeding of new varieties is a tedious process requiring skill, patience and time. That this is true is made clear, for example, by Dewey and Albrechtson in their account of breeding new varieties of cereals (116).

Suggested approaches to solution of the problem

In Fig. 1 is displayed a flow diagram of the major steps which are anticipated in arriving at the ultimate objective: To find, or to develop, a plant, or plants (exclusive of forage) tolerant to salinities characteristic of marine coastal waters and which can be used for food sources, including protein sources, for man and domesticated animals. Some initial, immediate approaches are:

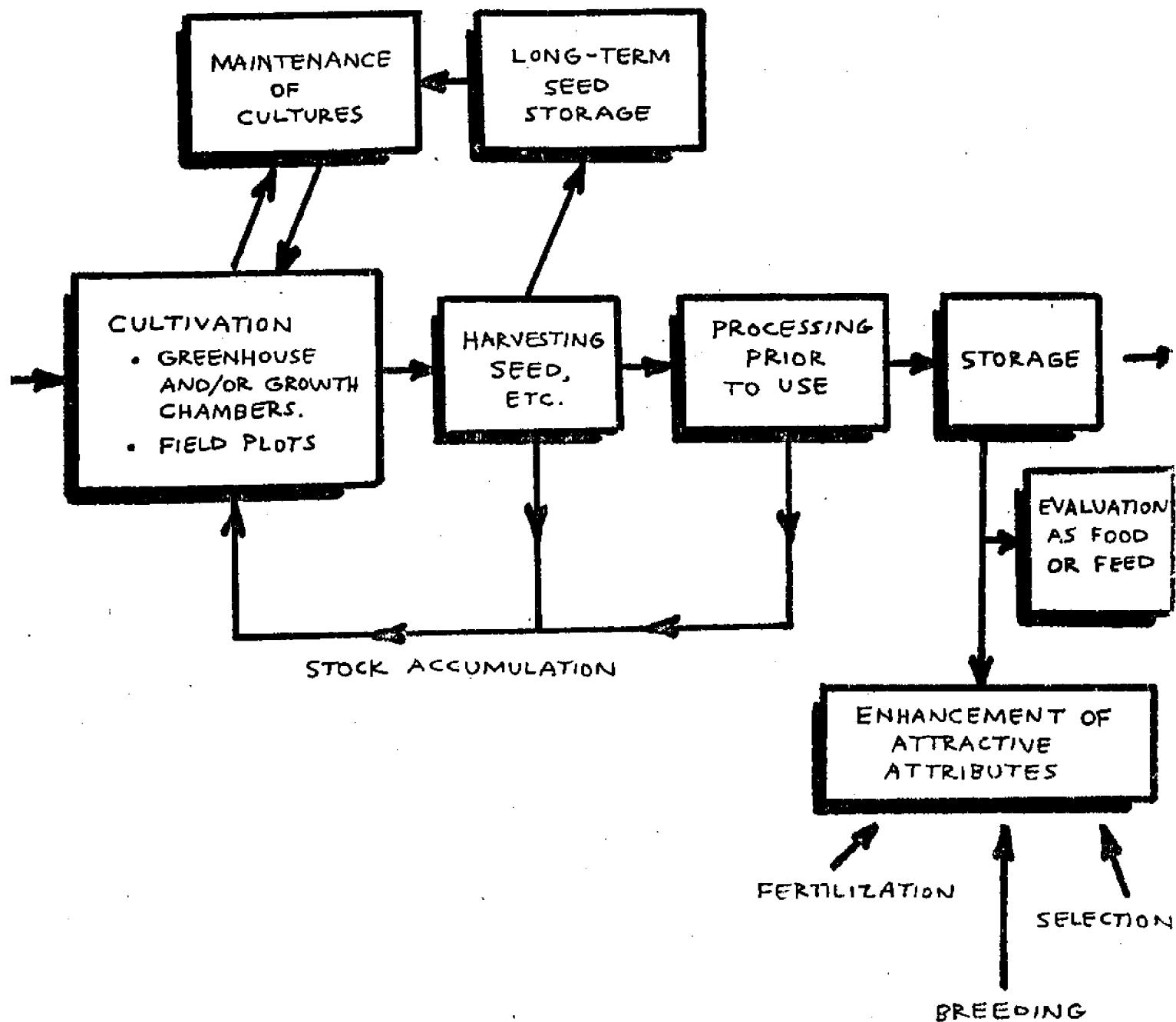
Fig. 1. Suggested steps in developing food plants
adapted to saline water



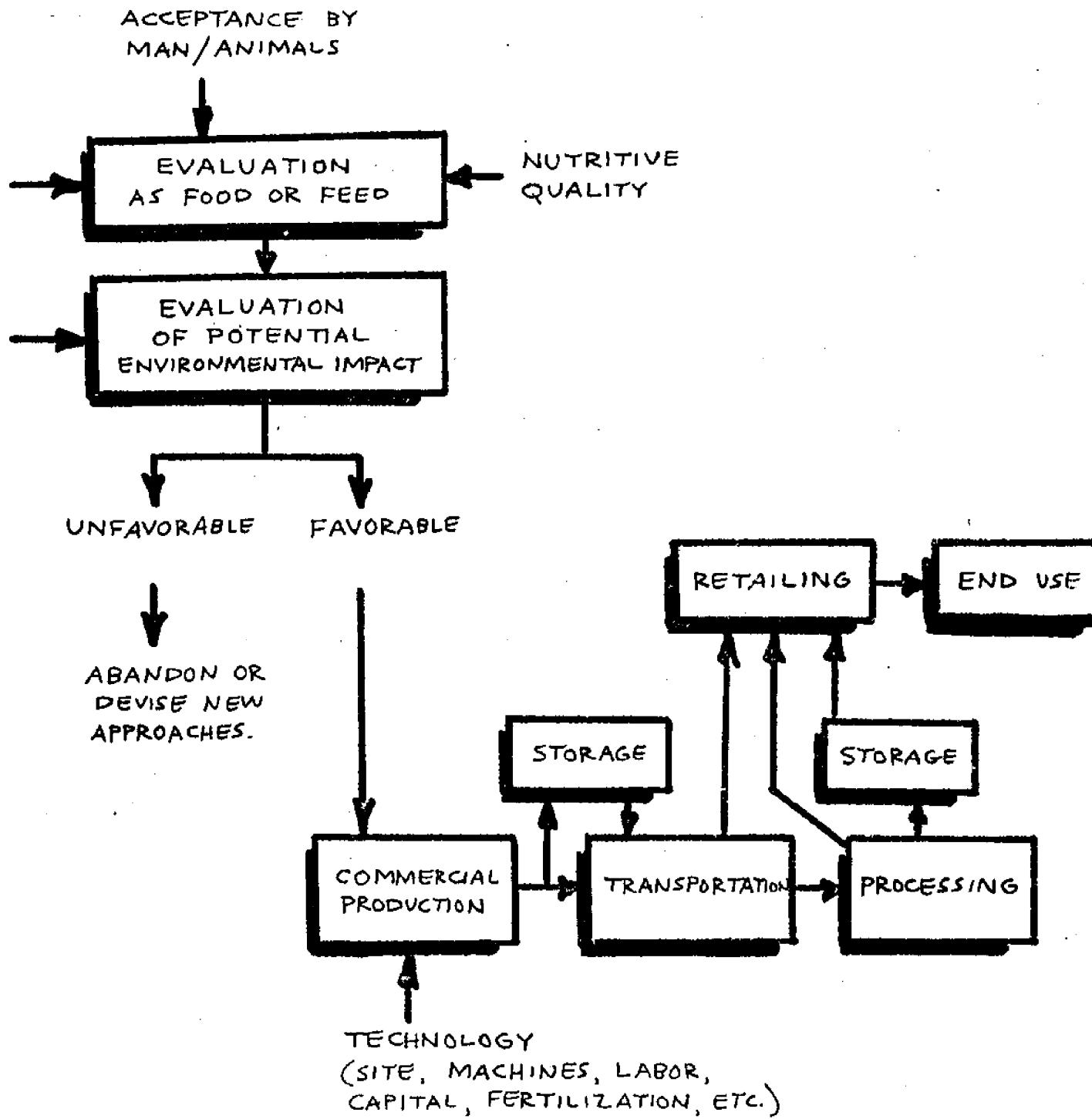
CRITERIA FOR SELECTION :

1. GROWS IN SALINE HABITATS NATURALLY.
2. PRODUCES ABUNDANT SEEDS.
3. PRODUCES LARGE SEEDS.
4. POTENTIAL FOOD ATTRIBUTES :
 - TASTE
 - EDIBLE (STURTEVANT, 98, ETC.)
 - SIMILARITY TO EXISTING FOODS.
5. POTENTIAL FOR ADAPTING TO AGRICULTURAL PRODUCTION :
 - SUSCEPTIBILITY TO DISEASES, INSECTS.
 - WEED CONTROL.
 - RESPONSE TO FERTILIZERS.
 - GENETICS
 - ADAPTABILITY TO EXISTING PLANTING, CULTIVATING, HARVESTING PROCESSES.
 - OTHER.

STRATEGIES FOR MARANHA PROJECT



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1. Identify species and/or varieties of plants which show promise of being adaptable to the long-range objective.
2. Establish cultures and/or seed sources of these plants using a nursery area irrigated with saline coastal water.
3. Obtain or produce significant quantities of promising plants for a preliminary evaluation of their suitability as potential food sources.
4. Initiate a breeding and selection program to enhance desirable attributes of promising plants using greenhouse or other facilities to accelerate life cycles.

It is expected that a number of plants could be considered as potential candidates in a program such as this. We would propose to concentrate first of all on species which are found growing in tidal wetlands and marine shore areas of temperate zones. Unless a plant shows substantial promise it will be abandoned in subsequent years. Our proposal is to focus as rapidly as possible upon a very limited number of most promising species, but additional candidates will be examined as they are discovered if they appear likely to be as promising as those under test.

More Specific Approaches Proposed as Suitable for Delaware

Crucial to the successful completion of the overall objectives of this program are two considerations: 1) That the candidate plants will be found growing naturally in saline water or in soils which are saline

and/or which are supplied with saline water. 2) Food preferences are so strongly enculturated that to select a crop which produced a totally unfamiliar food would greatly depreciate the chances of ultimate success (120).

Tide marshes of Eastern U.S.A. present a number of attributes that are immediately attractive for this program: 1) They are regularly supplied with abundant water from an essentially inexhaustible source, the ocean. 2) They regularly support pure or nearly pure stands of seed plants which thrive in this habitat. Moreover, they produce substantial yields (4,140), exceeding in this respect cultivated areas which routinely require a great deal of attention and substantial input of fertilizer, etc. A pure stand of Cord Grass, Spartina alterniflora, is reminiscent of a rice paddy, both in the water-saturated substrate and the pure stand of a vigorous grass. This, and other considerations, prompt one to ask: Could Spartina alterniflora be selected and managed to produce a reasonable yield of food? Would the seeds be suitable either as food for man or feed for animals? Observations by Woodhouse et al. (107) and Daiber (personal communication) indicate that seed production might be influenced by cultural conditions or strain differences. Another marsh plant which deserves consideration is Salt Grass, Distichlis spicata. If either of these should prove suitable, their culture probably would result in a minimal disturbance of the tide marsh contribution to the estuarine ecosystem. Moreover, they are perennials and probably could be established in pure stands more readily than plants which do not now play such a dominant role in

marsh communities. However, the seeds appear to be rather small. Possibly selection and genetic manipulation (e.g. tetraploidy) could overcome this handicap. Possibly other parts of the plant could yield food. The rhizomes of S. alterniflora are eaten avidly by geese (Garbisch, personal communication).

Eelgrass (Zostera marina L.) grows in shallow coastal waters. This plant has been used as a food source by the Seri Indians in the Gulf of California for years (142) and should be considered in our program. Other wetlands plants in local flora or from elsewhere which merit consideration are given in the Appendix. Plants which grow in shore areas should be considered also, though some of these, even if growing on coastal dunes, probably are less salt tolerant than tide marsh plants and probably will not tolerate flooding. Nevertheless, possible candidate plants include Beach Plum (Prunus maritima), Beach Pea (Lathyrus maritimus -- is there danger of lathyrism in this case?). Seeds of Marsh Elder "(Iva annua)" were used for food by American Indians in pre-Columbian times (104). Consideration must be given of course to edibility (98,99).

Criteria to be used in selecting candidate plants include:

1. Vigor of growth in saline habitats.
2. Yield of fruit or other edible portion.
3. General characteristics of edible portion, e.g. dry or fleshy, size, etc. In the case of seeds, large ones are preferable. (Many plants which grow in wetlands produce large numbers of seeds, but they are so small that they are probably unsuited for the purposes of this program.)

4. Quality of fruit or other edible portion.

- If it were large enough would it have commercial potential?
- Nutritional quality
- Palatability
- Similarity to existing foods

5. Potential for adapting to commercial production

- susceptibility to diseases and pests
- weed control
- response to fertilizers
- genetics
- adaptability to current planting, cultivating and harvesting machinery

In a large measure these criteria would be applied sequentially.

Obviously there would be no point in selecting a plant which did not grow vigorously in a saline habitat. However, it must be recognized that various saline habitats differ in many respects (see Waisel, 5, for a summary). For this project the crucial habitat should be tidal wetlands or coastal areas to which seawater (or brackish water) can be applied. Some of these criteria could be applied in the field after the initial selections have been made; others could be applied to plants in cultivation.

In most cases it probably would be necessary to make detailed studies of the life cycle for those plants which appear most promising. We will need to know, for example, suitable conditions for storage of

seeds, best means of germination, growth requirements, flowering habit and fruiting characteristics (i.e., does it shatter badly, etc.).

Culture studies would need to be undertaken. Some items to be considered here include site preparation and site management, (i.e., water control, salinity control, planting, weed, disease and pesticide control, harvesting technology).

It is proposed that the first step of course would be to identify candidate plants from a number of species. Enough material must be assembled to provide a broad spectrum of germ plasm. No doubt this would prove to be a more or less continuing process. At the outset two approaches could be used: (1) Collection of material, especially seeds, but possibly cuttings and/or transplants from the coastal flora of Eastern U.S.A., (2) Purchase and/or contribution of seeds from other regions through contacts with scientists or commercial seed sources. Special collecting trips to other regions might be advisable in the future. A recent publication edited by McKell, Blaisdell and Goodin (152) will be helpful in identifying inland plants adapted to saline habitats.

Seed from plants other than grasses should be sought, though the latter would appear more likely to yield success because they commonly dominate tidal wetlands. However, because of world need for high protein food sources, attention should be given to other families as well, e.g. legumes, chenopods and composites.

It is noteworthy that species of Atriplex (Chenopodiaceae) exhibit the so-called "Kranz" leaf anatomy (see 5) characteristic of those plants which use the 4-C acid shunt in photosynthesis (145). These plants use sunlight more efficiently in photosynthesis than plants without this attribute. The high photosynthetic efficiency of Spartina alterniflora (140) and our own observations of its leaf anatomy suggests that this plant likewise uses the 4-C acid pathway. This may be one reason why the tide marshes are so productive. With this in mind it might be useful to examine the leaf anatomy of other candidate plants. Other things being equal, those with this type of leaf anatomy would probably be more likely to produce high-yielding food crops.

Whatever plants are chosen, the seed will need to be given appropriate after-ripening treatments, in some cases in cold sea water, in others merely moist and cold, prior to germination. For some of the plants likely to be used, after-ripening techniques are given in available literature (102,107,121). Early germination would be attempted in growth rooms and/or greenhouses to provide seedlings for field planting. Other seed lots could be planted directly in the field. A combination of growing room (day-length controlled) and field production should make possible two seed crops per year of some species.

The usual approaches of inbreeding, cross-breeding and selection would be used to enhance desirable traits--selection first; breeding for genetic manipulation later. Proximate analyses would be used initially to estimate for food value.

Facilities

During the current year a 25-acre dredge spoil enclosed in a dike is being built at the Lewes facility of the College of Marine Studies. It will have to be graded appropriately and test plots laid out. We anticipate a range of soil characteristics from rather sandy ones, easily drained, to those made up largely of fine inorganic and organic materials. Water probably will percolate through the latter rather slowly. Hence, a variety of test sites will be available to test the adaptability of candidate plants to different substrate conditions.

An irrigation system will have to be designed and installed using water from the nearby tidal canal or stream. Recent publications (128, 132,133) suggest that flooding, drip or trickle irrigation techniques are better than spraying. We expect this facility to be available for the 1975 growing season.

Growing rooms, growth chambers and greenhouses are available on the Newark campus. Limited space, enough for a start, will be available in these. Laboratories and equipment for proximate analyses for food value are available.

Evaluation strategy

If we receive requisite financial support we are proposing to embark upon a project which will require a long time to achieve success (unless we find a commercial crop which is already adapted to our purposes). As an initial effort we propose a minimum of five years with

annual review by University-related personnel as well as major evaluations from outside the University as follows:

1. After two growing seasons, i.e. during the 3rd project year, the progress will be evaluated and continued support will be sought only if there is clear evidence that substantial progress is being made.
2. After four growing seasons, i.e. during the 5th project year, a more searching evaluation will be made. If at this point the prospects are not bright, this year will be a terminal year devoted to closing out the project and publishing the progress to date. If the prospects are bright continuation will be sought in terms of the most promising leads which have been developed.

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Appendix

The following are some plants which appear to merit consideration as candidate plants in a program such as this. They are divided into two categories:

- A. Plants being used now or formerly as food.
- B. Plants from local flora and/or elsewhere which appear to have promise for one reason or another.

(These lists were compiled largely from references 5,7,8,90, 91,103,119,130,138,142, but are drawn also from personal experience.)

A. Plants used as food, now or formerly.

Wild rice, Zizania aquatica, L.

Used for centuries by the Indians of north central U.S.A. Now being cultivated in Minnesota (100,102,121,122). A plant of fresh-water wetlands which ranges into brackish water of Eastern U.S.A. coasts.

Bulrush millet, Pennisetum typhoideum Rich. (Also called cattail, spiked or pearl millet and bajra.)

Essentially an African savannah staple. It may be associated with brackish water in Tanzania. An important food crop in India and Pakistan (98,146).

Barley, Hordeum vulgare L.

Some varieties rather salt tolerant (144). Among the most salt-tolerant crop plants tested by the U.S. Salinity Laboratory (8). Not clear whether or not it will tolerate water-saturated soils.

Appendix 2

Eelgrass, *Zostera marina* L.

Grows in shallow water of coastal waters. Used as a food by Seri Indians of Gulf of California (142).

Marsh elder, "Iva annua"

Seeds used by American Indians for food in pre-Columbian times (104). [There is some uncertainty about the name of this plant. According to Cronquist (personal communication) ". . . it is doubtful at best that it applies to anything in North America." It may be *Iva ciliata*, var. *macrocarpa* (148).]

Atriplex sp. (92-97, 131, 134, 137)

Farmed on a large scale in Tunisia (134).

Rice, *Oryza sativa* L.

Short-season, salt-tolerant varieties may be worth testing.

B. Plants from local flora and/or elsewhere which appear to have promise for one reason or another.

Grasses:

Seaside Arrowgrass, Triglochin maritima L.

Southern Arrowgrass, Triglochin striata R. & P.

Giant Cutgrass, Zizaniopsis miliacea (Miebx.) Doll & Aschers

Giant Setaria, Setaria magna Griseb.

Cord Grass, Spartina alterniflora Loisel.

Big Cord Grass, Spartina cynosuroides (L.) Roth

Salt Grass, Distichlis spicata (L.) Greene

Sea Oats, Uniola paniculata L.

Water millet, Echinochloa Walteri (Pursh) Nash.

Aeluropus litoralis

Hordeum marinum

Other than grasses:

Water Hemp, Acnida cannabina L.

Nodding Beggar Ticks, Bidens cernua L.

Beach Plum, Prunus maritima

Beach Pea, Lathyrus maritimus. Is there danger of lathyrism
in this case?

Aster tripolium

Orache and related plants, Atriplex spp.

INVITED PAPERS

WILD RICE DOMESTICATION AS A MODEL

Ervin A. Oelke¹Distribution of Wild Rice

The genus Zizania occurs extensively in nature in eastern North America, reaching from the northern end of Lake Winnipeg eastward along the northern shores of the Great Lakes and the St. Lawrence River. It occurs south from Lake Winnipeg to central Dakotas, western Nebraska and eastern Texas to the Atlantic Ocean, and along the coast as far south as central Florida. The best stands of wild rice are found along the margins of the tide water rivers of the middle Atlantic states, above the saline zone, and in shallow lakes, ponds, and sluggish streams in northern Minnesota, Wisconsin and southern areas of Ontario and Manitoba.

The genus was established in 1754 by Linnaeus, but the name was used in 1743 by Gronovius for a plant collected in Virginia by John Clayton. Confusion exists as to the number of species within the genus. Fassett in 1924 in his revision of the genus in North America considered all wild rice to be Zizania aquatica L. with three varieties under it. Later Silveus and Hitchcock both recognized a second species in North America Z. texana from south-central Texas which is a perennial, but today this species is found in Asia and was named Z. latifolia by Turezaninow in 1838. Dore in his review of the literature on the species in 1969 came to the conclusion that there are four species in the genus Zizania: Z. aquatica, Z. palustris, Z. texana and Z. latifolia. He questions the validity of Z. texana. According to

¹University of Minnesota

Dore the wild rice which grows in Minnesota would be classified as Z. palustris var. palustris or var. interior, but he indicates that in most modern works these are given under the combination Z. aquatica var. angustifolia.

Historical Use by Indians

The Indian name for wild rice is "Manomin" meaning "good berry." When white men came they called it by many names. Some were Indian rice, Canadian rice, squaw rice, black rice, Indian oats, blackbird oats, wild oats, water oats and marsh oats. However, the name which has survived over the centuries is wild rice and is used in commercial trade today. Some writers prefer to use one word "wildrice" to distinguish it from the wild types of Oryza sativa L.

The date which wild rice was first used for food is not known, but believed to have been 10,000 years ago when aboriginal man moved eastward into central North America. It is known that wild rice has been used for food by Indians of the Upper Great Lakes region for centuries, particularly by the Chippewa and Menomini tribes. The Chippewa and Sioux tribes had many battles over wild rice beds. The most important harvest of the year was wild rice for the Indians of the Upper Great Lakes Region. Early explorers reported that Indians would push their birch bark canoes into the wild rice stand while the grain was in the milk stage. They would bend a group of stalks together and wrap the heads with bark strips. After the grain had fully matured, it would then be harvested. Tying the heads together would reduce loss to birds,

rain and wind. This method was abandoned about 1800 and now natural stands are harvested by the canoe and flail method. One person pushes the canoe through the stand with a pole, while the other uses two small sticks to bend the stalks over the canoe and tap the panicles so the ripe grains fall into the canoe.

After the grain was gathered it was cured generally by laying the grain out on mats in the sun for several days or it was dried by laying the grain onto racks beneath which fires were built. Later large kettles were filled partially with grain and placed over a slow fire. The grain was constantly stirred with a paddle until completely dried or parched. The hulls were removed by digging a hole in the ground and lining it with skin. Parched grain was placed into the skin and Indians wearing mocassins would tread out the grain. After the hulls were removed from the grain, the chaff was removed by winnowing. The finished grain was stored in bags made of skins or cedar bark, or in birch bark boxes.

Large quantities of wild rice were gathered, parched and stored for use the year around. It was the principal vegetative food of the Indians who lived in an area where agriculture was difficult. In years when the wild rice crop failed, woodland Indians were hard pressed to survive the long winters.

Harvest and Processing of Grain from Natural Stands in Minnesota Today

In 1939 the state of Minnesota passed a law which regulated the harvest of Minnesota's 30,000 plus acres of natural stands which are not in Indian reservations. Indians have control of the wild rice in

their waters while the Department of Natural Resources regulates harvesting of other natural stands. Licenses are required by individuals to harvest and process wild rice. Because of the uneven ripening and shatter losses, natural stands are allowed to be harvested only for a 2 hour period every other day during the ripening period. Since 1939 when production records were kept, the amount of nonprocessed grain harvested from natural stands ranged from a low of 20,000 lbs. to a high of 3,216,000 lbs. Most of this is harvested by non-Indians. Harvest per canoe for a 2 hour period will range from 50 to 200 lbs. Much of the grain is sold to buyers at the lakeside who represent processors. Basically the grain is still processed in the same manner which the Indians used many years ago except for a 10 to 14 day wet curing (fermentation) before parching to obtain a more uniform product. Also, modern equipment such as gas heated parchers, Japanese rice hullers to remove the hulls, gravity tables and grading machines are used in the processing operation. Most of the grain harvested by Indians from their own reservations is sold to processors and processed in the same manner as the grain from other natural stands.

Commercial Production

Perhaps the first individuals to attempt to commercially produce wild rice were the Indians. Often suitable lakes or rivers were seeded to wild rice by mixing seed into clay, rolling it into a ball and dropping the clay ball into the water. In most cases this was successful.

Businessmen and botanists have thought about cultivating this plant for more than 100 years. Early European explorers collected seed for planting in Europe but these failed probably because the seed was not handled properly to remain viable. In 1828 Timothy Flint in "Geography and History" wondered why so little attention has been paid to wild rice. In 1852 Joseph Bowron suggested wild rice be seeded for agricultural purposes. In 1853 Oliver Kelly, founder of the National Grange, made the same proposal. Mechanical harvesting of private lands in Canada started in 1917 by H. B. Williams and Z. Durand.

In Minnesota growing wild rice in fields specially designed to grow wild rice was not begun until 1959 by the Chun King Corporation near Duluth. They collected seed from a natural stand and planted a 25 acre field which had dikes around it so the field could be flooded. The first two years they obtained good yields but the third year the field was completely destroyed by disease which turned out to be leaf blight (Helminthosporium sp.). This discouraged their efforts and the project was abandoned. In 1962 Al Johnson of the Johnson Construction Company in Minneapolis started growing wild rice in northern Minnesota and in 1964 Walter Heineman also started growing some. Both of these individuals used seed that was collected from natural stands. Then in 1965 Uncle Ben, Inc. from Houston, Texas started contracting acreage and this was the real beginning of the commercial production of wild rice. Success in these early years was due primarily because new acreage was continually being brought into production. In many cases there were

severe losses in 3 and 4 year old fields because of leaf blight. These early fields were planted with seed collected from various lakes thus the plants had the same characteristics as those growing in natural stands. Not all of the seed matured at the same time and when mature, they fell from the plant. These characteristics necessitated the development of harvest machines which did not cut off the plants but removed only the mature kernels from the panicle. Also, tracks had to be used instead of tires because of the wet field conditions. With this type of harvester 150 to 200 lbs/A of unprocessed grain could be collected. The potential yield, however, was at least 3 to 4 times this amount.

In 1963 an important discovery was made by Dr. Paul Yagya and Mr. Erwin Brooks who were with the Department of Agronomy and Plant Genetics of the University of Minnesota. They found a few plants in Mr. Johnson's field which retained their male flowers longer than the rest. In natural stands the male flowers fall from the plants almost immediately after the anthers shed their pollen. Dr. Yagya and Mr. Brooks deducted that perhaps the grains will also stay on longer after maturity. The seeds from these plants were collected and planted the following year. The plants indeed did not shatter their seeds as readily as those in the field from which they came. Later other plants were found with this characteristic. Dr. Yagya and Mr. Brooks left the University during 1965 and no one continued their work because funds were lacking, but Mr. Johnson increased the seed and in 1968 he had 20 acres. This discovery gave new impetus to the commercial growing

of wild rice. With this new selection yields of 1,000 lbs/A of un-processed grain could be harvested with regular rice combines used in rice production in California. As a result of this new selection and research now being done by the University, cultivated acreage increased from a few hundred acres in 1968 to 18,000 acres today.

Research Past and Present

In Minnesota from 1940 to 1960 several research proposals were made and a few funded to study the growth habit of wild rice and how to improve the harvest from natural stands. Some of the research was done by the State Department of Natural Resources and some by the Botany Department, University of Minnesota. It wasn't until 1963 that a small grant was made available to the Minnesota Agricultural Experiment Station by the Bureau of Indian Affairs. The purpose was to make a survey of the current and potential wild rice production, processing and marketing on several Indian Reservations in Minnesota and Wisconsin. This work was undertaken by Mr. Erwin Brooks, then a Graduate Research Assistant in the Department of Agronomy and Plant Genetics. During this time Mr. Brooks and Dr. Yagya developed an interest in wild rice and worked with the few individuals interested in commercially growing wild rice, particularly Mr. Al Johnson. It was during this time that they found the more shatter resistant plants in Mr. Johnson's fields in northern Minnesota. Both Mr. Brooks and Dr. Yagya left the University in early 1965 and due to lack of funds their work in the breeding area was discontinued. However, in late 1965 a small amount of money for one

graduate student was made available by the Experiment Station to study seed dormancy in wild rice. This work was done under the direction of Dr. Brun and completed in 1969. Mr. Brooks, when he left the University, was instrumental in organizing the Manomin Development Company in 1965 for the purpose of developing varieties of improved wild rice. They obtained a grant of \$185,000 for a 2-year period from the Economic Development Administration for support. Presently the company is still functioning, but only in producing wild rice for processing. The breeding program was dropped because of cost and slow progress, however they are using a variety developed by their breeding program.

The commercial growing of wild rice was beginning to expand and the Minnesota Agricultural Experiment Station could anticipate some serious problems. They requested the 1967 State Legislature to appropriate funds to develop disease and shatter resistant varieties. Also, some attention would be given to insects and cultural studies. These funds were not made available. Finally in 1971 through the efforts of the Wild Rice Growers Association the State Legislature appropriated funds to the Agricultural Experiment Station for breeding, cultural, disease and entomology research on wild rice. In 1971 there were about 10,000 acres of wild rice being grown commercially and the problems which were anticipated developed. The most serious of these was the complete destruction of some fields by leaf blight. In 1973 additional funds were made available for soil fertility and engineering research.

The primary objective of the plant breeding project is to develop disease and shatter resistant and earlier maturing varieties. The objectives of the culture and physiology project are to determine the best cultural conditions to obtain optimum yields with existing and new varieties and to investigate the physiological and morphological development of the wild rice plant. The disease project objectives are to identify the diseases and their incidence on wild rice and to study all aspects of their etiology and epidemiology, to study control measures and to cooperate with the plant breeders to develop disease-resistant varieties. The objectives of the entomology project are to study the biology of the wild rice worm and study methods of control, and to make a collection of all species of insects observed on wild rice and determine their economic importance. The soils project has the objective to determine the fertility requirements of wild rice for optimum yields. The objectives of the engineering project are to design and construct equipment for thinning wild rice fields, and to work with growers for timeliness of harvest and proper combine adjustments for minimum losses. All projects have an overriding objective which is to get results as quickly as possible for the growers so commercial production of wild rice can survive. The above projects involve 3 full time and 5 part time professional people plus 3 full time technicians.

Research on processing was initiated by the University of Wisconsin in 1970 through a grant from the Upper Great Lakes Regional Commission. This work is now continuing with funds from the USDA. Processing research is necessary to obtain a more uniform and better quality product than is presently obtained from the old system of processing.

Conclusion

Commercial production is well on its way in Minnesota, but there are still many problems to be solved. Considerable economic losses have occurred in the growing of wild rice because research in breeding and production was not started soon enough. Ideally, extensive research should have started 10 years ago before millions of dollars were invested in commercial growing of wild rice.

I believe that when a plant(s) is found in your search for angiospermous food plants which could be grown using water approaching or equal to salinity of the oceans, research on production and marketing should be started early in the program. Hopefully the production problems could be solved before large investments are made in attempts to grow the new crop.

The possibility of growing wild rice in the tidal wetlands is open to question. However, there are reports that wild rice has been found in the Connecticut and Delaware River where the salinity was about 1/5 or less of average sea water - where chlorine content was equivalent to about 7100 ppm of NaCl. It may be possible by collecting a considerable amount of germplasm from slightly brackish areas to select plants which will tolerate sea water salinity.

Discussion following Dr. Oelke's paper

(NJ) - To break dormancy is protracted storage in the cold necessary? Would cold shock do it?

(EAO) - We have tried alternating temperatures and it does shorten the dormancy time. Normally the seed is stored for 2-1/2 months at 35° F to break dormancy, but by alternating temperatures, cold (35° F) and hot (100° F for 8 hr), we can shorten this to 7 weeks. We also tried many chemicals. We've tried sulfuric acid, ethanol, etc. to extract any germination inhibitors. Getting rid of any inhibitors, plus giving the seed a cold treatment may be necessary to completely break dormancy. Even the seedlings that were derived from scraped seeds didn't seem to have as much vigor as those derived from seeds which had been stored at 35° F to break dormancy. It appears as though the seed requires some sort of a cold treatment for the seedlings to really have the vigor of those plants which come from seeds that have been stored in the cold.

(OPB) - At the present time, what is the approximate value of the crop per year in Minnesota?

(EAO) - We had about 1,000,000 pounds of unprocessed grain that came from natural stands last year and from commercial stands approximately 3,500,000 pounds.

(OPB) - How many producers were there?

(EAO) - There are approximately 85 to 90 units. Some of these units have several individuals involved. The price, presently is about \$1.75 for a pound of finished grain. Unprocessed grain will finish out approximately 30 to 45%. It varies depending upon the maturity of the grain at harvest and the amount of extraneous material in the grain.

(GFS) - The figures for yield were in terms of the green product?

(EAO) - Yield was in terms of the green or unprocessed grain, yes.

(OPB) - What is the cost of your research program at the moment?

(EAO) - Annually, we presently have \$105,000 from the state, and about \$15,000 from USDA.

(WJB) - Will you share with us the reason why rice research went down and back up in your state?

(EAO) - I suppose the major reason is because of the natural stands which are harvested by Indians and other people. There were people who were opposed to cultivating wild rice which they felt would ruin the price of wild rice. Other groups objected because of the Indians. Limited funding, at first, was made available by the Experiment Station at the request of some growers. It was not until there was a sizable acreage in the state and some on Indian reservations, that there were enough proponents of commercial production to have an influence on legislative appropriations. They worked through the legislature and money was appropriated specifically for wild rice research.

(WJB) - Through the Experiment Station?

(EAO) - Yes. The Experiment Station had asked for some money before we obtained funds. However, money was not appropriated until the industry persuaded some legislatures that money was needed for wild rice research.

(SN) - Do you know if there is any foliar uptake of nutrients by wild rice?

(EAO) - We did apply some foliar applications of iron.

(GFS) - Chelated?

(EAO) - Chelated. Some seemed to have been taken up some. Etiolated plants responded to this application.

(?) - You gave the price per finished pound. What is the cost per finished pound?

(EAO) - You mean what you can buy it for?

(?) - No, what is the farmer's cost, what is the cost to him per finished pound? He is getting paid \$1.75. What is the cost of agricultural production? Or are you talking the farmer's price?

(EAO) - He has to pay about 25¢ a pound to process it, so you can subtract that. It is hard to get cost estimates from growers because it varies with cost of the land, etc. They tell me they need to have \$1.75 in order to make a profit.

(?) - Would any farmer tell you otherwise?

(EAO) - We really haven't determined exact costs. However, in 1971 we sent a questionnaire to all growers asking what it cost to develop wild rice fields. The indicated average cost was about \$250/acre for land, equipment and development. Annual operating costs were about \$30 an acre. This means if they have a good crop the first year, about 200 lb. finished grain/acre, a grower could pay for his operation in one year. However, growers right now cannot rely on stability of production from one year to another. One year you can get 12 inches of rain. One year a disease wipes them out. More than anything else I think this whole program will have to focus in on stability of production in order for growers to estimate exact production cost per lb. of finished grain.

(?) - I noticed in your density studies that in all cases that the more dense, your yields were still going up.

(EAO) - That's the first year's stand. We were only up to 2.8 plants per sq. ft. We would like to have 4 or 5. My seeding rates weren't high enough. The seed I used came from commercial growers and we were trying to determine, using their seed lot, what they would have to plant, in lbs./acre, to get the kind of stand needed the first year to give them optimum yield.

(GFS) - What about going through after harvesting and drawdown and rototill to bury a lot of these seeds deeper and cut down the second year's stand that way?

(EAO) - We've thought about this. Or even ploughing and burying them six inches to reduce the stand. Some growers have tried this and they've ended up with rows. But eventually, if you rototill enough times, over a long enough period of time, you always bring a few seeds up to the top and so you'll still end up with a pretty dense stand.

(GFS) - How long do they live in the soil?

(EAO) - We don't know, but we do know that quite a few seeds will survive at least 3 years.

(RF) - What is the ploidy, is it 2n, or are there any polyploids?

(EAO) - It behaves as a diploid. That's all we know at this time.

(?) - What about waterfowl, do they like these?

(EAO) - Yes, it's very attractive. Wild rice is, of course, used as a water fowl habitat and they like wild rice. There have been a number of studies which show that wild rice is eaten by water fowl. There also have been some studies determining what use is made by water fowl of commercial wild rice fields. The number of pairs of mallards, for example were 10 times greater than before the fields were there. Formerly the areas were kind of swampy, but really not areas where pairs of water fowl nested, etc. So once an area has some wild rice fields, it is an ideal situation for ducks. In terms of increasing duck population it really is one of the better duck producing areas of the state now. It compares favorably with the southwestern part of the state which is considered the prime duck producing area.

(?) - Is there a loss problem? I've seen enormous flocks of snow geese which would consume a substantial amount of material if they were to stay in an area.

(EA0) - Losses to water fowl don't seem to be much of a problem. They migrate out of the area by the time wild rice is harvested. Serious losses, however, are caused by blackbirds just before and during harvest. Yield losses of 50% or more have occurred in some fields. Growers spend a considerable amount of time to keep blackbirds away.

SEAGRASSES AS POTENTIAL FOOD PLANTS

Richard Felger¹
and
C. Peter McRoy²

There are about 50 species of seagrasses in the nearshore seas of the world (den Hartog 1970). No other seed plants grow fully submerged in ocean water. There are 12 species of Zostera belonging to two subgenera; the subgenus Zostera, with four species including Z. marina, occurs along most of the temperate coasts of the Northern Hemisphere.

Seagrasses are well adapted to life in the nearshore sea, in fact they are restricted to that habitat. Productivity of a dense seagrass meadow during the growing season reaches 4 to 5 g of carbon per m^2 per day with an associated standing stock of about 1 kg dry weight per m^2 (McRoy and McMillan, in press). These rates are true for seagrasses whether in the tropics or in higher latitudes. This is the total amount fixed per day, which should be mostly vegetative. That is what the seagrass meadow, regardless of species and geographical region, attains as a maximum growth and standing stock when local conditions are optimal. The upper limits of these are apparently comparable on a world-wide basis. Although similar in quantity, the quality of the standing stock can be very different through the latitudinal range of the species. The best-known illustration of this is with eelgrass, Zostera marina, which on the Pacific Coast of North America ranges from the Bering Straits to the Gulf of California. Most seagrasses, including eelgrass, produce two kinds of stems (turions), vegetative and reproductive. These two are morphologically distinct and their production apparently depends upon environmental conditions,

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primarily water temperature as shown by Setchell (1929). The relative proportion of these two types of standing stock is apparently correlated with the length of the growing season when the water temperatures are between 15 and 20° C. These early ideas of Setchell's appear to be generally true, but more recent evidence suggests that it is a combination of light and temperature that controls the composition of the standing stock.

The Gulf of California is characterized by a continental, rather than oceanic-influenced, environment. Winter sea-water temperatures seldom fall below 12° C (54° F), and from mid-June to early September the shallow waters where Zostera occurs reach 27 to 32° C (84 to 90° F; Robinson, 1973). Sunlight in this desert region is intense. Setchell (1929) found that in the temperate waters off California eelgrass ceases to grow in water below 10° C (50° F) and becomes dormant. From 10 to 15° C vegetative growth takes place, and from 15 to 20° C reproductive growth occurs. Above 20° C growth ceases and the plants become quiescent.

Zostera marina in the Gulf of California is primarily a winter-spring plant. In the fall, as the water temperatures begin to drop, say in late October to early November, I have found very rapidly growing rhizomes. These consist of white shoots that have not surfaced from the mud and long shoots which develop in a matter of days or weeks. Finally the perennial rhizomes produce further rapid growth. These will begin to grow into the characteristic vertical turions. As noted above, these turions are 100% reproductive in the Gulf of California. (Along the eastern coast of the U.S.A. one can search fairly long and not find a fruiting or reproductive turion.) Rapid growth continues through the mild winter. As early spring temperatures approach 10 to 15° C the fruit begins to develop (see Robinson, 1973 for surface sea

water temperature records in the Gulf of California). Water temperature in April rises very sharply. The insolation is intense in this desert region. Massive ripening of the fruit occurs in April. The reproductive turions, which contain the ripe or rapidly ripening fruit, break off and float ashore in large quantities, often forming extensive rafts in the drift. Enormous quantities of it accumulate as beach drift. It is at this time that the Seri Indians have traditionally harvested eelgrass "grain" (Felger and Moser, 1973).

On the Pacific coast of Baja California the water temperatures are quite temperate. The summer water temperatures are cool. On the other hand, the Gulf of California is a continentally influenced sea rather than a marine or oceanic influenced one. Seagrass populations in the Gulf of California probably are isolated biologically from contact with the main populations on the Pacific side. The real question is the extremely high seed production in the Gulf of California. Is it environmentally induced, or are there genetic differences between this and other eelgrass populations? I believe it is at least very largely environmentally influenced and this would be of major significance in attempting to cultivate it as a crop elsewhere. But one suspects some degree of genetic differences from populations isolated in the Atlantic and Pacific Oceans. This question deserves investigation.

In the Gulf of California, Zostera marina occurs in places with strong currents, and this may be an important factor. For this reason, it seems doubtful if this plant can be grown in placid water. Circulation is probably essential. Furthermore, in temperate regions Zostera often occurs where it is exposed to the air at low tide (Phillips, 1972, den Hartog, 1970). In the Gulf of California it will not tolerate exposure to the air, presumably because of the high temperatures of this desert region. In the Gulf of California Zostera

occurs from about 1 meter of depth at mean low tide to at least 10 meters of depth, and dense stands apparently occur at most of these depths. At 8 to 10 meters depth, the reproductive turions commonly reach 1 to 3 meters in length.

The reproductive turions are crucial since these produce the seeds. The Zostera seeds are produced in spathes, with 1 to 11 spathes per turion (usually about 5 to 6). The maximum is 25. The seeds are small averaging only 6.5 mg. fresh weight or 2.5 mg. dry weight (oven dried), but are numerous. The usual air-dried weight is about 3.1 mg. This is the approximate dry weight after storage for some months. A spathe may contain 4 to 11 seeds, and ones with 8 to 10 seeds are common. The number of reproductive turions varies both locally and throughout the geographical range of Zostera in the Pacific. In the lagoons of the Bering Sea, although high productivity is attained, the standing stock consists largely of vegetative turions with only 2 to 3% reproductive ones (McRoy, 1970). Farther south at Puget Sound there are about 14% reproductive turions (Phillips, 1972). The most dramatic shift of these proportions occurs in eelgrass meadows in the Gulf of California where we recently found that 100% of the standing stock consists of reproductive turions in spring. It is not surprising then that the Seri Indians learned to exploit this high seed production (Felger and Moser, 1973, in press).

In a preliminary survey we examined the Zostera meadows in the Gulf of California near one of the Seri Indian villages during April, 1974. From this we can make some quantitative estimates of seed production. These are highly preliminary. The standing stock of Zostera we sampled was not particularly high and we do not yet know the true range. It averaged 227 g dry weight per m^2 and consisted of an average of 555 reproductive turions per m^2 . This is

an average figure for a fair sample. These plants produce an average of 19,000 seeds per m^2 ; this is standing stock. In other words, it is what we found in one day. We can only speculate how much more would have been produced the following weeks or had already been produced and was gone. The seed biomass, fresh weight, is 122 g per m^2 and dry weight is about 38.5% of this. Unfortunately no other estimates of seed production in seagrasses are available in the literature, but this can at least be compared with data on commercial crops. The average yield of rice in California from 1964 to 1969 was 5200 pounds per acre, or 583 g per m^2 , as opposed to 122 g per m^2 for the Zostera. This is just 5 times our estimate for seed production from standing crop in Zostera from the Gulf of California. Since rice is a managed, highly developed crop, it is not surprising that its seed production is much higher; but what is the potential for seagrasses?

Our data for the Gulf of California are minimal and we do not know the magnitude of the natural variation in the population. We probably have data towards the low end of the natural stock. From many years of work in Izembek Lagoon, Alaska, we know that standing stocks greater than 1 kg dry weight per m^2 in turion densities of several thousands per m^2 are possible for Zostera (McRoy, 1970). The Gulf of California material was only approximately 500 turions per m^2 so there is a chance that the observed seed yield could be multiplied by a factor of 4 or 5. This suggests that higher standing stocks are most likely also to exist in the Gulf of California and that seed production would in fact be several times greater than our initial estimate. This, combined with the development of skills necessary to manage the seagrass population adequately, makes it not unreasonable to assume that seed production of Zostera could be sustained at a level comparable to that of rice.

Each grain-like fruit of Zostera marina in the Gulf of California contains a single seed about 3.0 to 3.5 mm long, weighing 1.1 to 5.6 mg. The seed contains 13.2 percent protein, 50.9 percent starch, and about 1 percent crude fat (Felger and Moser, 1973). More recent investigation indicates that there may be considerable variation in nutritional content. No artificial hybrids of seagrass have ever been made. Zostera asiatica Miki, in the northeastern Orient, has a fruit 5.0 to 6.5 mm long (den Hartog, 1970). Thus it may be possible to hybridize and select for increased grain size.

In June 1973, using coarsely ground eelgrass flour prepared by Seri Indian women, the first bread from the sea was prepared by Hazel Fontana and Mahina Drees Felger for the Environmental Research Laboratory, University of Arizona (Maggio, 1973). The bread has a good flavor when fresh, and is somewhat like rye bread. However, it dries out rather quickly because of low oil content. The flour seems best used as a substitute for whole wheat flour and blended with some white flour. The crust is golden-brown but the bread is green. The whole grain, when toasted, seems somewhat like wild rice.

The Seri Indians traditionally harvested the seed of eelgrass as one of their major foods (Felger and Moser, 1973). No other people are known to have harvested seeds of a sea plant; however, it may be that no other region than the Gulf of California contains seagrass populations which produce large quantities of seed. The concept of farming a grain-like crop in seawater is most attractive and deserves considerable research effort (Felger, in press). However, there are serious obstacles and great caution must be taken to avoid adverse environmental effects.

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Discussion following Dr. Felger's paper

(NJ) - What did you use as a leavening agent for a loaf of bread?

(RF) - We tried various methods. We first baked some just as is, and when fresh it was quite tasty. However, it did not rise. Then we tried some ordinary yeast in it.

(NJ) - Did you mix any with commercial flour?

(RF) - Yes, the straight eelgrass was quite tasty when it was still hot, but it dried out very quickly. We then mixed it as one would ordinary whole wheat with a little bit of white flour. We found that with very little white flour it had more substance and could be baked into a respectable loaf. Ideally, we would like to have a large enough sample so that nutrition experts could experiment with it. As we were cooking it, and nibbling on it as it was being cooked, it had the smell and the flavor of wild rice, that is the whole "grain." So there is, I think, a rather wide latitude of possibilities.

(SN) - More or less two questions. I guess the second one is a sort of a general one, maybe to everyone here. Are you aware of whether Zostera or Ruppia or perhaps any of the other seagrasses, you mentioned Phyllospadix, can be grown in a pelagic phase.

(RF) - None are known.

(SN) - I know they do not grow naturally, but can they be grown in this way?

(RF) - It has never been done. Only last year the first report of any seagrass being used as a substantial food resource was published (Felger and Moser 1973). I think that eelgrass would not be a plant that you would attempt to grow under pelagic conditions. I am rather positive the plants would require the roots; that you could not grow them as Sargassum--that is without the holdfast.

(SN) - But something like Ruppia might grow?

(RF) - Ruppia could be grown without any holdfast but the seed is so tiny that it would be of little potential value as a crop plant. The seeds of Phyllospadix and Zostera are small but are substantially larger than those of Ruppia.

(SN) - That gets to the second question. If you know, or whether anyone else here knows, whether people working with leaf protein concentrates had tackled the halophytes.

(RF) - The protein content in seagrasses is very high. I think there is at least one paper published, from some work done on turtle grass, Thalassia, in Florida. This was harvested mechanically from wild fields, and did have a substantial quantity of protein in the leaf, but I do not think it would be considered as human food but rather as food for animals.

(SN) - The British anyway, perhaps Dr. Chapman would know, have a technology for extracting protein from terrestrial plants. I wonder if you would speculate about marine plants as a potential source of protein. Possibly using an analog of the process for fish-protein concentrate to separate it from leaf material which in itself is not palatable; to obtain a press cake as the end result. Some of the things like the iodine one might expect to get from some of the halophytic plants would be potentially of great benefit. I am wondering if the salt problems. . . .

(RF) - The salt needs to be washed or removed from vegetative portions but not from the seed. I think the latter is the most valuable part. The vegetative part is usable, but I cannot say very much about it. The vegetative productivity of sea grasses approaches the productivity of sugarcane, etc. and other high productivity terrestrial crops.

(VJC) - Sorry I cannot add anything to what you have said, but I would like to ask one question and to make one comment. It is said to be a common food of

turtles and dugongs. Now if it is a food of dugongs do you think it would be a potential food for human beings as a vegetable? I know nothing about it.

(RF) - I would presume that it (Thalassia) will probably be much like the vegetative part of Zostera and that it could be eaten. It is the white stem or the emerging part of Zostera that was most prized by the Pacific Coast Indians. I have eaten the vegetative parts of eelgrass, both cooked and uncooked, and I do not think it is a very important vegetable.

(VJC) - You mean, in other words, that you do not think people would eat it. It is a matter of people becoming acclimatized to a kind of vegetable they are not familiar with at the present time.

(RF) - There might be secondary uses for the vegetative part. I think probably fertilizer would be the highest use. There did exist a very substantial industry of harvesting Zostera for packing material and for fertilizer, and that collapsed when the wasting disease decimated the Atlantic and St. Lawrence Seaway populations.

(ETM) - They stuff furniture with it in New Jersey.

(RF) - Yes.

(VJC) - I want to comment on the wasting disease because I do not think I go along with you that it was simply the action of an ordinary decaying organism, because it also attacked the Zostera in New Zealand as well and decimated the beds there. That is a different species altogether. I think it really is a disease and I do not think it is just one of ordinary decomposers gone mad.

(JJR) - You mentioned that growth was better where the currents were higher.

(RF) - I do not have data, this is only a guess. I do not know that the growth is higher but in at least many of the stands there are strong currents.

(SN) - There is a study published by Tom Conover where he got a suspiciously good correlation between the standing crop of Zostera and current speed. But this nice straight line drops down. When one sees data like that I raise my eyebrows, but there is at least a graph available showing a very good relationship.

(RF) - It appears that there is a relationship.

(JJR) - Do you think there is going to be a problem in trying to cultivate it, because I am sure we cannot simulate the field conditions.

(RF) - I cannot answer that. That is certainly going to be a major problem. I do not think the cultivation can possibly be in the traditional ways used for cultivated fields. I think it would probably have to be in some sort of way in which tidal waters were used. I am fairly sure of that.

(IC) - What is the first step in processing when they gather up the sea wrack.

(RF) - The first stage is drying, and this is probably the crucial stage as to why other native people have not used it. The Seri Indians gather it only when the winds are just right. There is a name for a certain type of wind which is a drying wind. (Elsewhere, such as on the Pacific coast of Baja, California, or the coast of California, even if there were enough seed to gather, that time of year is foggy and damp and so it would probably not dry properly under "primitive" conditions.) The first stage is drying. Then after it is dried it is placed, in earliest times on a deerskin, then on tarps and now on plastic. After it is thoroughly dried it is threshed with a stout stick, and it does not take very long for the fruit to fall out.

(JS) - Did the Seri select these populations and transport them in any way?

(RF) - No. Their traditional culture is totally without agriculture. They probably did transplant a few terrestrial plants in historical times but this was very little practiced.

(JS) - What about the seed viability.

(RF) - I suspect that it is probably fairly high but I do not have data. I do not know whether it will germinate after being dried. We have gotten fairly good germination from seed collected wet, fresh, kept wet and immediately planted.

(GFS) - Kept wet in sea water?

(RF) - In sea water, yes, or damp. I do not know how long the viability would be. I suspect it would not be very long because there is a change from 6.5 mg./seed to 2.5 mg. when it is thoroughly dried, or from about 6.5 mg./seed to 3.1 mg./seed without oven drying.

(JS) - Are there any archeological findings.

(RF) - No, I have not been able to find any. There have been some sealed pottery vessels found in the Seri region that do have Zostera in them. But, I do not think they are very early. However, the traditional culture that we have been able to record is probably little changed from earlier centuries. Judging from the linguistic and cultural information I am sure this is a very old practice. One month of the year is the month of year for the harvest of Zostera. The name for the plant is very short, comparable to oak, oak tree, you cannot translate the word oak. Older terms tend to be that way.

(JJR) - What is the tidal variation in that area, is it as high as it is up north?

(RF) - No, it is much less. I do not know but I think it is about 3 meters, possibly 4 meters.

(GAP) - If the seed is harvested one month out of the year what are the keeping qualities of dried seed?

(RF) - It keeps well. It was one of the things that was stored against famine. Of course the air is very dry. It is put into a large pottery vessel, a pottery lid is put on it, and it is sealed with a type of native gum which is very similar to the Oriental lacquer, or lac. The Seri Indians were known to make the largest and thinnest pottery vessels probably of any people in the world. Some of them were very tall. It was known as eggshell work. I presume those large ones were not transported but as I said water was their main limiting factor. I imagine they developed very thin pottery so that it would not be any heavier than it had to be for carrying water. They certainly were very breakable.

TERRESTRIAL HALOPHYTES AS POTENTIAL FOOD PLANTS

V. J. Chapman²

Up to the present, terrestrial halophytes have not been generally regarded as plants suitable for human food. This is probably either because of the salt they contain, even when succulence indicates there is also water storage tissue, or, in the case of salt desert halophytes, because of their shrubby nature. Those who have been tempted to chew leaves or succulent stems in the field will have been impressed by the salty taste and considered that with abundant food available from other sources there was no justification for promoting any of the strictly halophyte species.

Maritime salt marshes are characterized in most parts of the world by grass species, mainly belonging to the genera Spartina and Puccinellia. In Europe marshes with extensive swards of Puccinellia maritima have traditionally been used for the grazing of sheep and cattle and so indirectly have contributed to man's food. In Morecambe Bay (Lancashire, U.K.) it has been estimated that one can graze 4 - 6 sheep per acre (Gray, 1972). On the Atlantic Coast of North America marshes with Spartina patens, Distichlis spicata and Puccinellia americana formerly were mown regularly for hay to feed cattle during the winter months. This practice has greatly decreased during this century but some marshes in New Jersey are still mown. In 1956 Burkholder reported that cattle grazed upon the extensive Spartina alterniflora marshes of Georgia.

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At the present time cattle graze on the recently developed S. alterniflora marshes in the Kaipara Harbour of New Zealand. More extensive use of S. alterniflora marshes is probably prevented by the relatively low level they occupy on the shore and the softness of the muddy substrate on which the species thrives best. The low shore level (around mid-tide) reduces the hours during which animals can graze with safety and also means more time required for staff to move the animals on and off the areas. Palatability to stock of other species of Spartina, e.g. S. foliosa, S. brasiliensis, S. montevidensis, does not appear to have been reported in the literature. Insofar as grazing of these grasses by domesticated animals is an indirect means of producing human food there would seem to be a case for experimenting with the palatability and response to grazing of these other species. This may be particularly appropriate since it is possible to create new Spartina marsh on mud flats and dredge spoil (Seneca, 1974; Bascand, 1970; Concern for Environment Inc., Md. Personal observation).

A recent inquiry by the National Research Council of the U.S.A. produced possible forage crops that could be grown on saline lands, so that again, if these were to be extensively introduced the production of human food would be indirect. Both Atriplex halimus and A. nummularia are reported to thrive on Israeli saline soils as well as the Chilean Prosopis tamarugo (Vietmeyer, pers. commun.; Mudie, 1974). The grass Stenotaphrum will grow on soils with some salt present but it would seem more important to develop strains of Spartina, Distichlis and Puccinellia as sward grasses. In particular species of Puccinellia

(P. nuttalliana, P. salinaria) from saline deserts should be investigated. In arid saline areas bush plants are likely to be more successful than grasses, but unless there is adequate fresh water for cattle to drink, forage development in saline areas cannot be successful.

In the tropics large areas of maritime soils are occupied by mangroves. Since many of these contain tannin in some quantity they have not provided any direct food value for man. They are principally used as a source of tannin, they yield an excellent charcoal and traditionally have been employed for railway sleepers, piles and house building (Chapman, 1974; Walsh, 1974). Provided the soil is firm enough, low-growing plants of Avicennia marina var. resinifera are certainly eaten by cattle in New Zealand. The attraction of this species and of the salt marsh grasses for cattle probably lies in their salt and mineral element content, since otherwise the cattle might need salt licks for successful rearing. Seedlings of Avicennia officinalis are reported as edible (Chapman, 1974; Mudie, 1974).

All the above, however, only yield food for man indirectly. The use of saline lands and of halophytes as food plants directly for man has not really been explored previously. It must be admitted that the outlook for new crops is not promising and one may quote Mudie (1974): "Prospects appear to be rather low for large scale use of halophytes as novel foods for human consumption." The difficulties of growing plants on distinctly saline soils and the excess presence of salt in such plants have undoubtedly determined man's disinterest in the past. However, at least three commonly used food plants have been derived by domestication and breeding from wild species that are traditionally regarded as coastal

plants. The common beetroot has been derived from the shoreline Beta maritima, the cabbage family is derived from the wild Brassica oleracea and garden asparagus comes from the wild Asparagus officinalis. In this last case successful cultivation usually involves the actual addition of substantial amounts of salt to the soil in springtime. Wild radish (Raphanus raphanistrum) is also a plant that grows on the sea shore though its roots probably do not penetrate into salt water.

In view of their origin it would seem worthwhile to try and develop strains of beetroot (6 wild species are known) and of the cabbage family that could be grown directly on saline soils. Mudie (1974) reports that Beta maritima will tolerate up to 3% of salt in the soil and hybrids have already been produced. Entirely new strains may have to be developed from the wild species or it may be possible to produce strains that will increasingly tolerate salt from the existing garden varieties of cabbage, broccoli, Brussels sprouts and cauliflower. Nineteen species of Brassica are reported in Bailey's Manual of Cultivated Plants as of economic importance. These include B. rapa (turnip), B. napa (rape) and B. campestris (field mustard). Whether or not any of these will tolerate some salt in the soil is not reported and it might be possible to develop strains that would. Some hybrids, using a salt-tolerant species as one parent, have already been produced (Mudie, 1974). These include Raphanus maritimus x R. sativus and Crambe maritima x C. abyssinica (a possible vegetable oil). One would expect less effort would be required to produce strains of Asparagus that would grow quite satisfactorily on

saline soils. There may be other wild species of Asparagus (300 are reported in Willis's Dictionary) that could be acclimatized to saline soils and which could form a source of animal food. It is a genus that should be examined for this possibility.

The Cruciferae (to which Beta, Brassica and Raphanus belong) is a significant family with other wild halophytic genera. One such genus that should be investigated is Cakile. C. maritima is a drift-line plant of Europe and C. edentula occupies the same position in the eastern U.S.A. The species must be capable of tolerating occasional high concentrations of salt in the soil water but studies would be needed to demonstrate whether they can tolerate continual high salt concentrations. The seeds are regarded as edible (Higgins, pers. commun.) and the fleshy leaves could well provide a vegetable. Since most drift-line plants are also nitrophiles it will be necessary also to study the nitrogen regime and requirements of the species and whether such requirements can be met on salt marshes. It could well eventuate that the species would grow admirably on salt marshes that have been irrigated with effluent from sewage treatment plants since it is rich in nitrogen. It should be noted that Cakile is a member of the Cruciferae a family that has provided many food plants for man. If it is found not to be suitable for man it could well prove to be a good forage crop for domestic animals. This is an aspect that should also be investigated. There are some 15 species of Cakile known and the other species should perhaps be investigated.

Three other genera in the Cruciferae contain maritime species. The most important of these is Crambe maritima the wild ancestor of the sea-kale. This normally grows at the base of cliffs and may require good

drainage (Chapman, 1964). There are 20 species of Crambe and some at least of these ought to be examined. Breeding experiments (see earlier) may show that wild Crambe maritima is capable of growing on well-drained salt marsh or salt-desert soil and from this a suitable food strain could perhaps be developed.

The genus Lepidium is widespread. Some 130 species are known and a few are used as salad plants, the best known being L. sativum or pepper-grass. Lepidium crassifolium is a common species of inland salt deserts of Eurasia. This species, at least should be investigated in order to determine whether it has any food value, and if so, then breeding experiments should follow.

Cochlearia is the third genus with about 25 species, some of which have been or are used in salads. Cochlearia anglica grows on shingle spits on European coasts but there are no reports of the degree of salt that it will tolerate in the soil. The species needs study both in respect of its utilization and also its capacity to tolerate saline conditions. Mudie (1974) reports that C. anglica is a Meso/Miohalophyte.*

Apart from the Cruciferae and Gramineae the family Chenopodiaceae is the other principal family that contains herbaceous genera commonly found in halophytic habitats.

In Great Britain the annual species of Salicornia (S. europaea, S. stricta, S. strictissima), known as Samphire, have been collected off the marshes and sold as a luxury item in Covent Garden market for many years. They can be cooked like asparagus and have a taste of their own.

*Mesohalophyte = 0-2% NaCl tolerant; Miohalophyte = 0-1% NaCl tolerant.

The same annual species can also be eaten raw in the field. The perennial species of Salicornia are not employed in this way, probably because there is more wood and less succulent tissue. In my view Salicornia does represent the principal genus of wild halophytes that should be subjected to immediate study. In the first instance attention should be directed to the annual species, not only those in Europe, but also S. utahensis, S. bigelovii and S. rubra in this country. Attempts should also be made to breed or select varieties that are highly palatable and productive. This will not be an easy task because of the nature of the flowers of Salicornia and it will present a challenge to the geneticist. At the same time there would appear to be a case for examining some of the perennial species, in order to ascertain if they have any culinary promise, e.g. S. perennis, S. australiensis. In addition there are allied genera found in salt deserts that could also be investigated for their food value. These include Arthrocnemum (20 species extending from Mediterranean to Australia), Halocnemum (one species in Eurasia) and Allenrolfea (4 species in North and South America). Species of all four genera are widespread in the world and representatives of every species should be collected together in one locality for trial purposes.

The species of Salicornia are very tolerant of high salt values and also of submergence and they are usually the first colonists of mud flats. Should they prove to be a valuable food plant, as they may well be, attention will have to be given to techniques of cultivation. It will be necessary to determine the uppermost levels at which they will grow and techniques will need to be devised to inhibit competition from

other species that grow naturally at higher levels. If any of the allied genera prove satisfactory their ecological requirements will all need to be studied in more detail than heretofore as well as their capacity to reproduce. This latter might prove to be the critical issue.

In New Zealand plants of Tetragonia trigyna (New Zealand spinach) grow on maritime sand dunes and leaves are collected from wild plants or it is grown in gardens as an alternative to traditional spinach (Spinacia) in the same family. Tetragonia certainly tolerates salt spray and Mudie (1974) reports that it will tolerate salt in the soil up to 3.0% NaCl. It has to be remembered that maritime dune plants are regularly subject to salt spray, but roots are generally in a fresh water table floating above a lower salt water table. This fresh water comes from precipitation and also from internal dew formation (Chapman, 1964). Since this species has a capacity to grow under saline conditions, breeding experiments should be undertaken to produce the best strains.

At the same time wild spinach (Spinacia) could be studied to see if it will tolerate any salt in the soil. The genus Atriplex with about 200 species is widespread, many of the species occurring as weeds. A. patula and its var. hastata is common on the driftline and reference has already been made to A. halimus and A. nummularia. Bailey (1949) reports that A. hortensis can be grown for vegetable purposes and it is therefore possible that other species could be used for this purpose or as forage crops for domesticated animals. The genus would certainly seem worthy of further investigation. Mudie (1974) lists the following species of Atriplex as Mio- or Meso-halophytes: A. confertifolia, A. nummularia,

A. semibaccata, A. elegans, A. hortensis, A. patula, A. Wrightii. The first three are potential forage crops whilst the last named could be a source of a grain.

Suaeda is a genus with 110 species, some annual and other perennial. Many of the species have a succulent foliage which might be the basis for a cooked vegetable. Some of the shrubby species (e.g. S. nudiflora) occur on inland saline areas and these also should be investigated. Initially annual species, such as S. maritima, would be the most promising candidates. If studies show that any of them are likely to be promising similar problems in respect of their cultivation could arise as in the case of Salicornia.

The genus Chenopodium, which is closely allied to Atriplex, has species which can be found as casuals around the landward edges of salt marshes. It would seem that they are not as tolerant to salt as Atriplex spp. C. amaranticolor is recorded by Bailey (1949) as sometimes being used for greens. For this reason the species ought to be examined for its degree of salt tolerance.

There are three other genera in the Chenopodiaceae that are common in saline habitats. These are Salsola, Kalidium and Anabasis. It does not appear that any species in these three genera currently have any food value. Because of this it is difficult to indicate whether they should or should not be examined. Salsola has some 150 species with a number (S. dendroidea, S. soda, S. platytheca, S. arbuscula) found in saline areas of Eurasia. S. kali with the spiny tips to the succulent leaves is not a likely candidate for a food source but some of the other

species might be more promising. They tolerate salt so that it remains to be established whether they have any food value. In the case of Kalidium with 4 species and Anabasis with 30 species it is again a matter of testing for potential food value for man or his animals. Kalidium caspicum and Anabasis salsa are both species that grow in saline soils. Kochia scoparia is reported as a mesohalophyte forage crop by Mudie (1974).

The family Aizoaceae with 300 species (sensu stricto) of the genus Mesembryanthemum is worthy of consideration. The species of Mesembryanthemum are essentially species of arid areas, but there are a few, such as M. australe, M. crystallinum, M. chilense, which grow on coastal cliffs where they must be subject to salt spray. The only species recorded as edible is M. edule which has an edible pulp. Any species which are reported as growing on coastal cliffs together with M. nodiflorum (Mudie, 1974) should be examined for their capacity to grow on saline soils, and at the same time they should also be studied with a view to establishing whether they have any food value.

Another halophyte genus in the Aizoaceae is that of Sesuvium. Eight species are recorded by Willis (1966) and two, S. portulacastrum and S. verrucosum, are widespread in the tropics and sub-tropics. The former is generally associated with mangroves and the latter with saline desert areas. Mudie (1974) reports them as Mesohalophytes. They should be investigated both for their use by humans or by domestic animals.

Crithmum maritimum, the rock samphire (Umbelliferae), is already used as a pickle but experiments may show that it could have a wider use.

Mudie (1974) reports it as a Meso/Miohalophyte so that it is salt tolerant but, based on its wild habitat on cliffs, it may have a drainage requirement. As a species it is certainly worthy of study.

On some salt marshes in Europe Plantago maritima occupies extensive areas. The leaves can be very succulent but whether they have any food value has to be determined. It would certainly seem to be a species capable of producing a large crop. Similarly Cotula coronopifolia (Compositae) is extensive in New Zealand on brackish marshes and would be easy of cultivation.

Vietmeyer (pers. commun.) informs me that Simmondsia trinanthis from Mexico-Arizona has been suggested as a possible species that would grow on saline areas and from which an oil, equivalent to that of sperm oil, could be extracted.

One tropical strand plant that might be investigated in more detail is the small tree Coccoloba uvifera, the sea grape. The fruit is said to be edible, and if so attempts should be made to see if the species will grow on sandy saline soils. Because of its natural habitat it is likely that the plants require good drainage. The tree might prove very successful on dredge spoil.

In concluding this contribution, attention should be drawn to the fact that the vegetation of maritime salt marshes plays a major role as a producer in the estuarine and offshore fisheries food chain. Replacement of native species by introduced species, even if halophytes, on any large scale might affect the ecosystem, especially if the plants are harvested so that little or no dead, decaying material is available for

the food chain. Before any attempt is made to use extensive areas of maritime salt marsh for food plants, it would be important to determine the acreage of salt marsh required to maintain in their present state adjacent estuarine and offshore fisheries. Only when this has been done could one say how much of present salt marsh should be available for cropping of food halophytes. In the case of interior saline deserts no studies have been made of their value to any of the adjacent ecosystems and it could well be that change of use, or more intensive use of interior saline regions would be more acceptable ecologically.

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Discussion following Dr. Chapman's paper

(RF) - I have some comments which might be of some interest. Allenrolfea seeds were harvested by the Indians in the Gulf of California. They are emphatic that the vegetative part was not edible.

(VJC) - O.K., there is one answer to a query.

(RF) - Salicornia was also eaten. There are Salicornia fields there; I have seen them completely inundated at high tide.

(VJC) - Yes, they would be at high tide, they are completely inundated.

(RF) - Rhizophora fruit has also been eaten. There are a number of reports of it being eaten. I do not think it was a major source.

(VJC) - I would not think so. The amount of tannin is pretty considerable and I think they would be an acquired taste. If I were picking I would go for Avicennia rather than Rhizophora.

(RF) - There was either a species or a cultivar of Distichlis, probably derived from Distichlis spicata, known as Distichlis palmeri that was grown in considerable quantities. This might be an very interesting plant. It was grown for its seed.

(GFS) - Where was it grown?

(RF) - At the head of the Gulf of California in the flood waters of the delta of the Colorado. I have seen it growing. I have seen what probably is Distichlis palmeri growing where it is now inundated with seawater. Considerable quantities have been recovered both in historical times and from the prehistoric era.

(GFS) - I had wondered about the possibility of looking for seed production from some of the tide marsh grasses. Distichlis is one I wondered about. Frankly I do not know whether Spartina ever produces fruits big enough so that they are worth considering here. We have looked at them very casually, always from a different point of view in the past, you see.

(VJC) - I must admit I ignored the grasses. They were the ones most likely to be used either for pasture or for hay--or for some other indirect use. I would think from the point of view of economics and running them it would be much easier that way than trying to harvest them, but I could be wrong.

(IC) - I can testify for Coccoloba, that is a rather tasty fruit. The flesh is thin.

(VJC) - I am glad to know that. I have seen it but never tasted it. Again breeding it might produce a really good grape-like fruit that is very attractive.

(IC) - The fruit varies greatly from bush to bush.

(VJC) - Yes, I'll bet it does.

(ETM) - Suaeda is very good cooked, the way people cook spinach. Also Atriplex patula var. hastata can be used in salads and also cooked.

(VJC) - A big potentiality here, I'm sure.

(GFS) - As a matter of fact, hastata is very nice to eat in the field. Just pick the leaves off and eat them, particularly the young plants.

(ETM) - That is what we do down at Henlopen when we go out on the marshes.

(VJC) - Salicornia is best when it is getting really fat and thick. Atriplex is best when it is young. I would not like to eat it in the autumn, I think.

(ETM?) - As it gets older the insects seem to have liked it better than you did.

(JCW) - You mentioned New Zealand spinach, what we know in this country as New Zealand spinach--which I think is the same thing--I've seen it in New Zealand, has a high oxalic acid content.

(VJC) - I have eaten New Zealand spinach cooked and it is perfectly all right. It is very pleasant.

(JCW) - We ate it during the War here.

(GFS) - Some of us have commented to each other that all of a sudden we are looking at these plants in a way we never looked at them before. We are turning the picture around and looking at the other side of it. I think this is what we must do.

POTENTIAL FOR ADAPTING PRESENT CROPS TO SALINE HABITATS

James W. O'Leary³

The title of this presentation implies that there is some question whether presently used food crops can be grown using water that is saline. If we agree on the definitions of these terms, then there definitely is a question. Food crops, in my usage, will mean those plants now being grown for their use as food by man and domesticated animals, and saline water means water with a salt concentration either equal to or closely approaching that of seawater. With these definitions in mind, it is clear that present food crops are being grown with water that may well be salty in many cases but is nowhere near that of seawater. Thus, the step from crop production under present conditions to crop production in saline habitats is indeed a giant one. As I see it, then, my charge is to assess the potential of successfully making that giant step. In order to do so, I will use the following approach.

First, the problem will be clearly defined. That is, the consequences of increasing salinity of the rhizosphere to plant growth will be elucidated, albeit in general or summary terms, so that it is clear exactly what problems have to be overcome in adapting plants to a habitat where salinity in the rhizosphere is extremely high. Second, I will discuss some of the ways that are potentially possible to overcome or prevent the growth reduction induced by the high salinity and the relative

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successes of attempts along those lines so far. Finally, I will consider those alternatives that seem most likely to further extend the adaptation of present crops to salinity, and I will give you my prejudiced judgments and those of others as to the potential of these.

Plant Response to Salinity

The equilibrium water status of a plant is dependent on the plant's environment. For a terrestrial vascular plant, that means the equilibrium plant water potential will be equal to, or less than, the soil water potential (O'Leary, 1970). That is, the soil water potential determines the maximum plant water potential that can be developed. It is for this reason that considerable emphasis is placed on maintaining soil water potential as high as is reasonably practical. It is important, also, to remember that continued water movement into a plant occurs only as long as the plant water potential is lower than that of the soil solution.

The value of the soil water potential (ψ_s) depends almost exclusively on matric (τ) and osmotic pressures (π). As the water content of a soil decreases, both matric and osmotic pressures increase, and ψ_s is lowered accordingly. Under nonsaline soil-water conditions, π is so small relative to τ that it usually is neglected.

As the salinity of the soil-water increases, π becomes more important. This is a matter of great concern because it makes possible the existence of low soil-water potentials, even at high soil-water content. For example, since there is such a close relationship between τ and soil-water content, measurements of water content or τ are the soil-water

measurements typically employed. However, if the salt content of the soil water was such that π_{soil} was 5 bars, then neither of those measurements would reveal the fact, and more important, the ψ_s would be -5 bars even at field capacity. Thus, it was recognized that the water potential gradient from soil to plant necessary for water movement into the plant could be non-existent under saline conditions even if abundant water was present in the rhizosphere. This led to the development, and acceptance for many years, of the concept of "physiological drought" (Stroganov, 1964). This view was popular for many years in spite of the demonstration many years ago that, as π_{soil} increased, so did π_{plant} (McCool and Millar, 1917). This is illustrated in Table 1.* Even though this demonstration of internal osmotic adjustment was confirmed several times in the following years, not until after the papers of Bernstein (1961) and Slatyer (1961) appeared did the realization of plant osmotic adjustment become widespread.

When the π_{plant} increases in response to increase of π_{soil} , there is not always a direct correspondence between the two. Sometimes the osmotic adjustment is less than complete (Janes, 1966, 1968; Meiri et al., 1970), sometimes it is complete (Slatyer, 1961), and π_{plant} even has been found to increase more than the increase in π of the root medium (Boyer, 1965). This osmotic adjustment occurs whether the increase in π of the root medium is slow or fast (Meiri and Poljakoff-Mayber, 1969, Ruf et al., 1967), within limits. Furthermore, the adjustment occurs whether the solutes responsible for the increase in π of the root medium are permeating (Eaton, 1927; Eaton, 1942) or non-permeating

*See page 113.

(Janes, 1966; Ruf et al., 1967), and it occurs in both glycophytes (Meiri et al., 1970; Slatyer, 1961) and halophytes (Black, 1960). In fact, π_{plant} even has been found to increase proportionally with decrease in soil moisture, under certain conditions (Padurariu et al., 1969). Thus, osmotic adjustment in plants is truly a response to decreased water potential in the rhizosphere and not simply a response to increased concentration of permeating solutes. The osmotic adjustment seems to be reversible, also (O'Leary, 1974).

Despite osmotic adjustment that occurs in plants, which should maintain the water potential gradient from rhizosphere to leaves (Bernstein, 1963a; Kramer et al., 1967), drought symptoms often have been observed on plants growing in saline conditions (Bernstein, 1961; Bernstein and Hayward, 1958). Thus, it appears that water transport to leaves may be reduced in osmotically adjusted plants under certain conditions. How this might occur can be seen from consideration of the generalized flow equation:

$$J_v = L_p (\Delta\psi)$$

where J_v = water flow across the root surface ($\text{cm}^3 \text{ cm}^{-2} \text{ sec}^{-1}$), L_p = hydraulic conductivity coefficient of the root surface ($\text{cm sec}^{-1} \text{ bar}^{-1}$), and $\Delta\psi$ = the water potential gradient from the external solution to the interior of the plant (bars). Even if $\Delta\psi$ is maintained, reduced water flow into the plant could occur if L_p is reduced. It has been suggested many times that permeability of roots may be reduced by increased salinity of decreased water content in the rhizosphere (Janes, 1968; Klepper, 1967; Kramer, 1950; Mees and Weatherley, 1957), and direct determination of L_p of the root surface in osmotically adjusted plants has confirmed that this in fact does occur (O'Leary, 1974).

Water stress in plants usually occurs when the capacity of the soil to deliver water to the plant becomes limiting, or when transpiration is occurring so rapidly that it outruns water absorption by the plant, even in soil containing adequate water. Whether or not transpiration rate exceeds absorption rate depends on the evaporative demand of the air and the resistance to water transport to the leaves. When evaporative demand is high, transpiration often exceeds water absorption, and water stress and wilting occur. In osmotically adjusted plants, increased root resistance makes such an event more probable since the evaporative demand of the air does not have to be so high for transpiration rate to exceed absorption rate. When this happens, the osmotically adjusted plant incurs a water deficit and suffers the same consequences as the wilted plant in a drying soil. This suggests that salinity damage might be less in higher humidity environments, and, in general, this has been found to be the case. Nevertheless, even in environments where water stress might not be expected to develop, the osmotically adjusted plants grow less than the same plants growing in a situation with lower salt content in the rhizosphere (O'Leary, 1971, 1974).

The pertinent question then becomes--what are the metabolic consequences of osmotic adjustment? That is, what are the changes in cellular metabolism resulting from the higher than usual π_{cell} that are responsible for the reduced growth in osmotically adjusted plants? That there are metabolic disturbances as a result of osmotic adjustment has already been suggested by the change in hydraulic conductivity of root cells. There has been a

reasonable amount of research on the effects of salinity on metabolic processes, and much of that work is reviewed elsewhere (Greenway, 1973; Mercado, 1973). The results of that extensive research are admittedly quite variable, and even contradictory in some cases. However, there are some generalizations that can be made. Enzyme activity and the corresponding metabolic processes are definitely affected by higher salt content and osmotic pressure in cells. Furthermore, most of the results fit the conclusion that salt stress, even in osmotically adjusted plants, induces premature senescence (O'Leary, 1971; Prisco and O'Leary, 1972, 1973).

In general, then, plants subjected to a high salt concentration in their rhizosphere really are faced with two major alternatives. They can exclude the salts and prevent the dangers associated with increased salt content in the cells while assuming the risk of water stress, or they can avoid the risk of water stress by absorbing the salts and assume the risks associated with the higher cellular salt content. In reality, many plants are intermediate in this regard. That is, some of the salts are excluded and some are absorbed, there is some degree of osmotic adjustment resulting from internal production of organic solutes, and there is some degree of growth reduction resulting from these activities. The truly salt-tolerant plants, i.e. halophytes, absorb the salts present in high concentration and tolerate the higher salt content in the cells. For non-halophyte plants, though, the level of salinity that can be tolerated, and the particular environments (i.e. hot or cold, dry or humid) in which such levels can be tolerated, is a function of the degree and manner of ion exclusion and osmotic adjustment.

Faced with those major alternatives or combinations thereof, then how can we adapt crops to more saline habitats? Basically, there are two alternatives:

- (1) Environmental Modification
- (2) Increase Salt Tolerance of Crops

I would like to consider each of these alternatives now and survey some of the attempts made along these lines so far.

Environmental Modification

This, basically, means changing the plant's environment to compensate for the harmful effects of the high salt content. In general, two approaches have been taken. The first is designed to change the root environment so the salt concentration at the root surface is changed favorably. One of the techniques is to use trickle or drip irrigation, which maintains the root zone at or near field capacity continuously. This keeps the matric pressure depression of soil water potential at the minimum (0.3 bar) continuously rather than having matric pressure fluctuate between about 0.3 bar and 1 or 2 bars as it does during wetting and drying cycles under normal surface irrigation schedules. This will allow for use of water with about 2000 ppm of added salinity at best, and this will not in itself increase the tolerable salt level much at all.

The other techniques of modifying the root environment involves the use of very porous, sandy soil which has been championed by Boyko and his

followers (Boyko, 1966, 1968). In brief, the principles upon which successful irrigation of plants with extremely saline water is based are as follows. With large pore spaces in the soil, the saline irrigation water rapidly leaches through the large pore spaces and only a thin film of water adhering to the soil particles remains. The pore space itself is saturated with moisture, and as a result of supposed temperature fluctuations water condenses on the root surfaces. Thus, the root surfaces are bathed with a film of pure water, and normal water uptake by the roots follows. Only a small percentage of the total root surface presumably comes into direct contact with the saline water. In spite of the evangelism of Boyko and followers, no large scale use of water with a salt concentration equal to or closely approaching that of seawater for irrigation is in evidence. There are several fallacies in the reasoning of why this should work, which probably explains why it has not become a common cultural practice.

The second approach to environmental modification involves taking advantage of high relative humidity to reduce transpiration to a minimum so the development of water stress is prevented. That is, the lowered water potential of the soil solution and the possible reduced root permeability are acknowledged, but it is desired to reduce the water loss to a minimum so that the reduced water uptake does not become limiting. Nieman and Paulsen (1967) at the U.S. Salinity Lab conducted a small experiment to test this hypothesis a few years ago with variable results.

Recently, Hoffman and co-workers at the Salinity Lab conducted a series of experiments which also tested this hypothesis (Hoffman and Rawlins, 1970, 1971; Hoffman et al., 1971). The results from those

experiments are summarized in Table 2.* The absolute humidity levels used in each of the experiments differed, but the important point is that in each of the experiments there was a wide difference between the low and high relative humidities. The general hypothesis that raising the humidity of the atmosphere reduces the harmful effect of saline water is well supported. The osmotic pressure of the solution around the roots that caused a 50% yield reduction was only 2.2 bars at low humidity for onion, but when the humidity was raised it took a solution with osmotic pressure of 4.3 bars to cause the same yield reduction. A similar relationship held for the other crops investigated, except cotton. It is interesting to note that the greatest effect of humidity was on those crops usually considered salt sensitive, and the least effect was on those crops considered salt tolerant. That suggests that a major part of the yield reduction in the salt sensitive crops was due to water stress, which was relieved by the high humidity. Conversely, in the salt tolerant crops, water stress did not seem to play an important part in the yield reduction due to salinity. Thus, it is not surprising that when the water stress effect was removed from the relatively salt sensitive crops, the salinity level corresponding to 50% yield reduction was not much different from that corresponding to a 50% yield reduction in the relatively salt tolerant crops. In spite of the demonstrated benefit of high humidity on use of saline water for crop growth, this does not seem to offer a means for extending the tolerable salinity level to anywhere near that of seawater.

*See page 114.

Increase Salt Tolerance of Crops

The second major alternative is to increase the ability of the plants to withstand the high salt concentration in the rhizosphere. The first approach is to try to compensate for the metabolic disorders resulting from the higher cellular osmotic pressure by application of the appropriate compounds.

For example, it is known that salinity reduces the amount of root-synthesized hormones that are delivered to leaves. Therefore, if one could apply directly to the leaves the deficient hormone in proper amount, this effect could be ameliorated. Some attempts have been made along this line with moderate success. Ben-Zioni et al. (1967) treated leaf discs from water or salt stressed leaves with kinetin and partially restored the impaired protein synthesis. Kaufman and Ross (1970) used kinetin to partially overcome salinity inhibition of germination. O'Leary and Prisco (1970) sprayed benzyladenine and gibberellic acid directly on leaves and partially overcame the salinity-induced growth inhibition. More research along this line might prove fruitful, but I doubt that it will be a practical approach to overcoming considerably high salinity levels.

That finally gets us to the question of breeding for more salt-tolerant plants. Two important and related questions that must be answered are:

- (1) Is there enough genetic variability in this characteristic within a species? That is, is there a gene pool rich in genetic variability that can be utilized to come up with a successful product?
- (2) Do we really know what features we want to incorporate in a plant in order to make it more tolerant of high salinity? In other words, do we know what it is about a salt-tolerant plant that makes it salt tolerant?

The answer to the first question is not easy. It depends on who you ask. When I ask people directly whether they think breeding can result in crop plants that are tolerant of sea-water level salinity, I get some answers of "definitely not" and some that say "no question about it." The characteristic common among those who say there is no question that we will be able to breed crop plants tolerant of high salinity is that they all are talking about barley or some other grass. Barley was grown with good yield at salinities up to 20,000 ppm over 20 years ago by Ayers et al. (1952), but even then, it required different levels at different growth stages for success. For example, the salinity had to be low during germination and early stages of growth. In fact, this is a fairly general characteristic of many plants, even halophytes; the low tolerance of salinity at germination coupled with a relatively high tolerance during more mature stages. Several grasses apparently can tolerate relatively high salinity. Agropyron (wheatgrass) often is cited as a good example. Dewey (1962) demonstrated tolerance of wheatgrass varieties up to 18,000 ppm, for example.

Some other opinions about the genetic variability available are given here.

Rains (1972) says that, "It may be too optimistic to expect a solution in the near future to the problem of how to use the millions of acres now considered to be too saline for optimal plant growth, but it is certainly not beyond possibility." He feels there is enough genetic availability there, and he makes a plea for plant physiologists and geneticists to work together in adapting economically important plants to saline habitats.

Epstein and Jeffries (1964) also made a similar plea. They said that "much is to be gained by an energetic pursuit of the possibilities of breeding for salt tolerance." They felt that breeding for salt tolerance has been done only on an exceedingly modest scale.

Epstein (1972) in his recent book, says this again, but he also points out that there is ecotypic variability even among halophytes. He, thus, says, "We therefore have the possibility of breeding salt tolerance into crop species, as well as the option of breeding economic usefulness into salt-tolerant wild plants. Neither of these strategies has yet been tried in any sustained, energetic manner."

The book Biology and the Future of Man (Handler, 1970) written by a panel commissioned by the NAS says that "It is now clear that all crop species have large stores of inadequately explored genetic variability."

Greenway (1973) also shares this optimism for breeding, referring to "large varietal differences in salt tolerance found for many species."

It is interesting that the supporting citation for that statement is a paper by Abel and McKenzie (1964) where they compared six varieties of soybeans up to 7500 ppm which starts out by saying, "Plant genera and species may differ widely in salt tolerance but, for most crops, varietal differences in salt tolerance are very small." Thus, it is not easy to say clearly whether the required genetic variability is present or not.

Bernstein (1963b) has not been that optimistic about the amount of genetic variability available and the chances of successfully exploiting it. I must admit that I have to side with the apparently minority opinion. Maybe not for the same reasons, but I don't feel optimistic at all about being able to make truly salt-tolerant plants out of crop plants as we know them now.

There is always a price to be paid for any significant adaptation made by plants. The trade-off that has to be made for increased ability to withstand saline environments undoubtedly will change the present characteristics of our present food plants. This might be as simple as lower yield or as severe as non-palatability. The things that make a plant a good halophyte and those that make a plant a good food plant may be incompatible. Much depends on the answers to the second question. That is even harder to answer.

Do we know what to breed for? It is interesting to note that most of the people referred to earlier who feel optimistic about breeding for salt tolerance and most of the people they cite for support feel that the varieties which were tolerant were so because of their ability to exclude ions. If this is so, and if ion exclusion then is what we should breed for,

that puts us right into the controlled environment situation where relative humidity can be maintained extremely high. Even if some osmotic adjustment occurs without ion uptake, it cannot account for very much of the needed adjustment. For example, Greenway (1973) calculated that at an external concentration of about 6000 ppm NaCl, in order to osmotically adjust by organic solute accumulation, the cell sap would have to contain 30 g/l of hexose or 60 g/l of disaccharides. This represents about 20% and 40% sugar on dry weight basis.

The answer to these questions--i.e., do we breed for ion exclusion?, do we breed for some internal osmotic adjustment mechanism that doesn't rely on ion uptake?--already is available. The experiments have been done for us. Halophytes presumably have "selected" themselves to "fit" their environment. How did they do it? Did they find another osmotic adjustment mechanism? No, they absorb the ions and they tolerate them. Thus, true salt tolerance probably has to involve the ability to absorb some of the salts present in high concentration and tolerate them.

How do they tolerate the salts? Frankly, we really don't know. There is some compartmentalism involved probably, but we don't know much about that at a cellular level. In glycophytes, it appears that chloroplasts are most sensitive to salt, then nuclei, and then mitochondria. In the few halophytes that have been studied in this manner, it seems like Cl^- content is higher in chloroplasts than in other organelles. It also is important to remember that whenever unequal distribution of ions occurs in cells, the problems of electrical balance and water potential equilibrium among cellular compartments must be overcome. This involves

alterations in organic acid production, for example. There is a lot of evidence for linking oxalic acid levels and internal ion balance under saline conditions. It will be important to know what these relationships are in cells of seeds and fruits of plants grown under highly saline conditions since oxalic acid is undesirable in food for human consumption.

The easiest specific directions one could give a plant breeder might be the type of enzymes for which to select, since much phenotypic plasticity is due to the isozymic composition, and assays for different isozymes is relatively straightforward. However, in the few cases so far in which comparison has been made of enzymes from halophytes and non-halophytes (Flowers, 1972a,b; Greenway and Osmond, 1972), it has been found that the enzymes from both kinds of plants were equally sensitive to salt concentrations. The investigators in those studies concluded that the differences in salt tolerance, therefore, were not due to enzyme differences in salt tolerance, but rather were due to the cell's ability to spatially separate the salt from the enzyme sites. Thus, there still is a strong feeling today that the vacuole is an ion sink which allows the cytoplasm to be relatively low in salt content.

Chances of Success?

In summary, I feel that the upper limit of salt tolerance for specific crops probably can be raised through recurrent selection procedures. However, to make that giant step from present tolerance

limits to saline habitats does not seem to have much potential. Too many attributes and activities would have to be too carefully integrated to make a plant a good halophyte and a good food plant to make it successful. To illustrate the difficulty of doing this sort of thing I would like to close with an illustration of a similar attempt already made.

One of the most intensively investigated areas of plant physiology over the past half dozen years has been the C_4 pathway of photosynthesis. Through comparative studies of C_3 and C_4 plants and through investigation of distribution and activities of specific enzymes, the spatial and sequential steps of these two pathways has been well explained. Bjorkman and co-workers (Bjorkman and Berry, 1973) have been able to hybridize a C_3 species and a C_4 species of Atriplex. The F_1 plants were intermediate between the two parents in anatomy and other features, but among the F_2 and F_3 plants, some could be found that had exactly the right anatomical arrangement for the C_4 pathway and also had the right biochemical characteristics. Yet none of them have been found to have a complete and integrated C_4 pathway. All of the known necessary characteristics are there, just what was specified in the "instructions," yet the coordination is not there. Bjorkman concludes, "Thus even though only a few genes may be involved in determining the genetic inheritance of each component of four-carbon photosynthesis, the requirement for a complete coordination of the anatomical and biochemical properties of the leaf could well make it impossible to introduce this pathway into plants lacking it."

I can't help but feel the same way about introducing salt tolerance into plants lacking it. That is, I can't visualize the development of a plant that has the attributes necessary to give it tolerance of irrigation water with salt concentration equal to, or closely approaching, that of seawater while also having the attributes necessary to make it a desirable food plant.

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Table 1 - Osmotic adjustment of corn roots in response to
 increased salinity of the soil solution¹
 [π = osmotic pressure]

π of growth medium (bars)	π of root cells (bars)
1.21	4.59
1.99	5.48
3.38	6.61
4.96	7.51
7.22	8.19

¹Adapted from McCool and Millar (1917)

Table 2 - Osmotic pressure (π) of soil solution necessary
to cause 50% reduction in yield¹

<u>Crop</u>	<u>π of Soil Solution (bars)</u>	
	"Low" Relative Humidity	"High" Relative Humidity
Onion	2.2	4.3
Radish	2.9	4.0
Bean	2.2	3.5
Cotton	5.0	5.0
Beets	6.0	7.0

¹Data adapted from Hoffman and Rawlins, 1970, 1971,
and Hoffman et al., 1971.

Discussion following Dr. O'Leary's paper

(LC) - Would you care to comment on the interaction between oxygen tension and salt tolerance? For instance, in this state under uniform salinity levels Spartina alterniflora is relatively poorly developed under low oxygen levels, but if the oxygen levels are increased it grows much taller. This seems to be pretty independent of salinity.

(JWO) - Does this mean relative flooding or nonflooding of the soil?

(LC) - Yes, and I think Dr. Chapman has hinted on that a few times when he has mentioned plants that stand salinity but require good drainage.

(JWO) - Two things. One, I do not have a good answer for you, and two, the way I think I will get out of it is by saying that sounds exactly what I came to hear Dr. Bernstein tell us.

(LC) - One other question. When you are talking about the influence of salt concentrations on metabolites, which obviously are going to be influenced, most of the work, of necessity, has been done under continuous salt concentrations. What would happen under a cyclic situation where you allow salt to the point where you begin to get damage but not quite reach that point, then go back down, then go back up? Could you utilize saline water in that way with some efficiency?

(JWO) - Yes and no. We have done something similar to that. I can say that the plant can reversibly osmotically adjust. When the salinity is increased the plant raises its osmotic pressure; then when the salinity is lowered the osmotic pressure comes back down. But the changes that take place in those cells that are once osmotically adjusted seem to be permanent changes, and some of these seem to be structural rather than physiological changes. On the other hand, if

you get away from the problems associated with permeability, etc. then maybe there are no serious problems since with many plants there are stages at which the tolerance is very high. Such as, once grain filling starts in many plants, they will take extremely high salinity levels, and at that point maybe you can switch over and just give them salt water.

(WSV) - It seems that Zostera has sort of carried your control of humidity to extremes.

(JWO) - I imagine it is very humid. But that is only part of the problem.

(WSV) - I would like to challenge just a bit, your conclusions with respect to the enzymes being transferred, because, as you said, the way that halophyte cells are adapted a very high salinity is basically by having a sink. They are using actually the vacuole as a sink. Now indeed if this is a common cellular structure to most of these plants, and indeed it is, the idea of transferring is a little different from the highly integrated enzymic-anatomical structure that one has in chloroplast arrangements, which is probably one of the most sophisticated systems that exists in any living organism. I do not think it would be quite impossible to transfer some of these genes back and forth in this case, as I would in the particular example you used.

(JWO) - Yes, I partly agree with you. In other words, what you are saying is that you could transfer the ability to accumulate ions in a vacuole to a plant. That probably could be done. But again, I think that begs another question. Even if the ion concentration is high in the vacuole there is going to tend to be water potential equilibrium between cell compartments. Hence, the water potential in the vacuole is going to be very low and is going to have to be reflected by a similar water potential in the cytoplasm. It has to be lowered some way, whether it comes up with higher concentrations of colloidal materials,

etc. to give it a higher matric pressure, or a higher osmotic pressure from organic solutes. Whatever these may be, the problem is still one of the metabolic rate of organelles sitting in that soup with the activity of the water at some low level. Now I've looked hard for data, but unfortunately there really is very little data to put one's hands on relating the growth of cells, of leaves or plants to the water potential in the cells, independent of turgor. I think somewhere along the line this should be done. Usually when water potential has been lowered it has been by causing the turgor pressure to go down. Then of course you get the typical water stress effect. But to maintain the turgor pressure high and the water potential low and observe the effects of that is more pertinent here. There are some suggestive data by McNulty of Utah on some halophytes he has worked with there. He has compared the growth of ones that grow in Salt Lake or around the margin of Salt Lake. If he lowers the water potential in the medium, or the salt content in the medium in which they grow, the growth is enhanced fantastically. Again, I think the tradeoff a plant makes by being able to tolerate salinity is to give up some of the rapidity of growth.

(WSV) - Is there evidence of energetic transfer of water in plant cells like there is in animals? Active transport of water takes place.

(JWO) - No.

(WSV) - But there is no evidence of this in plants? I am surprised.

(GFS) - It has been examined. The question has been asked but the conclusion is pretty generally no.

(WSV) - O.K., I'd better qualify that.

(JWO) - That's another one of those questions that it depends upon whom you ask. If you ask me I will categorically say no. There is definitely no chance of

active transport of water into plant cells. The permeability of the cell membranes, for example, is so high to water that the system would short-circuit so quickly that it would be very difficult to get active transport against an activity gradient.

gradient.

(NJ) - More of a comment, if you want to put me in one of the categories, I guess I am basically more optimistic. Also I am thinking mostly I guess in terms of cereal crops. On the other hand with respect to gene pools or germ plasm resources, in cereals, for example, we have around 30,000 in the world collection of wheat, and of the total about 16,000, maybe about 15,000, in barley. This is just a wild guess, but probably not 5% of this whole total has ever been used in making hybrids, which is our chief way of getting variability. Now when you look through these germ plasm resources sometimes you think there is nothing there. They have never found any cereal with a C₄ system in the small grains, as far as I know. They have in corn, of course. But other things are there in very, very small amounts. For example, high lysine in barley and high lysine in corn. There certainly were not many genotypes found with that. But you only need one or two to sometimes solve a problem. I want to make one more comment about the use of these. I guess I would always come down on the side that it is easier to work if you know what you are working with. But with a lot of these things, in the plant physiology area and other areas too, we really do not know the basic information. I just want to make the point that a plant breeder often does work without knowledge. In the case of barley it is very easy and efficient. It is not like dealing with a genotype of a barley, one genotype which can only respond within its very narrow capabilities, but you can take the full collection and work with them. This has been done. I expect you talked with Tom Ramage.

(JWO) - No, I did not.

(NJ) - He would have been one of the very optimistic ones.

(JWO) - I think if you asked Ramage he would be one of the most optimistic persons.

(NJ) - One technique needed to run the screen system is the male sterile gene and we have put together these populations. I have helped work on these with 1295 barleys. The wind blows the pollen across the field, and they form hybrid seed. On the male sterile barley, there won't be any seed. So you can determine if there is variability. Then you plant this on a highly saline soil and only the survivors will come through. They will pollinate so you keep on cycling this. We do not know a thing about what is happening but it works.

(JWO) - He presumably has been doing this for years.

(NJ) - I know he has and I do not know why he does not release it.

(JWO) - I have heard from various places as far away as thousands of miles that Ramage has a barley that presumably will grow in seawater, but I have not heard the details.

(JCW) - Is that not the adult plants, because I talked with him in February and he made a point of stressing that fresh water, or at most water much reduced in salt content from his usual saline water, had to be used through the seedling stage.

PROBLEMS IN MANAGING SALINE SOILS

Leon Bernstein⁴

The management of saline soils is usually dealt with under two headings, reclamation and salinity control. Reclamation is aimed at lowering soil salinity to levels that permit the culture of the desired crop plants when soils are initially too saline or have become too saline during previous cropping. Leaching, in conjunction with adequate internal drainage, reduces soil salinity. Soil amendments, such as gypsum or sulfur, may be needed to reduce excessive exchangeable sodium. Since we are presently considering crop production at sea water salinities, we may dispense with further consideration of reclamation and concentrate on the control of salinity during crop production, remembering, however, that reclamation may still be needed whenever salinity control has been inadequate.

Salinity control and the nonuniformity problem

Salinity control depends on uniform water application and infiltration. Nonuniform water penetration tends to produce the barren salt spots characteristic of salt-affected fields. Salt spots may be due to poor land leveling resulting in less water being applied to the high spots in the field. Soil heterogeneity within a field may cause less water infiltration in the less permeable areas in the field.

⁴U. S. Salinity Laboratory, ARS, U. S. Dept. Agr., Riverside, California

Some effects of variable soil salinity such as poor or irregular stands are apparent early in the crop season. Even low levels of salinity may inhibit germination because salts tend to concentrate near the soil surface as the result of evaporation. Furrow irrigation, by moving salts into the plant bed, may increase salinity in the seed row by 5- to 10-fold in a single post-planting irrigation. Moderate levels of salinity tend to retard germination; higher levels of salinity prevent germination. In the latter case, seed may remain dormant in wet saline soils for months and germinate normally when salinity is reduced by leaching rains. Such effects have also been noted in salt marshes and salt deserts where they may benefit reproduction by limiting germination to favorable periods of the year. Delayed germination in crop plants is, however, undesirable since it causes nonuniform maturation and complicates harvesting.

Selection of salt-tolerant crops

Sometimes soil salinity cannot be completely eliminated as, for example, when only saline irrigation waters are available. In such cases, only those crops that can tolerate the ambient salinity can be grown. Before describing the salt tolerance of crop plants we should consider the mechanisms by which salinity affects growth and yield. These mechanisms determine which salinity parameters are most closely related to plant response.

When isosmotic concentrations of single salts are added to nutrient solutions, almost any crop will exhibit differential growth effects. Thus, bean plants are inhibited more by CaCl_2 than by isosmotic NaCl ,

whereas maize plants show the reverse effect (Fig. 1). Beans avidly take up calcium causing potassium and magnesium deficiencies or nutrient cation imbalance. Maize, however, does not take up adequate amounts of calcium from saline solutions unless calcium is increased in concentration along with other cations. For both beans and maize the specific nutritional effects are corrected when salinity is induced by mixtures of the major cations rather than by single salts. Specific proportions are usually not critical. Since salinity in the field usually involves mixed salts rather than single salts, specific nutritional effects are relatively rare. However, some crops do develop nutritional deficiencies under saline conditions as, for example, blossom-end-rot in tomato and peppers (Ca deficiency) and sulfate-induced Ca deficiency in some lettuce varieties. In such cases, foliar sprays of dilute Ca salt solutions provide the needed calcium through foliar absorption. Except for a few such cases, the osmotic potential of the soil water is the salinity parameter that correlates best with plant response. Routinely electrical conductivity (EC) is measured instead of osmotic potential, since it is easily determined and is closely related to osmotic potential in the soil water. Since the EC of the soil water depends on the water content as well as on the salt content of the soil, we measure the EC of the soil saturation extract (EC_e) which approximates one-half the EC of the soil water at field capacity. The range of EC_e values and associated effects on crop production are given by the Scofield scale:

0 - 2 mmho/cm salinity effects mostly negligible

2 - 4 mmho/cm sensitive crops affected

4 - 8 mmho/cm most crops affected by salinity

8 -16 mmho/cm only tolerant crops yield satisfactorily

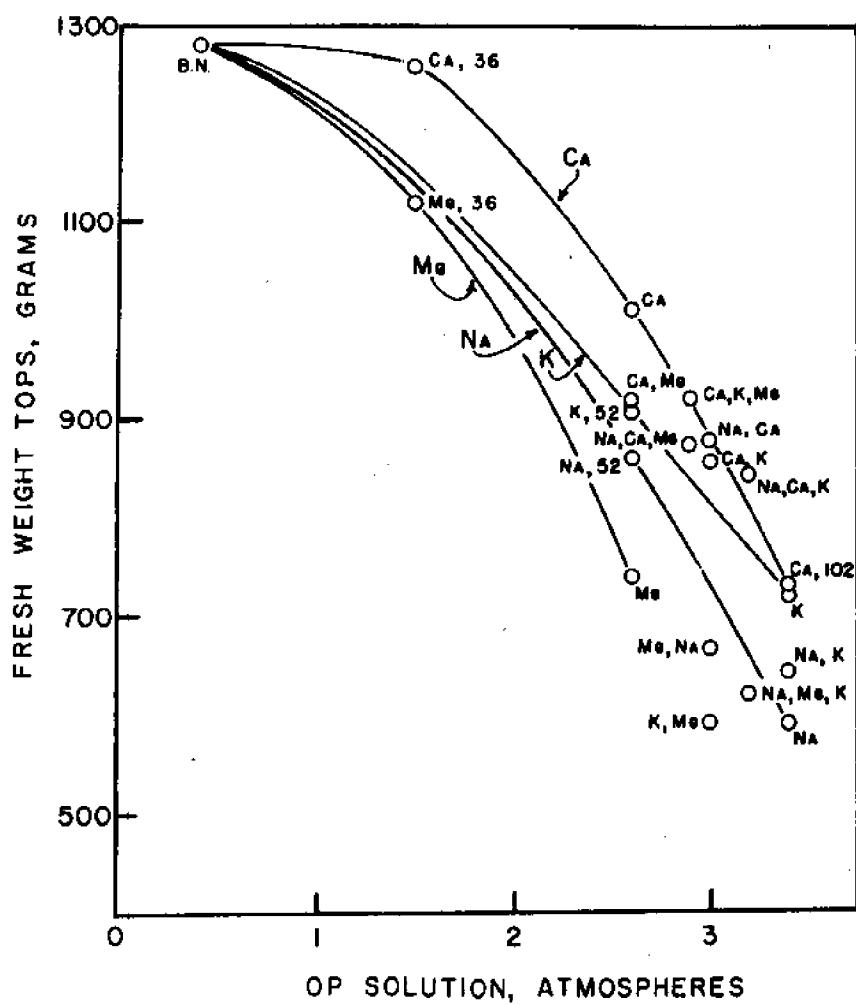


Figure 1. Relation of growth of sweet corn to osmotic pressures of media containing indicated chloride salts at 72 meq/l except for base nutrient (BN) and specified treatments at 36, 52, or 102 meq/l. (Bernstein, 1964a)

On the average, 1 mmho/cm is equivalent to 640 mg salts/liter.

In addition to the osmotic and nutritional effects of salinity, mention must be made of the specific toxic effects of chloride and sodium which occur mainly in woody species, i.e., most fruit trees, vines and woody ornamentals. Characteristic leaf burn symptoms in these species develop when leaf chloride reaches about 0.5% or leaf Na about 0.25% on a dry weight basis. Many Cl- and Na-sensitive fruit crops absorb Cl and Na through the leaves as much as a hundred times more rapidly as through the roots, making them highly susceptible to the toxic effects of these ions when the leaves are sprinkled with waters containing as little as a few meq/l of Cl or Na. Nonwoody field, forage, and truck crops are not specifically sensitive to Cl or Na injury except when sprinkled with brackish waters (i.e., waters containing about 20 meq/l or more of Cl or Na). Some fruit trees (avocado) and truck crops (cantaloupe) absorb so little Cl or Na through the leaves that they are not injured by foliar absorption of salt.

The salt tolerance of crop plants has been studied in artificially salinized plots brought to graded salinity levels by additions of salts (usually NaCl + CaCl₂ in equal parts by weight) in their irrigation waters. Growth, yield and quality are correlated with the measured EC_e's of 16 to 18 mmho/cm. In these experiments, the EC of the irrigation water approximated the EC_e of the soil. Therefore, a 50% decrease in yield occurred when the irrigation waters contained 10,000 - 12,000 mg of salts per liter or no more than 1/3 the concentration of sea water. Full yields are obtained at 2/3 the EC_e's causing 10% yield decreases.

Therefore, the sensitive crops including most of the vegetable crops produce maximum yields when the EC of the irrigation water does not exceed 1-1.5 mmho/cm. For the most tolerant crops, the EC_{iw} limit for full yields is 7-8 mmho/cm.

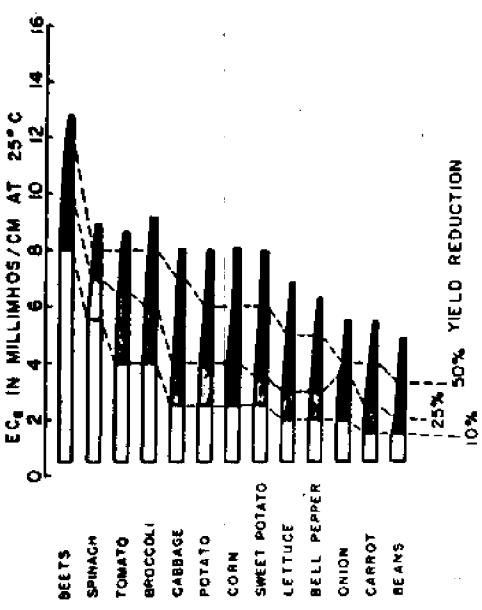
In most of these salt tolerance experiments, the 5 or 6 varieties of each crop that were studied exhibited little or no varietal differences in salt tolerance. Even when statistically significant differences were found, as among cotton varieties, the differences were small and occurred only at high salinities. Notable varietal differences in salt tolerance did occur in some forage species (e.g., bermuda grasses) and among fruit crop rootstocks that varied in their rates of chloride uptake and hence in tolerance to chloride in the root media. Because genetic stocks of most crop plants are so similar in salt tolerance, the use of existing varieties to breed for improved salt tolerance would probably achieve only limited success.

The salt tolerance data in Figure 2 are based on harvested plant products. Vegetative growth was variably related to harvest yields. Some of the more tolerant species, such as cotton and barley, exhibited much reduced vegetative growth at moderate salinities which, however, permitted full yields of fiber and grain, respectively. In other species such as maize, vegetative growth and grain yield were closely related.

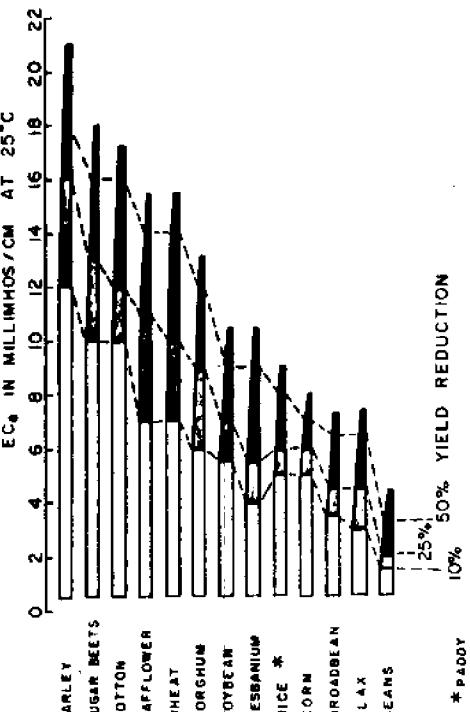
Irrigation Management

Irrigation is the most significant aspect of management for salinity control. Internal drainage must be provided, if it is not naturally

a. SALT TOLERANCE OF VEGETABLE CROPS



b. SALT TOLERANCE OF FIELD CROPS



c. SALT TOLERANCE OF FORAGE CROPS

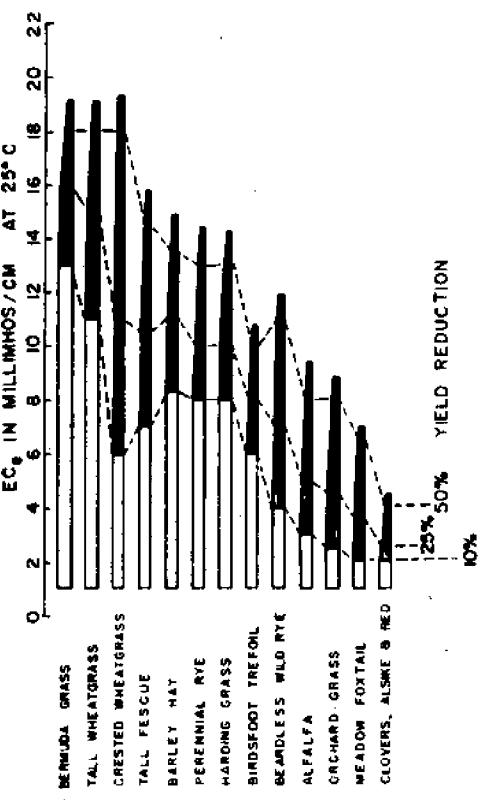


Figure 2. Salt tolerance of crop plants.

Indicated soil salinities (EC_e) were maintained from the late seedling stage to maturity except for sensitive seedling stages of small grains when EC_e did not exceed 4 mmho/cm. Crosslines indicate EC_e's at which yields were reduced 10, 25 and 50%. (Bernstein, 1964b)

adequate. Under saline conditions, plants absorb very little of the salt that is present in the water they take up. Thus, during an irrigation cycle, the residual soil water becomes progressively more saline. More frequent irrigations minimize the peaks in soil water salinity during irrigation cycles and maximize the growth potential for an irrigation water of given salinity. Recent studies with drip irrigation which provides small daily applications of irrigation water instead of larger, less frequent applications, showed the beneficial effect of more frequent applications of saline water. These studies also confirmed that sprinkling with saline water induced leaf injury that was absent when surface irrigation methods were used.

Although flood irrigation in level basins applies water uniformly, differences in soil permeability may induce differences in water penetration and localized salt accumulations. A slow rate of application that permits uniform infiltration in all parts of a field can minimize differences in soil salinity. Both drip irrigation and sprinkling have the potential of controlling water application and water penetration but, as already noted, sprinkling with saline water can be highly injurious.

To prevent excessive salt accumulation in the soil it is necessary to remove salts by the application of water in excess of consumptive use. The excess water applied may then remove salts from the root zone provided internal drainage is adequate. This concept is quantified in the term, leaching requirement. Leaching requirement (LR) is the fraction of total water applied that must drain below the root zone to restrict salinity to a level tolerated by the crop:

$$LR = \frac{v_{dw}}{v_{iw}}$$

where v is volume and dw and iw are drainage water and irrigation water, respectively.

Assuming strict salt conservation in the soil water system,

$$v_{iw} c_{iw} = v_{dw} c_{dw}$$

where c = concentration of salts. Therefore,

$$LR = \frac{c_{iw}}{c_{dw}} \cdot \frac{EC_{iw}}{EC_{dw}}$$

The minimum permissible LR (the leaching requirement) is determined for a given EC_{iw} when the maximum permissible EC_{dw} for a crop is specified.

Recent findings indicate that plants may concentrate soil water much more than was previously thought possible without injurious effects. Thus alfalfa produced equal yields when a 1 mmho/cm irrigation water was concentrated 8-fold (the previously recommended limit) or 16-fold (Fig. 3). Only when this irrigation water was concentrated 32-fold (LP = 3.1%) was yield reduced by 15%. However, when the EC of the irrigation water was 2 mmho/cm, yield was regularly 10% less than with the 1 mmho/cm water. Thus alfalfa was much more sensitive to the EC of the irrigation water than to the EC of the drainage water. A 1 mmho/cm increase in EC_{iw} affected yield about as much as a 20 mmho/cm increase in EC of the drainage water. The failure of plants to respond to the average EC of the irrigation water is explained by the differential uptake of water from zones of increasing salinity. Because of the inverse relationship

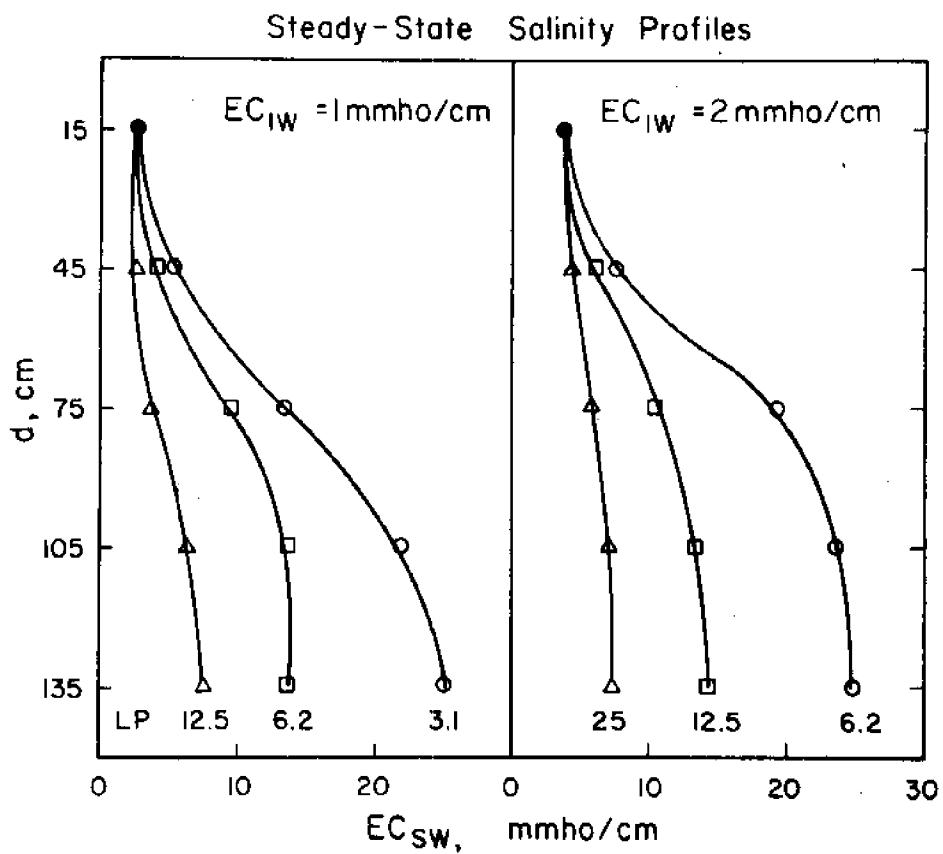


Figure 3. Representative steady-state salinity profiles in alfalfa root zones irrigated with 1 and 2 mmho/cm irrigation waters at 3 leaching percentages. (LP = 100 LF). d = soil depth; EC_{SW} = electrical conductivity of soil water. (Bernstein and Francois, 1973b).

of concentration to volume, most of the water is taken up from the least saline zone. At steady state, the mean salt concentration against which water is taken up (\bar{c}_a) is:

$$\bar{c}_a = \frac{c_i}{1-LF} \ln \frac{1}{LF}$$

Thus, effective salinity is directly related to the concentration of the irrigation water (c_i) but is related to LF mainly as a log function of the reciprocal of LF; i.e., geometric decreases of LF are required to influence \bar{c}_a appreciably.

There are, of course, limits to which plant roots can concentrate the soil water. When leaching was entirely discontinued in some treatments, alfalfa was able to increase the EC of the soil water to 35 mmho/cm. The same value is found by extrapolating the yield-salinity curve for alfalfa to zero yield at which water uptake is zero. Similar extrapolations for the most tolerant crop plants yield maximum soil water salinities of 40-45 mmho/cm, equivalent on the average to about 23,000 mg salt/liter. Thus the most tolerant crop plants become unable to absorb any water at a salinity about 2/3 that of sea water.

Although LR's have now been reduced to 1/2 or less of the previously recommended values, the LR is still large for highly saline waters. Even if crops are developed that tolerate sea water salinity, they will probably not be able to concentrate the sea water many fold, so that LF's may well be in the order of 0.5. (Cf. the stenohaline character of many oceanic plants). Seaside locations in which the tides supply fresh sea water daily and from which drainage of "ground water" could occur

naturally would be better adapted to sea water irrigation than would inland locations for which pumping costs and drainage requirements would probably be prohibitive.

Fertilization of saline soils

In the salt tolerance studies, plants were fertilized optimally to assure maximum yields. In some undeveloped countries and under some dryland conditions, lower fertility levels may be maintained and the response of plants to salinity under these conditions needs to be known. Also the suggestion has often been made that higher levels of fertility (superoptimal for nonsaline conditions) may offset the yield losses caused by salinity. In Figure 4, three possible salinity-fertility interactions are shown. In A, independent effects of salinity at high fertility (upper curve) and low fertility (lower curve) are shown. In B, fertility that is adequate under nonsaline conditions is assumed to become inadequate under saline (lower curve). In C, crop response to salinity under high fertility is shown to be absent under conditions of low fertility (lower curve).

Sand culture experiments with maize, barley, wheat and six vegetable crops have generally shown independent response to salinity and fertility (N and P levels) as in "A". When fertility was very severely limiting, a "C" type response was observed. In no case was there any evidence of a consistent B-type response although Ca-deficiencies in tomato and celery under saline conditions would represent a B-type response. Figure 1 shows that increased K levels do not increase salt tolerance of maize and this was confirmed in the later studies with even a lower base level of K supply.

Levels of P commonly used in solution culture studies (0.5-2.0 mM phosphate) were shown to cause P toxicity under saline conditions because reduced growth resulted in an accumulation of P to 1% or more in maize leaf tissues. To sum up, saline conditions do not require any special fertilizer practices, although response to fertility may be limited by strongly inhibiting levels of salinity. Poor soil conditions characteristic of some salt-affected soils may seriously restrict root development and so indirectly lead to nutrient deficiencies.

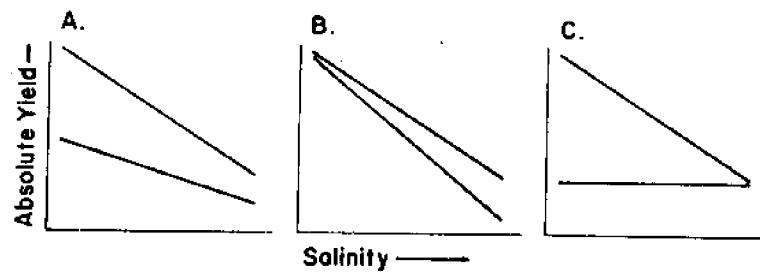


Figure 4. Types of salinity-fertility interactions. Upper line = optimal fertility, lower line = limiting fertility. (A) Independent effects of fertility and salinity. (B) Decreased salt tolerance and (C) Increased salt tolerance (relative basis) at limiting fertility. Conversely, B indicates a greater fertility response or fertilizer requirement and C a lower fertilizer response with increasing salinity (Bernstein, Francois and Clark, 1974).

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Discussion following Dr. Bernstein's paper

(GAP) - Suggested Dr. Bernstein comment about experiments with alternating salinity levels with tomato and pepper.

(LB) - Dr. Pearson remembered that he and I about 20 years ago did an experiment on alternating salinity. The question was raised earlier as to what effect this would have on salt tolerance. We used 2 test plants, pepper and tomato. With pepper we found that the response to salinities ranging between a very low level to something like 12 atm., a very high level, was just about equivalent to the average salinity that the plant experienced during the course of these systematic fluctuations. With tomato the response was even more drastic than would be predicted from the average salinity. So this sort of a thing has been looked at and variations, even systematic, carefully controlled high frequency variations of salinity, do not overcome the inhibitory effect of salt. The plant, in general, tends to respond to something like the mean salinity level.

WORKSHOP GROUP I

Workshop topics:

1. What are desirable attributes of candidate plants?
2. Which plants have such attributes?
3. Where might such plants be found?

Group participants: Moul, leader; Chapman; Cornman; Grant; O'Leary; Pihl; Ralph; Seibert; Woodhouse; Nixon, recorder.

The participants agreed to consider vegetative parts of plants as well as seeds and fruits. They classified essential attributes into three categories with respect to information available concerning them:

1. Some knowledge available

Prolific, with large fruits and/or edible vegetable parts, i.e., yield
 Readily digested
 Balanced content of protein, fat and carbohydrates
 Disease resistant
 Tolerant of up to 3.3% salt
 Useful by-products
 Fair to good quality food (palatability)

2. Very little known

Good breeder (genetic)
 Adaptable to range of climates, i.e., ecological and geographical adaptability
 Role of plant in larger estuarine ecosystem
 Processing problems minimal
 Seeds with high viability and high production
 Readily harvestable
 Accessible habitat
 Photosynthesis efficiency (C_4 -photosynthetic pathway)
 Resistant to "pollution" or environmental stress

3. Information largely lacking

Adaptable to intensive cultivation
 Weed control feasible
 Response to fertilizer
 Response to light intensity (non-saturating)
 Tillability

The group enumerated a number of potential candidate species and added their estimate of the attribute information category" (1, 2 or 3 above) and the plant part to be considered (s = seeds, f = fruits, v = vegetative parts):

<u>Candidate Plants</u>	<u>Information Category</u>	<u>Plant Part</u>
<u>Grasses</u>		
<u>Spartina</u> (15 species)	1	s, v (by-products)
<u>Bromus tectorum</u>	3 (?)	s
<u>Elymus arenarius</u>	2	s
<u>Elymus virginicus</u>	2	s
<u>Phragmites communis</u>	2	v (by-products)
<u>Distichlis spicata</u>	1 or 2	
<u>Distichlis palmeri</u> (?)	?	
<u>Setaria faberi</u>	2	s
<u>Setaria geniculata</u>	2	s
<u>Uniola paniculata</u>	2	s (by-products)
<u>Chenopodiaceae</u>		
<u>Salicornia</u> spp.	1	v
<u>Suaeda</u> sp.	1	v
<u>Atriplex patula</u>	2	v
<u>Atriplex</u> (desert spp.)	1	v
<u>Tetragonia trigyna</u>	1	v
<u>Cyperaceae</u>		
<u>Scirpus</u> spp.	3	(by-products)
<u>Juncaceae</u>		
	3	(by-products)
<u>Miscellaneous</u>		
<u>Prunus maritima</u>	2	f
<u>Rosa rugosa</u>	3	f
<u>Zostera marina</u>	1	s
<u>Ruppia</u>	2	s (brackish water)

<u>Candidate Plants</u>	<u>Information Category</u>	<u>Plant Part</u>
<u>Potamogeton pectinatus</u>	3	s
<u>Thallassia</u>	3	v
<u>Phyllospadix</u>	3	v, s
<u>Mesembryanthemum crystallinum</u>	2	v
<u>Sesuvium pertulacastrum</u>	2	v
<u>Typha angustifolia</u>	2	v (by-products)
<u>Typha domingensis</u>	2	v (by-products)
<u>Avicennia germinans</u>	2	v (seedlings)
<u>Polygonum glaucum</u>	3	s
<u>Coccoloba uvifera</u>	2	f
<u>Lathyrus japonicus</u>	3	s
<u>Lathyrus latifolia</u>	3	s
<u>Chrysobalanus</u> sp.	3	f
<u>Hibiscus palustris</u>		
<u>Cakile edulenta</u>	1	v, s
<u>Cotula coronopifolia</u>	2	s (?)
<u>Erechtites hieracifolia</u> var. <u>megalocarpa</u>	2	s (?)

Cultivated plants

Brassica spp.

Beet root

Cabbage

Radish

Barley

Rice

Asparagus

In the judgment of the group the following were "front runners":

Seeds: Spartina, Zostera, Elymus

Vegetative: Salicornia, Spartina, Zostera

Fruit: Prunus

WORKSHOP GROUP II

Workshop Topic:

"How should a program such as posed by the problem statement be carried out?"

- What are the first steps?
- What follows after these first steps?
- What parts of the program should (could) be conducted simultaneously?
- Which can be done sequentially? What sequence?

Group Participants:

Gaither, leader; Attaway; Benton; Fieldhouse; Goodman; Bergelin; Riley; Liebhardt, recorder.

Prior to answering the general questions posed in the Workshop Topic, the group felt a need to clarify and put the whole subject into perspective. This was done so that each member of the group would have a better idea of the overall thrust of the research.

Following is a general outline of the project as Group II sees the problem:

Goal 1 - To make substantial progress in 10 years toward identifying, domesticating and bringing to consumer acceptance plants tolerant to salt, i.e. 10,000 to 30,000 ppm. In accomplishing this the following will be determinatives:

- a. plants which bear seeds usable as foods
- b. leaf protein extract as a possible alternative food source
- c. total production in terms of:
 1. high, sustained yields
 2. large marine areas

Goal 2 - Identify plants tolerant of brackish water and grow halophytes under brackish conditions.

These halophytes might be grown in tidal areas, flood marshes, and/or inland areas. (Offshore areas were specifically excluded from consideration.)

Justification: Forecasts are for a further aggravation of the present circumstances which are characterized by:

1. Shortage of land
2. Shortage of water
3. Shortage of food

Accomplishing these goals will help ameliorate these shortages.

After identifying and accepting the above goals, the group addressed itself to the following questions:

1. What are the first steps during the first phase of this research?
2. What follows in the second phase and beyond?
3. What are important characteristics of staff and facilities? What will constitute a critical mass?

Other questions posed but not considered due to lack of time were:

4. What parts of the program should be conducted simultaneously and what parts can be accelerated?
5. What and where are important affiliations and contacts for the staff of the program? Also, where might one go for additional support?
6. What will these plants be competing against and what existing products might these plants complement?

In considering each question, points or ideas concerning it were submitted individually by members of the Group. Then a vote was taken to ascertain the sequential order to be followed and/or the importance of each idea. The results follow: (The designation M indicates that this a management decision or input. The rankings are the result of a consolidation of individual votes. A low number indicates a high rating. The responses are tabulated in order of the rating; not as they were developed by the Group.)

QUESTION #1. What are the first steps during the first phase of this research?

	<u>Sequence*</u>	<u>Importance*</u>
Disseminate conference results and solicit reactions	1	2
Complete the State of the Art Literature Review	3	1
Establish criteria for candidate halophytes	2	3
Make a list of candidate halophytes	8	4
Analyze candidates to see if criteria is met	4	10
Establish a seed bank for candidate plants	6	9
Define type of plant to be developed	10	6
Determine extent of potential resource extension	4	12
World solicitation for seed bank	9	8
Select smallest number of candidate plants	7	11
Identify underutilized coastal land resources	13	5
Identify characteristics of water adjacent to available lands	15	7
Design experiments and test facility	12	13
Grow test plants under simulated natural conditions	11	15
Environmental impact	14	14
Develop a management plan	M	M
Develop objectives for additional funding	M	M
Identify needed human and physical resources	M	M
Prepare 5-year plan for funding	M	M

*Steps listed in increasing magnitude of combined rating.
M ratings arbitrarily listed last.

QUESTION #2. What follows in the second phase and beyond?

	<u>Sequence</u>
Study physiological response of candidate selected	1
Selection program to maximize yield	2
Breeding and selection program	3
Continue or initiate early experimental programs	4
Develop cropping, production and harvesting systems	5
Establish field stations	6
Insect and disease observations	7
Study ways to modify environmental impact	8
Define promising sub-programs	9
Publish up-to-date program results (consider newsletter)	10
Establish a pilot commercial farm	11
Processing and marketing quality	12
Evaluate sociological-economical impact	13
Assess consumer acceptance	14
Check for pharmacological potential	15
Determine potential for environmental improvement	15
Develop economic parameter to go into business	17

QUESTION #3. What are important characteristics of staff and facilities?
 What will constitute a critical mass?

	<u>Importance</u>
Close-working team	1
Multidisciplinary staff	2
Critical mass of 5 professional people min. (if min. red tape)	3
Energetic and knowledgeable leadership	4
Food production orientation	4
Establish operational center (easy comm.)	6
Basic team: Director, Plant Breeder, Physiologist, Estua. Ecologist, Agronomist, Economist, Pathologist	7
Ample environmentally controlled space (phytotron)	8
Capability for organic and inorganic analysis	9
Need systematist, geographer, planner (1st year)	10
Plan for broadening staff and scope	11
Field station	13

WORKSHOP GROUP III

Workshop topic: What technological problems might be expected if the goals of this program are accomplished?

Group participants: Morehart, leader; Cotnoir; Oelke; Pearson; Smith; and Scarborough, recorder.

The group divided the topic into two areas of concern, namely:

1. identification of candidate plants, and 2. adapting of promising candidate plants for agricultural production.

1. Identification of candidate plants - discussion focused on the criteria for selection of candidate plants, suggested by Dr. G. Fred Somers, which stated that candidate plants should:

- grow in saline habitats naturally
- produce abundant seeds
- produce relatively large seeds
- possess potential food attributes of edibility, taste, and similarity to existing foods.

The criteria for selection were deemed sound and several areas of concern in respect to possible technological problems were identified:

- a) Logistics of germplasm collection and the identification of habitat requirements. Obviously plants must be collected and tested, but to do so implies a knowledge of plant and habitat characteristics. Two alternative approaches were recognized: 1) An empirical collection of species for testing under more or less standardized conditions, 2) A careful study of the microenvironment of promising candidate plants with a view toward simulating those conditions when culturing the plants.
- b) Soil survey. Candidate plants must be matched to specific soils and areas. This might be accomplished by characterization of the soil as to environmental factors, native fertility, analysis, topography and inundation.
2. Adaptation of promising candidate plants for agricultural production--the experience of the Minnesota research group (Oelke *et al.*) in the cultivation of Zizania aquatica served as a model for discussion of potential technological problems. The most important areas of concern were:
 - a) Soil management. One must consider the maintenance of favorable levels of nutrients. Undesirable species (weeds) might be controlled by either physical or chemical means. The physical construction of any necessary impoundment structures was not considered to be a major problem.

- b) Cultural practices. A number of factors need consideration:
1) Weed, insect and disease control; 2) Introduction of mycorrhizae, if necessary; and 3) Modification of present or future equipment needed for plant culture.
- c) Processing and storage. Modification of present technology will be dependent upon the crops which are selected.
- d) Energy input-output relationships will need to be evaluated.
- e) Economic feasibility. To achieve a demonstration of the economic feasibility of commercial production and marketing it will be important: 1) to attract funds for commercial development; 2) that the marketable product accommodate existing consumer preferences or that it be utilized with existing products.
(It is less expensive to modify products than to attempt to change consumer tastes or preferences.)

WORKSHOP GROUP IV

Workshop topics:

1. Selection, adaptation, and breeding of existing food crops to increase their salt tolerance.
2. Selection, adaptation, and breeding of halophyte plants as new, major food crop plants.
3. Use of halophytes as gene sources to develop "new" halophytic crops.

Participants: Vincent, leader; Bernstein, Felger; Garbisch; Jensen; Svec, recorder.

Their major recommendations were:

1. If the option is for the use of sea-water salinity level, then halophytes must be developed as food crops and/or new halophytic crops synthesized by genetic engineering and/or conventional breeding techniques.
2. If the option is for use of brackish water, then selection, improvement, and conventional breeding techniques must be used to increase tolerance to salinity in current food crops and this is the most likely, feasible route.

They summarized their discussion of the three Group IV workshop topics into four areas:

1. Adaptation of current food crops to sea water salinity is virtually impossible.
2. Adaptation of current food crops to brackish water salinity is a good possibility, is being done with certain crops, and has been demonstrated adequately to be feasible.
3. Information about halophytes is generally lacking and needs to be collected.
4. Synthesis of new crops has potential, but current techniques are undeveloped and possibilities may be long term.

These summary statements are derived from a consideration of the advantages or disadvantages of the three options outlined below:

A. Selection, adaptation, and breeding of existing food crops to increase their salt tolerance.

Advantages

1. Large body of physiological data presently exists.
2. Techniques for crop improvement exists.
3. Large germplasm exists, much is known about this germplasm.
4. Most valuable genes are known.
5. Acceptance and marketing is established.
6. Processing techniques are established.
7. Cultivation technology developed.

Disadvantages

1. There is an apparent finite limit to salt "tolerance," which precludes use of sea water salinity in such plants.
2. Poor prospects for use of existing crops due to lack of tolerance.
3. Would duplicate ongoing research to do this here.
4. Reduced yields possible from plants used.
5. Selection for tolerance may reduce palatability.

<u>Advantages</u>	<u>Disadvantages</u>
8. Includes crops of known tolerance to brackish waters. (Can use crops currently adapted to brackish water and saline soils.)	6. Possibility of results from effort low in terms of economic return.
9. Could yield possible short term positive results.	7. May require extensive environmental modification.
10. Could have major impact on food supplies.	
11. Specialty crops could be developed to utilize brackish water.	
12. Some demonstrated positive nutritional and palatability effects.	
13. Possible positive environmental impact.	
 B. <u>Selection, adaptation, and breeding of new halophyte plants as food crop plants.</u>	

<u>Advantages</u>	<u>Disadvantages</u>
1. "Tolerance" to all levels of salinity feasible. (High diversity of plant materials give range of salinity tolerance possible.)	1. Lack of information about salt tolerance physiology of halophytes.
2. Demonstrated high productivity in plants growing in sea water.	2. Effects of salinity on yield in halophytes little known.
3. Many species of edible halophytes available.	3. Germplasm pool of unknown size and distribution.
4. Potential in use of rhizome material as well as seed for food.	4. Genetics of halophytes poorly known.
5. Halophytes already used as secondary food source, may be suitable for human use (i.e. they have no toxic component now.).	5.* Germplasm is rapidly disappearing.
6. Some practical cultivation of halophytes already under way.	6.* Ethnic knowledge of edible halophytes is being lost.
7. Germplasm collection needed.	7. Vegetative reproduction generally indicative of low seed yield, with many exceptions (Dr. Felger mentioned many).
8. Ethnobotanic research provides a diverse germplasm pool.	8. Extensive requirement for inventory and evaluation of halophytes as food, considering farming, etc.
	9. Education of consumer will be necessary.

<u>Advantages</u>	<u>Disadvantages</u>
9. Allows use of many non-arable lands.	10. Breeding prospects long range and payoff period may be long term.
10. Many specialty crops possible (markets, use?)	11. Probability of major food production unknown.
11. Relatives to current food crop species are halophytes, therefore, plant breeding techniques may be used and useful.	(*Items starred could be used for justification)
C. <u>Use of halophytes as gene sources to develop "new" halophytic crops.</u>	
1. Include many of the advantages of use of current food crops.	1. "Halophytic" genes are unknown.
2. Possibility of short term success.	2. Physiology of halophytes little known.
3. No ongoing research	3. Standard plant breeding techniques probably not usable.
4. Many known halophytic close relatives to current food crop species, therefore plant breeding techniques may be used and useful.	4. Requires genetic engineering.
5. Long range promising.	5. Strong possibility of being totally unsuccessful.
6. Time span very long.	

Although each advantage or disadvantage may not have had the same support from each member, each member did have ample opportunity to get his ideas listed and those listed represent the total contribution of the committee.

GENERAL DISCUSSION

The concluding session of the Conference was devoted to a general discussion in which all present were invited to participate. The questions considered in this session were:

Could the goals of this proposed program be accomplished?

What would it take to accomplish them?

Would it be worthwhile?

The response to the first question was clearly in the affirmative. An uncontested statement was made that the adaptation of present land crops to sea-water salinity is unlikely¹. On the other hand, there are seed-bearing plants which grow successfully in areas subjected to inundation by highly saline water at every tidal cycle. Others grow where they are repeatedly drenched by spray from the surf. Still others grow in saline inland habitats. Confidence was expressed that one or more species from among these could be found with sufficient potential to be exploited in this program. Some concern was expressed for size of the seeds or fruits and other attributes less desirable

¹ Emanuel Epstein, who was not in attendance at this conference because of prior commitments, probably would have disagreed had he been present. In a private communication he reports "(1) that we are using a composite cross of barley incorporating over 6000 lines from all over the world to make selections for salt tolerance; (2) that barley genotypes differ markedly in this respect, affording therefore the genetic base for selecting and breeding for this trait; (3) that salt tolerance may vary appreciably during the life cycle of the plants, lines that are quite salt tolerant early (germination and establishment of seedlings) not necessarily being tolerant later on, and vice versa; and (4) that, for barley at least, salinization of solution cultures with a synthetic sea water salt mix is generally less harmful than salinization with NaCl only." Ed.

than conventional crops. Again the consensus was that this could be overcome by selection and breeding. We really don't know enough about seed-bearing halophytes to know what are the possibilities as to size of seed, dwarfism or other desirable characteristics, but the chances of success in developing a product that would serve as a food crop are good. Bernstein in commenting on the draft of this discussion emphasized

the slow growth and low productivity of most halophytes under highly saline conditions. Salt bushes (Atriplex spp. and Sarcobatus vermiculatus, etc.) are able to survive under saline conditions but grow best at quite low salinities. . . . Only Salicornia and obligate halophytes such as pickleweed (Allenrolfea occidentalis) have a broad range of tolerance extending to and beyond sea water salinities."

Reference was made also to recently developed techniques in cellular and molecular biology which would permit "genetic engineering" to produce new, desirable genomes. The potential for crossing halophytes with non-halophytes exists, but the requisite techniques are not yet available. Halophytes might serve as a gene source to create new crops. The presence of a gene for male sterility has facilitated mass selection for desirable traits in barley which permits a relatively rapid identification of desirable genes. In short, the consensus of the group was that species with the desired attributes could be found and/or developed and that the technology for their exploitation was either available or could be developed. If we are going to use sea water to grow food crops, halophytes must be developed.

Some specific points raised might be mentioned to point up this position. It was stated that there are some 19,000 miles of desert seacoast in the world. Possibly one could use sea water to irrigate such areas. Another way to go would be to grow in sea water. Culture of sea grasses in shallow water was cited as an approach. The possibility of using or developing salt marsh pools for culture of submerged halophytic seed plants was suggested. A question was raised about the potential food value of rhizomes, etc. which might be produced in muds of tidal flats or estuaries. The potential of using nutrients supplied to an estuary by sewage effluents was cited as a possible approach to food production with simultaneous environmental improvement. Reference was made to Ryther's use of sewage effluents plus sea water from Nantucket Sound in maintaining large cultures of diatoms to feed to oyster spat.

In addition to seeds, rhizomes and other plant structures should be considered.

Would it be worthwhile? One response was to ask if it would be morally defensible further to expand our food-producing potential to accommodate a concomitant increase in world population which might then suffer more massive starvation. An affirmative reply was given by conference members. The view was expressed that population stabilization was required. It was suggested further that the food supply situation was almost certain to become far more grave before population limitation has been effected. The current food shortage in parts

of the world was recognized and the view was expressed that this would be even more severe by the end of the century. It would take about that time to develop halophytic food plants. Hence, research should be started now to provide an alternative to conventional food sources. Germaine to the precarious food-supply prospect was a reference to a statement by Handler²:

We still have urgent needs to provide fundamental designs for extremely intensive, very high-yield agriculture, to learn how indeed to take advantage of offshore opportunities for intensive agriculture of molluscs and, perhaps, of higher marine organisms, to breed wheat of more useful protein content, to find suitable alternatives to the dependence of man, globally, on just a few staple crops--rice, wheat and corn. This dependence on only three cereal types offers the terrifying prospect of a worldwide pandemic of a virus to which no strain of one of these might be resistant.

(Underlining added.) Reference was made also to limitations that have appeared in varieties upon which the "Green Revolution" was founded.

The group expressed their view of what it would take to accomplish the goals of this program only in the most general terms, partly because this had been considered as one of the workshop sessions and partly because there was not time to come to grips with detail. The consensus was, however, that it would require a major effort over a rather long period of time. Only with substantial financial support on a continuing basis can the interest of qualified researchers be attracted and maintained. It was a task that should be guided by a mature scientist

²Philip Handler, Ed. *Biology and the Future of Man*, Oxford Univ. Press, 1970, p. 900.

(or scientists) willing to make the necessary commitment and not be overawed by the prospect of failure.

Briefly stated, the consensus of the group was that it definitely would be worthwhile. Whether it can or will be done is largely a question of funding.

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