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Review

Glassworts: From Wild Salt Marsh Species to Sustainable Edible Crops

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Abstract: Halophytes are naturally adapted in saline environments, where they benefit from the substantial amounts of salt in the growth media. The need for salt-tolerant crops increases as substantial percentages of cultivated land worldwide are affected by salinity. There are few protocols, guidelines, or trials for glasswort (*Salicornia* (L.) and *Sarcocornia* (Scott), belong to the *Amaranthaceae*) field cultivation. The high salt tolerance and content in bioactive compounds make glassworts one of the most important candidates for future use both for fresh and processed food, due to their functional and health properties. This review describes the glassworts respect to their biodiversity and the most important factors affecting propagation, salt tolerance traits, agro-techniques and yields, food uses and nutraceutical properties.

Keywords: agro-techniques; biodiversity; halophytes; propagation; *Salicornia* spp.; salt tolerance; *Sarcocornia* spp.

1. Introduction

The depletion of natural resources due to human activity, global change, and the increasing population have led to a great reduction in arable lands along with salinization of the soil and unavailability of freshwater. Only cultivating conventional crops that have a low tolerance to salinity and drought is therefore not recommended in the future [1]; new sustainable crops, with low inputs and strong abiotic tolerance, are thus needed.

Halophytes need a high-salt soil composition to develop properly [2,3]; their salt tolerance is related mainly to the ability to control ion uptake and the vacuolar compartmentalization of Na^+, K^+, and Cl^-, in order to maintain the osmotic balance between vacuoles and cytoplasm by the synthesis of osmotic active molecules [4,5].

Today edible halophytes are one of the most interesting groups of plants as they can be cultivated in marginal areas with seawater, or in saline areas near the sea, in beginning a potential cash crop [6].

Examples of edible halophytes include purslane (*Portulaca oleracea* L., [7]), marine fennel (*Crithmum maritimum* L., [8]), ice plants (*Mesembryanthemum cristallinum* L., [9]), Mediterranean saltworts (*Salsola soda* L., [10]), and glassworts (*Salicornia* (L.) and *Sarcocornia* (Scott), [11]).

This review describes the glassworts in respect to their biodiversity and the most important factors affecting propagation, salt resistance traits, agro-techniques and yields, food uses, and nutraceutical properties.

Glassworts: *Salicornia* (L.) and *Sarcocornia* (Scott) genus (*Amaranthaceae*, subfam. *Salicornioideae*), are divided into succulents which are annual, and edible halophytes which are perennial.

They are a difficult taxonomy because of the richness of the microspecies, subspecies, hybrids, and varieties. Kadereit et al. [12] found that *Salicornia* and *Sarcocornia* were separated from each other near the Middle Miocene (14.2–9.4 mya); however, actual lineages were diversified during the Early Pleistocene (1.4–1.8 mya).

2. Habitat and Apulian Biodiversity

Salicornia and *Sarcocornia* develop mainly in sandy or muddy saltmarshes that are flooded by the tide, in mudflats, sandflats, and sometimes in open saline areas. *Salicornia* is found around much of the coastline of Europe from the Arctic to the Mediterranean, as well as on the shores of both the Black Sea and Caspian Sea; it is also present sporadically where inland salines occur across Europe [13].

Annual *Salicornia* species have a much wider distribution than *Sarcocornia* in the Northern hemisphere and in South Africa. They are absent from South America and Australia [12]. Table 1 shows the origin of some species belonging to *Salicornia* and *Sarcocornia* genus [12,14–16].

Table 1. Origin of some species belonging to *Salicornia* and *Sarcocornia* genus [12,14–16].

Genus	Species	Subspecies	Origin
Salicornia	*europaea* L. (*Syn: S. herbacea* L., *S. brachystachya* G. F. W. Mayer, *S. ramosissima* J. Woods, *S. patula* Auct.)	*europaea*	From southern Spain to northern Scandinavia
		disarticulata	Atlantic coasts of Netherlands and southern England.
		marshallii	Atlantic coasts of Brittany and the Netherlands
S.	*perennans* Willd	*perennans*	North Africa and the Mediterranean region to the Baltic Sea and White Sean Asia to Yakutsk (Siberia), Japan, and Korean Peninsula
		altaica	Altai Mountains (Russia, Mongolia)
S.	*procumbens* Sm.	*procumbens*	Mediterranean and Atlantic coasts from Morocco to Scandinavia, inland occurrences in Turkey and Ukraine
		freitagii	Turkey (Anatolia)
		pojarkovae	Coasts of the White Sea (Russia) and Barents Sea (Norway)
		heterantha	Endemic in southeast European Russia (Rostov Oblast)
S.	*persica* Akhani	*persica*	Iran
		iranica	Eastern Mediterranean and Southwest Asia
S.	*dolichostachya* Moss		South of Italy (Apulia), Northern European Russia: White Sea coast
S.	*glauca* Delile (*Syn: s. macrostachya* Moric)		South of Italy (Apulia)
S.	*bigelovii* Torrey		Gulf of Mexico, Atlantic coast up to Maine, S California
Sarcocornia	*alpini* Lag.		Iberian peninsula
S.	*carinata* Fuente, Rufo & Sánchez Mata		Spain
S.	*fruticosa* L.		Coasts of the Mediterranean Sea and Atlantic (France)
S.	*hispanica* Fuente, Rufo & Sánchez-Mata		Southeastern Iberian peninsula
S.	*lagascae* Fuente, Rufo & Sánchez-Mata		Mediterranean coasts of the Iberian peninsula
S.	*obclavata* Yaprak		Turkey
S.	*perennis* Miller		Atlantic and Mediterranean coasts in West and South Europe and North Africa
S.	*pruinosa* Fuente, Rufo & Sánchez-Mata		Atlantic coasts of France, Spain, and Portugal

In south of Italy (Apulia Region), *S. europaea* L., known as common sea asparagus, is a characteristic pioneer species of the association *Thero-Salicornietea* [17]; the brackish lakes of Lesina (Figure 1) and Varano (Foggia Province) are rich in this wild plant species, that colonize damp and brackish soils, flooded by the tide for most of the year and dry during the warmer seasons [18]. There are *S. glauca* Delile and *Sarcocornia fruticosa* (L.) A.J. Scott too.

Figure 1. *Salicornia europaea* fuund at Lesina lagoon (Province of Foggia, Apulia, Italy).

In the south of Apulia, the "Torre Guaceto" coastal lagoon (Province of Brindisi—Figure 2) is a National Natural Reserve characterized by a wide number of halophyte plants; among these, *Sarcocornia fruticose* is one particular example. In the province of Taranto, "Salina dei monaci", *Sarcocornia* sp. grows in globe-like shrubs (Figure 3). It is richly branched, with long sterile shoots (in the current year) and fertile shoots (from the previous year) with leaves small and green. In the Province of Lecce, "Le Cesine" another glasswort was found by [19] on cliffs, where the salinity is the same as the sea: *Sarcocornia fruticosa* L.

Figure 2. *Sarcocornia* sp. seeds gathered from Torre Guaceto (Province of Brindisi, Apulia, Italy).

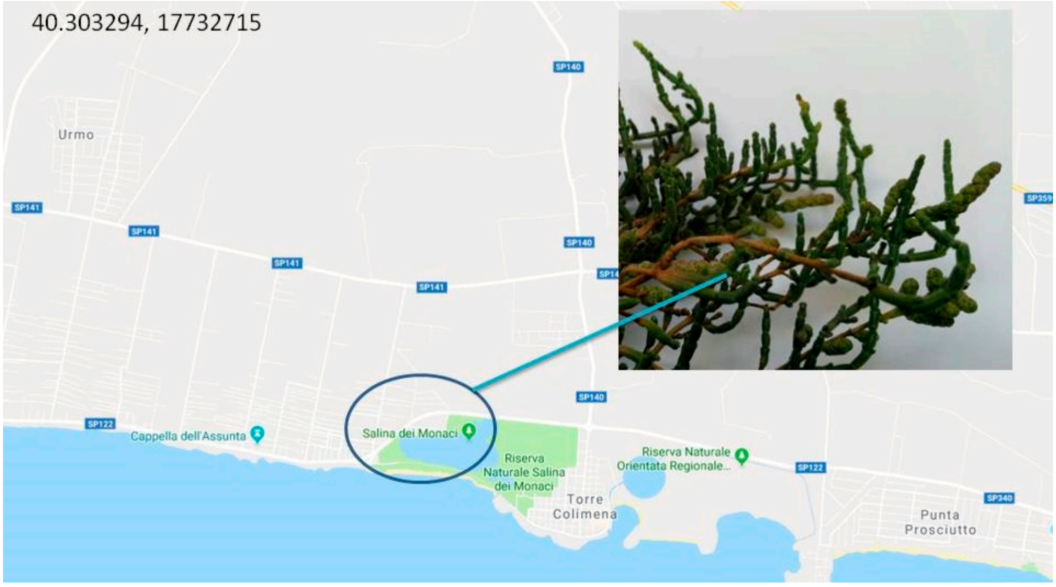

Figure 3. Adult plants of *Sarcocornia* sp. were harvested from Saline dei Monaci (Province of Taranto, Apulia, Italy).

3. Morphological Characteristics

As glassworts are characterized by an extremely reduced morphology, they can grow prostrate, erect, or branched [13]. Figure 4a shows that the leaves are very small and the assimilatory surface is composed of succulent branches with cylindrical internodes [20]. Axillary buds on the main stem develop into primary branches which produce secondary ones [21]. Annual species are usually green, but in autumn, near the end of the cycle, the stems turn red. In *Salicornia* spp. flowers are aggregated in a dense terminal, spike-like thyrses composed of three flowers: one central and two lateral (Figure 4b). In *Sarcocornia*, these are placed in horizontal rows [12]. Glassworts differ from all other *Amaranthaceae* since the seeds that lack perisperm [22]. The *Salicornia* seed is small, ellipsoid, dark (Figure 4c) and is characterized by heteromorphism: i.e., seeds from the same plant have a difference in size, color, or shape [23]. In *S. europaea* L. there is a wide variation in size: 0.4–0.9 mm [24,25]. Heteromorphism is also widespread in *Asteraceae* and *Amaranthaceae* [26,27] and is the result of an adaptation to desert environments, because each seed morph germinates under different conditions [28–31].

Figure 4. *Salicornia europaea*: (**a**) cylindric and succulent stem; (**b**) spike-like inflorescence; (**c**) seeds; (**d**) seedlings.

4. Propagation

Propagation can be carried out by both gamic and agamic techniques.

4.1. Gamic Propagation

Halophytes usually inhabit extreme soil parameters. This implies that seeds need strategies in order to overcome these situations: dormancy under hypersaline conditions and germination at high salinity levels [32].

Dormancy starts during the late autumn and ends with seed germination of glassworts in late April–early May [33]. The main advantage of germination in early spring is the abundance of water which involves low salt concentrations, ideal for germination. *S. europaea* (L.) and *Spergularia marina* (L.) have two or more different seed morphs and each seed has a different dormancy and salt tolerance [25,34,35]. In fact, the lateral seeds of *S. europaea* (L.) are more dormant than the central seeds (which are more salt tolerant), in order to maintain a long-term soil seed bank [25]. Orlovsky et al. [36] found that the germination of large seeds was three to four times higher than small seeds in the control and under 0.5–2% salt (both NaCl and 2NaCl + KCl + $CaCl_2$). This high dormancy typical of smaller seeds can be partly broken with chloride or sulfate salts (concentrations of 0.5 to 2%).

In order to overcome the dormancy period in specialized nurseries, seeds need to undergo a cold stratification: T = 5 °C for 30 days in the dark. Aghaleh et al. [37] and Lv et al. [38] reported that *Salicornia* seeds were exposed to sunlight and salinity using 30:70 or 50:50 seawater:freshwater. This phase ended in 14 days, leading to appropriate seedlings (Figure 4d).

The percentage and rate of germination decreased as salinity increased which is true for both seed morphs [36]. Although there is a greater success of germination under freshwater, halophytes can also germinate at high saline concentrations: for example, *S. europaea* can germinate at 600 mM NaCl [39,40].

Ungar [34] found that treatments with GA_3, play an important role in overcoming salt stress-induced dormancy in *Salicornia*, *Suaeda*, and *Spergularia*.

Several authors have described the recommended environmental parameters of germination: T = 15–25 °C day/5–20 °C night (never under 5 °C and over 30 °C); light = 12–16 h day/8–12 h night [38,39]. The germination phase is not only affected by salt concentration, but also by the salt type: Orlovsky et al. [36] found that large seeds have a good germination under NaCl between 0.5 and 2%, Na_2SO_4 and 2NaCl + KCl + CaCl between 0.5 and 3%, and $2Na_2SO_4$ + K_2SO_4 + $MgSO_4$ between 0.5 and 5%. Small seeds are stimulated by chloride salts under 0.5–1%, and sulfate salts under 0.5–3%.

4.2. In Vitro Propagation

In vitro propagation of *S. bigelovii* and *S. europaea* was studied [41,42] but "in vitro" culture system of succulent halophytes was not very successful so far. Lee et al. [41] developed in vitro propagation of *S. bigelovii* using the shoot tip culture method but the regeneration rate was very low; however, Shi et al. [42] established a method of *S. europaea* regeneration from mature embryos. Tissue culture of succulent halophytes using a mature embryo is not promising because of the microscopic size and non-availability of explants throughout the year.

Joshi et al. [43] found that in *Salicornia brachiata* an efficient shoot proliferation was observed with combinations BA (8.9 μM) + NAA (5.37 μM) + NaCl (500 mM) and BA (13.3 μM) + NAA (5.37 μM) + NaCl (250 mM) indicating that NaCl is required for the micropropagation.

5. Cultivation

5.1. Growth

Glassworts, in North Apulia, are typically cultivated from February–March to August–September in the acidic marshes near the brackish lake of Lesina, Cagnano Varano, and San Nicandro Garganico in open fields [44]. In Israel, *Salicornia* is grown using nests or greenhouses in soil, floating systems or plastic sheets [45] with perlite, dune sand, coconut fiber, or a commercial substrate mixed with sand (1:1 *v:v*) [46]. Singh et al. [3] showed that production (fresh and dry biomass) of *S. dolichostachya* moss, in hydroponic cultivation, was higher than plants grown in sand media; on the other hand, hydroponic cultivation can lead to chlorosis events.

Gunning [45] reported that *Salicornia* plants were fertilized with a nutrient solution (30:50 or 50:50 seawater:freshwater) with a N:P:K = 14:10:27 to achieve high yields.

A notable amount of biomass for *S. ramosissima* woods was achieved using artificial seawater containing 257 mM NaCl [3]; on the other hand, Rozemaa et al. [47] found that growth was depressed at low salt concentrations. Regarding irrigation, Singh et al. [48] showed that cultivation of *S. brachiata* in a greenhouse using reverse osmosis reject water with and without fluorine ion could be a sustainable solution for reject water management.

The main problem related to wild species introduced to cultivation, is the prevalence of non-commercial characteristics due to genetic diversity, for example, production homogeneity. Besides breeding programmes, with plant growth promoting bacteria (PGPB) could be an alternative in order to increase production. Bashan et al. [49], found that *S. bigelovii* increase production (height and weight) when inoculated with some PGPB, i.e., *Azospirillum halopraefrens*; *A. brasilense* (two different strains); *Vibrio aestuarianus* + *V. proteolyticus*; *Bacillus licheniformis* + *Phyllobacterium* spp. It is worth underlining that the cultivation of *Salicornia* could be beneficial in order to increase soil fertility, due to the presence of rhizobacteria in its roots [50].

In Apulia, harvesting, in open field, takes place in July–August; in Israel in August–September, and it is carried out manually in order to maintain the high quality of the final product; only fresh and tender parts can be sold. *Salicornia* can be collected several times during the year in greenhouses: The harvest can be repeated every two or three weeks (depending on the level of development). Plants are cut above 5 cm from the ground at a height of 10–15 cm [51]. This repeated harvesting enables the same plant to be cut from three to four times depending on the level of growth. The yield can reach 10–15 tons per hectare.

5.2. Flowering

Under natural conditions, when the day length decreases, the reproductive phase of glassworts begins with a differentiation in terminal fruiting spikes [52]. The optimal day length is different for high latitude and short latitude plants: in fact, northern glassworts (*S. europaea*) need 18 or more hours to prevent flowering; for *S. bigelovii*, 13 h are enough [51]. Flowering induction has many negative effects on both the production (intense decrease in growth) and production of non-saleable shoots and nutraceutical properties [51]. For perennial *Sarcocornia*, flowering can be controlled with a repeating harvesting regime [51]. Based on the results of Ventura and Sagi [46], nutrition management can also be used for flowering control. The regulation of Mo and N-NO_3 can prevent the reproductive stage, in fact, ammonium fertilization promotes flowering in *S. bigelovii*. In addition, the sowing date can be useful in preventing flowering: Seeds planted in November or December repress the reproductive stage; whereas, planting in January results in inhibition, because during the growing cycle, the day length increases [51].

5.3. Salinity Tolerance, Water Relations, and Gas Exchange

Glassworts are salt-tolerant species: Redondo-Gòmez et al. [21] showed that *S. fruticosa* has a considerable salt tolerance, compared with other halophytes, resulting in the greatest growth with 510 mM NaCl treatment. Similar results, regarding the optimal salt concentrations, have been achieved for different genotypes: for *Salicornia persica* Akhani, e.g., 200 mM NaCl [53]; 200 mM NaCl for *S. brachiata* [54]; 170–340 mM NaCl for *S. europaea*, *S. bigelovii*, *S. herbacea*, and *S. brachystachya* [55]. The photosynthetic apparatus of *S. fruticosa* also appears capable of tolerance prolonged high external salt exposure, suggesting plasticity.

The main salt tolerance responses of plants relate to an increased leaf thickness. Katschnig et al. [56] found that leaf succulence and diameter in *S. dolichostachya* were higher when plants were grown in 300 mM NaCl of nutrient solution compared to other treatments grown in from 0 to 500 mM NaCl. This is due to an increased accumulation of Na^+ and Cl^- ions in the vacuoles [57], which leads to a reduced leaf surface area and consequently an increased water use efficiency. In saline environments, in order to ensure the water uptake, a low water potential in the cells is needed [56]. Beside Na^+ and Cl^- ions, organic compounds such as glycine betaine are stored in the cytoplasm in order to guarantee a water potential equilibrium in the cells [58]. Organic solute as malate dehydrogenase can also act as an enzyme that stabilizes at high salt concentrations [59]. Jolivet et al. [60] also found that glycine betaine inhibits the betacyanins efflux when present in the external medium along with the oxalates. Glycine betaine is perhaps the main organic compound with osmoregulation properties for *Salicornia* spp. [61].

Another mechanism used to maintain a better water uptake is gas exchange regulation: Stomata conductance generally decreases for halophytes as a reaction to increasing salt concentrations. At high salt concentrations, as reported by Ayala and Oleary [62] for *S. bigelovii*, stomata conductance decreases, consequently the carbon dioxide fixation and transpiration rate also decrease, in order to obtain the best efficiency in terms of water use.

6. Bioactive Compounds

Halophytes can be used for many commercial purposes: Not only as fresh and processed foods, but also in terms of their high salt content, as biofuel, high nutritional oilseed, medical raw materials, as well as nutraceutical and functional foods [63,64].

Chenopodiaceae members are known to contain high amounts of crude proteins, sulfur, and minerals [65], which favor glasswort as an edible plant. *Salicornia*, developed in extremely saline environments, produces antioxidative metabolites, which are desirable in the human diet. Simple and complex sugars, alcohols, quaternary amino acid derivatives, tertiary amines, and sulfonium compounds are also useful for human nutrition, and are found on these plants [45].

Guil et al. [66] showed that sea asparagus has high levels of ascorbic and dehydroascorbic acids (more than 100 mg 100 g^{-1}), as well as carotenoids (5 mg 100 g^{-1}). *S. bigelovii* also show high content of β-carotene (15.9 mg 100 g^{-1} of fresh weight), and a high amount of vitamin A [67]. Both *Salicornia* and *Sarcocornia* showed a high content of polyphenols (1.2 and 2.0 mg GAE g^{-1} of fresh weight, respectively) [51]. Kang et al. [68] found that the freshwater cultivation of *Salicornia* had a higher phenolic and flavonoid content, than seawater cultivation.

Due to the specific biochemical composition of *Salicornia* seeds, they are very good for human health. The main molecules include linoleic (75.6%) and oleic acids (13.0%); in addition to palmitic, linoleic and stearic acids [63]. Proteomic analysis has also revealed a high protein content of the seeds [69]. Considering the main components, palmitic acid, tetracosanol, and octacosanol showed significant levels [70]. Octacosanol is a high-molecular-weight aliphatic alcohol and belongs to cholesterol-lowering drugs such as polycosanol [71].

In addition, the leaves of *Salicornia* are also a good source of fatty acids such as linoleic and oleic acids [72]. Finally, the presence of selenium has also been detected; which is an important micronutrient both for growth and has good antioxidant effects [73].

The *Salicornia* genus has antimicrobial, anti-tumor, antioxidant, and anti-inflammatory properties [74].

Abiotic stress, including salt stress, leads to the production of reactive oxygen species in the plants, which damage cellular membranes and enzymatic activity [75]; to combat salt-oxidative stress, antioxidative enzymes and small antioxidant molecules are produced. These molecules give medicinal properties to halophyte plants, which are used for several treatments for chronic disease, including diabetes, cancer [74]. Polysaccharides from *S. herbacea* at 0.5–4 mg mL^{-1} have been found to be antiproliferation of human colon cancer HT-29 [76]. Another study found that pentadecylferulate from *S. herbacea* has an antioxidant effect and, an anti-cancer response to human hepatocellular liver carcinoma HepG2 and human lung adenocarcinoma epithelial A549 cells [77]. The methanol extract of *S. herbacea* has shown antibacterial activities, mediated by interference with cytochrome and several enzymes [78]. Osteoporosis is a bone disorder, caused by a higher bone adipogenesis (differentiation of stem cells into mature adipocytes): *S. herbacea* extract has been found to inhibit adipogenesis [69].

Besides the health properties of *Salicornia*, there are also some negative aspects: *Chenopodiaceae* members are known to contain a high oxalate content, which could be harmful to consumers [65].

7. Food Uses

The edible parts of glassworts have tender leaves and shoots can be used in a fresh salad, or boiled like spinach without salt, and then coated with extra virgin olive oil (Figure 5). The color, after cooking, resembles seaweed, and the flavor and texture are similar to young spinach or asparagus. Sea asparagus is often used as an accompaniment to fish or seafood [45].

Figure 5. Apulian traditional dish: boiled *Salicornia* with extra-virgin olive oil and garlic.

S. europaea L. is currently included in the list of traditional Apulian vegetables.

In Hawaii, it is often blanched and used as a topping for salads or as an accompaniment for fish [79]. The seeds of *S. bigelovii* can be used to make edible oil; however, it is not always edible because it contains saponins, which can be toxic. *S. brachiata* is used as fodder for cattle, sheep, and goats [80]. In Sri Lanka, it is used to feed donkeys [81].

In India, shoots can also be transformed into beverages such as nuruk (fermentation starter), makgeolli (Korean rice wine), or vinegar [82,83]. One study found that Salicornia enhances fermenting microbe propagation and improves vinegar quality [84]. Other authors have found that these plants can be used as a source of salt for several dishes. Indeed, *S. herbacea* powder can be transformed into spherical granules, which may be used as NaCl [85].

8. Conclusions

In the last few years, interest in halophytes cultivation has increased; however, scientific papers and multiple large scale experiments are very limited. There are few protocols for glassworts field cultivation and few guidelines for small cultivations or trials.

The high salt tolerance and content in bioactive compounds makes glassworts one of the most important candidates for future use both for fresh and processed food, due to their functional and health properties.

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