
Feasibility of Halophyte Domestication for High-Salinity Agriculture

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Abstract

We discuss the process of domesticating wild halophytes to serve as crop plants using seawater irrigation. First steps in this domestication involve determining whether halophyte species exist that may produce significant amounts of a usable product under seawater irrigation and that this is a sustainable agronomic practice. This is followed by development of strategies to improve crop productivity via selecting appropriate species for domestication and then affecting agronomic traits through plant breeding. We demonstrate that halophytes may be productive under seawater irrigation, that this management system may be sustainable, and there are demonstrated pathways toward domestication.

Keywords

New crops • Crop domestication • Salinity • Salt-affected soils • Seawater • Drainage water reuse • Halophytes

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1 Introduction

Concomitant with increased human population and demands for food, fiber and energy crops has been a worldwide increase in irrigated agriculture. Unfortunately, this has also resulted in increases in salinized cropland where most non salt-tolerant crop plants are unproductive. This, along with a desire to utilize naturally saline soils or water for crop production, has led to interest in alternative, salt-tolerant crop plants and cropping systems often using saline water. Only limited progress has been made in developing salt-tolerant varieties of

conventional crops, due to the complex anatomical and physiological attributes needed to confer tolerance and the multigenic nature of tolerance mechanisms [1–3]. A more prudent approach may be to attempt to domesticate wild halophytes that have evolved inherently high salt tolerance [4]. Halophytes are defined as plants which complete their life cycle where salt concentration is equivalent to at least 200 mM NaCl in the external medium equal to 11.6 g L⁻¹ Total Dissolved Solids (TDS) under conditions similar to those that might be encountered in the natural environment [5], whereas others use 5 g L⁻¹ TDS to define a halophyte [6]. In general, 5 g L⁻¹ TDS is considered to be the extreme upper limit for salt content of irrigation water for conventional (i.e., glycophytic crop plants) [7].

In this overview paper, we address three points that have been raised as obstacles to the use of halophytes as crops. First, that halophytes have inherently low productivity; second that irrigation with saline water is not a sustainable practice; and third that as wild plants, halophytes have numerous traits that may make them undesirable as crop plants.

2 Halophyte Productivity

Interest in halophyte crop production began during 1950s [8–10]. An international effort to develop halophyte crops was undertaken in the 1970s, enunciated as the “Biosaline concept” for production of food, fuels and chemicals using non-traditional soils and water supplies [11], such as reclaimed drainage water from irrigated crop land or seawater. However, the concept was met with skepticism by many agricultural scientists. U.S. Department of Agriculture Salinity Laboratory stated, “We do not anticipate practical use of seawater for agriculture nor high levels of production per unit area of halophytes” [12]. More recently, a halophyte ecologist, concluded, “A sustainable agriculture based on irrigation with seawater on a large scale seems to be still an utopic illusion” [13]. These statements were largely based on the assumption that halophytes are not as productive as conventional crops. Here productivity was sometimes defined as in traditional cropping

systems, generally as mass of usable product (e.g., seeds or fruits) per unit of area over a cropping season. However, in some cases emphasis was only on total plant biomass and did not include harvest index (the proportion of total plant biomass that represents a usable product) in making these comparisons. Nevertheless, field and greenhouse trials conducted over the past 40 years clearly show that halophytes can maintain high productivity of biomass and seeds/fruit on root zone salinities up to seawater and beyond.

The evidence for a tradeoff between high salinity tolerance and reduced growth rates has been previously given [3]. They compared relative growth rates (RGR) by measuring total plant biomass of euhalophytes (the most tolerant species, able to grow on seawater) and less tolerant miohalophytes (less tolerant but able to grow on brackish water) with non-halophytes under both saline and non-saline conditions. The growth rates of the three classes of plants did not differ significantly ($P \leq 0.05$) under non-saline conditions, showing that halophytes are not inherently slow growing plants. As expected, halophytes outperformed non-halophytes under saline conditions. Furthermore, the salinity for optimal RGR of the euhalophyte *Salicornia dolichostachya* was 300 mM NaCl (17.1 g L⁻¹) in the greenhouse, and that high productivity (total plant biomass) was maintained up to full seawater salinity in field experiments [14].

A series of productivity trials have been undertaken with halophytes under agronomic conditions, with salinities varying from brackish (1–20 g L⁻¹ TDS) to full-strength or even hypersaline salinity (30–40 g L⁻¹ TDS) [15]. Some of these have involved plot trials of several hundred ha (Fig. 1). Table 1 lists biomass and seed yields of a selection of halophytes under cultivation and gives references to publications. Biomass yields of the most productive species have been in the range of 10–20 t ha⁻¹, within the range of conventional forage crops. Seed yields of the euhalophytic species *Salicornia bigelovii*, a potential oilseed crop, have ranged from 1 t kg ha⁻¹ under large-scale cultivation to 2 t kg ha⁻¹ in small plot trials, under full seawater irrigation. These are similar to yields of conventional oilseed crops [22].



Fig. 1 Upper panel: 200-ha *Salicornia bigelovii* farm irrigated with seawater in Eritrea, Africa. Lower panels: mechanized *Salicornia* harvest and center pivot irrigation with seawater in Raz Al Zawr, Saudi Arabia

Table 1 Examples of halophyte biomass and seed yields under in different agronomic settings

Location and species	Yield (dry tonnes ha ⁻¹)	Soil type	Irrigation salinity (g L ⁻¹)	Reference
Safford AZ				[16]
<i>Atriplex barclayana</i>	14.7	Loam	0.6	
<i>A. nummularia</i>	12.3	Loam	0.6	
San Joaquin CA				[17]
<i>A. barclayana var sonora</i>	11.1	Clay	1.0	
<i>var barclayana</i>	9.2	Clay	1.0	
Marana AZ				[18, 19]
<i>A. lentiformis</i>	20.1	Loam	2.0	
Puerto Penasco Mexico				[20, 21]
<i>A. lentiformis</i>	17.9	Sand	4.0	
<i>Batis maritima</i>	17.4	Sand	4.0	
<i>Salicornia bigelovii</i>				
Biomass	15.4	Sand	4.0	
Seed	2.0	Sand	4.0	

3 Sustainability of High-Salinity Agriculture

The initial reaction of agricultural engineers to the prospects of high-salinity agriculture was negative. Starting in the 1950s, institutions such as the USDA Salinity Laboratory in Riverside, California, began emphasizing the hazards that even mildly saline irrigation water poses to crops and soils [23]. Irrigation water with a salinity of only 1.44 g L^{-1} TDS was classified as presenting a very high salinity hazard and was declared to be not suitable for irrigation under ordinary conditions [23]. In the 1970s, recommendations for managing salinity called for large leaching fractions to maintain crop productivity, and surface or subsurface drainage systems to convey saline water away from the fields for off-site disposal [7, 24]. Of course, these recommendations were based on the reality that agriculture at that time was dependent on glycophytic (non salt-tolerant) crop species with very low levels of inherent salt tolerance.

However, attitudes towards the use of saline water are changing. It was realized early on that while sodic (high sodium) water can cause dispersal of clay particles that impairs permeability, this effect disappears when the total electrolyte concentration exceeds about 15 meq (e.g., $0.85 \text{ g L}^{-1}\text{NaCl}$) [25]. Hence, high salinity water is not inherently damaging to most soils. Faced with the need to recycle saline drainage water within irrigation districts, Qadir and Oster evaluated over 30 years of research from around the world and concluded that high-salinity water may be used as part of sustainable agricultural systems where disposal of drain water outside the district is not possible [26]. Furthermore, a reevaluation of crop leaching requirements has concluded that previous guidelines recommended much more water than was actually needed, due to the high degree of self-regulation in the plant-soil-water system [27]. The new recommendations recognize that plants do not respond to the average root zone salinity, as was assumed in the original recommendations, but instead use water from the lowest-salinity portion of the root zone, which is near the soil surface for flood-irrigated plants.

This is fortuitous, as fresh water supplies are under increasing pressure for multiple uses, and disposal of large volumes of agricultural irrigation drainage water has become problematic due to environmental concerns. Hence, a paradigm shift is occurring in many elements of the agricultural community towards the potential use of saline water for crop production.

A number of multi-year plot trials have been conducted with halophytes with no reported decrease in yield or negative impacts in soil structure due to saline water irrigation [16–18, 20, 21, 28]. Perhaps the longest continually operated halophyte trials were conducted at Kino Bay, Mexico [29]. This 20-ha farm was flood-irrigated with $2\text{--}3 \text{ m year}^{-1}$ of seawater from 1986 to 2010 to produce *Salicornia bigelovii* as an experimental oilseed crop. Crop yields obtained in yield trials in 2007–2008 showed biomass and seeds yields were still within the range of conventional crops [30].

There was also concern that extreme (and uneconomical) agronomic practices would be required to produce halophytes on high salinity water. Seawater along coastal deserts typically contains $38\text{--}42 \text{ g L}^{-1}$ TDS, whereas optimal growth is obtained at half this salinity [14]. At seawater salinities, frequent irrigation and a generous leaching fraction are required to maintain halophyte productivity. In lysimeter studies, maximum productivity of *S. bigelovii* required 3 m year^{-1} of seawater in a coastal desert environment in Mexico [31]. Approximately 35 % of this was the leaching fraction, required to maintain the soil solution in the root zone at 80 g L^{-1} TDS or lower. This is at the high end of water application rates for conventional crops in arid zone irrigation districts. However, in large flood-irrigated plantings, irrigated at 3–5 day intervals, as much as 5 m of water can be applied over a cropping season [30, 31].

Analysis of pumping costs supports the use of seawater for irrigation, even in large quantities under certain circumstances. Pumping costs, whether expressed as dollar costs for electricity or liquid fuel, or as carbon equivalents to take into consideration the carbon balance, are a function of the volume of water pumped and the lift of the well. Typical agricultural wells lift water

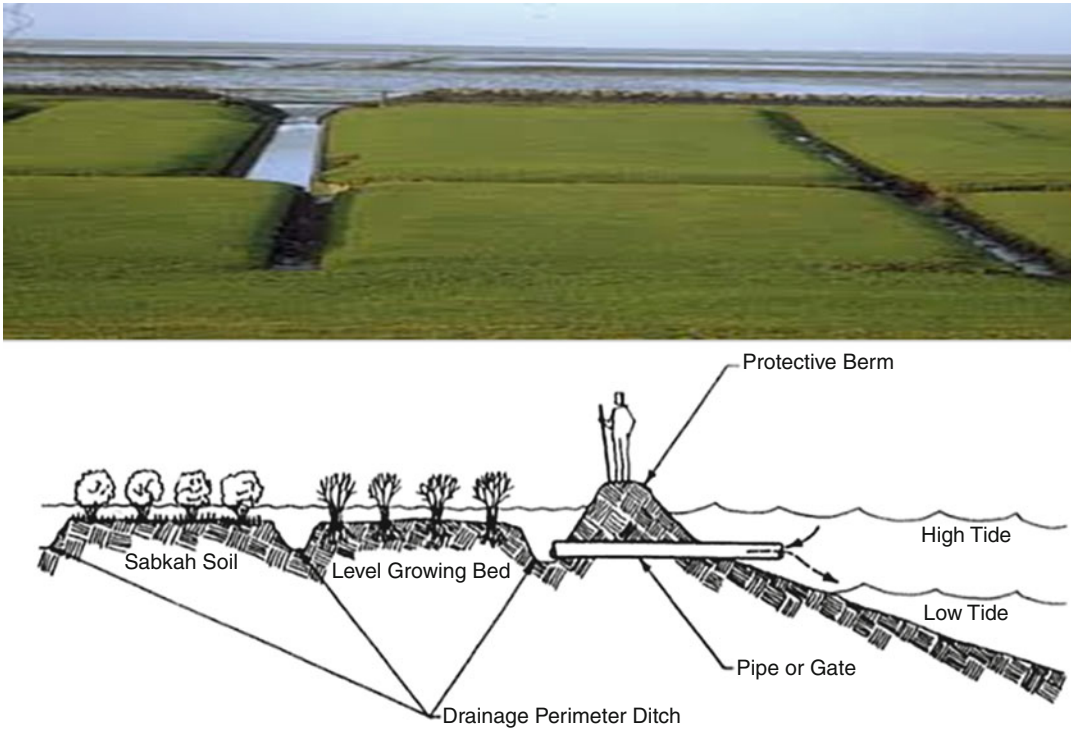


Fig. 2 Tidally irrigated *Salicornia bigelovii* beds at Jubail, Saudi Arabia

from 20 m to as deep as 100 m, whereas the lift of typical coastal seawater wells is only 3–10 m. Furthermore, tides can be used to irrigate crops without the need for pumping in some locations (Fig. 2) [28]. A demonstration project conducted for the Electric Power Research Institute concluded that the total carbon expenses of producing, harvesting, baling and delivering to roadside a halophyte crop on seawater was one-third the amount of carbon fixed and similar to conventional proposed biofuel crops [28].

has been responsible for affecting such traits in most crop plants [32]. Very little has been reported on selective breeding of halophytes, with the exception of a preliminary study on *Salicornia bigelovii* [33]. Hence, the following sections outline a strategy for improving halophytes similar to what has been accomplished with other wild plants, with the goal of determining if halophytes might offer special challenges not presented by the numerous species of wild plants previously domesticated.

4 Considerations for Domestication

Perhaps the greatest impediment to uses of halophytes as cultivated plants has been undesirable crop characteristics in these wild species. Traits such as uneven germination, lack of seed retention, and toxic substances in tissues, while adaptive for wild plants, are not typically desirable in crop plants. Genetic modification, whether conscious or natural, during long periods of domestication

4.1 Basic Considerations

Here we define domestication as consistent successful cultivation and harvest of a formerly wild plant under commercial agricultural conditions. Domestication is typically a long-term process and the timeframe to domesticate a crop can be on the order of decades [32, 34].

Before undertaking any experimentation, the first obvious steps are to consider the desired product(s) within the context of available botanical

and agronomic resources. Halophytes can be grown to produce oilseeds, grains, forage, fuel, food, medicine, chemicals, timber and fiber [30, 35] or be used for soil or water conservation or remediation [36, 37]. Economic assessments should be conducted to ensure that there will be a market for products and that they may be produced at a cost that is competitive with conventional crops, although this can be difficult given the agronomic unknowns associated with halophyte culture. Additionally, the desired crop should not adversely affect water supplies or land that could support conventional agriculture.

A primary consideration is where the crop might be grown. For example, if one is considering growing a crop in coastal land using seawater, then one is limited to halophytes with high salinity tolerance (euhalophytes), and thus there are fewer species from which to sample. For growing crops in inland brackish water of lower salinity, then there are a greater number of species to consider. It is advantageous to examine species from climate regimes and perhaps latitudes similar to those where the potential crop is being planted, as the candidate species will be better adapted to local environmental conditions. More generally, consideration of plant growth and development including the plant's life cycle in nature is critical in identifying candidate species for evaluation and in developing agronomic practices for their production. There are both annual and perennial halophytes that under consideration for domestication, as well as monocots and dicots, and monoecious and dioecious species [30].

4.2 Domestication Syndrome

The domestication syndrome is defined as the suite of traits whose expression indicates that a recent domesticate has diverged from its wild ancestors and is adapted to cultivation [38, 39]. These traits may include seed retention (loss of seed shattering), loss of seed germination inhibitors, synchrony of germination, flowering and fruit development, and increase in fruit or seed size; changes in secondary metabolites (e.g., loss of bitter or toxic compounds) [39, 40].

Many wild halophyte species are known to have various seed dormancy mechanisms to allow them to germinate under ideal conditions in nature [41]. Seed ripening and retention may also be a major factor limiting halophyte domestication. For example, although seed yields of *S. bigelovii* under seawater irrigation can approach conventional oilseed crops under optimal conditions, yields are reduced under mechanical harvest due to uneven seed ripening and shattering of seeds [30]. Similarly, the seeds of *S. bigelovii* contain saponins, which can have deleterious effects on animal growth limiting the use of oilseed meal in animal diets [21, 30]. However, a 25 % larger seed size in populations was reported in plants that had been cultivated for several crop cycles and harvested with mechanical equipment, suggesting that at least this species is subject to improvement through mass selection [33].

4.3 Development of Crop-Appropriate Production Regimes

A critical element in many crop domestication strategies involves the development of agronomic systems that are appropriate for the new domesticate and the target environments in which its use is proposed. In the case of most crop plants, this process occurred mostly via cultivator empiricism, often with significant trial and error over hundreds of years [39]. Modern crop domestication aims to greatly accelerate this process and to replace unsystematic cultivator activity with deterministic planned experimentation. In most cases of modern crop domestication, an existing agronomic system is modified for a new crop. This might not hold for halophytes, however, as there are constraints of the use of highly saline water that do not exist for conventional crops.

4.4 Plant Breeding

In some cases, heritable genetic variation may exist in domestication syndrome traits within

wild plants that could be efficiently exploited within plant breeding programs [32]. Indeed, some modern crops exist in various states of domestication and some such as the cranberry (*Vaccinium* spp.) are commercially viable with very little domestication [40], indicating that it may be feasible to grow some crops without complete control of reproduction. However, it is important to note that near domesticates like cranberry or many forage plants are successful as crops because they can be grown in environments that are very similar to those in which the plant occurs in nature [32].

Plant breeding tactics within halophytic species could vary from traditional mass selection and progeny testing to marker - assisted breeding, to using deterministic genetic modification approaches [34, 42]. As in all crop improvement through plant breeding [43], affecting the domestication syndrome or productivity characteristics in halophytes will depend on the existence of (1) heritable and useful genetic variation for traits of interest, (2) a means to consistently identify this variation, and (3) an ability to regularly replicate agronomically acceptable phenotypes within target environments. Experiences with food crop domestication [32, 39] have shown that meeting each of these requirements is by no means trivial, and genetic improvements have often been based on hundreds of experiments, often conducted over decades, and with many failures. For the vast majority of halophytes we are just at the beginning of this process and we know very little about each of the key foundations required for significant crop improvement.

5 Conclusions

In order to manage the growing demand for agricultural products, utilization of marginal lands and water sources should be considered. We believe that halophytes can be grown using high salinity water in soils that could not support conventional crops. Halophyte crop yields can equal yields of conventional crops grown on freshwater. Additional steps toward domestication will require identifying the correct plant species for the target

environment and application and eventually improving wild plants through crop breeding.

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