

Halophytic Crops for a Salinising World

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Abstract. Soil salinisation is an increasing problem for agriculture, affecting the most productive crop areas in the world – those cultivated under irrigation in arid and semi-arid regions. In addition, a significant fraction of the world's land surface is naturally saline and is not available for agriculture. Cultivation of these salinised areas, if possible, would contribute to the increase in food production needed in the next few decades to feed a growing world population. Unfortunately, our present crops are all salt-sensitive, to a greater or lesser degree, and classical breeding has not succeeded in improving their resistance to salinity. Similarly, genetic engineering approaches have not yet delivered commercial salt-tolerant 'biotech' (GM) crops. Yet a small percentage (ca. 0.25%) of wild angiosperm species – *halophytes* – are adapted to saline soils in their natural habitats, and many are able to complete their life cycle at salinity levels similar to, or even higher than sea water. Halophytes could be cultivated in salinised land already lost for agriculture, and also in naturally saline, marginal soils, using brackish water, reclaimed industrial/urban waste water, or even sea water for irrigation. Most important, this 'saline agriculture' will not compete with conventional crops for increasingly scarce resources, such as fertile land and good-quality irrigation water. Several salt-tolerant taxa are being investigated as potential 'new' halophytic crops and others can be developed in the near future, to be used, for example: i) as human food or for animal feed; ii) for production of biofuels: biomass generation for bioethanol, and biodiesel obtained from oleaginous seeds; iii) for the production of secondary metabolites with medical, nutraceutical, cosmetic or other industrial applications; iv) as new ornamental plants, for gardening and landscape architecture. As the crop potential of many of these species is unknown and some may have undesirable agronomic characteristics, we propose that more effort should be invested in the domestication of promising halophytic taxa, establishing breeding programmes to transform these amazing wild plants into useful crops.

Keywords: crop productivity, food production, halophytes, plant breeding, saline soils, salt stress, salt tolerance

INTRODUCTION

At present, agriculture provides enough food to feed – theoretically – the whole world population of more than 7×10^9 people: about 2700 Kcal/person/day. It is obvious that food is not equally distributed, worldwide or within countries, since near 900 million people in the world are undernourished, and several million die of hunger every year (Stop the hunger, 2013). In any case, since the mid 1980s, the increase in food production has not been as fast as population growth and, at present, the average amount of food per person is actually decreasing. If this trend does not change in the near future, by 2050 there will be no enough food for the ca. 9.2×10^9 people who are expected to be living then on earth. Therefore, we need to apply all available strategies to increase food production in the next few decades. This will be a quite complicated task, considering some additional difficulties we will face, such as the decreasing area of land available for agriculture, due to urban and industrial development in many developing countries but also to the spread of desertification brought about by global

climate change – mostly in arid and semiarid regions – or the increasing scarcity of water for irrigation. In addition, these improvements of crop yields should be achieved in the frame of a sustainable agriculture, without depletion of natural resources or further degradation of the environment (Boscaiu *et al.*, 2012).

For all crops, average yields are only a fraction of record yields, and these losses – which are generally higher than 50%, and can be over 80%, depending on the crop (Buchanan *et al.*, 2000) – are mostly due to abiotic stress conditions affecting the plants in the field. Drought and salt stress, specifically, are the major causes reducing crop yields worldwide (Boyer, 1982). In particular, soil salinity is an increasing problem for agriculture, affecting the most productive crop areas of the world, those cultivated under irrigation in arid and semiarid regions – they represent less than 15% of global arable land, but produce more than 40% of world food (Munns and Tester, 2008). At present, there are about 230 million hectares of irrigated land in the world, and more than 20% of this area is seriously affected by salt. This ‘secondary salinisation’ – of anthropic origin – is due to the progressive accumulation in the soil of toxic ions dissolved in irrigation water, and is a major contributor to the loss of more of 10 million hectares of arable land every year (Owens, 2001); the problem is expected to worsen in the near future, again because of the foreseeable effects of climate change. Salinisation of crop land is by no means limited to ‘modern’ agriculture. Archeological findings and old written records have provided solid evidence for the progressive soil salinisation in ancient – more than 4000 years ago – Mesopotamian agriculture, which made impossible wheat cultivation (it was slowly substituted by barley, a more salt-resistant crop); this process continued for centuries and finally – together with silt accumulation in the irrigation channels – led to the collapse of the Sumerian civilisation, around 1700 B.C. (Jacobsen and Adams, 1958).

In addition to the loss of agricultural land due to human intervention, there are huge areas of naturally saline soils, about 6% of the world’s land surface; these marginal soils have never been cultivated because of their high soil salinity. It is obvious that scientific or technical advances allowing crop growth in these salinised areas will contribute to the urgently needed increase in food production.

HOW COULD SALINE SOILS BE CULTIVATED?

Most wild plants and all our major crops are glycophytes; that is, salt sensitive: they cannot survive relatively low levels of salt in the soil, although there are quantitative differences between species in a continuous range, from very sensitive to somewhat salt-resistant taxa. In a ‘salinising’ world, genetic improvement of salt tolerance has become an urgent need for the future of agriculture, at least in arid and semiarid regions. Salt-tolerant crops cultivated under irrigation would maintain high yields despite salinisation of the soil, or could be irrigated with low-quality, brackish water – thus saving good-quality fresh water for human consumption or other uses; they could also be used to reclaim land already lost for agriculture due to secondary salinisation, or could even be grown in naturally saline, marginal soils (Rozema and Flowers, 2008; Rozema *et al.*, 2013).

Classical breeding has met very limited success when trying to develop crop varieties with improved resistance to salt stress. This is not unexpected, since salt tolerance is a very complex, multigenic trait and, in addition, most crops do not have salt-tolerant wild relatives that could contribute this specific character. Among our major cultivated plant species, only sugar beet (*Beta vulgaris*) is relatively resistant to salt stress, since its wild ancestor – the sea beet, *Beta maritima* – is an halophyte (see below).

As an alternative to traditional breeding, generation of salt-tolerant transgenic plants through genetic engineering has been tried for the past two decades; some apparently positive results were already obtained more than ten years ago in tomato overexpressing a vacuolar Na⁺/H⁺ antiporter (Zhang and Blumwald, 2001), but were later challenged as they were found to be non-reproducible. More recent research has provided new promising approaches, and transgenic plants showing significant increases in salt stress tolerance have been produced (Bourgon *et al.*, 2007; Møller *et al.*, 2009). However, these studies are being carried out in laboratory set-ups with model plants – mostly *Arabidopsis thaliana* – and it is not yet known whether their results can be extended to crops in the field. In short, although genetic engineering will probably succeed in the medium or long term, it has not yet delivered commercial salt-tolerant ‘biotech’ (GM) crops.

HALOPHYTES AS ALTERNATIVE CROPS FOR A SALINE AGRICULTURE

Given the difficulties to adapt our present crops to conditions of increasing salinity, it may be worth to consider the possibility to ‘domesticate’ wild species naturally adapted to high levels of soil salinity in their natural habitats – the *halophytes* – to transform them in useful ‘new’ crops. Halophytes have been defined as those plants specific of saline ecosystems, where they are able to survive and complete their live cycle in the presence of soil salinity levels equivalent to, at least, 200 mM NaCl (Flowers *et al.*, 1986; Flowers and Colmer, 2008); in fact, many of them can easily stand salt concentrations higher than that of seawater. Halophytes represent a small percentage of all angiosperm species, 0.25% (Flowers *et al.*, 2010); that is, about 350 species, widely distributed in different plant families and genera. It should be relatively simple to establish breeding programmes to improve the agronomic characteristics of some promising halophytic taxa, since they already possess the desired trait of salt tolerance, which is the most difficult to manipulate.

As mentioned above, once halophytic crops are developed and established, they could be cultivated in land affected by secondary salinisation, as well as in naturally saline, marginal soils, using low-quality water – brackish water, reclaimed industrial/urban/farm wastewater, sewage, wastewater from aquaculture, or even seawater – for irrigation. Halophytes could be used by poor farmers in developing countries in ‘subsistence-type’ agriculture, to help feed themselves and their livestock, but also cultivated as large-scale commercial cash-crops. Most important, this ‘saline agriculture’ will not compete with conventional crops for increasingly scarce resources, such as fertile land and good-quality irrigation water, and will also save large amounts of fresh water needed for domestic and industrial uses.

Some halophytic taxa have been traditionally collected from nature and used as human food or animal feed, so that there is already some information available on them – at least, we know that they are edible! These and other species are being investigated as possible new crops, and many others can be developed in a relatively short time. Saline agriculture has the potential to contribute significantly to the global supply of food, and to provide a wide range of interesting – and profitable – plant-derived products: biofuels, fiber, and secondary metabolites with medical, nutraceutical, cosmetic, culinary or other industrial applications. The possible use of halophytes as ornamentals, or for the stabilisation and/or rehabilitation of degraded land should also be considered. Therefore, halophytes represent a practically untapped resource, which could be important for agriculture in the near future; this will require investing more effort in basic and applied research on wild salt-tolerant taxa, and to develop appropriate breeding programmes to realise their full potential.

To support the ideas mentioned in the previous paragraphs, in the next sections a few specific examples of the practical uses of halophytic crops will be described and discussed.

HALOPHYTES AS FOOD FOR PEOPLE

‘Gourmet’ vegetable crops. Different halophytic species have been traditionally used as food by people collecting them from nature, and have a great potential to be transformed into vegetable crops for saline irrigation. Most are eaten as raw vegetables, for example in fresh salads, and some also cooked or pickled. Apart from their palatability, these plants are, in general, rich in protein, antioxidant compounds and/or essential nutrients – minerals, vitamins, amino acids and/or fatty acids – as illustrated by the following examples (Ventura and Sagi, 2013, and references therein). *Aster tripolium*, popularly used to prepare fresh salads or eaten as a cooked vegetable, is rich in minerals and polyphenols. *Atriplex hortensis*, an herb suitable for growing in kitchen gardens, is also consumed in green salads and has high protein and amino acid contents. *Batis maritima*, which can be eaten raw, cooked or pickled, contains essential amino acids and tocopherol antioxidants (vitamin E). *Inula crithmoides*, also consumed in salads or pickled in vinegar, is a dietary source of iodine. *Plantago coronopus*, used as salad greens, contains relatively high levels of vitamins A, C and K, and minerals. All plants mentioned above can be grown using irrigation solutions containing high salt concentrations, over ~ 200 mM NaCl, although, depending on the species, they may show variable reductions in yield as compared to standard irrigation. Other potential halophytic crops, which are also rich in vitamins, minerals, antioxidants, omega-3 fatty acids and other nutrients, are not as salt-tolerant, but could still be cultivated with saline water, only of lower salt concentration.

Among those halophytes with highest potential to be developed as vegetable crops, several species of the related genera *Salicornia* (annual plants) and *Sarcocornia* (perennial) have attracted particular attention, due to their extremely high salt tolerance and a long history of consumption by man. Species of the two genera – and obviously within each genus – are so similar that are very difficult to differentiate by non-specialists. Therefore, plants considered as *Salicornia europaea*, the most commonly used species, may in fact belong to different, related taxa. *Salicornia* and *Sarcocornia* plants have been traditionally used as vegetables – mostly as fresh salads – in coastal communities. People collected them from wild populations to be self-consumed, or sold in local markets. These plants are rich in minerals, fatty acids and antioxidant compounds, such as polyphenols. There have been several field trials of *S. europaea* in different countries, with promising results. In fact, there are also some examples of small-scale commercial cultivation of this species using seawater for irrigation, for example in Ensenada, Mexico; the production – freshly harvested plants – is mostly sold directly to trendy restaurants in Europe and USA. With this previous knowledge and experience, breeding programmes to transform *Salicornia* into a ‘standard’ crop should be relatively simple, based on selection of the best genotypes and improvement of marketing characteristics: uniformity of the product in taste, size and colour, constant supply to the market, etc (Ventura and Sagi, 2013).

Oilseeds. Many halophytes have oleaginous seeds, with high content and appropriate composition of fatty acids and lacking or containing low levels of toxic compounds, so that they can be used to extract oil for human consumption. Specifically, a high percentage of unsaturated fatty acids (USFA) is the main characteristic for an edible oil to be considered as ‘healthy’. To establish their potential to be used as a source of edible oil, the oil content and composition have been determined in seeds of different halophytes, for example in *Arthrocnemum macrostachyum*, *Alhaji maurorum*, *Cressa cretica*, *Halopyrum mucronatum*,

Haloxylon stocksii and *Suaeda fruticosa* (Weber *et al.*, 2007). The seed oil content in these species ranged from 22% to 25%, and all contained a relatively high fraction of USFA. From a nutritional point of view, oil from *S. fruticosa* seems to be the best, with 74% USFA, followed by *H. stocksii* (69%), *H. mucronatum* (70%), *C. cretica* (64%), and *A. macrostachyum* (65%), while *A. maurorum* showed the lowest percentage (54%); for all species, the oil was very rich in linoleic acid, which represented 97-99% of the total USFA.

A *Salicornia* species, *S. bigelovii*, is one of the most interesting taxa for saline agriculture, since – as other congener species – it can be grown with seawater irrigation. Seed yields are similar to those of soybean and other oilseed crops, about 2 tons per hectare per year. Seeds are rich in oil and proteins (ca. 30% each) and, as in the examples mentioned above, contain high quality edible oil, with a high content of polyunsaturated fatty acids (70% of linoleic acid).

Grain crops. The practical advantages of harvested, dry grains (mainly seeds of cereals or legumes) over other plant foods such as fresh vegetables, fruits and roots or tubers are obvious: ease of mechanical harvest, long-term storage, handling, and transport. These characteristics would be maintained in future halophytic grain crops. One possibility is based on the domestication of *Distichlis palmeri* (Glenn *et al.*, 2013), a salt grass endemic to the delta of the Colorado River, in the northern Gulf of California. This is a perennial species, with grain similar to rice in size and nutritional value, and highly salt-tolerant; in fact, it can grow under flooded conditions – like paddy rice – in seawater. Apparently, it does not pose any problem for human consumption, since it was used as food by the Cocopa people who inhabited the region. However, its agronomic characteristics and, therefore, its crop potential are as yet unknown, and further characterisation of the species will be required before efficient breeding programmes can be designed.

The situation is totally different with other halophytic grain species, quinoa (*Chenopodium quinoa*), which should be considered as an ‘established’ – not ‘new’ – crop, since it had been cultivated in the Andean region for thousands of years. When the Spanish conquistadors arrived, they – or, rather, the priests who accompanied them – banned the cultivation of this plant, which was associated with religious rites of the indigenous population. Quinoa is considered as a ‘pseudocereal’, the seeds are rich in starch and high-quality protein, and contain all the essential amino acids, trace elements and vitamins, but are gluten-free. The essential nutrients are found in the nucleus of the grain, unlike cereals like rice or wheat, in which they are located in the hull and are lost unless whole grains are consumed. The interest in this seed crop is increasing all over the world, due to its exceptional nutritional quality (e.g., Vega-Galvez *et al.*, 2010).

The crop shows an extraordinary adaptive capacity to extreme ecological conditions: it can grow from sea level to almost 4000 m, withstands temperatures from -4°C to almost 40°C and relative humidity from 40% to 88%. Quinoa is extremely salt-tolerant, able to grow at salinities higher than seawater, but also remarkably resistant to frost and water stress; it is a very water-efficient plant, producing acceptable yields with rainfall of 100 to 200 mm. This adaptability to such a disparate array of environmental conditions makes quinoa a unique candidate for cultivation in many different regions of the world: high mountains, littoral and inland saline soils, arid lands... In fact, apart from the Andean countries where the species originated, it has been successfully grown – at a small scale – in the USA and Canada, several EU countries, Kenya in Africa, and in the Himalayas and the plains of Northern India, in Asia; in all cases, high yields have been obtained. The seeds can be found in western countries in specialised shops or in the ‘bio-food’ shelves of supermarkets, but the market is still very limited. Considering all its properties, it is not surprising that quinoa has been

defined as ‘an ancient crop to contribute to world food security’ (FAO, 2013), and that FAO has declared 2013 as the ‘International Year of Quinoa’.

HALOPHYTES AS FEED AND FODDER FOR LIVESTOCK

It is clear that, in principle, all halophytes that can be used as food for humans, either as vegetable crops (e.g., *Aster tripolium*) or grains (e.g., quinoa), could also be used to feed animals. However, for the efficient use of saline agriculture to produce forage for livestock, several factors – which are still poorly known, in general – should be considered, such as biomass production, the voluntary feed intake by the animals, and the nutritional value of the product (Norman *et al.*, 2013). Halophytes that are efficient salt-accumulators probably should not be used as the only (or main) feed source for the animals, since their diet would contain too high and unhealthy levels of sodium. The same can be said for products or byproducts containing excessive amounts of toxic or deleterious compounds. The final use of halophytes as feed or fodder for livestock will depend on the specific animals to be fed: while camels and goats will eat almost anything, poultry is especially sensitive to the feed composition. For example, the seed meal remaining after extraction of oil from *S. bigelovii* seeds can be used as a protein supplement in fish and ruminant diets, replacing conventional counterparts; however, its high saponin content prevents its direct use as a protein source in poultry feeds (Glenn *et al.*, 2013).

Among the different halophytic species that are being investigated as potential forage crops, particular attention has been devoted to *Atriplex lentiformis* – as well as to other taxa of the same genus with similar properties. *A. lentiformis* is a perennial, deep-rooted desert shrub which can be grown with seawater irrigation; since the seeds do not germinate under high salt conditions, cultivation of this species requires to sow the seeds in nurseries, to produce seedling that will be then transplanted to the field. In addition to its salt-tolerance, *A. lentiformis* is also highly tolerant to drought and extremely efficient in water use. The nutritional quality of the plant leaves is similar to alfalfa – the most important forage crop grown around the world. However, not all characteristics of *Atriplex* are positive: it has a low-energy content compared to conventional forages, and contains some anti-nutrients, whose elimination or at least reduction should be a clear breeding objective. It also shows a tendency to become woody with age; therefore, even though it is a perennial species, probably the best would be to cultivate *Atriplex* as an annual, limiting the number of harvests of the leaves (Glenn *et al.*, 2013).

HALOPHYTES FOR BIOFUEL PRODUCTION

Biodiesel production from oilseeds. In principle, all species with oil-rich seeds could be used for obtaining biodiesel. This includes those mentioned above as suitable for production of edible oil (*Suaeda fruticosa*, *Arthrocnemum macrostachyum*, *Salicornia bigelovii*, etc.); in this case, we will have two possible alternative uses for essentially the same product (although higher purification may be required for human consumption), the choice between them will probably be determined by economic reasons and marketing strategies. To these species, we can add those oleaginous halophytes not suitable for the food industry – due to the presence of toxic compounds, or to an inappropriate oil composition (e.g., very low content in unsaturated fatty acids). It should be pointed out that the possible uses of oils are not limited to human consumption and biofuel production, as they have many additional industrial applications, as lubricants, additives for paints or glues, etc.

Bioethanol production from lignocellulosic biomass. At present, large-scale industrial production of bioethanol is based on sugar or starch-rich food crops, such as sugarcane, maize and other cereals, or soybean, which leads to direct conflict with the food sector. Therefore, the focus of research has shifted to other potential sources or fermentable sugars, such as lignocellulosic biomass obtained from non-food crops – despite technical problems concerning the large-scale and efficient hydrolysis of cellulose with specialized cellulases. Some fast-growing halophytic grasses, such as *Phragmites karka*, *Halopyrum mucronatum*, *Desmostachya bipinnata*, *Panicum turgidum* and *Typha domingensis*, can provide biomass with a lignocellulosic composition appropriate for its downstream processing into sugars: high content in cellulose (26-37%) and hemicelluloses (24-38%), but very low (< 10%) in lignin, which interferes with the hydrolysis of cellulose; therefore, these species – and other halophytes with similar characteristics – are promising candidates for bioethanol production (Abideen *et al.*, 2012).

In the same area of biomass production, it is interesting to mention a trial carried out for several years in Israel (Eshel *et al.*, 2010). Individuals of five different *Tamarix* species (salt-tolerant, fast growing trees) were planted and grown in the Negev desert, irrigated either with reclaimed sewage from the nearby city of Eilat (moderately saline, EC ~ 3 dS/m), or with brine from a local desalination plant (EC = 7-10 dS/m). The net production of aboveground organic biomass was quite high, ranging from 26 ton/ha/yr (for those trees grown under high-salinity conditions) to 52 ton/ha/yr (for the sewage-irrigated trees). Similar studies have been undertaken with *Euphorbia tirucalli* plants. These data point to the possibility to use fast-growing halophytic woody species – trees and shrubs – for biofuel production, with advantages over other salt-tolerant plants such as grasses, in that higher yields of biomass can be obtained.

SUMMARY AND PERSPECTIVES

As mentioned in the previous sections, halophytes can provide food for humans and livestock – as fresh vegetables, edible oils, grains, protein seed meal, forages – as well as energy, as a source of biofuels (biodiesel and bioethanol). In addition, although not the focus of this review, many of these salt-tolerant plants synthesise secondary metabolites of commercial interest, for their medicinal, aromatic, cosmetic, culinary or other traditional household uses. Some of them can be marketed as ornamentals, because of the beauty of their flowers or their general attractive appearance. And we should not forget their potential for the stabilisation and/or rehabilitation of degraded land, e.g. for reclaiming land lost for agriculture due to secondary salinisation.

Halophytes are wild species – although some may have been cultivated at a small scale for centuries – which cannot compete in purely economic terms (yield, agronomic and marketing characteristics) with our standard crops, domesticated thousands of years ago and improved over the centuries. However, in a world with an urgent need to increase food production, with huge areas of naturally saline soils unsuitable for conventional agriculture, and with a serious problem of secondary salinisation of the most productive arable land, halophytes represent an important natural resource, as yet practically unexploited, for the quick development of a sustainable ‘saline agriculture’. Different halophytes can be grown in all types of saline soils, using saline water for irrigation – even seawater in case of the most salt-tolerant species – and, therefore, not competing with conventional crops for resources, such as fertile land and fresh water, which are becoming increasingly scarce.

As wild plants, however, in many cases their crop potential is unknown, or they have undesirable agronomic characteristics. It may be necessary, for example, to select the best

genotypes for particular agro-ecological conditions, to reduce the content of toxic compounds or anti-nutrients, to increase yields or to improve marketing characteristics (uniformity of the product in taste, size, colour, etc.), and to tailor standard agricultural practices to particular species. In short, some of the common objectives of traditional plant breeding and agricultural practice.

We think that more effort (and money) should be invested in the domestication of the most promising halophytic taxa, establishing appropriate breeding programmes to transform these amazing wild plants into useful crops. This should not be too complicated and could be achieved in a relative short time, since the plants already possess the most important – and most difficult to introduce – trait: salt tolerance. In any case, the benefits of developing a ‘saline agriculture’ based in the cultivation of these new halophytic crops are worth the effort.

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