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REVIEW: PART OF A SPECIAL ISSUE ON HALOPHYTES AND SALINE ADAPTATIONS

The development of halophyte-based agriculture: past and present

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• **Background** Freshwater comprises about a mere 2·5 % of total global water, of which approximately two-thirds is locked into glaciers at the polar ice caps and on mountains. In conjunction with this, in many instances irrigation with freshwater causes an increase in soil salinity due to overirrigation of agricultural land, inefficient water use and poor drainage of unsuitable soils. The problem of salinity was recognized a long time ago and, due to the importance of irrigated agriculture, numerous efforts have been devoted towards improving crop species for better utilization of saline soils and water. Irrigating plants with saline water is a challenge for practitioners and researchers throughout the world.

• **Scope** Recruiting wild halophytes with economic potential was suggested several decades ago as a way to reduce the damage caused by salinization of soil and water. A range of cultivation systems for the utilization of halophytes have been developed, for the production of biofuel, purification of saline effluent in constructed wetlands, landscaping, cultivation of gourmet vegetables, and more. This review critically analyses past and present halophyte-based production systems in the context of genetics, physiology, agrotechnical issues and product value. There are still difficulties that need to be overcome, such as direct germination in saline conditions or genotype selection. However, more and more research is being directed not only towards determining salt tolerance of halophytes, but also to the improvement of agricultural traits for long-term progress.

Key words: Agrotechniques, *Aster tripolium*, biofuel, cash crops, *Crithmum maritimum*, *Euphorbia tirucalii*, halophytes, *Pennisetum clandestinum*, *Salicornia*, saline agriculture salinity, *Sporobolus virginicus*, *Tamarix jordanis*.

INTRODUCTION

Water is generally considered a renewable resource, but its availability for human needs is limited by its chemical and physical properties and its global distribution. Freshwater comprises about a mere 2·5 % of total global water, of which approximately two-thirds is locked in glaciers at the polar ice caps and on mountains (Gleick, 2009). Constant accessibility to freshwater from rivers and lakes is of the utmost importance, particularly for irrigated agriculture, industry and households. Almost 20 years ago Postel *et al*. (1996) estimated that global water use constituted 54 % of accessible runoff, with 65 % of this going to agriculture, frequently for irrigation. The disparity between the geographical distribution of water and that of the human population further aggravates the problem of freshwater scarcity.

In many instances, irrigation causes an increase in soil salinity due to overirrigation of agricultural land, inefficient water use and poor drainage of unsuitable soils. Most known agricultural crop plants are salt-sensitive glycophytes, the growth of which is severely inhibited when grown under saline conditions. Therefore these plants cannot be produced economically with saline water. The United States Department of Agriculture estimates that, worldwide, 10 million hectares of arable land are lost every year to salinity as a result of improper irrigation.

The problem of salinity was recognized a long time ago and, due to the importance of irrigated agriculture, numerous efforts have been devoted towards improving crop species for better utilization of saline soils and water (Malcolm, 1969; Mudie, 1974; Epstein *et al*., 1980; O'Leary, 1984). The decrease in dry matter production of several crops in response to increasing salinity was estimated by Munns and Tester (2008), revealing a 50 % decrease at 80 mM NaCl for rice (*Oryza sativa*), at 100 mM NaCl for durum wheat (*Triticum turgidum* ssp. *durum*) and at 120 mM NaCl for barley (*Hordeum vulgare*). Conversely, 'salt-loving' halophytes, which occur in the wild throughout the world, live and reproduce in salt marshes, sea shores, estuaries or saline deserts (Epstein *et al*., 1980). Halophytes are capable of tolerating a wide range of salinities, even beyond seawater concentration (approx. 500 mM NaCl), thus providing a basis for the development of an extensive spectrum of halophytic crops covering large fields of application (Yensen, 2006).

This current review aims to reassess agricultural production systems from the past and in the present that use halophytic plants converted into agricultural crops. The main focus is placed on multifaceted applications ranging from production of animal feed to gourmet vegetables, and from ornamentals to biofuel, sometimes realized by one and the same plant species.

FROM THE PAST TO THE PRESENT DAY

Irrigating agricultural crops with seawater was and still is one of the biggest challenges for farmers and for plant researchers, whose main efforts are directed to discover solutions to the problems. Driven by the need to expand the use of natural resources, Hugo and Elisabeth Boyko, respectively a geophysicist and plant-ecologist, demonstrated in the early 1960s the possibility of cultivating crops with full-strength seawater, and thus paved the way for pioneering research of seawater agriculture (Boyko and Boyko, 1964). They hypothesized that the combination of the high soil permeability to water and the good drainage capability of sandy soils together with the use of excess quantities of seawater may be the basic factors allowing the development of this field of agriculture. To prove the concept, these scientists showed in a small-scale experiment that two plant species with extremely different ecological requirements, *Agropyrum junceum* and *Juncus arabicus*, could be grown successfully, for fibre production, on dunes irrigated with various seawater dilutions over a period of about 1·5 years (Boyko and Boyko, 1959). In subsequent experiments it was demonstrated that certain local barley strains could complete their life cycle when irrigated with seawater containing up to 4·2 % salt (Boyko and Boyko, 1964). Nearly simultaneously, similar hypotheses were tested, and the potential of two grasses, *Agropyron elongatum* and *Puccinellia capillaris*, was demonstrated for ground cover and for grazing when grown on saline wastelands, (Rogers and Bailey, 1963; Malcolm, 1969).

Nevertheless, the majority of agricultural crops are highly sensitive even to small amounts of sodium chloride. Maas (1990) summarized research that showed that soil salinity even less than 2 dS m^{-1} resulted in yield reduction of vegetable crops such as beans (*Phaseolus vulgaris*, yield decline of 19 % per dS m^{-1}), peppers (*Capsicum annuum*, 14 %), corn (*Zea mays*, 12 %) and potatoes (*Solanum tuberosum*, 12 %). Thus, the main ambition of those interested in saline agriculture was to increase the number of crop species that could produce economic yields while growing under unfavourable saline conditions. To realize this goal, two research directions were proposed: (1) crossing of salt-tolerant relatives within sensitive crop lines by traditional breeding methods (Yeo and Flowers, 1989); and (2) domestication of naturally salt-tolerant plants. Many research efforts worldwide were devoted to the first strategy, with high expectations that improved lines could be developed (Epstein *et al*., 1980). However, breeding for salt tolerance proved to be a difficult task, as this is a multigenetic trait (Flowers and Yeo, 1995; Flowers *et al*., 2010), and the numerous attempts resulted in only few salt-tolerant lines.

The second route, exploiting the potential of natural halophytes, was followed by another group of researchers, led by Elisabeth Boyko. A 6 year plant introduction programme was conducted oriented mainly toward the development of agricultural and pasture material suitable for dryland conditions (Nurock, 1960). The resulting ecological desert garden was the first milestone for a plant collection of xerophytes and halophytes, particularly those with economic potential (Boyko, 1962). Follow-up research started in 1982 with a new project for systematic collection and evaluation of halophytes for fodder production irrigated with saline water (Pasternak, 1990). About 140 halophytic species were evaluated in a large experimental plot on the Mediterranean coast. The importance of comparing a broad range of halophytes, collected from most of the world's continents, under the same environmental conditions was highlighted. Based on visual observations obtained three times a year during three sequential years (1983–1985), a list was compiled including 78 plant species that could grow successfully even if irrigated with 100 % seawater and an additional 22 species that produced well at 15 % seawater (Pasternak, 1990). The HALOPH database was initialized by this list, then further extended and finally published by Aronson (1989). According to Aronson's criteria, HALOPH included about 1560 plant species that were able to grow when exposed to ECi (electrical conductivity of the irrigation water) of 7–8 dS m^{-1} during significant portions of their life cycle. One rubric of the HALOPH database was dedicated to the economic uses of the different species, modified from the code developed by G. E. Wickens and co-workers for the Survey of Economic Plants for Arid and Semiarid Lands (SEPASAL), Royal Botanic Gardens, Kew, UK (Aronson, 1989). Aronson's data have since been extended by Menzel and Lieth (2003). An additional version on halophytes and their uses, based on Aronsons' data, was developed by Yensen (http://www.ussl.ars.usda.gov/pls/caliche/Halophyte.query). Most recently, an interactive version, the eHALOPH database, was compiled and can be found at http://www.sussex.ac.uk/affiliates/halophytes.

The initial enthusiasm for growing *Atripex* spp. successfully with highly saline water and its fodder potential for small ruminants as a rich N source (up to 17 % crude protein under 100 % seawater) was stifled by the very low animal intake (0·3–0·4 kg dry matter d^{-1}) and its low metabolic energy content (approx. 1·5 Mcal kg^{-1} d. wt) (Pasternak *et al*., 1985; Pasternak, 1990). Therefore, it was concluded that *Atriplex nummularia*, although highly salt tolerant, is a poor food source and its use as a fodder crop is limited. Conversely, additional studies conducted in the Mediterranean basin showed that *Atriplex* spp. could successfully be used as a complementary nutrient source, although energy supplements (e.g. barley) were necessary for small ruminants fed on salt-tolerant forage-based diets (Le Houerou, 1992; El Shaer, 2010). Based on this conclusion, and since halophytic grasses do concentrate salts in their leaves to a lesser extent than dicotyledonous halophytes and thus should have a higher net caloric value, a new line of testing several halophytic grass species at lower irrigation salinity (ECi 9·5 dS m^{-1}) was initiated in the late 1980s (Pasternak, 1990). Indeed, several American accessions of saltgrass (*Distichlis spicata*) were examined and showed considerable promise for selection as fodder crop for ruminants (Bustan *et al*., 2005).

Glenn *et al*. (1999) presented an overview summarizing the dominant research groups conducting field trials with halophytes under saline irrigation, working in arid zones of the USA ['The Environmental Research Laboratory of the University of Arizona' (Glenn *et al*., 1996) and the 'Halophyte Biotechnology Center', University of Delaware (Gallagher, 1985)], Australia (Malcolm, 1969) and northern Africa (Le Houerou, 1996). Since then numerous researchers have joined the field of halophyte crop cultivation, not only from dry regions, but also from areas with ample rainfall encountering the problem of salinity on coastal areas or inland salt pans. The groups of Rozema in The Netherlands (de Vos *et al*., 2013; Katschnig *et al*., 2013; Rozema and Schat, 2013), Koyro

(Koyro *et al.*, 2011) and Papenbrock (Buhmann and Papenbrock, 2013*a*, *b*) in Germany, Abdelly in Tunisia (Ksouri *et al.*, 2012) and Khan in Pakistan (Gul and Khan, 2003) introduced additional halophytic species as new cash crops and presented novel growing techniques. In particular, the field of renewable energy and ecological sustainability (e.g. purification of land-based aquaculture effluents) gained importance (Shpigel *et al.*, 2013). There has been a shift from producing halophytes as animal feed or salty vegetables for human consumption, to the mass production of non-food crops. Cultivation of halophytes as ornamental plants for either landscaping or floriculture is still in its infancy. In the field of ornamentals, most efforts are still directed towards testing glycophytes for improved performance under salinity (Cassaniti *et al.*, 2013). Since Boyko (1966) set the important first milestones in saline agriculture, many ideas have been tested and several discarded, but the '*ne plus ultra*' has yet to be found (http://www.cost.eu/domains_actions/fa/Actions/FA0901). Koyro *et al.* (2011) presented 12 major uses for halophytes, *inter alia* food, feed, wood, chemicals, landscaping, ornamentals, industrial raw materials and bioremediation. However, introducing non-domesticated halophytic plant species as agricultural crops with reasonable income for the growers will require the refinement of growing protocols and selection of improved varieties. To date, the scientific literature still focuses mostly on basic research questions dealing with plant salt tolerance mechanisms, and thus refers to small-scale experiments (Koyro *et al.*, 2011). As Boyko concluded in 1966 'Agrotechnical details for economic purposes have to be worked out . . .'; therefore, scaling-up to larger field experiments and intensifying genotype selection directed towards economic crop production should be the primary activities for future directions (Glenn *et al.*, 2013). However, many novel ways for the utilization of halophytes were proposed recently through the COST action 'Putting Halophytes to Work, From Genes to Ecosystems' and have made a significant input in advancing these matters for future halophyte growers (http://www.cost.eu/domains_actions/fa/Actions/FA0901).

FODDER-YIELDING HALOPHYTES

High palatability, digestibility and good nutritional value (high protein and low fibre, ash and oxalate contents) signify high fodder quality (El Shaer, 2006). Since salt accumulation reduces the nutritional value and feeding quality of most plants, the future prospects of *Atriplex* species as useful fodder crops, even in combination with other energy sources, were described as rather limited by Pasternak (1990). A different tactic was proposed by Barrett-Lennard and Setter (2010), who recognized the importance of feeding mixtures of plants, such as *A. nummularia*, with herbaceous species and annual grasses, which together fulfil the requirements of an effective fodder crop and can be grown at moderate salt levels. This approach has been further discussed by Norman *et al.* (2013), who highlighted the critical importance of voluntary feed intake (palatability, post-ingestive feedback) and nutritive value (metabolizable energy, salt, antioxidants, toxins) as factors affecting production of livestock. A concluding remark made by Norman *et al.* (2013) for successfully using the mixed plant system (halophytic grasses and shrubs) was to take advantage of the benefits of using halophytes while managing their negative consequences.

The potential of halophytic grass species as fodders was also investigated by Pasternak (1990) and Bustan *et al.* (2005). Indeed, although less salt tolerant than species of *Atriplex*, the ash content of all tested *Distichlis spicata* accessions never exceeded 11 % of the dry matter, about half the amount found in the salt-accumulating chenopods, highlighting its potential as a fodder crop (Bustan *et al.*, 2005). The protein content of *D. spicata* varied widely between the accessions, and ranged from a minimum of 9·2 % to a maximum of 18·9 % of dry matter, similar to the protein content reported by Pasternak (1990) for *A. nummularia*. In Pakistan, cultivating the halophytic species *Leptochloa fusca* (Kallar grass) not only resulted in high productivity [20 t dry matter ha^{-1} from 4–5 cuts per year (Mahmood *et al.*, 1994)], but also successfully improved the soil conditions of the existing saline sodic soils, showing increased vegetation growth after a 5 year period (Hollington *et al.*, 2001). The anatomical adaptation of grasses for salt secretion evidently contributes to the maintenance of low leaf salt levels and relatively low (compared with those existing in dicotyledonous halophytes) Na/K ratios (Flowers and Colmer, 2008). Liphschitz *et al.* (1974) reported the existence of active salt-secreting glands on the leaves of Rhodes Grass (*Chloris gayana* Kth.). In a similar manner, Bermuda grass (*Cynodon dactylon*) was determined as a salt-secreting species (Liphschitz and Waisel, 1974; A. Eshel and Y. Waisel, 2007, unpubl. res.), which was confirmed by Hameed *et al.* (2013) by an increased number of vesicular trichomes for the exclusion of toxic ions. Thus these plants attract interest as important candidates for economic utilization in saline environments (Liphschitz *et al.*, 1974).

Grasses have also been used in combination with other chenopods apart from *Atriplex* species. *Salicornia bigelovii* was tested as a protein-rich fodder crop for saline irrigation (Glenn *et al.*, 1991), but its high ash content (up to 39 %) limited its nutritional potential and its fodder quality (Basmaeil *et al.*, 2003; Y. Ventura, J. Miron and M. Sagi, 2012, unpubl. res.). To overcome this problem, Glenn *et al.* (1992) substituted 50 % of a Rhodes Grass-based fodder with *S. bigelovii*. Plants were grown on complete seawater and directly after harvest the plant biomass was soaked in seawater. This action reduced the NaCl content by half to approx. 8–13 %, resulting in an ash content of 16·7 %. Glenn *et al.* (1992) also noted that the protein content of the *Salicornia* biomass was higher if the seeds were not removed prior to animal feeding. The conclusion drawn from an experiment feeding *S. bigelovii* straw or seed meal to lambs showed that this halophyte could be used as an acceptable feed substitute in arid coastal regions where fresh water for crop irrigation is limited (Swingle *et al.*, 1996). In another study, the replacement of 12·5 % alfalfa by *Salicornia herbacea*, the locally occurring *Salicornia* in Kuwait, in the basal diet resulted in the highest body weight gain and feed consumption of Australian wither lambs, as compared with the other treatments (Abdal, 2009). On the other hand, in a camel feeding trial, the incorporation of 25 % seawater-irrigated *S. bigelovii* biomass in the diet had an adverse effect on the nutritive value of the feed in comparison with Rhodes Grass diet. In particular, ADF (acid detergent fibre) and NDF (neutral detergent fibre) digestibility decreased by approx. 50 and 20 %, respectively, which might have indicated an increased flow of undigested dietary components out of the rumen (Basmaeil *et al.*, 2003). The usefulness of *Salicornia* spp. as an animal feed for ruminants seems to be directly related to its salt content, which can be adjusted by the plant portion in the diet. Selection for low-salt-accumulating varieties may increase the feeding value of *Salicornia* for small ruminants. For other species, Belal and Al-Dosari (1999) successfully included 40 % *Salicornia* meal in fish (Nile Tilapia) feeds as a replacement for the conventional fish meal diet, with no adverse effect on fish growth and body composition.

NEW GENERATION HALOPHYTES – FOOD AND GOURMET VEGETABLES

Halophytes (e.g. *Crithmum maritimum*, *Portulaca oleracea*, *Salicornia* spp. and *Aster tripolium*) have been consumed by humans for centuries, and to date are still often gathered from the coastal salt marshes and inland salt pans of Europe (Franke, 1982; Wagenvoort *et al*., 1989; Davy *et al*., 2001; Simopoulos, 2004; Tardio *et al*., 2006). These species are well known for their ability to synthesize secondary metabolites, which have several functions, such as osmolytes and scavengers of reactive oxygen species (Hasegawa *et al*., 2000). The secondary metabolites include simple and complex sugars, amino acids, quaternary ammonium compounds, polyols and antioxidants (e.g. polyphenols, β-carotene, ascorbic acid and ureides; Parvaiz and Satyawati, 2008; Ventura and Sagi, 2013). Osmolytes can potentially be utilized in functional food, which is defined as having disease-preventing and/or health-promoting benefits (Stuchlík and Žák, 2002; Buhmann and Papenbrock, 2013*a*). The modern awareness of a healthier diet may promote additional markets for halophytes with high nutritional potential, evident in the rapidly growing consumption of products from some halophytic plants (e.g. quinoa; Panta *et al*., 2014). Such alternative crops may find niches in the demanding market for novelties, while taking advantage of a range of saline irrigation water sources. Several halophyte products such as *Salicornia* spp. and *Aster tripolium* are already being sold as sea vegetables and salad crops on the European markets at comparatively high prices (Böer, 2006). A number of additional halophytes, e.g. *Salsola soda*, *Crambe maritima* and *Beta maritime*, have a great potential to be released as novel sea vegetables to the market. The non-seasonality and year-round availability was an important step in the dissemination of the *Salicornia* crop and should be realized for any further halophyte vegetable (Böer, 2006, http://www.scribd.com/doc/102170797/Saline-Crops-From-Halophyte-Research-to-Sea-Vegetable-Markets). A broad range of saline water sources and soil salinities, from drainage water originating from sub-surface drainage systems used to lower saline shallow water tables, up to complete seawater, can be used for halophyte vegetable cultivation (Grieve and Suarez, 1997; Ventura *et al*., 2011*a*; Ventura and Sagi, 2013).

The South American seed crop quinoa (*Chenopodium quinoa*) has a long history of cultivation and, within the existing 2500 accessions, some are able to cope with salinity levels present in seawater (approx. 40 dS m^{-1}). Due to its high tolerance not only to salinity but also to other abiotic stresses (drought, frost and wind) and the exceptional nutritional quality of the seeds (rich in vitamins, minerals, essential amino acids and fatty acids), this 'old crop' gained interest in the Western world's diet and was nominated to contribute to global food security (Adolf *et al*., 2013). Presently, in Bolivia, one of the largest quinoa producers, grain yields are low (<0·5 t ha^{-1}), but potential yields may reach 3–5 t ha^{-1} through optimizing cultivation conditions (Gómez *et al*., 2011; Adolf *et al*., 2013).

Although the effect of salinity on secondary metabolites has been extensively studied with respect to plant salt tolerance, these compounds have seldom been referred to in terms of quality parameters of a commercial product: they can enhance the nutritional value of a crop and may differ between plant species and even between genotypes within the same species. The content of secondary metabolites may also be further influenced by agrotechnical practices (Ventura *et al*., 2011*a*), which include irrigation water quantity and salinity, plant fertilization, harvest time and cycle, and harvested plant material (young or old leaves) (Ventura *et al*., 2010, 2011*a*, 2013). An example of improvement of the quality of a leafy vegetable by plant fertilization was presented by Ventura *et al*., (2013) for *Aster tripolium*. This highly salt-tolerant plant species was considered a potential halophytic cash crop and it is already cultivated in pilot projects in The Netherlands, Belgium and Portugal (Lieth and Mochtchenko, 2002; Geissler *et al*., 2009*a*). Nevertheless, the introduction of *A. triopolium* as a salt-resistant vegetable crop met unexpected difficulties (Ventura *et al*., 2013). When cultivated on soil suitable for saline irrigation (96 % sand, 0·8 % silt, 3·1 % clay, <0·1 % organic matter, pH 8), a specific micro-element deficiency that affected product quality (leaf yellowing) was indirectly induced by the high pH. Therefore it is clear that growing protocols need to be adapted to the existing cultivation conditions, taking not only salt tolerance into account.

An additional halophytic species with cash crop potential is *Crithmum maritimum*, which was known for its antiscorbutic property. In the past, leaves were collected by sailors along the maritime cliffs (Cunsolo *et al*., 1993). To date, the salt tolerance, secondary metabolite content and antioxidant capacity of *Crithmum* have been studied extensively (Cunsolo *et al*., 1993; Guil-Guerrero and Rodríguez-García, 1999; Ben Hamed *et al*., 2005; Ben Amor *et al*., 2006; Meot-Duros and Magné, 2009; Atia *et al*., 2011) using non-domesticated plant material, collected from the wild. A study comparing four ecotypes revealed differences in yield, leaf appearance, polyphenols and ascorbate content (Y. Ventura *et al*., unpubl. res.). These results highlight the genetic differences and the potential for selection of genoptypes with high yield and high nutritional metabolite content.

The annuals *Atriplex hortensis* (red orach) and *Tetragonia tetragonioides* (New Zealand spinach) are both halophytic plant species suggested as spinach substitutes (Wilson *et al*., 2000; Słupski *et al*., 2010). *Atriplex hortensis* has been cultivated for its edible leaves since ancient times and is still grown in kitchen gardens as a pot herb (Wilson *et al*., 2000). *Atriplex hortensis* is more salt tolerant than *T. tetragonioides* (Wilson *et al*., 2000). In an agronomic study carried out in Israel, early flowering of *A. hortensis* in the spring season led to a very short harvest period, during which only two sequential harvests could be performed. Shifting to a selective harvest regime, in which only marketable size shoot tops were removed, resulted in five harvest cycles, before flowering occurred. In a greenhouse experiment, maximum yield of 2·2 kg m^{-2} fresh biomass was obtained under an irrigation salinity of 4 dS m^{-1} for the attractive variety, Purple Orach, which declined to 1·4 kg m^{-2} at 8 dS m^{-1}. Since only shoot tops of marketable quality were harvested, no further yield loss was recorded for the final marketable product (M. Myrzabayeva, Z. Alikulov, Y. Ventura and M. Sagi, unpubl. res.). *Atriplex hortensis* has been recommended as a substitute or supplement to spinach (*Spinacea oleracea*) due to their similar chemical composition (Carlsson and Clark, 1983). Likewise, *T. tetragonioides* (New Zealand spinach) was considered to be of good nutritional value, with the exception of sulphur amino acid deficiency. Moreover, culinary and technological processing (blanching–freezing–storage–cooking) caused a significant increase in total amino acid content, except for methionine and cysteine, in this species (Słupski *et al*., 2010).

Inula crithmoides was proposed as a candidate for saline agriculture by Zaruyk and Baalbaki (1996). This species is traditionally consumed in Lebanon, but is less commonly used in other Mediterranean countries such as Spain and Italy (Zaruyk and Baalbaki, 1996; Guarrera *et al*., 2006; Tardío *et al*., 2006). In a potted-plant experiment, growth of *I. crithmoides* was reduced only at salinities exceeding 20 dS m^{-1}, reaching a yield of 18·3 g d. wt per plant in an 87 d experiment (Zaruyk and Baalbaki, 1996). A 1 year long pot experiment, with monthly sequential harvests, produced a maximum yield of 30 and 6 kg m^{-2} fresh biomass at 50 mM (approx. 5 dS m^{-1}) and 200 mM NaCl (approx. 20 dS m^{-1}), respectively (Y. Ventura and M. Sagi, unpubl. res.). Marketable yield, defined as undamaged shoot tops, accounted for >50 % of the total fresh biomass at the highest tested salinity (200 mM NaCl). The potted plants could recover after harvest throughout the year, even under prolonged saline irrigation. Leaves of two *I. crithmoides* genotypes (Ramat Negev and UAE) were tested for their nutritional ingredients, and their fatty acid profile was established (Table 1): the content of a nutritionally important group of unsaturated fatty acids, the long-chain (C16–C20) polyunsaturated fatty acids (PUFAs), particularly those desaturated at either C3 or C6, known as ω3 and ω6 essential fatty acids, was tested (Stuchlík and Žák, 2002). *Inula crithmoides* contains a high total lipid content with a significant portion of ω3 fatty acids found as 18:3ω3 and 16:3ω3. Compared with other halophytic plants, *I. crithmoides* ranked second after the ω3 leader *Portulaca oleracea*: Guil-Guerrero and Rodríguez-García (1999) found total fatty acids to be 3·8 % of dry matter in *P. oleracea* collected from the wild and 3·4 % in *I. crithmoides* depending on the genotype and salinity (Table 1), followed by *C. maritimum* with 3·0 and 2·2 %, for wild collected (Spain) and 50 mM NaCl-irrigated plants from Tunisia, respectively (Guil-Guerrero and Rodríguez-García, 1999; Ben Hamed *et al*., 2005). Both the genetically inherited high fatty acid content of a certain plant species and irrigation salinity have a significant impact on the total lipid content as well as on the PUFA profile.

Salicornia and *Sarcocornia* species, in particular *S. bigelovii*, have been tested for several applications: gourmet food, animal feed and oils for biodiesel. When grown for human consumption as a gourmet vegetable, only young, vegetative shoots of *Salicornia* or *Sarcocornia* should be used. Daylength manipulations and multiple harvesting are agrotechnical practices used in this case to ensure high market value (Ventura *et al*., 2011*a*, *b*). The total lipid content of both *Salicornia* and *Sarcocornia* shoots grown in seawater was 21 and 17 mg g^{-1} dry matter, containing 48·2 % ω3 fatty acids, respectively (Ventura *et al*., 2011*a*). Differences between the plant genera (*Salicornia* and *Sarcocornia*) and their respective genotypes leave a large gap for further investigation in order to optimize the nutritional value of these plants. *Salicornia* and *Sarcocornia* also contain antioxidant compounds, namely polyphenols, β-carotene and ureides. Increasing salinity increased the content of those compounds (Ventura *et al*., 2011*a*). The high NaCl content in the shoot may have only a minor impact on the plant's nutritional value, since as a gourmet product it is consumed in small quantities.

ANTINUTRITIONAL FACTORS

In addition to the accumulation of high value nutritional components, halophytes also accumulate undesired factors. Among these antinutritional factors are oxalates, nitrates, phenols, saponins, tannins and salts (Kumar, 1991). Table 2 summarizes antinutritional factors in potential cash crop halophytes and the agrotechnical practices that can be applied in order to decrease their content and improve the product quality.

TABLE 1. *Fatty acid methyl ester (FAME) profile (in % of total fatty acids in dry matter) of two Inula crithmoides genotypes (Ramat Negev and UAE) grown in pots irrigated with solutions containing different concentrations of NaCl*

FAME	Salinity (mM NaCl)							
	Ramat Negev				UAE			
	0	50	100	200	0	50	100	200
16:0	13·9^{bc}	14·5^{ab}	14·7^{a}	14·8^{a}	13·2^{c}	13·4^{c}	14·5^{ab}	14·0^{abc}
16:1	2·2	1·8	2·1	2·3	2·4	1·9	1·8	2·3
16:2	1·0^{ab}	1·2^{a}	1·2^{a}	1·1^{ab}	0·7^{b}	0·8^{ab}	0·8^{ab}	0·7^{b}
16:3ω3	2·4^{cd}	2·2^{d}	2·2^{d}	2.1d	7·8^{a}	8·1^{a}	5·5^{ab}	4·9^{bc}
18:0	3·3^{ab}	3·3^{ab}	3·2^{ab}	3·4^{a}	2·6^{bc}	2·6^{bc}	2·4^{c}	2·3^{c}
18:1ω9	1·8^{ab}	1·5^{ab}	1·4^{b}	1·5^{ab}	1·7^{ab}	1·9^{a}	1·6^{ab}	1·6^{ab}
18:2	28·4^{a}	28·9^{a}	28·5^{a}	29·3^{a}	24·1^{b}	26·3^{ab}	26·9^{ab}	26·1^{ab}
18:3ω3	45·7^{a}	44·7^{a}	45·1^{a}	44·4^{a}	44·3^{a}	41·0^{a}	42·9^{a}	45·6^{a}
Others	1·4^{c}	1·8^{bc}	1·5^{c}	1·2^{c}	3·2^{ab}	3·9^{a}	3·6^{a}	2·4^{abc}
Total omega-3	48·0^{ab}	46·9^{b}	47·3^{b}	46·5^{b}	52·1^{a}	49·1^{ab}	48·4^{ab}	50·5^{ab}
Total fatty acids (% d. wt)	3·41^{a}	2·99^{bc}	2·88^{c}	2·85^{c}	3·26^{ab}	3·12^{abc}	2·88^{c}	3·41^{a}

Values are means of three replicates.
Different letters within the row indicate a significant difference, $P < 0·05$.

TABLE 2 *Antinutritional factors in cash crop halophytes*

Plant species	Antinutritional factor	Agricultural activity to reduce the content	Reference
Portulaca oleracea	Oxalate	Reduce NO_3 fertilization in favour of NH_4	Palaniswamy *et al.* (2002)
Salicornia/Sarcocornia	High ash content	Wash harvested biomass in seawater	Glenn *et al.* (1992)
	Saponins in seeds	Careful leaching with running water	Glenn *et al.* (1991); Eganathan *et al.* (2006)
Aster tripolium	Nitrate accumulation	Adjust iron fertilization	Ventura *et al.* (2013)
Atriplex hortensis	Oxalate, nitrate, Saponins, phenolics	May be decreased during processing. Would not present problems for ruminants.	Carlsson and Clarke (1983)
Atriplex nummularia	Oxalate	Reduce NO_3 fertilization in favour of NH_4. Selection of low oxalate genotypes	Al Daini *et al.* (2013)

Purslane (*Portulaca oleracea*) is considered moderately salt tolerant (EC 6·3 dS m^{-1} is a threshold for yield reduction) and possesses the highest leaf ω3 fatty acid content (4 mg g^{-1} wet weight) in green leafy vegetable yet examined (Kumamoto *et al.*, 1990; Simopoulos, 2004). Furthermore, this plant species is cultivated commercially in Mediterranean regions and the fleshy leaves and stems are used in salads (Shannon and Grieve, 1999). Unfortunately, purslane also accumulates large amounts of oxalates (Palaniswamy *et al.*, 2004). The oxalate content in purslane was found to be influenced by salinity (Teixeira and Carvalho, 2009), NO_3/NH_4 fertilization ratio (Palaniswamy *et al.*, 2002), harvesting stage (Palaniswamy *et al.*, 2001) and variety (Carvalho *et al.*, 2009; Szalai *et al.*, 2010). An increase in ammonium at the expense of nitrate did not influence vegetative biomass parameters significantly, but did lead to a significant decrease in oxalate content in leaves and stem (Palaniswamy *et al.*, 2002). A similar finding of high oxalate levels, which could be counteracted by ammonium nutrition, was described for *Atriplex nummularia*, a halophytic shrub widely used as forage for ruminant production in saline farming systems in Australia (Al Daini *et al.*, 2013). Ammonium application in *A. nummularia* not only reduced leaf oxalate levels, but, in contrast to the study of Palaniswamy *et al.* (2002) in purslane, also significantly decreased the relative growth rate and total plant dry matter. Importantly, the same authors discussed the possibility of genotype selections as useful breeding objectives for achieving low oxalate content. Antinutritive secondary substances (e.g. nitrate and oxalic acid) found in *Atriplex oleracea* may be reduced during processing and therefore may not diminish the nutritional value of the plant (Carlsson and Clarke, 1983).

Microelement deficiency may result from soil alkalization as a side effect of soil salinization (Grattan and Grieve, 1999). As a secondary effect of low iron availability in sand dune soils (pH 8), nitrate was found to accumulate in leaves of *A. tripolium*, when irrigated with 50 mM NaCl. Enhanced nitrate reductase activity, induced by the application of iron fertilizer in a chelate form, reduced the leaf nitrate content. Concomitantly, leaf colour was restored after chlorosis, which in turn improved its market value (Ventura *et al.*, 2013).

HALOPHYTES FOR LANDSCAPING AND ORNAMENTALS

Success in the floriculture industry is largely based on the availability of new and attractive ornamental plant varieties, there being a constant demand for novelties (Zaccai, 2002). Due to the primary importance of their external appearance, ornamentals are traditionally irrigated with the highest quality water, as salinity usually affects their yield and quality (Shillo *et al.*, 2002). Valdez-Aguilar *et al.* (2009) noted that salinity could cause adverse effects on the visual quality of ornamentals including reduced plant growth, distorted flower growth and yield quality, foliar injury and reduced stem length. Still, efforts were made to test a broad range of floricultural glycophytes for their salt tolerance and the possibility of irrigating them with low quality brackish water, recently reviewed by Cassaniti *et al.* (2013). The application of halophytic plants for landscaping and ornamental purposes seems to be a very attractive solution for the economic utilization of saline soil. Many halophyte species produce attractive flowers. Based on the HALOPH database (Aronson, 1989), Cassaniti and Romano (2011) investigated halophytes native to the Mediterranean region and listed 13 families with about 42 species having ornamental potential.

Besides its value as a vegetable crop, *Aster tripolium* produces attractive lilac-colour flowers with yellow stamens in the centre (Fig. 1), during its second year of growth. In nature, the flowers appear from July to September. The seeds require a stratification period of 14 d at 4 °C in moist soil before germination (Ramani *et al.*, 2006). Germination was reported to be restricted by salinities >1·5 % NaCl (Ungar, 1995). Both characteristics may have important impact on establishment on saline soils or where only saline water is available for irrigation. Although the salt sensitivity during germination may be an impediment for direct sowing in saline soil, it may be solved through pre-cultivation and subsequent transplanting to the final location. *Aster tripolium* subsp. *tripolium* and the smaller subsp. *pannonicus* (not suitable for vegetable production because of its bitter taste), with distinct morphological differences (leaf size and shape, leaf colour, leaf number and growth habitus; Sági and Erdei, 2002), may have high potential both as cut flowers and for the cultivation in flowering pots. *Aster tripolium* has been the subject of many investigations concerning its salt tolerance mechanism from several points of view, including growth response (Shennan *et al.*, 1987*a*), elevated atmospheric CO_2 concentrations (Geissler *et al.*, 2009*a*, *b*), leaf fatty acid profile (Ramani *et al.*, 2004), stomatal closure (Kerstiens *et al.*, 2002) and ionic regulation (Shennan *et al.*, 1987*b*). However, no study has analysed the effects of salt on flowering. The genetic material of *A. tripolium* seems to possess great potential for selection regarding flower appearance (Fig. 1). Therefore, the desired application–purpose, appropriate agrotechniques and salinity levels should be determined in order to direct the

FIG. 1. *Aster tripolium* flowers. (A) *Aster tripolium* subsp. *pannonicus* growing in September in a salt meadow named 'Nagylapos', in Törtel, Hungary (photograph by Professor Laszlo Erdei). (B) Inflorescences with increased amount of petals. (C) Flowering branch, kept for 6 d in double-distilled water after cutting. B and C were grown in 5 L plastic pots irrigated with 50 mM NaCl.

flowering period. Post-harvest treatments for cut flowers should also be developed to guarantee quality and shelf-life comparable with those of non-halophyte cut flowers.

MULTIFUNCTIONAL APPLICATIONS OF HALOPHYTES

Crithmum maritimum seems to have the potential to become a multipurpose halophytic cash crop. The aromatic, succulent leaves are appreciated on one hand as a salty vegetable (fresh or pickled), and on the other hand the approx. 30 cm high umbrella-like, delicate inflorescences may be attractive for ornamental purposes. *Crithmum maritimum* grows in rocky coastal environments in the Mediterranean region, where it is often subjected to sea spray (Ben-Hamed *et al*., 2004). Indeed, Franke (1982) mentioned that this plant may be used in rock gardens close to the sea, not exclusively for its flowers, but also for its decorative succulent leaves. Special care should be devoted to the germination as the germination of hulled seeds of *C. maritimum* decreased when exposed to salinity levels >15 dS m^{-1} (Conesa *et al*., 2008). Moreover, Atia *et al*. (2006) reported that germination was significantly inhibited when NaCl concentrations exceeded 50 mM (approx. 5 dS m^{-1}).

Due to their easy cultivation, even at seawater salinity, *Salicornia/Sarcocornia* have been the subject of numerous research trials which demonstrated their multipurpose applications that include biodiesel, oil, bioremediation, forage, vegetable, probiotic and ornamental usages (Table 3). In addition to *Salicornia/Sarcocornia*, numerous other halophytes have been listed for more than one application (Table 3). *Inula crithmoides*, proposed by Zurayk and Baalbaki (1996) as a saline crop, consumed in Lebanon, yields profusions of attractive yellow flowers from July to August, which make it a candidate for flowering pots as well as landscaping. *Mesembryanthemum crystallinum* is a well-studied model plant for abiotic stresses,

TABLE 3. *Halophytic plant species and their multiple application potential*

Scientific name	Uses	References
Aster tripolium	Vegetable	Ventura *et al*. (2013)
	Ornamental	Lieth (2000)
Crithmum maritimum	Vegetable	Meot-Duros and Magné (2009)
	Ornamental	Ben Dov *et al*. (1993)
	Edible seed oil	Zarrouk *et al*. (2003)
Inula crithmoides	Food and fodder	Zuryak and Balbakki (1996)
	Ornamental	Franke (1982)
Mesembryanthemum crystallinum	Vegetable	Herppich *et al*. (2008)
	Ornamental	Jessop (1986)
Atriplex hortensis	Vegetable	Wilson *et al*. (2000)
	Ornamental	
Salicornia/Sarcocornia spp	Biofuel/oilseed crop	Glenn *et al*. (1991, 2013)
	Bioremediation	Webb *et al*., (2012, 2013); Sphigel *et al*. (2013)
	Forage	Glenn *et al*. (1992); Imai *et al*. (2004)
	Meal by-product of oil extraction from seeds	Attia *et al*. (1997)
	Vegetable	Ventura and Sagi (2013)
	Probiotics	Sarker *et al*. (2010)
	Ornamental	Ventura and Sagi (2013)
Sporobolus virginicus	Ground cover, fodder	A. Eshel and Y. Waisel,(unpubl. res.)
Pennisetum clandestinum	Ground cover, fodder	Muscolo *et al*. (2013)
	Biomass	Muscolo *et al*. (2013)

which induces the switch from the C_3 to CAM photosynthetic mechanism (Bohnert and Cushman, 2000). It can be grown as an ornamental ground cover (Jessop, 1986). Herppich *et al.* (2008) tested the effects of saline irrigation on plant growth, physiology and leaf quality of a rare vegetable crop of *M. crystallinum*, commonly known and cultivated in California, India and the southern hemisphere, reporting that irrigation with 150 mM NaCl did not have a negative impact on plant quality.

Pennisetum clandestinum and *Sporobolus virginicus*, salt-tolerant grass species, were investigated for their potential as salt-resistant ground cover and pasture plants with good nutritive properties (Tables 3 and 4). Root, as well as shoot, growth decreased significantly when plants were irrigated with saline water, but no further reduction could be observed among all salt treatments ranging from 80 to 240 mM NaCl (Fig. 2). Moreover, Muscolo *et al.* (2013) pointed out that *P. clandestinum* is more resistant to salinity during germination than during vegetative growth, an important characteristic for starting a ground cover crop on marginal, salinized soils. The same authors also mentioned the use of *P. clandestinum* as a source of renewable bioenergy, as it contains lignocellulotic compounds that could be hydrolysed to produce high amounts of biogas.

TABLE 4. *Yield of the perennial grasses in September 2006*

Species	Irrigation water	f. wt (t ha^{-1} month^{-1})	% d. wt	d. wt (t ha^{-1} month^{-1})
Sporobolus	Reclaimed	4·20 ± 2·18	66·87	2·81 ± 1·46
virginicus	Brackish	5·58 ± 2·68	45·88	2·56 ± 1·23
Pennisetum	Reclaimed	7·19 ± 1·20	41·17	2·96 ± 0·49
clandestinum	Brackish	9·92 ± 2·61	33·57	3·33 ± 0·88

The salinity of the brackish water ranged between 7 and 10 dS m^{-1}. The salinity of the reclaimed sewage was 2–3 dS m^{-1}. The grasses were cut monthly by a tractor-drawn mechanical harvester (A. Eshel and Y. Waisel, unpubl. res.).

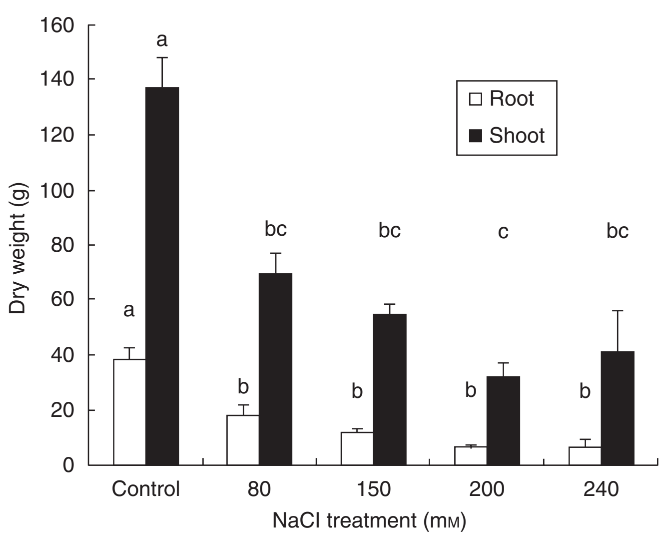

FIG. 2. Effects of increasing NaCl concentration on dry root and shoot biomass of kikuyu grass (mean ± s.e.). Lower case letters denote statistically significant differences between treatments (Tukey HSD, $P < 0.001$) (A. Eshel and Y. Waisel, unpubl. res.).

INDUSTRIAL USES OF HALOPHYTES

The utilization of halophytic plants as a source of renewable energy has emerged during the last decade (Rozema and Flowers, 2008). Recently, the use of glycophytic crops, such as maize, sugarcane or soybean, which can be easily used for production of bioethanol or biodiesel, was criticized, because the resource allocation for bioenergy production competes with food production. Furthermore, not only food crops, but also non-food crops such as switchgrass (*Panicum virgatum*) or short rotation woody perennials including willow and poplar depend on the existing scarce freshwater and arable land resources (Dominguez-Faus *et al.*, 2009). Therefore, the use of halophytes as bioenergy feedstock may be advantageous, since they may occupy a niche of unused marginal or saline lands where irrigation with available saline water is possible.

Eshel and co-workers trialled two desert halophyte plants, *Tamarix* spp. and *Euphorbia tirucalii*, for biomass production under extreme desert conditions (Eshel *et al.*, 2010, 2011). Among the four tested *Tamarix* species, *Tamarix jordanis* was selected for its high cellulose and low hemicellulose and phenol contents; preferable characteristics for ethanol fermentation (Santi *et al.*, 2014). *Tamarix aphylla* (erect type) trees produced 52 and 26 t ha^{-1} organic biomass when irrigated with reclaimed sewage (EC approx. 3 dS m^{-1}) or brine (EC approx. 7–10 dS m^{-1}), respectively. *Euphorbia tirucalii*, a desert succulent from East Africa, was suggested as a potential biofuel crop by Nobel Laureate Melvin Calvin >40 years ago (Nielsen *et al.*, 1977; Calvin, 1980). In recent experiments it exhibited a 60-fold weight increase 18 months after transplanting, when irrigated with saline sewage (EC 8–10 dSm^{-1}), generating a crop rich in carbon and hydrogen that has potential for being directly converted into biofuel (Eshel *et al.*, 2010).

A second approach is the cultivation of oilseed crops for biodiesel production using direct seawater irrigation, which is readily available in coastal areas of arid regions. *Salicornia bigelovii*, being highly salt tolerant and producing up to 30 % seed oil, was a primary candidate (Weete *et al.*, 1970; Glenn *et al.*, 1991; Alsaeedi and Elprince, 2000). However, the uneven seed ripening and their small size (0·6–1·2 mg) may result in approx. 50 % grain loss when harvested mechanically (Glenn *et al.* 2013), emphasizing the need to develop a special mechanical harvest technology for seed harvesting of this plant. Another disadvantage of growing *S. bigelovii* is the need to grow the plants for a relatively long period, approx. 100 d at cool temperatures, to initiate flowering (Glenn *et al.*, 1998) which is rather difficult in warm areas. However, breeding programmes for *S. bigelovii* demonstrated that accessions with improved seed and biomass yields could be obtained, indicating that improvement can be achieved over a relatively short period (approx. 5 years) (Zerai *et al.*, 2010).

An additional potential biofuel candidate with positive prospects to become a commercial crop is *Kosteletzkya pentacarpos* (syn. *K. virginica*), the seashore mallow, an oilseed-producing perennial halophyte (Gallagher, 1985). *Kosteletzkya pentacarpos* may be cultivated on large, saline marginal lands that can be irrigated with saline water (Gallagher, 1985). Therefore, (1) the biofuel crop does not compete with land suitable for conventional food crops; (2) utilizes areas of fallow land; and (3) liberates freshwater resources for more vital purposes.

The seeds of *K. pentacarpos* contain 18–22 % oil, which has a similar composition to cotton-seed oil, an edible oil and currently one of the oils used successfully for biodiesel production. Still, due to limited breeding and selection, the seed yield of *K. pentacarpos* is relatively low (up to 1500 kg ha^{-1}) as compared with soybean (approx. 2300 kg ha^{-1}) (Moser *et al.*, 2013). Nonetheless, the plants' perennial growth habit should allow for the development of multiple harvests, resulting in increasing yields with plant age due to the larger number of branches produced (www.ceoe.udel.edu/Halophyte/Growing%20Seaside%20Biodiesel%20proposal%20FINAL.pdf). The low disease susceptibility as well as retention of seed (non-shattering; Moser *et al.*, 2013) are additional helpful traits for mechanizing harvesting and efficient phytosanitary control.

THE USE OF CONSTRUCTED WETLANDS FOR MARINE EFFLUENT PURIFICATION

Coastal marine aquaculture development is frequently associated with negative environmental impacts and competition for resources (Bunting and Shpigel, 2009), because marine aquaculture effluents contain particulates, organic matter (including algae), nitrogen and phosphorus. Constructed wetlands, originally designed for effluent purification of non-saline water (Craft, 2005), might be used to deal with pollutants from marine aquaculture. The main principle of constructed wetlands is based on a combination of physical, chemical and biological processes that can be divided into four major elements: (1) plants; (2) soil and sediment; (3) microbial biomass; and (4) an aqueous phase containing contaminants. The inorganic nutrients from marine fish and shrimp culture could serve as fertilizer for plants and promote their growth and development. Since marine effluents are moderate to highly saline, the use of halophytes for their purification is advantageous. The relatively new approach of combining aquaculture and cultivation of halophytes as cash crops is gaining interest, with several recent papers demonstrating the purification capacity of constructed wetlands planted with *Salicornia/Sarcocornia* under different climatic conditions (Buhmann and Papenbrock, 2013*b*; Turcios and Papenbrock, 2014) ranging from a warm climate system (Shpigel *et al.*, 2013) to temperate climatic conditions (Webb *et al.*, 2012, 2013). Shpigel *et al.* (2013) concentrated on the effect of nutrient load under two different hydraulic flow regimes on *Salicornia* performance as a biofilter and biomass producer. Here, it was concluded that the surface flow regime with *Salicornia* would probably be more efficient in facilities with low nutrient load (e.g. fish hatcheries), whereas a subsurface flow regime would be more efficient with high nutrient load (e.g, super-intensive fish farms) (Shpigel *et al.*, 2013). In this study, seawater-grown *Salicornia persica* yields ranged between 17 and 26 kg m^{-2} $year^{-1}$ fresh biomass in all the treatments, comparable with previous investigations [15–26 kg m^{-2} $year^{-1}$ f. wt by Glenn *et al.* (1991); 8–9 kg m^{-2} $year^{-1}$ f. wt by Glenn *et al.* (1998); 1·2–2·4 kg m^{-2} $year^{-1}$ d. wt by Lu *et al.* (2010); and 1·7 kg m^{-2} $year^{-1}$ d. wt by Ventura *et al.* (2011*a*)]. Year-round *Salicornia* production in warm water aquaculture systems may have an advantage as compared with seasonal and irregular harvesting, practised throughout much of Western Europe (Bunting and Shpigel, 2009). As a reliable biofilter for waste water treatments throughout the year, the plant can provide income as an animal feed and a source of nutraceuticals. However, further assessments are needed in order to understand fully the market potential of cultured *Salicornia*, which may change with the use of the crop (gourmet vegetable, animal feed, oilseed crop or for the nutraceuticals industry).

FUTURE PERSPECTIVES

During the last decade, public awareness regarding successful establishment of halophytes has grown (Böer, 2006; Rozema and Flowers, 2008). Nevertheless, scientific documentation of large-scale experiments is limited, and no cultivation protocols are available for halophyte crops, as exist for conventional crops. To date, only one breeding programme has reported selection for yield parameters using *Salicornia bigelovii* as an example for an oilseed crop (Zerai *et al.*, 2010) and only a small number of investigations have evaluated the potential of the existing genetic material. There is a need for long-term experiments proving the sustainability of halophyte crop production and their economic prospective for future growers. Halophytic crops should undergo the same process undergone by conventional agricultural crops (breeding for improvement of agricultural traits such as yield, taste and mechanical harvesting over extended time periods) so that during short time spans economically profitable and consumer-acceptable products can be attained.

Moreover, halophytic crops can make use of marginal soils and saline irrigation water, both of which are inapplicable for conventional crop production. However, to ensure lasting sustainability of saline agricultural, the correct choice of adequate cultivation systems is of utmost importance. Sandy soils existing in coastal areas or inland sand dunes may be ready available for large-scale halophyte production without the risk of salt contamination occurring on fertile soils through Ca^{2+}/Na^{+} exchange and subsequent clay dispersion. Likewise, underground freshwater contamination should be avoided by the existence of sufficient deep water tables or adequate drainage. On the other hand, closed cultivation systems, which are separated from the natural soil, may offer a wide range of possible applications: hydroponics, constructed wetlands, artificial growth media (perlite, vermiculite and coconut fibres) and any suitable combination of these.

The almost infinite availability of saline water highlights the importance of halophytes as a source of renewable energy, particularly since they do not compete with glycophytic food crops. There are still difficulties that should be overcome, such as direct germination in saline conditions or genotype selection. However, more and more research is directed not only towards determining salt tolerance of halophytes, but also towards the improvement of agricultural traits for long-term progress (yield, palatability, chemical composition and mechanical harvesting), testing market potential and finally securing farmers' income. Perhaps time will ultimately be the determining factor advancing halophyte cultivation, when prices for fossil and alternative energy resources will exceed the halophyte biofuel production costs.

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