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Halophyte crop cultivation: The case for *Salicornia* and *Sarcocornia*

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ABSTRACT

Increasing soil salinization and the growing scarcity of fresh water dictate the need for a creative solution to attain sustainable crop production. To accomplish this aim, the domestication of inherently salt tolerant plant species with economic value is proposed as a straightforward methodology. Most studies investigating salt tolerance mechanisms are linked to small, experimental systems that cannot be generalized to the real agricultural context. The crops *Salicornia* and *Sarcocornia*, however, with their extreme salt tolerance and long history of consumption by humans, make the ideal model plants on which to base a halophyte growth strategy. New applied technologies were developed for leafy vegetable production using small-scale greenhouse and in-field studies. Several cultivation systems adapted to the irrigation water salinity and the available soil conditions are described. Daylength manipulation and a repetitive harvest regime partially elucidated the flowering patterns of *Salicornia* and *Sarcocornia* and showed that flowering should be prevented for maximal vegetable production. Additionally, the beneficial effect of saline irrigation on quality parameters via the enhancement of stress-induced secondary metabolites with antioxidant capacity should be considered during cultivation. This review summarizes the recent developments in growing halophytes for food production with saline irrigation, using *Salicornia* and *Sarcocornia* as a case study.

1. Introduction

Halophyte plants growing near seashores have been collected since ancient times as food, for their medicinal qualities, and for their high salt contents (Davy et al., 2001; Lieth, 2000). The current interrelated crises of dwindling fresh water supplies and increasing soil salinization have awakened new interest in plant species that possess inherent salt tolerance, especially those plants that can achieve high, economically lucrative yields. The majority of our agricultural crops are salt sensitive glycophytes, however, and in spite of the promising results that emerged from initial attempts to cultivate glycophytes under saline regimes using conventional breeding programs, the overall results of these programs were disappointing (Flowers et al., 2010). Epstein et al. (1980) optimistically proposed a new developmental strategy of genetically adapting plants to saline conditions. Their concept was based on the screening, selection, and back cross-breeding (with salt tolerant germplasm) of conventional agricultural crops to increase their salt resistance. Fifteen years later Flowers and Yeo (1995) summarized the disappointing overall results of the efforts toward genetic manipulation, out of which only a handful of salt tolerant varieties emerged. Possible reasons for the low rate of success, according to Flowers and Yeo, included the low priority generally afforded the salinization problem, the poor level of collaboration between plant breeders and plant physiologists, and the genetic complexity of salt tolerance, which is a multigenic trait.

Expressed at the whole plant, tissue and cellular levels, salt tolerance involves morphological, physiological and biochemical adaptations (Koyro et al., 2011). In any plant, the adjustment to higher salinity is regulated by activating a cascade of genes responsible for building the molecular network involved in stress sensing, signal transduction, and finally, the expression of specific genes and metabolites (Türkan and Demiral, 2009). The lack of a single, key gene for salt tolerance, therefore, greatly complicates the work of plant breeders and is a strong indication that any efforts toward creating salt tolerant crop plants based on altering a single genetic factor will probably end in failure (Flowers, 2004).

Just as the successful development of conventional crops relied in the past on the domestication of wild plants, the most straightforward method for acquiring salt tolerant crops for the future should begin with halophytes (Flowers, 2004). Similar to the process undergone by many of our traditional crops, such as rice, wheat and corn, potential halophyte crop plants must be admitted to conventional breeding programs whose collective goal is to convert them from wild plants into crops with high yields (Rozema and Flowers, 2008). Despite the scientific community's understanding of the importance of selecting and cultivating a viable halophyte crop plant, most halophyte research has typically focused on merely revealing the existence of extreme salt tolerance or of tolerance mechanisms while neglecting the crop's

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Table 1
Yields obtained from halophyte crops grown under field conditions.

Plant species	Salt concentration	Yield (kg m^{-2} $year^{-1}$)	Reference
Aster tripolium	40 mM	14.0[a]	Ventura and Sagi (unpublished)
Atriplex lentiformis	500 mM	1.8[b]	O'Leary et al. (1985)
Atriplex triangularis	150 mM	21.3[a]	Gallagher (1985)
Batis maritima	500 mM	1.7[b]	O'Leary et al. (1985)
Salicornia europaea	500 mM	1.5[b]	O'Leary et al. (1985)
Salicornia persica	100 mM	15.0[a]	Ventura et al. (2011b)
Sarcocornia fructicosa	100 mM	28.0[a]	Ventura et al. (2011b)

[a] Expressed in fresh weight.
[b] Expressed in dry weight.

commercial potential. In a pioneer study, Zerai et al. (2010) demonstrated in *Salicornia bigelovii* that sufficient genetic diversity exists among wild accessions and cultivars to support a genetically-based crop improvement scheme within the relatively short seven-year breeding program. Unfortunately, the entire investigation was based on only a few traits of agronomic importance, and none of the lines have been tested yet under field conditions.

Since halophytes vary widely in terms of their salt tolerance ranges and their natural growth rates, the general salt restriction limits under which optimal yield will be achieved needs to be determined before starting cultivation. A quick-check system proposed by Koyro et al. (2006) may be capable of providing the initial answers about a prospective plant's salinity tolerance threshold under idealized, reproducible growth conditions. However, the authors also stated that this system can only be the first step in a halophyte's development as a cash crop plant. Subsequent upscaling to larger greenhouse experiments or field studies under local conditions to test yield and product acceptance constitute the next stage toward the commercial cultivation of halophytic crops.

Halophytes can yield as much as conventional crops, even when irrigated with seawater (Glenn et al., 1999; Ventura et al., 2011a). However, growth optimums for most halophytes range from 50 to 250 mM NaCl (Flowers et al., 1986), but for some extreme examples, that value is between 200 and 400 mM NaCl (Flowers and Colmer, 2008). These results were usually obtained from short-term studies (14–60 days) under controlled environments, and the data provided for yield performance are typically based on extrapolations from small-scale experiments (Flowers and Colmer, 2008; Zurayk and Baalbaki, 1996). Field trials simulating agronomic growing conditions are rarely reported (Glenn et al., 1999) and we thus summarized here yields obtained from halophyte plants grown in field experiments irrigated up to seawater salinity (Table 1).

Although the agricultural development of halophyte crops is still in its infancy, plant irrigation with saline water at small-scale production sites using seawater, diluted seawater, or brackish water is already being practiced (Glenn et al., 1998; Lieth, 2000). The diversity of halophyte plants translates into a wide range of potential applications (Koyro et al., 2011). Halophytes have been tested as fodder crops (Bustan et al., 2005; El Shaer, 2010), for phytoremediation (Manousaki and Kalogerakis, 2011), as renewable energy sources (biofuel) (Eganathan et al., 2006), for the treatment of saline aquaculture effluent (Brown et al., 1999), as landscaping ornamentals (Zia et al., 2008) and as food for human consumption (Ventura et al., 2011a).

Seawater agriculture as proposed by Glenn et al. (1998) appears to be the extreme in halophyte farming. The constant supply of a high salt concentration like that of seawater will effectively reduce the list of potential halophyte species to only the most salt-tolerant crops. The use of brackish water, for instance, with its much lower salinity than seawater, may spread the number of halophytic crops that can be grown, thus providing a more viable option for commercial agriculture (Rozema and Flowers, 2008). The cultivation of halophytic plants will require redefining agrotechnical practices, which, in turn, will need to be fine-tuned for each particular crop and its intended utilization. For example, it is essential to optimize the irrigation quantity at each salinity level (brackish or seawater) to allow salt leaching below the root zone, consequently avoiding soil salinization (Lieth, 2000; O'Leary, 1988).

Using *Salicornia* and *Sarcocornia* as examples, we summarize a decade of applied halophyte research. Included in the review are greenhouse experiments and long-term field studies that investigated the agrotechnical practices for the production of halophytes as leafy vegetables at low to moderate salinity and at seawater salt concentration.

2. Halophytes as vegetables and herbs – *Salicornia/Sarcocornia* as a case study

Among the wide diversity of existing halophyte species, those with the greatest economic potentials as crops will contribute to the most promising strategies for sustainable agriculture in marginal environments (Koyro et al., 2011; Lieth, 2000). To reduce the large pool of available halophytes to those with the greatest potentials to be domesticated as vegetable crops, first one should evaluate the existing knowledge about the plant's traditional uses and applications and estimate today's market demands. Many plant species have been used traditionally as herbs and vegetables, and accounts of their uses often can be found in ethnobotanic reviews and literature (Davy et al., 2001; Guarrera et al., 2006; Simopoulos, 2004; Tardío et al., 2006).

The growing interest of the past decade in cultivating crops under saline conditions has led to the rediscovery of the potentials of several, promising halophytic plant species to be farmed as leafy vegetables (Table 2). Until today, those plants have been gathered regularly from wild populations and sold at local farmers markets, and they enjoy only minor cultivation that is often limited to private backyards and kitchen gardens (Wilson et al., 2000).

Non-cultivated plant material typically exhibits low uniformity and the quality of its produce is unpredictable. Furthermore, its supply is notoriously inconsistent, confined to the natural growing season, and limited by the local abundance of the plant species (Schippmann et al., 2006). Therefore, prerequisite to its commercial cultivation as a gourmet vegetable are the selection of superior genotypes and the definition of the plant's reproducible growing conditions, which are necessary to ensure a constant market supply and the success of the new crop.

The gourmet vegetable and herb market demands products of the highest quality. In addition to the requirement that the marketed product be visually appealing in terms of freshness, color, and packaging, it should also consistently reach the market at the same maturity level, have a particular taste recognized by its consumers, and be of sufficient nutritional value to warrant its gourmet status (van der Voort et al., 2007). In particular, a product's levels of nutritionally valuable metabolites, such as omega-3 fatty acids, phenolic compounds, antioxidants or minerals, are used to decide whether it

Table 2
List of halophyte plants with highest potential as vegetable crop for saline irrigation.

Plant species	Salt tolerance level	Popular uses	Nutrient composition	Reference
Aster tripolium	300 mM[a]	Fresh salads, cooked vegetable	Minerals, polyphenols	Koyro et al. (2011)
Atriplex hortensis	>250 mM[a]	Pot herb, colorful salad greens	Protein, amino acids	Wilson et al. (2000), Carlson and Clarke (1983)
Batis maritima	200 mM[b]	Eaten raw, cooked or pickled	Essential amino acids, tocopherol antioxidants	Debez et al. (2010)
Cochlearia officinalis	100 mM[a]	Fresh salads	Vitamin C	de Vos (2011)
Crambe maritima	>100 mM[a]	Fresh salads	Phenolics, antioxidants	de Vos et al. (2010)
Crithmum maritimum	150 mM[a]	Fresh and pickled as spice and for salads	Vitamin C, antioxidants	Franke (1982), Ben Hamed et al. (2004), Ben Amor et al. (2005)
Diplotaxis tenuifolia	~150 mM	Mixed salads		de Vos (2011)
Inula crithmoides	400 mM[b]	Salads, pickled in vinegar	Iodine	Tardío et al. (2006), Zurayk and Baalbaki (1996)
Mesemyranthenum crystallinum	400 mM[c]	Salad green or quickly cooked		Herppich et al. (2008), Agarie et al. (2007)
Plantago coronopus	250 mM[a]	Salad greens	Vitamins A, C, K, minerals	Koyro (2006)
Portulaca oleraceae	<140 mM[a]	Salad greens, cooked vegetable	Omega-3 fatty acids, Vitamin C, α-tocopherol, β-carotene	Simopoulos (2004), Yazici et al. (2007)
Salicornia sp. and *Sarcocornia* sp.	>500 mM[a]	Salad greens, vegetable	Minerals, fatty acids, polyphenols	Ventura et al. (2011a)
Tetragonia tetragonioides	174 mM[a]	Frozen like spinach	Antioxidants, amino acids	Wilson et al. (2000), Słupski et al. (2010)

[a] Refers to the salinity level in the irrigation solution that results in a 50% reduction in yield.
[b] Refers to the salinity level for maximum growth.
[c] Significant reduction in growth.

meets the standards of 'functional food' for health enthusiasts (Del Giudice and Pascucci, 2010).

2.1. *Salicornia as an oilseed crop*

To date, one of the most successful examples of halophyte cultivation is probably *Salicornia*. The plants of this annual genus are characterized by an extreme reduced morphology of apparently leafless shoots (Davy et al., 2001). As a salt marsh pioneer plant, *Salicornia* possesses extreme salt tolerance and can be grown with saline irrigation water whose salt concentration may even be as high as that of full-strength seawater (Ventura et al., 2010). But for *Salicornia* to become a commercial halophyte crop it must also be capable of high-yield production under saline conditions for its cultivation to be economically viable (O'Leary, 1988).

In their quest for those additional characteristics, Glenn and his co-workers thoroughly investigated *S. bigelovii* (Glenn et al., 1991), which belongs to the North American tetraploid branch of *Salicornia* (Kadereit et al., 2007). Its seeds' high oil and protein contents compare favorably with those of the major oilseed crops of the world, prompting the proposal that halophytes' greatest promise may be as oilseed crops for the production of vegetable oil lined up for food or industrial uses (O'Leary and Glenn, 1994). Additionally, the mean annual yield of 0.2–0.25 kg seeds m^{-2} from a single harvest equaled or even exceeded those of freshwater irrigated oilseed crops, thus fulfilling the preconditions for a successful halophyte crop (Glenn et al., 1998). In a breeding program initiated in 1997 for *S. bigelovii* aimed at enhancing the biomass production and seed yield of wild germplasm through both hybridization and pedigree breeding, Zerai et al. (2010) showed enhancements in seed yield and seed-oil content, demonstrating that *S. bigelovii* is amenable to improvement.

Besides their cultivation for oilseed production, *S. bigelovii* and other *Salicornia* species are multifaceted, practical crops, and as such they have generated major research interest (Lu et al., 2010). Most studies have focused on salt tolerance mechanisms (Moghaieb et al., 2004), specific chemical constituents with medicinal importance (Rhee et al., 2009), and its potential as a forage crop (Abdal, 2009; Glenn et al., 1992). Only minor attention was paid to vegetable cultivation, notwithstanding *Salicornia*'s long history of human consumption appreciating the salty taste and its high nutritional value (Lu et al., 2010; Mudie et al., 2005). Long before industrialized agricultural production and the widespread cultivation of certain crops, plants were typically gathered from the wild instead of being cultivated and used by the local people living near where the plant grew naturally, which is the coastal area for *Salicornia* (Mudie et al., 2005). There are currently projects to promote *S. bigelovii* vegetable production in Mexico, where growers can exploit the subtropical climate to supply the European markets with *Salicornia* shoots as an off-season product during the seasonally cold weather from September until June (OASE Foundation, 2009).

2.2. *Salicornia and Sarcocornia are vegetable crops with similar appearance*

Different species of the *Salicornia* genus are suitable for vegetable production. These have been accepted by the consumer, who is exclusively interested in the young green plant parts that are sold in the markets as 'Samphire' or 'Sea asparagus.' The latter name probably reflects the shape of the shoots, which resemble the tops of green asparagus. Nevertheless, these plants exhibit a reduced phenotype during vegetative growth, contributing to the large phenotypic plasticity and correspondingly notoriously difficult taxonomy of *Salicornia*, making the identification of most species a virtual impossibility for non-specialists (Kadereit et al., 2006, 2007). As a consequence, the names *Salicornia europaea* or *Salicornia herbacaea* were frequently used broadly to combine most of the species into a single group of the genus. Plants that were part of the same genotype but that were located in different regions were often given different names. Moreover, even the closely related perennial *Sarcocornia* was incorporated into the genus of its annual counterpart, further indication of this complexity (Davy et al., 2001, 2006). The identification and separation between *Salicornia* and *Sarcocornia* species based mainly on their growth habit and flower morphology, which more recently were underpinned by molecular tools (Kadereit et al., 2006, 2007). Specifically, *Salicornia persica* and *Sarcocornia fructicosa* can be easily distinguished by their annual

Table 3
Salt tolerance limits for the germination of *Salicornia* and *Sarcocornia* spp.

Plant species	Salt concentration (mM) at which germination was reduced from 75–100% to about 10% and less
Salicornia brachystachya	240
Salicornia bigelovii	1000
Salicornia brachiata	600
Salicornia dolistachya	240
Salicornia europaea	850
Salicornia herbacea	1700
Salicornia pacifica var. *utahensis*	860
Salicornia patula	340
Salicornia persica[a]	>500
Salicornia rubra	1000
Salicornia virginica	600
Sarcocornia fructicosa	1030
Sarcocornia fructicosa[a]	500
Sarcocornia perennis	1030
Sarcocornia quinquifolia	690

Adapted from Khan and Gul (2006).

[a] From Ventura et al. (2011a).

and perennial life forms and flower characteristics forming a characteristic triangle with a larger central and two smaller lateral flowers in *Salicornia* versus being arranged in a horizontal row in *Sarcocornia*. (Kadereit et al., 2007; Ventura and Sagi, unpublished). Nevertheless, both genera produce similarly succulent shoots that are highly suitable as a vegetable (Ventura et al., 2011a). On the other hand, regarding cultivation practices for halophyte vegetable production, it is of the utmost importance to elucidate the biological differences among *Salicornia* species, and between the two genera of *Salicornia* and *Sarcocornia*.

2.3. Salinity and Salicornia/Sarcocornia germination

When the entire crop cultivation process, from planting to harvest, exploits saline irrigation, the salt responses of all plant developmental stages must be considered. Despite the ability of halophyte plants to grow and proliferate in highly saline surroundings, their seeds are sensitive to hyper-saline conditions (between 0.2 and 0.6 M NaCl) during germination (Khan and Gul, 2006). Under high salt concentrations, the water potential of the medium is reduced, thereby impeding the water uptake of imbibing seeds. Germination will therefore occur only after the salt stress is relieved to a certain threshold (Woodell, 1985). In nature, *Salicornia* and *Sarcocornia* germination generally coincides with the lower sediment salt concentrations associated with winter and spring (Davy et al., 2001, 2006). Moreover, the temperature regime has a strong impact on the germination rate of *Salicornia* species, which further interacts with the salinity levels. For example, the germination rate of *Salicornia rubra* at 1 M NaCl salinity was enhanced through a 25/35 day/night temperature regime to values above 10% germination rate as compared to lower temperature regimes, at which the final germination rate remained below 10% germination (Khan et al., 2000).

Under laboratory conditions, the best germination was found using either fresh water or water with low saline concentrations (Ventura et al., 2011a). Decreased germination rates were observed for concentrations above 50 mM NaCl (Meot-Duros and Magné, 2008), nevertheless the germination limits for *Salicornia* and *Sarcocornia* spp. are realized only at extreme hypersaline conditions of sometimes more than a 2-fold of seawater concentration (Table 3). *S. persica* and *Sar. fructicosa* genotypes exhibited significantly different germination rates for salinity levels above a concentration of 50% seawater (~250 mM NaCl). Germination rates declined fast with increasing seawater salinity, but for most of the genotypes they ranged from 30% to 70% when irrigated with a 75% seawater (~375 mM NaCl) concentration (Ventura et al., 2011a).

When halophytes first began to be cultivated, freshwater irrigation was recommended for the early stages of germination to ensure that seedlings were firmly established (Gallagher, 1985). But from the perspective of applied research, *Salicornia* and *Sarcocornia* can be germinated with irrigation water comprising concentrations of up to 75% seawater. Differences in genotype and germination rate, however, have to be taken into account and can be compensated for by altering the quantities of seeds used to germinate the crop (Ventura et al., 2011a).

3. Yield potential and harvesting regime

The yield potential of a halophyte plant depends on the plant species and the salt concentration to which the crop is subjected during cultivation (Lieth, 2000). Unfortunately, most scientific records of halophyte biomass production and yields refer to laboratory experiments, while field studies have seldom been reported. Yields are often presented as fresh or dry biomass per pot or per single plants, not taking into account plant densities under field conditions (Koyro et al., 2011; Zerai et al., 2010). In addition, time frames for growing cycles and/or harvesting periods may vary widely between plant species, regions, and growing seasons. The low quality and high variability of existing yield data on halophyte cultivation, therefore, greatly reduces the value of comparisons between halophyte cultivars, especially when the data has been derived from small-scale greenhouse studies.

During six years of field trials in Mexico, Glenn et al. (1998) reported an annual average of 1.7 $\mathrm{kg\,m^{-2}}$ of dry biomass for *S. bigelovii* when grown with seawater for oilseed production. The total biomass produced after a single harvest equaled that of several other halophyte plants and was only slightly lower than freshwater-irrigated alfalfa hay, lending this *Salicornia* species promise as a forage crop (Glenn et al., 1998). For vegetable production, only fresh and tender plant material is acceptable. Thus the repeated harvest of the same plants during a single growing season has a twofold advantage: (i) accumulated final yields per area higher than for a similar crop harvested once per season and (ii) improved product quality by cropping only young shoot tips.

Accordingly, we developed a repetitive harvest regime by which the plants were cut (about 5 cm above ground level, resulting in a "cutting table") for the first time when their shoot sizes were approximately 10–15 cm long. After shoot re-growth, the plants underwent several repeated harvests, of which they were cut back to the height of the cutting table (Ventura et al., 2011b). Plant re-growth capacity and time intervals between subsequent harvests were shown to be important criteria. Our comparison of fixed harvest regimes—cutting the plants every 2, 3 or 4 weeks—showed that the highest yield (16 $\mathrm{kg\,m^{-2}}$ during a six months harvest period) was obtained using the 3-week interval for *Salicornia* (Ventura et al., 2011a). More frequent harvests led to clear declines both in the accumulated yield (11 $\mathrm{kg\,m^{-2}}$ during a six months harvest period) and in the yield per single harvest expressed in shorter shoot size with reduced marketable value (Sagi, unpublished). Longer time intervals effectively raised the cutting table height and resulted in a reduction in yield (14 $\mathrm{kg\,m^{-2}}$ during a six months harvest period) as the cutting into undesired wooden shoot parts, now higher on the shoot due to the extended time between harvests, was avoided. The overall slower growth rates and low yields of *Sarcocornia* when irrigated with full-strength seawater were probably the reason for the lack of any significant effect by harvest regime on yield (Ventura et al., 2011a).

The total number of harvest cycles per growing period varied among *Salicornia* species and within the genus *Sarcocornia*. *S.*

bigelovii was limited to three to five harvest cycles when cultivated in Mexico with seawater (Oasis Foundation, 2009). An in-field study showed that six harvest cycles were possible for *S. persica* grown on sand dune soil in the desert in Ramat HaNegev, Israel, using irrigation water with a moderate salinity of 10 dS m^{-1}. Until plants started flowering, an average fresh biomass yield of 14.9 kg m^{-2} was obtained for the 7-month summer cultivation cycle (Ventura et al., 2011b).

In the same experiment in Israel, two *Sar. fructicosa* genotypes were compared to the *Salicornia* species for biomass accumulation, and a completely different cropping pattern—characterized by an endless sequence of harvesting cycles (currently, at least for three years)—was demonstrated for *Sar. fructicosa*. Specifically, members of this initially slow-growing genus regained growth with time, and the harvest period was not interrupted due to the loss of flower induction when the repetitive harvest regime was employed. Finally the *Sarcocornia* plants accumulated, depending on the genotype, roughly double the biomass amounts produced by *Salicornia* during a one year cycle of continuous harvesting (Table 4). Furthermore, the *Sarcocornia* harvest period could be extended to 17 harvest rounds spread over more than two years of continuous cultivation. Total fresh biomass yields of 63.2 and 46.9 kg m^{-2} were recorded for the two genotypes, with no need to reestablish the cultivation plot with new plants (Ventura and Sagi, unpublished). Ventura et al. (2011b) emphasized that the repetitive harvest regime most likely prevented flowering in the perennial *Sarcocornia*, since non-harvested plants flowered in the same manner as did the annual *Salicornia*. Thus, the genetic background of the perennial *Sar. fructicosa* plays an important role in terms of harvest duration and yield potential, and it should be considered before beginning vegetable production of 'Sea asparagus'.

3.1. Preferred cultivation system for Salicornia vegetable production

In Israel, *Salicornia* and *Sarcocornia* cultivation for vegetable production is typically practiced under simple nets or in greenhouses on land areas of 0.5–1 ha. For the products of these crops to be successfully marketed as vegetables, the young shoots must be harvested manually, a labor intensive element critical to halophyte crop production. Different cultivation protocols, therefore, have been tested for *Salicornia* vegetable production. For example, the easiest and most straightforward way to produce *Salicornia* is to cultivate it in native sand dune soils watered with drip irrigation, as has been successfully accomplished by some farmers in the Dead Sea and Ramat Hanegev areas (Fig. 1A and B). Low precipitation (average yearly rainfall 90 mm), the loose soil structure of dune sand, and the absence of shallow ground water in those semi-arid desert areas combine to enable crop irrigation with saline water at salt concentrations of 10 dS m^{-1} (Pasternak and De Malach, 1995). For edaphic conditions that do not allow this kind of culture, growing systems detached from the native soil have been developed (Fig. 1C–E). Although soilless culture systems using inert culture media, e.g., perlite or dune sand, are more labor intensive and costly, their irrigation regimes can comprise any desired salt concentration. This was realized by growing *Salicornia* in troughs built from plastic sheets (Fig. 1C and D) or in seawater-fed constructed wetlands, to which the plants were transplanted in floating units (Fig. 1F and H).

In addition to irrigation with seawater, the feasibility of using nutrient rich effluents, such as hyper-saline drainage water (Grattan et al., 2008) or saline aquaculture effluent (Brown et al., 1999), for the cultivation of *Salicornia* was investigated in small lysimeter experiments. Adapting this approach to a practical application, e.g., irrigation with moderately saline aquaculture effluent (EC 4 dS m^{-1}), was tested in Israel using a subsurface flow-through system in which the *Salicornia* crop was placed in coconut fiber-filled sleeves (Fig. 1G). Fast regrowth after the harvests led to average yields of 18.6 ± 0.9 kg (n = 6) fresh biomass m^{-2} during five months of cultivation (Ventura and Sagi, unpublished). Moreover, when grown in constructed wetlands (Fig. 1F), *Salicornia* and *Sarcocornia* were shown to function as efficient biofilters for the removal of nutrients from mariculture effluent while concurrently producing high yields of valuable by-products of vegetables, oilseed crop, or raw materials for the pharmaceutical industry (Shpigel et al., 2007). A production level of 20–30 kg m^{-2} $year^{-1}$ of fresh *Salicornia* biomass in the constructed wetlands is thought to remove 1–3 g m^{-2} day^{-1} of nitrogen (Shpigel et al., 2007).

In conclusion, a wide range of cultivation systems exists, which can be adapted by each grower for his specific cultivation purposes. The determining aspects for the final choice of application for any halophyte farming venture will depend primarily on irrigation water salinity, its quality and on the type of soil available.

3.2. Effect of day length on flowering and yield

Under natural conditions, the shortening day length of late summer causes the annual *Salicornia* to produce short segments that ultimately form terminal fruiting spikes in which the seeds are produced (York et al., 2000). After flower initiation, vegetative growth slows down rapidly, with the end result being a reduction in yield and the production of undesired flowering *Salicornia* shoots with no market value (Ventura et al., 2011b). Very few studies have investigated the conditions for the onset of flowering in this genus, and they focus mainly on *S. bigelovii* (York et al., 2000). Flowering in this species was promoted by short day length, with 15 h being proposed as a critical value for induction (Fu and Zhao, 2003). Cultivated *S. europaea* was reported to flower precociously when plants were only a few weeks old, and this early termination of vegetative growth restricted further plant development (Davy et al., 2001). High radiant flux densities in the immediate crop environment were anticipated to prevent precocious flowering, but the exact conditions leading to flower initiation in *Salicornia* are still not well understood.

The flowering behaviors of *Salicornia* species from different geographic locations were recently compared with those of two *Sarcocornia* genotypes (Ventura et al., 2011b). The research demonstrated that flowering could be controlled through morning and evening day length extensions executed by applying light of low radiant flux densities (Ventura et al., 2011b). For *Salicornia* whose geographical origin is on a latitude similar to that of Israel, the 13.5-h day length could be suitable to prevent flowering, but *Salicornia* species from the northern latitudes needed at least 18 h of light to delay the onset of flowering (Ventura et al., 2011b). The sensitivity to flower induction and to geographical origin, based on latitude values, were also correlated for *S. bigelovii* (York et al., 2000). From an applied point of view, the use of artificial light to extend day length during the season when it is decreasing is an efficacious means to extend the harvest period of European annual *Salicornia* species. In addition to the photoperiodic effect, flowering can also be inhibited in the perennial *Sarcocornia* (see above), but not in the annual *Salicornia* species, by practicing a continuous harvest regime, probably due to their perennial and annual growth habits, respectively (Ventura et al., 2011b).

Interestingly, a comparison of moderately saline (10 dS m^{-1}) water with 100% seawater showed that the salt concentration of the irrigation water affected the flowering of neither *Salicornia* nor *Sarcocornia* species (Ventura et al., 2011b). However, further experiments to elucidate the regulation of flower induction in *Salicornia* and *Sarcocornia* species are needed. In regions where mild winter climates make this crop a realistic possibility for year-round

Table 4

Fresh biomass of *Salicornia* (DS, RN, N) and *Sarcocornia* (VM, EL) genotypes after a one-year growing cycle that began in March. Plants were grown under field conditions on sand dune soil irrigated with moderate salinity (10 dS m^{-1}) in Ramat Hanegev, Israel. Harvesting was stopped after the 6th harvest for *Salicornia*, because of flower initiation. Values are means ($n = 4$).

Harvests		Fresh biomass (kg m^{-2})										Annual total
		1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	
Salicornia persica	DS	0.83	1.58	2.83	3.38	4.21	3.21	Flowering				16.04
	RN	0.67	1.70	2.72	2.81	2.69	2.81	Flowering				13.40
	N	0.31	1.89	3.52	3.55	3.38	2.54	Flowering				15.19
Sarcocornia fructicosa	VM	0	0.88	1.16	2.26	2.70	3.37	4.52	4.30	3.63	5.61	28.43
	EL	0	0.52	0.97	1.52	1.83	1.39	2.86	2.35	3.28	5.32	20.04

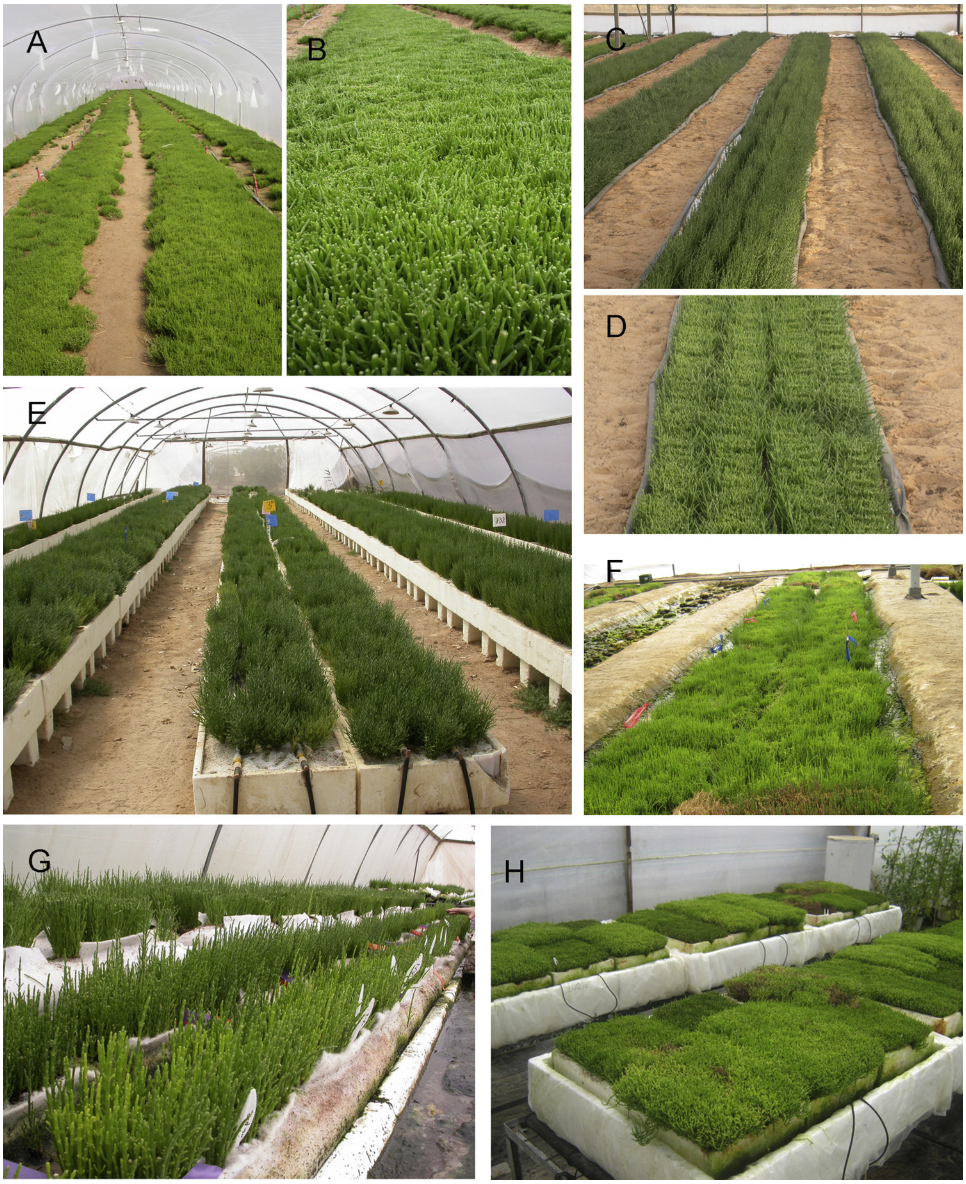

Fig. 1. Cultivation systems for *Salicornia* and *Sarcocornia*. (A) Plants growing on native sand dunes, irrigated with drip irrigation. (B) Sand dune culture after harvesting to 'cutting table' height. (C) Troughs build with plastic sheets, detached from native soil. (D) Troughs after the harvest. (E) Drip irrigated soilless culture, detached from native soil. (F) Surface-flow constructed wetland fed with marine effluent. (G) Sleeve cultivation irrigated with saline aquaculture effluent in subsurface-flow system. (H) Units filled with perlite floating in seawater.

cultivation, controlling its flowering pattern will strongly benefit future halophyte vegetable growers.

4. Quality of the vegetable

Leafy vegetables are important, easily accessible sources of nutrients, including minerals, vitamins and antioxidant compounds, for human consumption (Rubatzky and Yamaguchi, 1997). Moreover, to date, interest in certain ‘functional foods,’ which are endowed with exceptional nutritive values, is increasing (Del Giudice and Pascucci, 2010). The new potential halophyte crops, cultivated as cash crops using saline water, meet those special nutritional demands. Although the potentially negative health impacts of the high sodium and chloride levels in halophyte vegetables are often mentioned, they can be offset by the need to add little or no salt to halophyte dishes during food preparation. So far, however, the effects of salinity on the quality parameters of the marketable product have received much less attention in the literature than those on yield (Maggio et al., 2011).

In all plants, glycophytes and halophytes alike, tolerance to salinity relies primarily on the controlled uptake of ions by the root system, the compartmentalization of toxic ions in the vacuole, and the synthesis of organic compatible solutes (Flowers and Colmer, 2008; Shabala and Mackay, 2011; Zhu, 2001). In addition, plants have evolved an efficient system to counteract the oxidative damage caused by reactive oxygen species (ROS). The up-regulation of ROS-scavenging antioxidative enzymes and the synthesis of small, non-enzymatic molecules with antioxidant properties—such as ascorbate, glutathione, alpha tocopherol, flavonoids, anthocyanins, carotenoids and polyphenolic compounds—constitute the main detoxification strategy (Türkan and Demiral, 2009; Zhu, 2001). Although the primary reason for the changes in the biochemical composition of halophyte leaves is to combat salt stress, those changes are ultimately responsible for the quality of the vegetable product (Maggio et al., 2011).

The accumulation by the plant of organic solutes and mineral ions differs widely between plant families and species. This issue is among the top priorities of vegetable growers as vegetable composition, particularly of the edible plant parts, change substantially as the plant is exposed to increasing salinity (Grieve et al., 2001; Maggio et al., 2011). Sodium and chloride are the main ions accumulated when plants are irrigated with saline water. *S. persica* shoots (Table 5) grown in seawater accumulated 1.6 g Na^+ and 2.9 g Cl^- 100 g^{-1} edible portion in a process that confers on the plant the salty taste sought after by consumers (Ventura et al., 2011a; Wagenvoort et al., 1989). The salt content of *Sar. fructicosa* was found to be in a similar range, while that of the halophyte *Aster tripolium* exhibited about one third less Na^+ at the same salt concentration (Geissler et al., 2009; Ventura et al., 2011a). In comparison, the amount of Na^+ found in non-halophyte leafy vegetables, albeit grown at much lower salt concentrations (11 dS m^{-1}), ranged from 0.14 g to 0.42 g (Grieve et al., 2001). Much less attention is devoted to Cl^- in terms of nutrition, but as a competitor for $NO_3{}^-$ it may contribute to the maintenance of low $NO_3{}^-$ levels in the commercial part of the plant (Grattan and Grieve, 1999; Maggio et al., 2011; Sagi, unpublished).

The amounts of other ions—like the major essential ions K^+, Mg^{2+} and Ca^{2+}—that confer nutritional value on the product typically decrease with increasing irrigation water salinity, predominately as a result of competition with Na^+ during uptake (Flowers and Colmer, 2008). Koyro (2006) cultivated the halophyte *Plantago coronopus* in seawater as a potential leafy vegetable and reported a reduction in the major essential ions. Nevertheless, the calcium content of this plant species grown at seawater salinity was about eightfold that of *Atriplex hortensis*, another leafy vegetable halophyte, when grown with less than half-strength seawater salinity (Wilson et al., 2000). Interestingly, under increasingly saline regimes, *Salicornia* and *Sarcocornia* showed enhanced values for these nutritive ions, whose final contents in edible portions was comparable to those in non-halophyte vegetables grown at moderate salinity (Grieve et al., 2001; Ventura et al., 2011a).

Plant development in hypersaline environments is associated with the accumulation of metabolically compatible solutes. The increase in osmolytes probably has multiple functions, including osmotic homeostasis maintenance and oxidative detoxification through ROS sequestration (Zhu, 2001). Flowers and Colmer (2008) summarized the prominence of organic compounds, such as simple and complex sugars, sugar alcohols, quaternary amino acid derivates, tertiary amines and sulfonium compounds, during species-specific responses to salt stress. Specifically, antioxidant compound enrichment of the consumed plant part is highly desired for the human diet. The general thoughtfulness points to compounds, such as ascorbic acid (vitamin C), β-carotene and polyphenols, which are all well-known for their antioxidant activities. The total ascorbic acid content in salt-treated mangrove plants decreased, but salinity accelerated the activity of ascorbate peroxidase and glutathione reductase, two enzymes essential for maintaining the redox-states of ascorbate and glutathione, probably as a part of the antioxidative defense system against salt treatment (Parida et al., 2004). In the highly saline-adapted shoots of *S. bigelovii*, the total ascorbic acid content amounted to ca. 6 mg 100 g^{-1} fresh product (Lu et al., 2010), values in the similar range of those for non-halophyte leafy vegetables, such as spinach (7 mg 100 g^{-1}) and lettuce (<2 mg 100 g^{-1}) (Proteggente et al., 2002).

S. bigelovii was also found to be rich in the lipophilic antioxidant β-carotene, with 15.9 mg 100 g^{-1} fresh weight, which makes the plant a good source of vitamin A (Lu et al., 2010). Considerably lower values were reported by Ventura et al. (2011a), whose plants exhibited different responses to salinity (Table 6). The β-carotene content decreased slightly for *S. persica* but significantly increased for one of the *Sar. fructicosa* genotypes at higher seawater percentages, with values found to be in the range of seaweed and spinach—4.0 and 5.1 mg 100 g^{-1} fresh weight, respectively (Isabelle et al., 2010). The total phenolic content also makes an important contribution to the total antioxidant capacity. In *Salicornia* and *Sarcocornia*, total polyphenols are high (1.2 and 2.0 mg GAE g^{-1} FW, respectively) (Ventura et al., 2011a), such that they are far above the lower limit of other, non-halophytic leafy vegetables rated as rich in phenolic compounds (>0.5 mg GAE g^{-1} FW) (Isabelle et al., 2010).

Organic compatibles, which function to balance the osmotic potential in the vacuole due to accumulated Na^+ and Cl^- ions, are synthesized by the halophytes with differences in their carbon (C) and nitrogen (N) costs (Flowers and Colmer, 2008). *Salicornia* and *Sarcocornia* accumulated considerable amounts of sugars to attain total soluble solute values of 6.3% and 7.6%, respectively (Ventura et al., 2011a). Both genera are also proline accumulators (Sagi, unpublished). Also remarkable but noticed much less in non-legumes are the ureides, whose levels rise with increasing salinity. These nitrogen-rich compounds are proposed to play an energy-conserving role for nitrogen transport during carbon-limited stress conditions in *Salicornia* (Ventura et al., 2010). Moreover, their noteworthy antioxidant capacity, determined for H_2O_2 detoxification (Brychkova et al., 2008), provides additional nutritive value to the *Salicornia* vegetable (Ventura et al., 2011a). Hence, both *Salicornia* and *Sarcocornia*, despite or perhaps because they were cultivated with highly saline water, are ideal leafy vegetables containing nutritional metabolites rich in antioxidant compounds that are indispensable to the human diet.

Table 5
Cation and anion content (mg 100 g^{-1} FW) in the shoots of *Salicornia persica* and *Sarcocornia fructicosa* grown with seawater salinity.

	K^+	Na^+	Mg^{2+}	Ca^{2+}	NO_3^-	PO_4^-	SO_4^-	Cl^-
Salicornia persica	303	1557	100	47	189	75	53	2958
Sarcocornia fructicosa	286	1498	123	63	227	44	106	2846

Adapted from Ventura et al. (2011a).

At the cellular level, plants irrigated with saline water prevent damage to their cellular membranes by altering membrane fatty acid composition (Allakhverdiev et al., 1999). Salt tolerance was found to be enhanced by higher levels of unsaturated fatty acids in the plant membranes, which changes membrane fluidity and how protein complexes are stabilized in the thylakoid membranes of photosystem II (Allakhverdiev et al., 1999). Leaves of wild edible plants with culinary uses are a rich source of essential unsaturated fatty acids, such as α-linolenic acid (C18:3ω3) and linoleic acid (C18:2ω6), whose benefits to human health are well-known (Simopoulos, 2004). The leaf total fatty acid content of edible plant species, including halophyte and non-halophyte species, collected in the wild ranged from 1.46 g 100 g^{-1} DW for *Plantago major* to 3.81 g 100 g^{-1} DW for *Portulaca oleracea* (Guil-Guerrero and Rodríguez-García, 1999). In terms of added value to the consumed product, the annual *Salicornia* (2.12 g 100 g^{-1} DW) outperformed the perennial *Sarcocornia* (1.73 g 100 g^{-1} DW) in terms of total fatty acid content and of its omega-3 portion when grown with 100% seawater (Ventura et al., 2011a).

In summary, both *Salicornia* and *Sarcocornia* possess high salt tolerance that goes hand in hand with a corresponding strong potential for reestablishing ion and osmotic homeostasis, characteristics that combine to promote a high quality vegetable product by enhancing its nutritional value.

5. Effect of N fertilization during seawater cultivation

Growing *Salicornia* and *Sarcocornia* in hydroponic cultivation units using seawater may contribute immeasurably to sustainable agricultural production in coastal desert areas (Ventura et al., 2010). Salinity-induced nutrient imbalances significantly affect macro and micro nutrient availability to the plant (Grattan and Grieve, 1999). The high sulfate concentrations in seawater may strongly impair the availability of molybdenum to the plant (Howarth and Cole, 1985), thus limiting the molybdenum cofactor (Moco) biosynthesis essential for the activities of all molybdo enzymes, of which nitrate reductase (NR) and xanthine dehydrogenase (XDH) are involved in plant nitrogen assimilation (Sagi et al., 1997, 1998). The application of molybdenum as a foliar spray during seawater cultivation enhanced yield by accelerating the activities of both NR and XDH in plants fed either nitrate or ammonium (Ventura et al., 2010). Yet nitrate was the preferred N-source for *Salicornia*, resulting in 60% higher yields compared to ammonium fertilized plants. On the other hand, ammonium fertilization enhanced the total ureide content by up regulating XDH activity. Thus, under conditions of high salinity and fertilization with ammonium, ureides fulfill a dual function by saving energy through economic N transport (1:1 C:N ratio) and by supporting the antioxidant system via their ROS scavenging capacity (Brychkova et al., 2008; Ventura et al., 2010).

Table 6
Quality parameters of *Salicornia persica* and *Sarcocornia fructicosa* grown with seawater salinity.

Quality parameters	*Salicornia persica*	*Sarcocornia fructicosa*
EC (dS m^{-1})	44.9	48.2
TSS (%)	6.4	7.9
Total polyphenols (mg GAE 100 g^{-1} FW)	121	205
β-Carotene (μg 100 g^{-1} FW)	4690	5080
Total ureides (ng 100 g^{-1} FW)	776	1017
Protein (mg 100 g^{-1} FW)	253	359
Fatty acid content (mg 100 g^{-1} FW)	241	176
Omega-3 fatty acid content (mg 100 g^{-1} FW)	115	72

Adapted from Ventura et al. (2011a).

Unexpectedly, regardless of whether photoperiodic light was added, ammonium fertilization enhanced flowering in seawater-cultivated *S. bigelovii*, an effect that was partially counteracted by molybdenum application (Sagi, unpublished). These findings show that the onset of flowering is affected not only by day length manipulation, but also by plant nutrition, which can be regulated by fertilization with nitrogen and molybdenum. More in-depth study is needed to address the many unanswered questions about the interaction of plant nutrition and salinity and their corresponding effects on the flowering behavior of *Salicornia* and *Sarcocornia* species.

6. Future prospects and concluding remarks

In this short review, we examined some of the basic and applied aspects of halophyte cultivation for economic vegetable production, taking *Salicornia* and *Sarcocornia* as examples. The future use of halophytes to combat soil salinity and water scarcity in semi-arid and arid regions is inevitable. Therefore, the methodologies investigated for *Salicornia* and *Sarcocornia* may serve as a template for the development of additional potential halophyte species. Numerous halophytes are suitable as leafy vegetables, but their commercial production is still in its infancy. The majority of research studies, which refer to wild halophyte germplasm collected at distinct locations, investigate the plant response to general salt stress. The immediate scaling-up of the work with a promising halophyte into a field investigation will markedly advance halophyte domestication. Moreover, placing part of the experimental stage of the developmental process in the farmers' fields should shorten the time frame needed for a relatively unknown halophyte to become a recognized crop that starts to generate economic profits.

Modern, commercial halophyte production will require firstly selected genetic plant material expressing superior quality characteristics that give stable, reproducible results under saline conditions. Secondly, agrotechnical practices, including germination and seed production, should be adapted and proved for specific crops to promote sustainable cultivation in a world of increasing salinity.

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