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Review

Biological and Agronomic Traits of the Main Halophytes Widespread in the Mediterranean Region as Potential New Vegetable Crops

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Abstract: Salinity is one of the oldest and most serious environmental problems in the world. The increasingly widespread salinization of soils and water resources represents a growing threat to agriculture around the world. A strategy to cope with this problem is to cultivate salt-tolerant crops and, therefore, it is necessary to identify plant species that are naturally adapted to high-salinity conditions. In this review, we focus our attention on some plant species that can be considered among the most representative halophytes of the Mediterranean region; they can be potential resources, such as new or relatively new vegetable crops, to produce raw or minimally processed (or ready-to-eat) products, considering their nutritional properties and nutraceuticals. The main biological and agronomic characteristics of these species and the potential health risks due to mycotoxigenic fungi have been analyzed and summarized in a dedicated section. The objective of this review is to illustrate the main biological and agronomical characteristics of the most common halophytic species in the Mediterranean area, which could expand the range of leafy vegetables on the market.

Keywords: salt tolerance; *Salicornia*; *Suaeda*; *Atriplex*; *Portulaca*; novel food; hydroponic cultivation; mycotoxigenic fungi

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1. Introduction

The increasing salinization of both soils and water resources, which is mainly due to anthropic activity, has created a new interest in salt tolerant plants as potential crops for saline environments [1,2].

Halophytes are the plants with the highest level of salt tolerance resulting from several morphological, physiological, and biochemical traits, such as osmotic adjustment; ion compartmentalization and homeostasis; detoxification of reactive oxygen species; salt secretion; and other mechanisms that are not yet fully understood [3–5]. Halophytes can survive in very saline soils and exploit water resources of moderate-to-high salinity. The optimal salinity for the growth for most halophytes ranges from 50 to 250 mM NaCl; however, they can grow and produce as much as conventional crops even when irrigated with seawater, so with a molarity greater than 500 mM [6]. In general, halophytes are highly versatile plants and, in addition to their role in coastal-area preservation and as valuable scientific models for the investigation of salt-tolerance mechanisms, their exploitation as food and non-food crops could be a winning strategy in a salinizing world.

The cultivation of halophytes under greenhouse conditions—either in soil or in a soil-less system—or in an open field, to produce raw or minimally processed vegetables (i.e., ready-to-eat or fresh-cut products), in particular for gourmet cuisine, is of growing interest [7–9]. The edible parts of these species are appreciated due to their salty taste and high content in antioxidant compounds and essential nutrients (minerals, vitamins amino acids and/or fatty acids) [10,11]. Halophytes also contain ingredients of functional foods and active principles for medicinal supplements [12–15].

In the Mediterranean regions, the most abundant halophytes are found mainly in medium–high marshy areas; in most cases, these are directly connected to intertidal areas and are subject to sea water flooding. The floristic composition of these environments is closely linked to the topography and seasonal fluctuations in salinity, which can reach very high values—sometimes higher than that of sea water in the period of maximum evapotranspiration. The hyper-halophilous communities are dominated by therophytes or chamaephytes, annual or perennial shrubs, or grasses, while the sub-halophilous ones are characterized by hemicryptophytes and geophytes of different families. Among the typical plants, we can include many species of Amaranthaceae, such as *Salicornia* spp.; *Suaeda vera* J. F. Gmel. and *S. maritima* (L.) Dumort.; *Halimione portulacoides* (L.) Aellen; *Soda inermis* Fourr. and *Atriplex* spp.; and some species of Poaceae such as *Puccinellia distans* (Jacq.) Parl., *Sporobolus aculeatus* (L.) P. M. Peterson, *Thinopyrum acutum* (DC.) Banfi, and *Hordeum maritimum* Huds. These are often associated with other halotolerant species, including *Limbarda crithmoides* (L.) Dumort.; *Galatella tripolium* (L.) Galasso, Bartolucci and Ardenghi; *Artemisia caerulescens* L., *Juncus* spp.; *Limonium* spp.; and *Plantago coronopus* L.

The objective of this review is to illustrate the main biological and agronomical characteristics of the most common halophytic species in the Mediterranean area, which could expand the range of leafy vegetables on the market.

2. Halophytes: Definition and Complexity

Halophytes represent an ancient and remarkable ecological group of annual or perennial plants with very complex features, whose definition and classification are still not univocal and often controversial [16]. The species belonging to this group are very different from an ecological, morpho–physiological, and taxonomic point of view; therefore, their definition can be subjective and vary a lot in the literature according to the different interpretations. However, following the most popular definition used in the literature, halophytes can be identified as plants that grow naturally, and complete their life cycle in environments that contain a higher salt content than most plant species can tolerate [17].

The occurrence of halophytism is widespread throughout the plant kingdom and appears to have evolved several times, lending support to the concept that many glycophytes may have halophyte genes permanently switched off, but under mutagenesis, may revert to halophytism [18]. In fact, all four plant kingdoms contain members that are adapted to saline habitats; however, they occur in greater numbers among the thallophytes, such as red and brown algae, and terrestrial or aquatic spermatophytes. These plants are mainly distributed in arid or semi-arid inlands and saline wetlands along the tropical and sub-tropical coasts, as well as in temperate zones [17].

Halophyte plants and their natural habitats have attracted the attention of many naturalists and writers since very remote times. Allusions to salt-tolerant plants in saline soils along the banks and margins of salty waters date back to the mid-1500s, and data on halophytes were already very consistent in the 1700s. In *Hortus Cliffortianus* and *Species Plantarum*, when describing plants, Limneo often provides information on the salinity of their habitat [19].

The introduction of the word 'halophyte' probably dates to the Russian botanist Peter Simon *Pallas*; in the early 1800s, he wrote that species of *Salicornia*, *Salsola*, *Suaeda* and related plants, all previously included in the Chenopodiaceae and now included in Amaranthaceae family following APG classification, "must be united under what he believes is an appropriate name for *Halophyta*" [20]. In contrast to the term 'halophyte', the name 'glycophyte' was proposed by Stocker (1928) [21] for plants growing in soils with a low salt content. Most cultivated plants are glycophytes. Given the great biodiversity of these plants and the difficulty in distinguishing between salt-tolerant glycophytes and halophytic species, estimating the number of halophyte species and their diffusion is more difficult.

According to Houérou (1993) [22] and Glenn et al. (1999) [23], there are about 6000 species of terrestrial and marine plants in the world that are classified as halophytes. These represent 2% of the angiosperms, and some of them are under continuous taxonomic revision. Of these, approximately 1100 are widespread in the Mediterranean basin, with a wide range of levels of tolerance to salinity. Actually, it is possible to refer to the online database of salt-tolerant plants, namely eHALOPH [24], which is constantly updated. It is based on the records of Aronson (1989) [25] and includes plants that tolerate a soil electrical conductivity (EC) of at least about 8 dS/m, corresponding to about 80 mM NaCl concentrations [26]. The eHALOPH Halophyte Database currently identifies more than 1500 species as salt-tolerant, albeit without labelling them as 'halophyte'. Other authors report a greater number of halophytic species but, despite the difference, most detailed lists represent only 0.5% of all angiosperms [27].

The complexity of the halophyte group is also linked to the multitude of ecosystems that species can contribute to from all over the world. These habitats can be either natural or non-natural, and include semi-deserts, salt meadows, brackish swamps, mangrove forests, irrigated lands, and even urban areas. Many of the natural habitats are highly threatened due to both natural and anthropogenic factors, such as urbanization, tourism, and pollution. The effects of climate change are increasingly adding to the threats to which natural halophytic habitats and vegetation are exposed. Many saline habitats are likely to disappear due to rising sea levels, as these communities generally do not have the ability to relocate to more inland sites. The conservation value of these ecosystems has recently been assessed in the EU project 'Red List of habitats', which are classified as 'Near Threatened' (Arctic coastal salt marsh, and Mediterranean and Black Sea coastal salt marsh), 'Endangered' (Baltic coastal meadow) or 'Vulnerable' (Atlantic coastal salt marsh) [28]. In addition, many countries are facing the loss of agricultural soil due to secondary salinization resulting from irrigation, fertilization, and climate change. Nearly 20% of the total irrigated land area (45 million hectares) is already affected by salinization [29]. In regions with saline soils, halophytes could be alternative crops to glycophytes to produce food, forage, and fibers, and for industrial purposes. Moreover, when halophytes are grown as companion plants of glycophytes, the negative effect of salinity is alleviated by the uptake of toxic ions by the former species, as found by Colla et al. (2006) [30] and Karakas et al. 2021 [31].

3. Classification of Halophytes

Halophytes are very peculiar both physiologically and morphologically, and in some cases, are of great phytogeographic interest. It is, therefore, not surprising that they have been the subject of many studies in various fields of botany, and still are today.

The survival of halophytes is strongly influenced by the salinity in the root zone or, sometimes also by salt spray, as this can happen in saline semi-deserts, in brackish marshes, or on beaches. These types of environments have both negative effects on plants, due to the high osmotic pressure of the soil solution and the toxic effect of salt, and positive ones, as it reduces competition with other plants and may prevent diseases and parasites [32].

When a plant's response to salinity is considered, we usually refer to NaCl, although halophytes are also strongly influenced by other salts, such as $MgSO_4$, $NaSO_4$ or KCl. Halophytes can be also described as plants that survive in environments where the salt concentration is around 200 mM NaCl or more [33]. For example, the most salt-tolerant halophytes, such as *Suaeda salsa*, can complete their life cycle in soils containing 200 to 500 mM NaCl [34]. Many studies have also shown that suitable high salt concentrations can enhance the growth of halophytes in comparison with low or negligible salinity [35,36]. This is proven at both the morphological and physiological level, with a greater biomass accumulation and better seed quality [37], and a higher photosynthetic efficiency [38,39].

By contrast, glycophytes have a limited tolerance to salinity, showing significant reductions in biomass under saline conditions. Among the glycophytes, two types are described based on their degree of sensitivity: salt-sensitive and salt-tolerant. Glycopyhytes include species, such as rice or soybean, that can suffer irreparable damage starting from very low concentrations (less than NaCl 50 mM), and others, such as barley or beets, that can tolerate much higher NaCl concentrations (even those close to 200 mM) [3]. From the morpho–functional point of view, no single factor is of major importance for the ability to survive at high NaCl salinity. Therefore, there are no peculiar characteristics that univocally define all the halophytic species, being a very heterogeneous and systematically complex group. The combination of several mechanisms often enhances the salt tolerance of individual species [40].

However, the evolution of multiple specific morpho-anatomical adaptations and functional characteristics is evident, aimed at fighting the saline environment and even benefiting from it. These adaptations are mostly related to the prevention of leaf water loss by transpiration, with dilution of the salts absorbed in excess or, in some cases, with their excretion. These characteristics are found mainly in the leaves and stems, since they are the plant organs most rigorously exposed to environmental conditions. Among the most important characteristics may be the reduction or absence of leaves, the abundance of glandular trichomes or saline glands, the greater development of supporting tissues, the development of atypical secondary growth, and leaf succulence. Typical succulent halophytes are, for example, species of *Salicornia* and *Sarcocornia*; these are two very interesting genera that appeared in Eurasia in the Middle Miocene period, and that have long represented difficulties for taxonomists due to their growth form with very small leaves and flowers. Although the response of halophytes to the multiple stressors of saline environments is well known (Figure 1), their classification in relation to the total number of flowering plants [41] continues to be very uncertain.

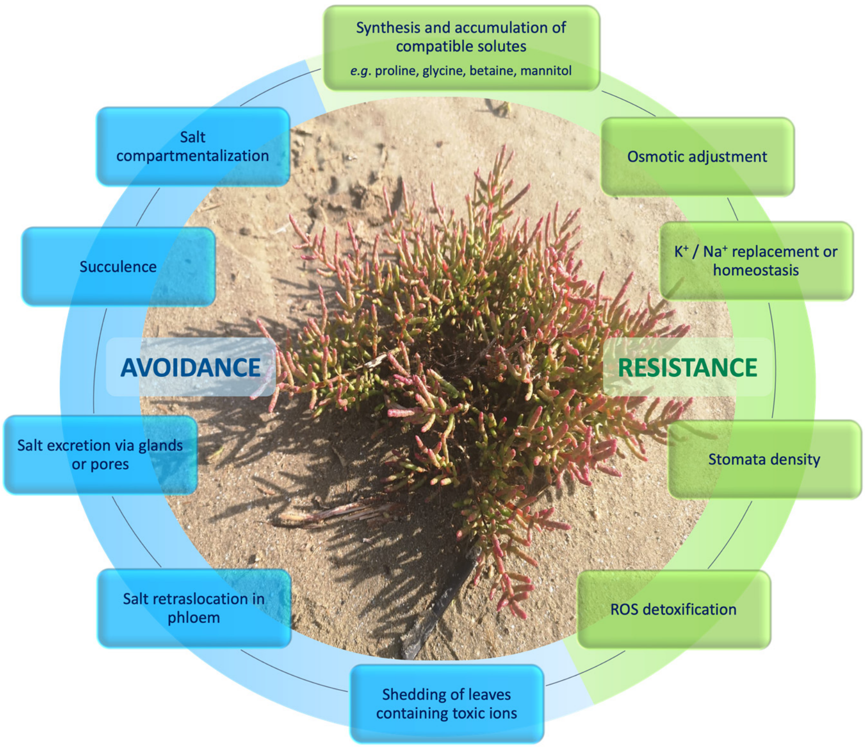

Figure 1. Response mechanisms to salinity stress by halophytic plants. Photo credit: Tiziana Lombardi.

As previously anticipated, due to their taxonomic and ecological complexity, even today, there is no consensus on a univocal definition. It is, therefore, difficult to draw a complete list of halophyte species, partly due to the problem of defining the lower limit of salt tolerance at which a plant should be considered a halophyte. Of course, this difficulty is reflected at the environmental level, in the vegetational subdivisions and zonation of communities dominated by halophyte species.

Halophytes are classified in various ways based on multiple factors, such as general ecological behaviour and distribution; plant growth response to salinity; salt intake rate; the presence or absence of saline glands, physiotype, etc. [32].

3.1. Response to Internal Salt Content

One of the first proposed classifications for flowering plants was based on their response to internal salt content, and divides halophytes into salt-regulating or and salt-accumulating types [42]. Based on their internal salt contents, halophytes were later also classified as excluders versus includers [17].

3.2. Eco-Physiological Aspects

Eco-physiological aspects can be used to differentiate the halophytes in obligate, facultative, and habitat-indifferent species [17]. This classification is based on what Ingram introduced in 1957, albeit without any definition of "low", "moderate", and "high" salinity. All three types of halophytes have better growth and development than glycophytes in saline environments [17].

- Obligate halophytes, mostly the Amaranthaceae members, are species with optimal growth at moderate or high salinity (NaCl 0.1–5%); they cannot grow at lower salinity, as they require salt as part of their nutrition to activate or de-activate several salt-sensitive enzymes. These species frequently exhibit an activation of these enzymes, both at very low Na^+ concentrations (below the physiological optimum) and at seawater Na^+ concentrations (considered excessive).
- Facultative halophytes are plants with the ability to grow on salty soils, but their optimal growth is observed in low-salt or non-saline conditions. Many dicotyledons such as *Aster tripolium*, *Chenopodium quinoa*, *Glaux maritima*, and *Plantago maritima*, but also some *Poaceae*, *Cyperaceae* and *Juncaceae*, belong to this group.
- Habitat-indifferent halophytes normally grow on salt-free substrates, but in saline conditions they thrive better than sensitive species. This group includes the plants that can live in disturbed or stable habitats. In some of these, such as *Festuca rubra*, *Agrostis stolonifera* and *Juncus bufonius*, there are significant genetic and morphological differences between the populations living on salty soils and those on salt-free soils.

3.3. Salt Tolerance

According to their salt tolerance, Chapman (1942) [43] grouped the halophyte under two groups: (i) eu-halophytes, subdivided into the three subgroups meso-halophytes, meso-euhalophytes, en-euhalophytes; (ii) and mio-halophytes.

- *Eu-halophytes* (extreme halophytes) are plants that can grow in seawater or tolerate more than 200 mM NaCl (up 5%), and occur almost exclusively in environments of high salinity [26]. Following the eHALOPH database, this group contains 333 species, members of 70 families of flowering plants. The 75% of eu-halophytes belong to just 19 families. Eu-halophytes are rather rare amongst flowering plants, representing just 0.4% of the 350,699 accepted names in 'The Plant List' within 20% of its 642 families. Some species of *Atriplex*, *Salicornia*, *Suaeda*, and *Salsola* can be included in this group.
- *Mio-halophytes* are plants that grow in habitats with low levels of salinity (less than 0.5% NaCl).

Much later, Grigore and Toma (2010) [44] proposed a new classification of halophytes, distinguishing the extreme halophytes from meso-halophytes, and dividing the extreme halophytes between irreversible and reversible. Thus, based on the analysis of the anatomical features of some taxa and ecological factors, they concluded that succulent Amaranthaceae (e.g., *Salicornia europaea*, *Suaeda maritima*, *Halimione verrucifera*) that grow only in very salinized environments, are irreversible halophytes. Conversely, reversible halophytes (e.g., *Atriplex* sp., *Bassia* sp., and *Camphorosma* sp.) are not strictly related to high salinity, and are able to pass from highly salinized areas to less salinized soils.

Based on the different mechanism of salt tolerance, halophytes can be further classified as follows [45]:

- *Salt-excluding* (root-excluding type) are halophytes (also known as pseudo-halophytes) that protect the shoot from salinity through apoplastic barriers in the roots and interveinal recycling of ions. Mangrove vegetation shows such a type of tolerance.
- *Salt-excreting* (endo- and eso-recretohalophytes) are plants that avoid cellular damage by releasing excess salts to the outside via specialized structures called salt glands—such as species of *Limonium*, *Tamarix*, *Spartina*, *Avicennia*, and *Frankenia*—or from epidermal bladders on the leaves, such as species of *Atriplex* and *Chenopodium*.
- *Salt-accumulating* are plants able to accumulate salts that are compartmentalized into vacuoles and used for osmotic adjustment, e.g., *Salvadora persica*, *Sesuvium portulacastrum*, *Suaeda nudiflora*.

3.4. Habitat and Geographical Distribution

The classification based on the habitat and geographical distribution includes hydro-halophytes and xero-halophytes [46]:

- *Hydro-halophytes* are halophytic plants that need aquatic conditions or wet soil. Species growing in aquatic environments belong to this group, such as the mangrove forests, tidal marshes or coastal lagoons, and the brackish marshes of the temperate zone. *Zannichellia palustris* and *Althenia filiformis* are typical hydro-halophytes in the Mediterranean area [47,48].
- *Xero-halophytes* grow in environments with dry soil due to high evapotranspiration. Most plants living in desert areas and succulents belong to this group. *Atriplex canescens* or *A. halimus* are xero-halophytes that tolerate both salt and drought stress.

4. Mediterranean Halophytes

In the Mediterranean regions, Amaranthaceae are the dominant angiosperm family, with halophyte species such as *Salicornia* sp., *Sarcocornia* sp., *Suaeda* sp., *Salsola* sp. and *Atriplex* sp. They are followed by Poaceae, such as *Hordeum* sp., *Puccinellia* sp., and *Sporobolus* sp. [25,26]. Halophyte species are mostly found in coastal brackish areas that are subjected to periodic flooding.

The halophytes reported in Table 1 were selected for this review.

The choice took advantage of both their diffusion and importance at an environmental level in the Mediterranean regions, and their degree of salt tolerance recognized by the main international databases such as eHALOPH. The species were then characterized from a botanical point of view and investigated regarding the availability of data on their potential as food-crop sources. Some data have also been provided on the distribution and availability of these species on the Italian territory, with reference to the Tyrrhenian coasts [49,50] (Figure 2a,b). These areas represent an important germplasm reserve for the use of local varieties or ecotypes. The species are reported with the scientific and common name, the type of halophytism, and the edible organs.

For all the species considered, we followed the taxonomic nomenclature reported by Bartolucci et al. (2018) [51], except for *Soda inermis*, herein kept as *Salsola soda*. This is due to the taxonomic difficulties of not being fully clarified by the Angiosperm Phylogeny Group classification [52], related to the revisions of the genus *Salsola*, from which the taxon *Soda* was separated with the only species *Soda inermis*.

Table 1. List of halophytes selected on the basis of their diffusion in the Mediterranean region and their type of halophytism according to eHALOPH [24].

Botanical Name	**Family**	**Common Name in English, French, German and Italian**	**Type of Halophytism**	**Edible Organs**
Atriplex littoralis L. (Syn.: *Atriplex patula* L. var. *littoralis* (L.) A. Gray)	Amaranthaceae	Grassleaf orache, Arroche du littoral, Strand-meide, Atriplice litorale.	Psammophyte	Leaves
Atriplex prostrata Boucher ex DC (Syn.: *Atriplex latifolia* Wahlenb. = *Atriplex hastata* L. var. *prostrata* (Boucher ex DC.) Lange)	Amaranthaceae	Hastate orache, Arroche couché, Spiess-meide, Atriplice prostata	Eu-halophyte Meso-hydrohalophile	Leaves
Beta vulgaris L. subsp. *maritima* (L.) Arcang. (Tuscany, Sardinia, Sicily)	Amaranthaceae	Sea beet, Bette maritime, Wilde übe, Bietola marittima	Mio-halophyte	Leaves
Cakile maritima Scop. subsp. *maritima*	Brassicaceae	Searocket, Roquette de mer, Strandrauke, Ravastrello di mare	Psammophile Halo-nitrophilous	Leaves
Halimione portulacoides (L.) Aellen (Syn.: *Atriplex portulacoides* L.)	Amaranthaceae	Sea pursiane, Arroche faux-pourpier, Strand-salzmeide, Porcellana di mare	Eu-halophyte Hydro-halophyte	Leaves
Portulaca oleracea L. subsp. *oleracea*	Portulacaceae	Common pursiane, Purcelane, Portulach, Porcellana	Xero-halophyte	Leaves Stem
Salicornia perennans Willd. subsp. *perennans* (Syn.: *Salicornia europaea* auct.; *Salicornia patula* Duval-Jouve).	Amaranthaceae	Grasswort, Salicorne etaleé, Pannonien glasschmaiz, Salicornia patula	Eu-halophyte Xero-halophyte	Stem
Salicornia perennis Mill. subsp. *perennis* (Syn.: *Sarcocornia perennis* (Mill.) A.J.Scott subsp. *perennis*).	Amaranthaceae	Perennial grasswort, Salicorne vivace, Ausdauernde gliedermeide, Salicornia radicante	Eu-halophyte Hydro-halophyte	Stem
Salsola soda L. (Syn: *Soda inermis* Fourr.)	Amaranthaceae	Monk's beard, Soude commune, Soda-salzicraut, Agretto	Eu-halophyte	Leaves Young stem
Suaeda maritima (L.) Dumort. (Syn.: *Chenopodium maritimum* L.)	Amaranthaceae	Sea-blite, Soude maritime, Strand-sode, Sueda marittima	Eu-halophyte Mesohydro-halophile	Leaves Young stem
Suaeda vera J.F. Gmel (Syn.: *Suaeda fruticosa* (L.) Forssk. subsp. *vera* (J.F. Gmel.) Maire & Weiller).	Amaranthaceae	Shrubby sea-blite, Soude vraie, Strauchige sode, Sueda vera	Eu-halophyte Halo-nitrophilous	Leaves Young stem

Figure 2. Salt marsh vegetation of Tyrrhenian coasts (Italy): (**a**) *Salicornia perennis* communities; (**b**) *Salicornia perennans* communities. Photo credit: Andrea Bertacchi.

The species and subspecies *Halimione portulacoides*, *Salicornia perennans* subsp. *perennans*, *Salicornia perennis* subsp. *perennis*, *Salsola soda*, *Suaeda maritima* and *S. vera* are exclusive to brackish areas. *A. prostrata*, *B. vulgaris* subsp. *maritima*, and *Portulaca oleracea* can be found in both brackish areas and internal saline soils. *Cakile maritima* subsp. *maritima*, and *Atriplex littoralis* are halophytes that grow exclusively in dune environments.

The main multidisciplinary traits of the 11 selected species are reported in Appendices A—C.

5. Halophytes as Potential Novel Crops

The Mediterranean basin is extraordinarily rich in wild, edible halophytes that grow in both coastal and inland salty areas. The use of wild halophytes for food, and for ethnomedicine, is very ancient. Many plant species have been used traditionally as herbs and vegetables, and accounts of their uses can often be found in ethnobotanic literature [53–55]. This suggests a high potential for Mediterranean halophytes to undergo exploitation by the food industry towards the production of new products with functional and healthy properties, such as beverages, salad mix, microencapsulated oils, food additives, antimicrobial agents, etc. Different parts of halophytes can be consumed, such as the leaves, young shoots, seeds, flower buds, roots, and fruits.

Examples of wild, edible halophytes belong to the genera *Atriplex*, *Bassia*, *Beta*, *Cakile*, *Chenopodium*, *Crithmum*, *Plantago*, *Portulaca*, *Salicornia*, *Salsola*, and *Suaeda*. Some halophytes have received attention as potential food sources due to their beneficial effects [7,12,56,57].

To overcome salinity, plants adopt various strategies. A common characteristic of salt tolerance is the leaf accumulation of L-proline. It is an amino acid commonly synthesized in the cytosol and stored in the chloroplasts, and its accumulation rises to 80% of the amino acid pool when plants are exposed to environmental stress [58]. Proline is well known for its osmoprotectant activity, such as its ability to change cell osmotic pressure, so its presence helps halophytes to counteract salty soils. Therefore, proline is considered to play a pivotal role in defense /protective mechanisms, as the scavenging activity against reactive oxygen species, to provide stabilization of the cellular membrane and play the role of a metal chelator [58]. Another compound accumulated by halophytes is glycine betaine, which interact with macromolecules (proteins, enzymes) and contribute to the mitigation of salinity stress [59]. *Salsola soda* (Syn.: *Soda inermis*) is an example of a glycine betaine accumulator [60].

Some halophytes are also a good source of nutraceuticals. For instance, *Salicornia perennis* (Syn.: *Sarcocornia perennis* subsp. *perennis*) is used in the human diet for its nutraceutical components. *S. perennis* leaves are rich in proteins (6.9 mg/100 g d.w.), polyunsaturated fatty acids (PUFA; linolenic acid is about 21% of PUFA), and minerals such as Ca, Mg, Fe and K [7]. *Salicornia ramosissima* is used as gourmet food due to the presence of antioxidants as phenolics compounds, and of α- and γ-tocopherol [7]. *Suaeda maritima* (Syn.: *Chenopodium maritimum*) contains a good amount of Ca, Mg, Fe, Zn, and Cu, which represent up to 10% of the allowed daily intake (ADI) and are a good source of vitamins such as beta-carotene and lutein, vitamin A, and vitamin C [11]. Phenolic compounds and/or derivatives, such as phenolic acids (e.g., gallic acid), phenylpropanoids (e.g., cinnamic acid, caffeic acid), flavonoids (e.g., quercetin and kaempferol) and lignans, are often present in *Suaeda* sp., *Sarcocornia* sp., and other halophytic species. *Suaeda vera* might be a valuable source of phenolic compounds due to its antioxidant, anti-inflammatory, and anticancer properties [61], as well as bioactive flavonoids, and other beneficial properties. Likewise, the leaves of *S. vera* accumulate sugars, especially galactoarabinans, which have a good antioxidant-activity effect and contribute to cell stability [62].

However, other plants accumulate sugar alcohols (e.g., mannitol, inositol, sorbitol) to maintain cell homeostasis. The leaves of *B. vulgaris* spp. *maritima* contain several nutraceutical compounds, such as tocopherols, phenols, ascorbic acids, and some fatty acids, although their consumption could be limited by the presence of malic and oxalic acid [12]. In *Cakile maritima*, the leaf content of minerals, vitamins, and amino acids, such as proline and glycine, increases in response to salt treatment [57,63]. *Portulaca oleracea*, also named "Global Panacea" by the World Health Organization, contains 3% carbohydrates, 2% protein, as well as various vitamins (especially vitamin A) and all the essential minerals. Its leaves are rich in flavonoids and contain alkaloids, including dopa, dopamine, and noradrenalin. *Portulaca* is a good source of Omega-3 fatty acids (α-linolenic acid and linoleic acid), contained in the leaves, stems and flowers. The presence of various bioactive compounds confers to *Portulaca* several pharmacological properties, such as antimicrobial, antioxidant, anti-inflammatory, antidiabetic, neuroprotective, antiulcerogenic, and anticancer activity [64]. More information about the biochemical characteristics of the 11 selected species are illustrated in Appendices A–C.

6. Cultivation of Halophytes in Hydroponic Greenhouse

As potential new vegetable species, halophytes are also candidates for greenhouse cultivation, which can allow year-round production of high-quality products with an efficient use of resources such as water, fertilizers, and manual labor. In the last three decades, protected horticulture has developed in many regions, particularly in the Mediterranean countries (e.g., Spain, Italy, Turkey, and Morocco), where the mild climate during winter makes it possible to produce many crops in simple structures [65]. The increasing competition arising from the globalization of production and marketing, the greater awareness of the environmental impacts provoked by intensive cropping systems, the increasing demand for healthy foods, and the shortage of resources such as water, are forcing greenhouse growers to apply more sustainable growing techniques. The use of greenhouses with better climate control and more advanced growing technologies, such as drip fertigation, hydroponics (or soil-less culture), and integrated control over pests and diseases, are the most relevant aspects of the development of the greenhouse industry worldwide.

Many soilless growing systems have been designed and tested for greenhouse crop production. Nowadays, the term "hydroponics" includes all methods and techniques for cultivating plants without soil in artificial substrates (aggregate culture) or in an aerated nutrient solution (liquid or water culture) [66]. Aggregate culture is generally used for row crops with low crop density and long growing cycles, such as Solanaceae, Cucurbits, and strawberry, while water culture is adopted for short-cycle and high-density crops such as leafy vegetables and herbs [66].

We searched SCOPUS for documents on the hydroponic cultivation of halophytic species using the following search strategy (last access: 15 February 2022): TITLE-ABS-KEY (halophyte* OR halophytic*) AND (hydroponic* OR aquaponic* OR aquaculture OR soil-less). We found 260 research articles published between 1983 and the beginning of 2022; almost half of these have been published since 2017, demonstrating the recent interest of plant scientist in this subject. Much attention has been paid to the utilization of these species in integrated or multitrophic marine aquaponic systems, in which halophytes are cultivated in undiluted or diluted seawater along with aquatic species such as fish, crustaceans and seaweeds [67]. In these systems, halophytes play a fundamental role in the bioremediation of effluents from aquaculture [68].

The halophytes most studied in hydroponics and aquaponics are the following: *Salicornia dolichostachya* [69], *S. perennans* [70,71], *S. ramosissima* [69,72], *S. bigelovii* [73], *Sarcocornia neei* [74,75], *Halimione portulacoides* [9,76,77], and *Portulaca oleracea* [78–82]. The crop yield observed in some halophytic species grown in soil-less culture is shown in Table 2, along with other information on growing conditions. We are not aware of any studies conducted on the hydroponic production of the other species selected for this review (Table 1). The hydroponic techniques mainly used for halophytes are deep culture, floating system, and sand culture. Singh et al. (2014) [69] found that in *Salicornia dolichostachya* and *S. ramosissima*, the harvestable biomass was greater in hydroponic culture than in sand culture.

One of the main advantages of a hydroponic system over soil cultivation is that plant growth rate, and then crop yield, are increased as result of better mineral nutrition and water uptake. In Israel, under field conditions, *Salicornia persica* produced 13.4 to 16.0 kg/m^2 of fresh biomass in six months when grown under field conditions on sand dune soil and drip-irrigated with moderate salinity (10 dS/m), or 18.6 kg/m^2 when grown in an unheated greenhouse on coconut fiber-filled sleeves irrigated with moderately saline aquaculture effluent (EC 4 dS/m) [83]. In *Salicornia europaea* cultivated for two months in a floating system in the typical greenhouse climate conditions of summer in Central Italy and using groundwater or diluted seawater (with salinities ranging between 10 and 30 g/L), the production of fresh shoots was between 7.10 and 9.78 kg/m^2, depending on the salinity of the nutrient solution [70].

Small dimensions and fast growth rate make some halophytes good candidates for the hydroponic production of fresh-cut baby leaves, which are increasingly used for mixed salads. Baby leaves are young plants harvested two to four weeks after seed germination. In addition, hydroponic culture allows the improvement of product quality by appropriate management of the nutrient solution [84]. Tender and very clean leaves and shoots are generally harvested in hydroponic systems, and this facilitates the washing operation with minimal processing. There is a growing interest in the fresh-cut baby leaves of halophytes [15], and some studies have demonstrated the good adaptation of purslane [85,86] and sea fennel [14].

Among soilless growing methods, the floating system is the simplest and most cost-effective technique to produce baby leaves at high crop density [86].

Intensive cropping systems, such as greenhouse hydroponics, enhance crop productivity but could affect the produce quality of wild edible plants, particularly as regards their nutritional, nutraceutical and organoleptic traits [87]. Recently, in a study conducted with three species of halophytes (*Mesembryanthemum nodiflorum*, *Suaeda maritima* and *Sarcocornia fruticosa*), harvested from the wild in two different locations in Portugal or cultivated hydroponically, it was found that cultivated plants are more succulent, and have fewer fibers and antioxidants than wild plants [11]. Increased succulence is a positive trait from an organoleptic point of view.

Table 2. Fresh biomass production of some halophytic species grown in hydroponics under different growing conditions, and at different plant density and salinity levels of the nutrient solution.

Species	Location (Country)	Growing Technique	Growing Season and Environment	Growing Cycle (Days/Month)	Plant Density (Plants/m^2)	Salinity Level	Fresh Biomass (kg/m^2)	Note	Reference
Halimione portulacoides	Portugal	Hydroponics (floating system)	Growth chamber	10 weeks	110–220	20 g/L NaCl	3.1–5.4		[9]
Halimione portulacoides	Portugal	Hydroponics (floating system)	Growth chamber	10 weeks	220	20 g/L NaCl	3.41–5.40		[77]
Portulaca oleracea	Jordan	Soil-less substrate	Unheated greenhouse, March–July	5 months		5.5–6.5 dS/m	14.6–26.9	Total yield depended on genotypes	[80]
Portulaca oleracea	Spain	Hydroponics (floating system)	Unheated greenhouse, July	15 days	2050	2.7 dS/m	1.64–2.66	Total yield depended on genotypes	[78]
Portulaca oleracea	Spain	Microgreens	Growth chamber	4 weeks		0–80 mM NaCl	1.51–1.97	Yield was greater at higher salinity	[81]
Portulaca oleracea	Canada	Hydroponics (floating system)	Controlled-climate greenhouse	26 days	266	0–10 mM NaCl	4.90–5.73		[79]
Portulaca oleracea	Alabama, US	Mixture of Jiffy mix, sand, and soil	Controlled-climate greenhouse	60 days	20	Hoagland nutrient solution	0.54		[82]
Salicornia bigelovii	Canada	Hydroponics (floating system)	Controlled-climate greenhouse	28 days	266	6–200 mM NaCl	0.33–1.69	The greatest yield was found at 200 mM NaCl	[73]
Salicornia dolichostachya	Germany	Sand culture or hydroponics (floating system)	Controlled-climate greenhouse	42 days	37	257–513 mM NaCl	0.86–1.06	Yield was greater in floating system than in sand	[75]
Salicornia europaea	Italy	Hydroponics (floating system)	Greenhouse, summer	58 days	60	0–30 g/L (artificial sea salt)	4.80–9.84	The lowest yield and the highest yield were found at salinity of 30 and 10 g/L	[70]
Salicornia ramosissima	Germany	Sand culture	Hydroponics (floating system)	5 weeks	-	257–513 mM NaCl	1.06		[69]
Salicornia persica	Israel	Coconut-fiber-filled sleeves	Unheated greenhouse	5 months	-	4 dS/m	18.6		[83]
Suaeda glauca	Canada	Hydroponics (floating system)	Controlled-climate greenhouse	27 days	266	6–200 mM NaCl	4.02–5.65	The lowest yield was found at 200 mM NaCl	[88]

7. Health Risks Associated with the Consumption of Cultivated Halophytes

For the economic development of halophytic crops, the possible presence of health-hazardous substances must be considered for nitrate and oxalate—which generally accumulate, to a large extent, in species belonging to the Amaranthaceae [89,90]—and Na, with regard to irrigation with saline water. The risk associated with the presence of heavy metals and other environmental pollutants is not considered in this review, as this risk is minimized if halophytes are grown under controlled conditions with safe irrigation water; this is in contrast with the harvest of these plants in the wild, which is prohibited in most areas where these species could be collected.

7.1. Nitrates

Nitrate (NO_3^-) may be harmful to human health as it can be converted to nitrite (NO_2^-) causing methaemoglobinaemia or carcinogenic nitrosamines [89]. According to the World Health Organization (WHO) and the European Commission's Scientific Committee on Food (SCF), the ADI for NO_3^- is 3.7 mg/kg b.w. (222 mg for an adult weighing 60 kg), while the USA Environmental Protection Agency (EPA) has set an ADI of about 7.0 mg/kg b.w. The main sources of NO_3^- in human diet are drinking water, cured meat and vegetables; the latter generally provide 30% to 94% of the daily dietary intake of NO_3^- [89].

The European Commission has established maximum limits for the NO_3^- content in some vegetable species marketed for fresh consumption or as frozen products: 3000 mg/kg f.w. for spinach (*Spinacea oleracea*); 2000–5000 mg/kg f.w. for lettuce (*Lactuca sativa*); and 6000–7000 mg/kg f.w. for rocket salad (*Eruca sativa*, *Diplotaxis* sp., *Brassica tenuifolia*, *Sisymbrium tenuifolium*). The limits depend on growing conditions. For instance, the limits are higher for vegetables grown in the fall–winter season and under cover, compared to those grown in spring–summer and in an open field. Limits to NO_3^- levels have been set in other European countries for other species [89]. We are not aware of the maximum NO_3^- levels set for the halophytes selected for this review.

Many leafy vegetables easily accumulate NO_3^- in their edible tissues under growing conditions that enhance NO_3^- uptake by the roots (e.g., high NO_3^- concentration in the growing medium) while NO_3^- reduction is hampered. For instance, low solar radiation limits leaf photosynthesis and the availability of reducing equivalents (ferredoxin and NADPH) for NO_3^- reduction, and this account for large NO_3^- accumulation in plants grown in winter with abundant nitrogen fertilization. Hydroponic cultivation stimulates root mineral uptake and can enhance more NO_3^- accumulation in leaf tissues compared to soil cultivation [91]. On the other hand, plant mineral nutrition can be controlled by the adjustment of the nutrient-solution composition. For instance, nutrient-solution deprivation [92], or the replacement of NO_3^- with Cl^- [93], during the last few days of cultivation can reduce leaf NO_3^- content to below the limits set by EU Regulation 2008 [94]. Nitrate accumulation is hampered when plants are grown with high NaCl in the growing medium due to the competitive interaction between NO_3^- and Cl^- [95]. In the halophyte *Suaeda salsa* (L.), NO_3^- reduction and assimilation were stimulated by Cl^- application, with a consequent reduction in leaf nitrogen accumulation [94]. Nitrate content can vary very much within species and cultivars, and the degree of NO_3^- accumulation is associated with the location of nitrate reductase activity and the plant's capacity of NO_3^- accumulation on halophytes marketed for human consumption. Recently, Labiad et al. (2021) [14] reported that NaCl concentration and leaf spray with methyl jasmonate did not affect the NO_3^- concentration of baby leaves of hydroponically grown *Crithmum maritimum*, which ranged between 229 and 296 mg/kg f.w. It was calculated that a daily consumption of 100 g of *C. maritimum* leaves did not reach the ADI of NO_3^- for adult persons. However, the content of NO_2^- was between 453 and 970 mg/kg f.w., and the same daily intake of baby leaves largely surpassed the ADI for nitrite (3.6 mg, according to SCF) [89].

In a greenhouse experiment with *Salicornia europaea*, grown in summer in an aerated water culture with different concentrations (0, 10, 20 and 30 g/L) of a synthetic sea salt

(Instant Ocean^{TM}), shoot NO_3^- content averaged 3397 mg/kg f.w. in the controls and was much lower in salt-treated plants, with no major differences across salinity levels (the mean value was 1374 mg/kg f.w.) [70].

7.2. Sodium

Sodium is one of the most abundant elements on earth and in seawater, and along with Cl^-, is by far the dominant ion in saline soils [96]. Halophytes tolerate a high concentration of Na in the root zone, and some of them require NaCl for optimal growth and development [97]. Although root control of Na uptake and the excretion of Na salts via specific organs (such as salt glands) are among the mechanisms of salt tolerance in some halophytes, most of them are eu-halophytes and accumulate large amounts of Na^+ and other ions; these are compartmentalized in vacuoles for osmotic adjustment. Therefore, the consumption of halophytes grown in saline conditions originates the risk of excessive intake of Na. According to the World Health Organization [98], the recommended ADI of Na for adults is 2 g per day, as greater intake increases the risk of hypertension and cardiovascular diseases.

In wild plants of *Beta vulgaris* subsp. *maritima*, *Cakile maritima*, *Portulaca oleracea* and *Salicornia europaea*, harvested in the South-East Spain, the Na content of fresh, edible organs was 171, 308, 42 and 884 mg/100 g f.w., respectively [63]. In *Sarcocornia perennis* subsp. *perennis*; *S. perennis* subsp. *alpini*; *S. ramosissima*; and *Arthrocnemum macrostachyum*, collected in the South of Portugal, edible tips contained, respectively, 2049, 1029, 910 and 1393 mg Na/100 g f.w. [7]. When *Halimione portulacoides* was grown hydroponically in artificial seawater (20 g/kg) under non-limited nutrient conditions, at harvest, fresh leaves contained 750 mg Na/100 g f.w. [9]. In the aforementioned study performed by Boni (2020) [70] with hydroponically grown *Salicornia europaea*, the shoot Na content was 471, 1299, 1672 and 1806 mg/100 g f.w. at salinity level of 0, 10, 20 and 30 g/L, respectively. Therefore, when halophytes harvested in the wild or cultivated with high sodium concentration in the growing medium are consumed, much attention must be paid not to exceeding the ADI recommended by the WHO. On the other hand, dried halophytes such as *Salicornia* spp. and *Halimione portulacoides* can replace Na salts to produce low-Na foods [99,100].

7.3. Oxalate

Oxalate is an anti-nutritional factor contained in many foods, although those rich in oxalate, such as some vegetables, generally play a minor role in human diet [101]. Oxalate can bind to several minerals, thus reducing their bioavailability in humans. Oxalate can reduce the availability of Ca due to the formation of an insoluble complex that is contained in the most urinary stones of kidney. Almost all the species considered in this review (Table 1) belong to Amaranthaceae, which includes some vegetables naturally rich in oxalates such as spinach, Swiss chard, and mangold [102]. A general guideline from the American Dietetic Association is to restrict the daily intake of oxalate to 40–50 mg/day [103]. Among the species considered for human consumption, undoubtedly, the most investigated halophyte is purslane, as it is a good source of omega-3 fatty acids, amino acids, and vitamins. However, this species also contains high concentrations of antinutritional factors, such as NO_3^- and oxalate [104]. The oxalate content found in hydroponically cultivated purslane ranges from 800 mg/kg f.w. [105] to more than 6000 mg/kg f.w. [106], and it has been known to reach 7700 mg/kg f.w. in plants collected in the wild [107]. With such high contents, a few grams would be enough to exceed the maximum recommended daily intake of oxalates. In purslane, the oxalate content depends on the genotypes [106,108], nitrogen nutrition [105,109], and harvesting stage [110]. Decreasing the nitrogen supply and the NO_3/NH_4 ratio in the culture solution has been known to reduce the oxalate content of stems and/or leaves of purslane grown in hydroponics [105,106,110]. Carvalho et al. (2009) [108] found a reduction in the oxalate content of purslane leaves when NaCl was added to the hydroponic solution. In a recent work with purslane microgreens, cultivated in a growth chamber under different light conditions, oxalic content significantly decreased when plants were illuminated with red and blue, or red, blue, and far-red LEDs. The nutrient solution contained 80 mM NaCl, compared with the controls grown under fluorescent light with a NaCl-free nutrient solution [81].

7.4. Mycotoxigenic Fungi and Mycotoxins in Edible Halophytes: A Potential Health Risk?

The parts of the halophyte plants used for nutrition could become potential natural sources of mycotoxins, if contaminated by mycotoxigenic fungal species.

Mycotoxins are a series of secondary metabolites produced by a variety of filamentous fungi that can grow on a diversity of crops and are associated with important morbidity and mortality in humans and animals, as well as with major economic losses. Exposure to mycotoxins can occur by inhalation, dermal contact, and primarily by ingestion. Because of their low molecular weight, thermostability and wide spectrum of toxicity, the management of the contamination of food and feed with mycotoxins is problematic [111]. Moreover, it is important to note that climate change is expected to significantly increase mycotoxin production by fungi [112].

A very large number of mycotoxins (>300) has been identified in agricultural products; correspondingly, mycotoxigenic species can be found in all major taxonomic groups, but the most important are produced by many species of the genera *Aspergillus*, *Penicillium*, *Alternaria*, and *Fusarium* [113]. Of the great number of known mycotoxins, only a few are commonly found in fruits and vegetables: aflatoxins (produced by several *Aspergillus* species); ochratoxin A; patulin and citrinin (by *Penicillium* and *Aspergillus* species); alternariol and derivatives (by *Alternaria* species); and trichothecin (by *Trichothecium roseum*) [114,115].

Mycotoxins rarely cause outbreaks via fresh food, but they are still a risk factor for foodstuffs of plant origin [116]. The contamination of fruits and vegetables with fungi that produce mycotoxins can occur in the field, at harvest and during transportation, and in storage. The presence of fungi on fresh products does not always lead to mycotoxin contamination but reveals that there is a potential risk, because many environmental factors can trigger the formation of mycotoxins [114]. Mycotoxins produced on fresh products may be found in their host tissues even after the fungal mycelium has been eliminated. This is critical for the safety of consumers, since apparently healthy parts can be used as ready-to-eat fresh products or dried food preparations [117,118]. In this regard, careful attention should be paid to the composition of the mycoflora on the edible parts, and to the presence of mycotoxigenic fungi.

Many scientific papers report the presence of endophytic fungal populations inhabiting several species of halophytes. Endophytic fungi generally reside within plants without causing any disease symptoms and have gained the attention of many researchers for their ability to produce bioactive metabolites [119–121]. However, recent findings highlight the possible contribution of endophytic strains in differentiating new lineages with an uneven mycotoxin assortment during the exploration of new ecological contexts [122]. Thirumalai et al. (2020) [123] pointed out the importance of investigating the endophyte community of leafy vegetables, especially those with a longer shelf life, for their mycotoxin production.

Therefore, against this background, the data relating to the endophytic, and/or mycotoxigenic fungal species reported on the halophytes described, have been presented in Appendices A–C. The examples confirm that representative fungal genera containing mycotoxigenic species have been frequently reported on halophytes. Therefore, symptomless infections could cause serious food-safety problems, as the plant can look normal, but it may contain mycotoxins.

Many mycotoxin-producing fungal species belonging to the *Aspergillus* and *Penicillium* genera have been isolated from low-water-activity environments (aw below 0.8) due to their adaptive xerotolerance/halotolerance [124,125]. Maciá-Vicente et al. (2008) [126] found a high occurrence of *Aspergillus fumigatus* and members of *Pleosporales*, such as *Alternaria* species, in saline environments. Recently, Calabon et al., 2021 [127] reviewed the fungal biodiversity in salt-marsh ecosystems. They found 486 taxa associated with different hosts, of which 95.27% (463) belonged to the phylum Ascomycota, and the *Pleosporales* was the largest order with 178 taxa recorded. Moreover, *Pleosporales* and *Alternaria* spp. are known to produce heavily pigmented spores and/or mycelia (especially melanin) that may protect the fungi in a high-salinity environment (UV radiation, desiccation, and extreme temperatures) [128].

Interestingly, within the *Pleosporales* order, some fungal genera have a host and habitat preference and can be found in marine or saline habitats in association with various kinds of halophytes. The majority of the *Neocamarosporium* species described so far were found in association with *Atriplex hastata*, *A. prostrata*, *Beta vulgaris*, *Halimione portulacoides*, *Salicornia* spp., and *Salsola* sp.; halotolerance seems to be a typical characteristic of this fungal genus [129,130]. The importance of the problem addressed is confirmed by recent observations of the presence of mycotoxigenic fungi and their mycotoxins in some halophytic plants [131,132].

Although toxicological assessments and guidelines are in place to curb the impact of many contaminants on public health, these safeguards cannot be applied to naturally occurring mycotoxins. For this reason, the health risk posed to the consumer by natural mycotoxins appears more serious than the health risk posed by man-made pesticides, preservatives, and other food additives [133,134].

7.5. Pathogenic Bacteria Potentially Associated with Edible Halophytes

To the best of our knowledge, there are no studies on the microbial contamination of halophytes intended for human consumption. Nevertheless, we can assume that the contamination of halophyte-based food preparation due to bacteria follows the general guidelines adopted for other vegetables. Bacteria such as *Aeromonas* spp., *Bacillus cereus*, *Campylobacter* spp., *Clostridium botulinum*, *Escherichia coli*, *Listeria monocytogenes*, *Salmonella enterica*, *Shigella* spp., *Staphylococcus* spp., and *Yersinia enterocolitica* are generally associated with fresh vegetable produce. Among these, *E. coli*, *L. monocytogenes* and *S. enterica* have been found to be responsible of most fresh-produce outbreaks in the United States [135].

The fresh vegetable market, including halophytes, is expanding due to global changes and to consumer habits being more oriented toward healthier lifestyle choices. On the other hand, the diffusion of foodborne illness is often associated with the intake of ready-to-eat preparations. These are consumed without being exposed to processing treatments, and pathogen contamination may be uncontrolled as a result. *Listeria monocytogenes* and *Staphylococcus aureus* have been proven to have the ability to survive in different types of salad over a range of temperatures, depending on the type of preparation and storage conditions [136]. In fresh-cut vegetables, the microbiological standard for *Salmonella* spp. is absence in 25 g of foods [137]; for *Listeria monocytogenes*, the standard is absence in 25 g before the food has left the immediate control of the producer, and <100 cfu/g in products that are placed on the market during their shelf life [137]. Studies on the presence of enteric pathogens in fresh-cut vegetables indicate that contamination with pathogens occurs infrequently [138]. However, in a recent study, increased consumption of fresh produce was correlated with increased outbreaks of microbial infection of these products [139].

The presence of halophyte species in food preparation is desirable to contribute to the preservation of biodiversity and improving sustainable practices; the development and application of accurate practices in the preparation and prevention of cross-contamination are essential to preclude the presence of pathogens.

8. Conclusions and Future Perspectives

Global climate change and soil degradation due to progressive salinization are now quite evident. In this context, halophytes can be of fundamental importance both for the restoration of salinized lands, and as a commercial alternative to traditional crops.

Some halophytes (e.g., *Portulaca oleracea* and *Salicornia* spp.) are cultivated and consumed as a novel source of nutraceutical components, conferring beneficial effects, such as proline. Further compounds that are well represented are phenolic compounds and/or derivatives, fatty acids, vitamins (tocopherols and ascorbic acid), and some minerals.

For these purposes, multidisciplinary investigations are crucial, starting with the identification of the species, subspecies and ecotypes, and subsequently characterizing their ecological, nutritional, and organoleptic properties, for their use as crop plants. This approach may not always be simple, as the halophytes, especially some members of the Amaranthaceae, often have high intraspecific morphological and physiological variability.

The cultivation and commercial production of edible halophytes is still in early stages; in the European market, their consumption is recent, and therefore not covered by any food-safety regulations. Despite the promising future for multiple uses of edible halophytes, there is still little knowledge of natural mycotoxin contamination in these plants, and more investigations are required before conclusions can be drawn on the health risks associated with their consumption.

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Appendix A

The systematic, morphological, and biochemical characteristics of the species considered in the present work (Table 1) are reported below. Nomenclature follows the APG IV classification system [52].

AMARANTHACEAE Juss.—Dicotyledons, annual or perennial, shrubs, or herbs. Leaves are simple without stipules, succulent or reduced in some taxa. Small flowers, bisexual or unisexual, in flower heads or spikes. Simple perianth of 3–5 scary tepals. Stamens equal in number to the tepals, and alternated with petaloid staminoids. Fruit is utricle or pyx. Seeds with annular embryo surrounding the mealy albumen. Cosmopolitan.

Appendix A.1. Genus Salicornia L.

The genus *Salicornia* includes several annual and perennial plants, divided into a series of diploid and tetraploid species and subspecies [140], difficult to distinguish based on macroscopic characteristics. The genus name derives from the Latin 'sal' (salt) and 'conus' (horn), due to the shape of the branches. These plants have articulated stems, succulent and apparently aphill, with very small flowers (hermaphrodites) that are difficult to observe. These are normally inserted in terminal racemes consisting of triflorous dicases, inserted at the axil of leaf-like bracts, in correspondence with each node. In this Appendix, following updates of Bartolucci et al. (2018) [51], reference is made to subspecies *Salicornia perennans* Willd. subsp. *perennans*, and *S. perennis* Mill. subsp. *perennis*. Other authors include the latter species in the genus *Sarcocornia* [141,142]. The two species are both diploid (2n = 18).

Appendix A.1.1. *Salicornia perennans* Willd. subsp. *perennans* (Syn.: *Salicornia europaea auct.*; *Salicornia patula Duval-Jouve*; *Salicornia herbacea* (L.).) Eu-halophyte

<u>Botanical traits</u>

Biological form: scapose therophyte.

Morphological characteristics: Stem 5–40 cm tending to purple with ripening, very branched at the base. The inflorescence is trifloral with the central flower much larger than the lateral ones. Mature seeds covered with curved and often hooked hairs.

Habitat: salt marshes, soils muddy clay-asphyxial, basic and hypersaline. *S. perennans* is widespread along almost all the Italian coasts. It grows in lagoons and basins subjected to periodic flooding of seawater and at the edges of the salt flats, along the coasts.

Chorological type: W-Europe (Euri-Medit.)

Flowering period: September–November.

S. perennans tolerates a NaCl concentration of more than 1000 mM, although its optimal growth has been observed at 200 mM [143]. The plants contain large amounts of minerals, especially Ca, Mg and iodine (I), and osmolytes such as betaine and choline [144].

Biochemical traits

The plant is cultivated for its oilseed used in human consumption and as a forage crop in saline coastal environments.

Wang et al. (2021) [145] performed metabolomic characterization of the leaves of *S. europaea*, and discovered 694 metabolites involved in the tolerance to salt conditions: flavonoids, alkaloids and coumarins, and the branched chain amino acids, glucosamine, maltose, and glucose. At a high salt concentration (500 mM NaCl), the succulence is due to the Na^+ content of the cell, which promotes the osmotic adjustment and increases the proline and other osmolyte content, maintaining cell turgor [146]. The first investigation on the effects of salt stress in *S. europaea* was elucidated in 2009 [147] by looking at the growth parameters, free proline content, ion accumulation, lipid peroxidation, and several antioxidative enzymes activities of in vitro plantlets. At high salt concentration (300 mM), peroxidation of lipid membranes occurs, reflecting free-radical-induced oxidative damage at the cellular level [148], counteracted by the increase in polyphenol content and enzymatic scavenger activity (peroxidase and superoxide dismutase). *Salicornia* shoots are also a good source of fatty acids such as linoleic and oleic acids [12,54].

The oilseeds of *S. herbacea* (Syn.: *S. perennans*) are rich in proteins [149] and linoleic (75.6%) and oleic acids (13.0%); they also contain a significant amount of palmitic, linoleic, and stearic acids, as well as tetracosanol, and octacosanol [149]. The composition is very similar to the composition of safflower oil. The extracts exhibit activity against different kinds of oxidative stress, inflammation, diabetes, asthma, hepatitis, cancer, and gastroenteritis [150].

Plant mycobiota

The analysis of the fungal community structure in *Salicornia europaea* in Poland revealed the presence of nine orders, and among them, the most representative were *Pleosporales* (main genus Alternaria) and Eurotiales (including the genera Aspergillus and Penicillium) [151,152].

Pleospora sp., *Alternaria alternata*, and *A. phragmospora* were the major endophytes found in *Salicornia europaea* in Japan [153].

Lopes et al. (2020) [132] investigated the presence of potentially mycotoxigenic fungi and the occurrence of aflatoxins (AFB1, AFB2, AFG1, AFG2) and ochratoxin A in fresh and powdered samples of *Salicornia* spp. (wild and cultivated) in Portugal. Potentially toxigenic fungi (*Aspergillus flavus*, *A. fumigatus*, *A. niger*, and *Penicillium* sp.) were present in most of the analyzed samples, and relevant levels of AFB1 > 5 $\mu g\ kg^{-1}$ and total aflatoxins (sum of AFB1, AFB2, AFG1 and AFG2) > 10 $\mu g\ kg^{-1}$ were found in various samples. Ochratoxin A was not found in any of the samples. It is interesting to note that a sample of *Salicornia* supplied by a local producer exhibited very high levels of contamination, but no aflatoxins were found in the samples grown either in greenhouses or in hydroponic cultivation. The presence of aflatoxins may not be considered a serious problem for those who consume *Salicornia* occasionally; however, this halophyte is widely used as forage [154], which, if contaminated, could be a risk to both animals and humans.

Appendix A.1.2. *Salicornia perennis* Mill. subsp. *perennis* (Syn.: *Sarcocornia perennis* (Mill.) A. J. Scott subsp. perennis). Eu-halophyte

Botanical traits

Biological form: succulent chamaephyte.

Morphological characteristics: Bushy stem 50–60 cm, rooting at the nodes. The inflorescence is 3-flowered with the central flower a little larger than the lateral ones. Mature seeds covered with short, curved hairs.

Habitat: hypersaline margins of the brackish areas where *S. perennans* also grows, often dry in summer.

Chorological type: Medit.-Atlant.

Flowering period: September–November.

Biochemical traits

The halophyte *S. perennis* contains high levels of proteins (6.9 g/100 g d.w.) and n-3 polyunsaturated fatty acids (PUFA)—particularly linolenic acid (21.1% of total FA)—and low concentrations of toxic metals, below the limits imposed by the European Commission. The plant is also a good source of minerals, particularly Na (64.1 mg/g d.w.), and manganese (31.4 mg/g d.w.). Other detected natural minerals include the presence of Ca, Mg, Fe and K. Leaf extracts show great antioxidant potential due to the content of total phenols (20.5 mg GAE/g d.w.), carotenoids (280 mg/100 g d.w.), and tocopherols (vitamin E, 1.2 mg/100 g d.w.) [7]. In addition, flavonoids, such as kaempferol and quercetin, and to a lesser extent, gallic acid and other hydroxy-benzoic acids, have been reported in *Sarcocornia* species; the intake of 100 g of edible portions (wet weight) of *S. perennis* would cover 71% of said recommended daily dose, to reduce the risk of cardiovascular and coronary heart disease [7]. Other metabolites, such as pectic polysaccharides, can protect the immune and reproductive systems of mammals against toxic chemical-inducers of oxidation reactions. All the cited compounds confer important biological properties, such as antioxidant, anti-inflammatory, hypoglycemic and cytotoxic activity [6].

Plant mycobiota

Petrini and Fisher (1986) [155] found 32 species of endophytic fungi in apparently healthy stems from 20 tussocks of *Salicornia perennis* on a salt marsh at Dawlish Warren, Devon, UK. The most frequent colonizers belonging to the order *Pleosporales* were *Pleospora salicorniae* and *P. bjorlingii*, and two species of *Stagonospora*. Other isolates were *Alternaria alternata*, *A. tenuissima*, *Cladosporium tenuissimum*, *Coniothyrium* sp., *Hypoxylon bipapillatum*, *Leptosphaeria* sp., *Phoma* sp., *Pleospora herbarum* and *Septoria* sp.

Appendix A.2. Genus Suaeda Forssk ex J.F. Gmelin

The *Suaeda* genus includes about 100 species, mainly halophytes with fat leaves; they grow in saline and alkaline wetlands and deserts almost all over the world but are primarily extra-tropical. The species are annuals or perennials, dwarf shrubs or, rarely, trees. The genus is known to be taxonomically very complicated due to its high polymorphism [156].

The two species *Suaeda maritima* (L.) Dumort., and *S. vera* J. F. Gmel, described below, are both diploid with 2n = 36.

Appendix A.2.1. *Suaeda maritima* (L.) Dumort. (Syn.: *Chenopodium maritimum* L.; *Schoberia maritima* (L.) C.A. Mey). Eu-halophyte/halo-nitrophilous

Botanical traits

Biological form: scapose therophyte.

Morphological characteristics: A 30–80 cm plant, first glaucous and then, with ripening, tending to red. Leaves (8–16 mm) with a semi-circular section, the lower opposite, the others alternate, never pointed. Flowers in glomeruli at the axil of the leaves on the upper branches.

Habitat: Mainly salty coastal areas, both on sandy soils in the back dune and clayey soils, where there is an accumulation of organic remains; it is also ecologically useful in swamp formations due to its ability to trap mud.

Chorological type: Medit.-Occid.

Flowering period: July–August.

Biochemical traits

Suaeda maritima is a succulent halophyte, suitable for human consumption due to the high concentrations of proteins, fiber and minerals [11]. The leaves have a pleasant, salty taste due to the high salt content [157]. *S. maritima* contains a noticeable content of various minerals, such as Ca, K, Mg, Fe, Zn and Cu, and the consumption of 20 g of fresh leaves could represent 2–10% of the recommended daily intake [11,158]). It is also rich in vitamins. Regarding fat-soluble vitamins, β-carotene represents the most important provitamin A (9.30–20.7 mg/100 g d.w.). The species also has high content of lutein (20–89 mg/100 g d.w.) in comparison with other vegetables. These metabolites are involved in many physiological processes, such as immune response, and the prevention of vision-degenerative diseases related to age in humans and animals [159]. The content observed in Vitamin A is 5.39 mg/100 g d.w., showing similar values to those of species with good sources of vitamin A (e.g., spinach 5.45 mg/100 g d.w.) [11]. *S. maritima* shows a content of ascorbic acid (Vitamin C) above that of other vegetables, such as parsley and broccoli [11,160]. In addition, other antioxidant metabolic compounds, such as total phenolic, flavonoids and condensed tannin, are detected in *S. maritima* [11]. The most representative compounds are chlorogenic acid, cinnamic acid, catechin hydrate, coumaric acid, luteolin-7-O-glucoside. The results of such work confirmed the direct correlation between the content of phenolic compound flavonoids, with the antioxidant activity of the extracts.

The cultivated plants of *S. maritima* showed a different nutritional profile compared with wild plants in [11]: leaves had a higher content of moisture, ash, and fiber. High water content and succulence are the result of a high concentration of osmolyte solutes, such as proline and glycine betaine, that contribute to the regulation of turgor [157].

Plant mycobiota

The genetic diversity of the fungal endophytes isolated from halophytic plants, sampled from salt marshes located in west and South Korea, was studied using the internal transcribed spacer (ITS) region as a DNA barcode for the classification of the specimens. Generic richness and diversity were determined by counting the genera present in the fungal communities in plant samples. In *S. maritima* sampled in west Korea, 7 genera and 7 species were found, and the most abundant genera were *Alternaria* and *Cladosporium* [161]. In South Korea 11 genera and 21 species were isolates from *S. maritima* samples and the most dominant genus was Fusarium, followed by the genera *Penicillium* and *Alternaria* [162]. The endophyte assemblage of *S. maritima* in India was dominated by *Camarosporium palliatum* as indicated by its mean density of colonization [163].

Appendix A.2.2. *Suaeda vera* J. F. Gmel (Syn.: *Suaeda fruticosa* (L.) Forssk.; *Suaeda fruticosa* (L.) Forssk. subsp. *vera* (J. F. Gmel.) Maire & Weiller; *Chenopodium fruticosum* (L.). Eu-halophyte (Halo-nitrophilous)

Botanical traits

Biological form: nano-phanerophyte.

Morphological characteristics: A plant that can reach one meter in height, with woody, very branchy and glaucous stems with semi-cylindrical and slightly more pointed leaves (8–15 mm) than *S. maritima*.

Habitat: salty and nitrophilous soils, but soils of calanchive and internal marly areas.

Chorological type: Cosmopol.

Flowering period: June–July.

Biochemical traits

The obligate halophyte *S. fruticosa* is known to increase its content of sugars, protein, and proline under high salt concentration [164]. Both the leaves and seeds are edible and used for human consumption. Succulence is one of the mechanisms used by this species to protect itself from salt stress [164]. Regarding sugars, the composition seems related to that of galactoarabinans, by the presence of pectin-like polysaccharides and neutral monosaccharides (including arabinose, mannose, galactose, rhamnose, glucose, and xylose). These polysaccharides possess significant potential in antioxidant activity effect [62]. Other phytochemicals with antioxidant activity—such as phenols, flavonoids, tannins, proanthocyanidins, and carotenoids—have been isolated from *S. fruticosa* extracts, reproducing the therapeutic benefits of these plants, and also used as herbal tea [165]. Alkaloids and saponins have also been detected, to enlarge their phytopharmacological use. *S. fruticosa* produces numerous seeds under saline conditions and contains about 25% oil [12], four saturated fatty acids (11.04%), and six unsaturated fatty acids (89.06%) [166]. These nutritional components promote the consumption of the leaves and seeds of *S. fruticosa* as food and feed. Unsaturated fatty acids (linoleic and oleic acids) confer the ability to overcome damage to the cell membrane under stress conditions, by controlling the expression of desaturase genes [167]. This plant is used in folk medicine for its hypoglycemic and hypolipidemic activity [12]; a good anti-inflammatory effect was also detected in polysaccharide extracts [62]. Interesting anticancer activity against human lung carcinoma and colon adenocarcinoma cell lines were reported for dichloromethane extracts [168].

<u>Plant mycobiota</u>

Fisher and Petrini (1987) [169] found that *Camarosporium* spp. (85.3% in stems) and *Colletotrichum gloeosporioides* (30% in leaves) endophytically colonized *S. fruticosa* in England.

Appendix A.3. Genus Salsola L.

Recently, the *Salsola* genus has been revised with the creation, among others, of the new taxa Soda (which would therefore include *S. soda* species as *S. inermis*). However, the original classification is still maintained in this review, as the new taxonomic classification has not yet been fully clarified in APG IV. The species of *Salsola* are mostly subshrubs, shrubs, small trees, and rarely, annuals. The leaves are mostly alternate, rarely opposite, simple, and entire. The bisexual flowers have five tepals and five stamens.

Salsola soda *L. (Syn.:* Soda inermis *Fourr.). Mio-halophyte (halo-nitrophilous)*

<u>Botanical traits</u>

Biological form: scapose therophyte.

Morphological characteristics: 20–120 cm tall, often red with ripening; leaves 20–40 mm long, succulent, opposite and slightly sharp; axillary flowers.

Habitat: salty coastal areas on both sandy soils in the back dune and clayey soils, where there is an accumulation of organic remains.

Chorological type: Paleotemp.

Flowering period: July–August.

<u>Biochemical traits</u>

S. soda represents a valid alternative crop for saline soils, because of its accumulation and tolerance to very high levels of Na [60]. Therefore, *S. soda* is considered a "bio-desalinating companion plant" for tomatoes and peppers in saline soils in the Mediterranean area [60]. Its cultivation can be achieved in different saline (NaCl) concentrations and in desalinized soils [170]. *S. soda* (Syn.: *S. inermis*) is also considered a glycine-betaine accumulator. Various Salsola species, including the species *S. soda*, have been examined for their phytochemical composition, showing the presence of alkaloids, flavonoids, saponins, coumarins, and sterols [171–173]. The shoots contain flavonoid glycosides and triterpenoid saponins [174]. In particular, the presence of quercetin 3-O-β-D-glucuronopyranoside may confer functional nutraceutical and medicinal properties. In fact, shoot extracts have been found to exhibit hypoglycemic, antioxidant, anti-cholinesterase, and antimicrobial activity [172,175]. Alkaloids present in the extracts from *Salsola* species have been evaluated against Alzheimer's disease [172].

Appendix A.4. Genus Atriplex L.

The genus *Atriplex*, with about 300 species, is the richest in species of the Amaranthaceae family. It has worldwide distribution, occurring on all the continents except Antarctica. Annual or perennial herbs or shrubs. The inflorescences consist of axillary or terminal spikes or spicate panicles, or axillary clusters of glomerular flowers. The flowers are unisexual. Some species are monoecious, others dioecious.

Appendix A.4.1. *Atriplex littoralis* L. (Syn.: *Atriplex patula* L. var. *littoralis* (L.) A. Gray). Halo-nitrophilous

Botanical traits

Biological form: scapose therophyte.

Morphological characteristics: both 40–120 cm high, with erect angular stem and lanceolate linear leaf lamina.

Habitat: seacoasts, ruderal and sub-saline habitat.

Chorological type: Europe and Paleotemp.

Flowering period: July–October.

Atriplex littoralis germination and growth are reduced at salinities higher than 1% NaCl [176]. The plant accumulates salt in the seeds and bracteoles (~40–50%) [177]. In adult plants, the salt is accumulated in the aerial parts, like other halophytes in the Amaranthaceae.

Biochemical traits

Regarding the 300 species belonging to the *Atriplex* genus, the species *A. littoralis* has not been deeply investigated for phytochemical content and biological activity. The plant is rich in flavonoids, glycosides, alkaloids, amino acids, minerals, saponins, and phytoecdysteroids [178].

Plant mycobiota

Some *Alternaria* species (*A. alternata*, *A. raphani*, *A. tenuissima*), *Cladosporium oxysporum*, *Fusarium moniliforme* and *F. tricinctum* were found in *Atriplex littoralis* sampled at various growth stages from an inland salt marsh in Canada [178,179].

Appendix A.4.2. *Atriplex prostrata* Boucher ex DC (Syn.: *Atriplex hastata* L. var. *prostrata* (Boucher ex DC.) Lange; *Atriplex latifolia* Wahlenb.). Halo-nitrophilous

Botanical traits

Biological form: scapose therophyte.

Morphological characteristics: both 40–120 cm high, with erect angular stem and hastate/triangular leaf lamina.

Habitat: seacoasts, ruderal, and sub-saline habitat.

Chorological type: Europe and Paleotemp.

Flowering period: July–October.

Biochemical traits

Atriplex prostrata is a facultative halophyte. Seed germination has been known to decrease by 25% at 200 mM NaCl [179]. In saline environments, Na accumulation is associated with a decrease in the content of K, Ca and Mg, and with reduced plant growth and photosynthesis [180]. However, some antioxidant enzymes have been known to increase in the aerial organs while the lignin content decreases [181]. Polyphenol content has been shown to increase with external salt concentration [182], but different behaviour of polyamines and ethylene was observed: spermine, putrescine and spermidine content decreased under saline conditions, while ethylene increased together with proline [183].

Appendix A.5. Genus Halimione Aellen

Monoecious annual or perennial herbs with silvery grey stems and leaves. The leaves are opposite in the lower part and alternate in the upper part of the plants. The leaf blade is oblong with entire margins

Halimione portulacoides *(L.) Aellen (Syn.:* Atriplex portulacoides *L.). Eu-halophyte*

Botanical traits

Biological form: chamaephyte.

Morphological characteristics: species up to 80 cm tall has a prostrate stem, often rooting at the nodes; opposite leaves with lanceolate lamina, up to 60 mm long, with obtuse apex.

Habitat: salty and clayey coastal areas.

Chorological type: Circumbor.

Flowering period: June–July.

Biochemical traits

H. portulacoides is an obligate halophyte with succulent leaves. The optimal growing condition was assessed at 200 mM NaCl; however, this species can tolerate up to 1 M NaCl [184]. Anthocyanins, polyphenols, and proline increases significantly with salinity, being maximal at 1000 mM NaCl [185]. The activity of superoxide dismutase (EC 1.15.1.1, SOD), ascorbate peroxidase (EC 1.11.1.11, APX), and glutathione reductase (EC 1.6.4.2, GR) is significantly stimulated by salinity in the leaves of H. portulacoides, whereas catalase (EC 1.11.1.6, CAT) activity is maximal in the 0–400 mM NaCl range. Leaves contain phenolic compounds, mostly sulphated flavonoids that confer high antioxidant activity [184].

The salt tolerance of *H. portulacoides* can be attributed to the leaf waxes containing long chain chloroalkanes. Recently, the polar lipid profile of leaves has been determined and classified in over five classes of phospholipids, three classes of glycolipids characterized by the presence of PUFA (n-3 and n-6 FA), and one class of glycosphingolipids [186].

High productivity and a capacity to grow in soil contaminated by heavy metals also make this species potentially useful for saline soil reclamation and phytoremediation purposes, and even as fodder plants [187]. Volatile organic compounds have been detected in the root exudates [168].

Plant mycobiota

Specific works on fungi associated with *H. portulacoides* date back to the 1960s [188,189]. In these studies, different fungi were identified. Mycoflora of leaves of *H. portulacoides* growing in two salt marshes showed a high presence of Alternaria tenuis and other *Pleosporales*, together with *Cladosporium herbarum*. More recently, these finding were confirmed by molecular studies (BOX-PCR fingerprinting, and sequencing of the ITS region of the ribosomal DNA cluster) performed on 111 isolates obtained from the roots, stems, and leaves of *H. portulacoides*; this revealed that 74.5 % belonged to the order *Pleosporales* [190]

Appendix A.6. Genus Beta L.

This genus consists of annual, biennial, or perennial species. The stems, erect or procumbent, have alternate leaves, ovate-cordate to rhombic-cuneate; the margins are mostly entire, with obtuse apex. The inflorescences are long spike-like cymes or glomerules, and flowers are bisexual.

Beta vulgaris *L. subsp.* Maritima *(L.) Arcang. (Syn.:* Beta maritima *L.) Mio-halophyte*

Botanical traits

Biological form: hemicryptophyte (rarely therophyte).

Morphological characteristics: 20–80 cm tall, with many erect angular stems; flowers in leafy ears; spatulate leaves up to 220 mm long and with reddened petiole.

Habitat: pebbly coastal soils.

Chorological type: Euri-Medit (Atl.).

Flowering period: June–August.

Biochemical traits

The leaves of *Beta vulgaris* subsp. *Maritima* constitute a healthy food against digestive disorders, burns, throat pains and anaemia [191]. Shoots' fresh weight is increased with salinity [192]. Under salt stress, sea beet roots revealed a higher content of Cl^{-} and Na^{+}, and a lower content of K^+ [192]. Mg content is increased in shoots and roots, while Ca is less affected by salinity.

In a comparative study with other halophytes, *B. vulgaris* subsp. Maritima showed an appreciable content of malic acid (51.36 mg/100 g d.w.) and oxalic acid (581 mg/100 g d.w.) [191]. The four chemical structures of tocopherols were detected, but α-tocopherol (vitamin E activity) was the major component. Total phenols (62 mg/100 g d.w.), total flavonoids (21.6 mg/100 g d.w.), and vitamin C (20 mg/100 g d.w.) were also present in the leaf extracts, and the antioxidant activity was significantly correlated with the antioxidant compounds [191]. The basal leaves contain fatty acids, such as α-linolenic acid, linoleic acid, and palmitic acid. The aerial parts contain essential oil rich in sesquiterpenes (69.5%) with a prevalence of γ-irone (26.3%) [193]. They showed antioxidant, cytotoxic, anticholinesterase and anti-tyrosinase activity.

Appendix B

BRASSICACEAE Burnett—Dicotyledons, herbaceous, annual, and perennial, and shrubs. Leaves without stipules, flowers arranged in racemes, panicles, or corymbus heads or spikes. Each flower has four petals, set alternating with the sepals, and six stamens. Fruit is silique or silicle. Cosmopolitan.

Appendix B.1. Genus Cakile Mill.

Annual plants with an erect or decumbent stem. The common species in Europe and North America grow close to the coast, often in dunes. Their leaves are fleshy. Flowers are typically pale mauve to white, with petals about 1 cm in length. Each fruit has two sections, one that remains attached to the adult, and another that falls off for dispersal by wind or water.

Cakile maritima *Scop. subsp.* maritima. *Halo-nitrophyle (Psammophile)*

Botanical traits

Biological form: scapose therophyte.

Morphological characteristics: Stem 10–30 cm tall, often devoid of leaves. Odd-pinnate divided leaves (max 50 mm long); small lilac flowers; siliqua (10–20 mm) formed by two superimposed articles, the lower more or less rhombic, the upper conical.

Habitat: sandy coasts, in the dune belt of drift lines.

Chorological type: Medit.-Atl.

Flowering period: January–December.

Biochemical traits

Cakile maritima (Sea Rocket) is a facultative halophyte that tolerates high salt concentration.

Under salinity conditions, fatty acid contents have been detected in the leaves, with ω-6 PUFAs as the major fatty acid group (17.88%) [168]. Amino acids—such as GABA, proline and glycine—and sugar content increased, while the phenolic content decreased, in plants subjected to high salt concentration [194]. Other metabolites, such as flavonoids, flavonoid glycosides, sinapic and chlorogenic acid derivatives, are not affected by salinity [57].

Cakile maritima has a high antioxidant capacity and maintains a high content of α-tocopherol when exposed to short-term NaCl treatment [195]. The leaves contain high levels of vitamins, proteins, and minerals [196]. Several minerals (Na, K, Ca, Mg, S) are detected in leaves—as are micronutrients such as Fe, Zn, and B—depending on salt level concentrations [57]. The ratio of Ca/P (about 1.0) is considered a good value for good Ca and P intestinal absorption. Oxalic acid content and the oxalic acid/Ca ratio are high in *C. maritima*, while the ratio of K/Na is low [196].

Plant mycobiota

Many mycotoxigenic *Alternaria* species (e.g., *A. alternata*, *A. mali*, *A. arborescens*) were isolated from fresh tissues of *C. maritima* in Tunisia. The *Alternaria* population showed that most of the strains (90%) produced at least one of four assessed mycotoxins (alternariol, alternariol methyl ether, tenuazonic acid, and altenuene), sometimes at very high levels [131].

Appendix C

PORTULACACEAE Juss.—Monotypic taxon that only contains the genus *Portulaca*. Dicotyledons, succulent annual herbs growing flat on the ground. Small, fat leaves. Small flowers with 2 sepals, 5 to 7 short-lived petals, and typically 6 to 40 stamens (sometimes more or less). Fruit is capsule. Sub cosmopolitan.

Portulaca oleracea L. subsp. oleracea. Xerophyte

Botanical traits

Biological form: therophyte.

Morphological characteristics: stems are round, thick, succulent and mostly prostrate. They range in colour from light green to reddish brown. The leaves are alternate or nearly opposite and sessile along the stems. The leaves are rather thick and succulent. The small, yellow flowers occur singly or in small, terminal clusters, and consist of five yellow petals and two green sepals. Fruit is capsule and splits open around the middle.

Habitat: ruderal areas and occasionally in salty soils.

Chorological type: (Sub-Cosmopol.) Cryptogenic.

Flowering period: May–October

Biochemical traits

Portulaca oleracea is an underutilized halophyte plant, already consumed as a vegetable in a variety of ways around thew world [197]. Nowadays, it is rich in omega-3 and omega-6 fatty acids (ω-3 and ω-6-FAs) as well as proteins, carbohydrates, carotenoids, vitamins A and C, and minerals [198]. Secondary metabolites are also present in the whole plant (leaves, stems, and roots) with a high content of phenolic compounds, especially lignans, which are important for ethno-pharmaceutical use [198]. The extract of this species is considered a potential source of melanosis-inhibiting compounds, for its diphenol oxidase-inhibiting activity [199]. Recently, microgreens of purslane have been produced under salinity to emphasize the potentiality of this plant cultivation; the content of total phenolics, flavonoids, carotenoids, and fatty acids, as well as the total antioxidant capacity content, are positively affected by salinity in *P. oleracea* microgreens grown with 80 mM NaCl in the nutrient solution [81].

Plant mycobiota

Some culturable endophytic fungi of *P. oleracea*, collected from Hohhot, Inner Mongolia, belonged to the genera *Penicillium* and *Fusarium* [200]. *Fusarium solani* was the most common species identified on the roots of *P. oleracea*, collected from the El-Kharga Oasis in Egypt. In addition, the entomopathogenic fungus *Beauveria bassiana* was found in leaf tissue for the first time in 2021 [201].

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