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Halophyte based Mediterranean agriculture in the contexts of food insecurity and global climate change

--Manuscript Draft--

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Abstract:	<p>The loss of agro-biodiversity, climate changes and food insecurity are major challenges in the Mediterranean countries with potentially multidimensional consequences. With respect to salinity, approximately 18 million ha, corresponding to 25% of total irrigated land in the Mediterranean area, are salt affected. Intensive cropping and the excessive use of expensive inputs such as water and fertilizers aggravate this situation. Understanding how we could improve crop productivity in salinized environments is therefore critical to face these challenges. Our comprehension of fundamental physiological mechanisms in plant salt stress adaptation has greatly advanced over the last decades. However, many of these mechanisms have been linked to salt tolerance in simplified experimental systems whereas they have been rarely functionally proven in real agricultural contexts. The sustainability of farming systems in salt affected Mediterranean soils can be effectively achieved by the use of salt-tolerant halophyte plants even more effective through the use of intercropping, crop rotation and aquaponics. Moreover, if these halophyte plants are removed from the soil to grow other species, pressure on generating salt-tolerant crop plants would be reduced and much healthier crop plants would be cultivated in less stressed saline soils. This paper will focus on the sustainable practices based on the cultivation of halophytes in saline soils by highlighting some experimental activities carried out at laboratory and field levels in the last few years.</p>
Suggested Reviewers:	Hans-Werner Koyro Hans-Werner.Koyro@bot2.bio.uni-giessen.de He has a long experience with halophyte research. Tim Flowers t.j.flowers@sussex.ac.uk He has a long experience with halophyte research.
Response to Reviewers:	

Tunis, 22 July 2021

Dear Editor,

I herewith re-submit you a revised version of the manuscript entitled “Halophyte based Mediterranean agriculture in the contexts of food insecurity and global climate change” to be considered for publication in Environmental and Experimental Botany.

The manuscript has been thoroughly revised according to the comments raised by the editor and two Reviewers of the previous submission, which have been very helpful to improve the review.

I hope this new revised version of the manuscript can now be acceptable for publication in Environmental and Experimental Botany.

Sincerely yours,

Karim Ben Hamed

Corresponding author

RESPONSES TO REVIEWER COMMENTS

The authors would like to thank to the reviewers for all comments and suggestions that greatly improved the quality and clarity of the manuscript. The responses to the comments of the reviewers are included below and required changes are made to the revised manuscript.

Editor comments:

In line with the comments from the referees, please also address my comments 1 to 5.

1) See if there is more recent literature on the extent of salinization in Europe (the references you quote are generally ten years old) and if there is not more recent data note this in your conclusions to the section.

Response: This information is now included in section 1 (Page (P): 3; Lines (L): 64-66)

2) Condense Sections 2 and 3 to a single short section highlighting those aspects of the physiology of halophytes relevant to title of your review. The adaptations seen in halophytes have been extensively reviewed.

Response: Sections 2 and 3 are now condensed to a short section (Section 2 in the revised Mn).

3) Section 4.1 and 4.2. Please combine these sections, tabulate the data available and evaluate the value of intercropping rather than describing published data. Tables are a valuable way of presenting data without the need for extensive text; the real value of a review is in drawing conclusions from 'all' the published data.

Response: Following the Editor's request, these sections are now combined (Section 3) and details of results were tabulated (Table 1, Table 2).

4) Sections 4.3 is worthy of its own section as is Section 4.4. Section 5 should be integrated into the other sections

Response: Section 4.3 and 4.4 become section 4 and 5, respectively. Section 5 is now integrated into section 3, section 3.2 with a revised title "Potential uses of halophyte biomass, after desalination process"

5) Throughout please gather and analyse the data available to present conclusions rather than summarise already published data.

Response: Done

Reviewer comments:

Reviewer #1:

The authors submitted a manuscript with the title "Halophyte based Mediterranean agriculture in the contexts of food insecurity and global climate change".

The title is very promising, the topic is relevant and the authors are authorities in their fields of research. In the highlight the original ideas are well reflected. Halophytes might be able to desalinate the soil and increase the productivity of corresponding (glycophyte) crop plants species. Therefore, some halophytic species might be suitable to be used as intercropping and

rotating species to reduce soil salinity. Many Mediterranean halophytes are well accepted in the population because there is a tradition and therefore there is a demand on the Mediterranean market.

1) However, many parts of the review remain superficial without revealing new insights or directions.

Response: We revised the review accordingly.

2) Also the list of references is far from being complete and up-to-date.

Response: Done. We apologise for the missing references. All the references highlighted by the reviewer were checked. Some of them were correctly cited in the reference list while a couple of them were badly written and this prevented their matching in the list (as for Meyer, and Simpson). Others were indeed uncited and were added in the revised manuscript.

3) Actually, there is a disproportional number of articles from the labs of the authors included.

Response: We tried to cite the available references published by the different authors, that would be the most relevant to the focus topic of the review.

4) Chapter 3 and Figure 1 can be deleted because both contain known facts published many times already that are not relevant to the focus topic.

Response: According to reviewer's suggestion, Chapter 3 and Figure 1 of the original submission are now deleted.

5) The other figures are highly simplified as can be found like this in many textbooks. Here it would be important to design graphs or schemes that reflect, for example, the remediation effects of halophytes.

Response: Following the reviewer's suggestion, figure 2 and 3 were deleted, and replaced by a figure (Figure 1 in the revised Mn) that describes generally the remediation effects of halophytes on saline soils.

6) What is the fate of the plant material containing high salt concentrations after remediations processes? That is a major question not touched in detail here.

Response: Done. We agree with the reviewer about the importance of stressing this point and, accordingly, a paragraph on this aspect of phytoextraction was added in the revised manuscript. In this context, the cultivation of halophyte crops and their harvest for a productive use as fodder, feed, raw material for extraction of pharmaceuticals, food additives, etc., deserves a particular importance, contributing to effective removal (P5, L 116-140)

7) Tables containing species and data of intercropping and crop rotations systems, either successful or less successful results, from the Mediterranean area are essential for this review.

Response: Following the suggestion, one table (Table 1) is added, summarising the results reported in literature on intercropping and rotation systems. This way, description of results was a little bit rearranged, pointing mainly to discuss success or failure of these approaches.

8) Chapter 4.3. contains only 4 references although it is a very important topic and many more approaches are currently underway, in the middle east and elsewhere.

Response: According to this comment, this section (section 5 in the revised Mn) was improved.

9) For Chapter 4.4. many more successful examples can be described, maybe also summarized in a table.

Response: As required by the reviewer, in the revised manuscript we described more examples of halophyte aquaponics (Section 6) and integrated them into a table (Table 2).

10) Chapter 5 is titled "Economic applications..." but no economic data are included, only potential applications. Again, more facts would be of interest for the reader.

Response: This section is now inserted in section 3, as suggested also by the Editor, with a revised title "Potential uses of halophyte biomass, after desalination process"

11) Also the conclusion remains rather descriptive and vague and there are not clear recommendations or pleas.

Response: The conclusion was revised accordingly.

Minor

12) The paper is well written, there are only some spelling errors in species names and references.

Response: Done

Reviewer #2:

The review by Hamed et al. "Halophyte based Mediterranean agriculture in the contexts of food insecurity and global climate change" is very interesting.

1) Nonetheless, I found things that need changing and/or need clarification or need to be rewritten for improved clarity. The requested changes are all highlighted in yellow, and the changes required shown in a sticky note, in the attached pdf.

Response: We thank the reviewer for all the valuable suggestions in the attached reviewer pdf file. We revised the Mn following the highlighted requests and addressed the questions and comments shown in this file.

2) Among them, please give a better discussion of the topic of soil desalination as mentioned in a few notes.

Response: Done. According to this comment and as you commented in the pdf file, soil desalination by halophytes was highlighted in section 2 and section 3 (P5, L116-140), also supported by a figure (Figure 1 in the revised Mn) that describes the possible remediation effects of halophytes on saline soils.

3) The figures need appropriate legends as those shown in the manuscript are inexistent or insufficient for a complete comprehension of them. Further, Figure 1 is not cited in the text.

Response: These figures are deleted.

4) There are several references missing in the bibliography and/or not well cited in the text.

Response: We apologise for the missing references. All the references highlighted by the reviewer were checked. Some of them were correctly cited in the reference list while a couple of them were badly written and this prevented their matching in the list (as for Meyer, and Simpson). Others were indeed uncited and were added in the revised manuscript.

5) Further, the text needs to be uniformised as the citations are properly formatted: they are cited in different ways.

Response: We have checked the format of the whole manuscript including the lack references and formating some references. All the literature cited has been checked in depth.

Highlights

- Halophytes can desalinize the soil and increase the productivity of crops
- Some halophytes are used as intercropping and rotating species to reduce soil salinity
- Many halophytes are efficient when they are integrated in aquaponic systems
- Many Mediterranean halophytes have potential multipurpose uses.
- Halophytes may find niches in the demanding Mediterranean market.

1 **Halophyte based Mediterranean agriculture in the contexts of food insecurity and**
2 **global climate change**

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14

15 **Highlights**

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22 **Abstract**

23 The loss of agro-biodiversity, climate changes and food insecurity are major challenges in the
24 Mediterranean countries with potentially multidimensional consequences. With respect to
25 salinity, approximately 18 million ha, corresponding to 25% of total irrigated land in the
26 Mediterranean area, are salt affected. Intensive cropping and the excessive use of expensive
27 inputs such as water and fertilizers aggravate this situation. Understanding how we could
28 improve crop productivity in salinized environments is therefore critical to face these
29 challenges. Our comprehension of fundamental physiological mechanisms in plant salt stress
30 adaptation has greatly advanced over the last decades. However, many of these mechanisms
31 have been linked to salt tolerance in simplified experimental systems whereas they have been
32 rarely functionally proven in real agricultural contexts. The sustainability of farming systems
33 in salt affected Mediterranean soils can be effectively achieved by the use of salt-tolerant
34 halophyte plants even more effective through the use of intercropping, crop rotation and
35 aquaponics. Moreover, if these halophyte plants are removed from the soil to grow other
36 species, pressure on generating salt-tolerant crop plants would be reduced and much healthier
37 crop plants would be cultivated in less stressed saline soils. This paper will focus on the
38 sustainable practices based on the cultivation of halophytes in saline soils by highlighting some
39 experimental activities carried out at laboratory and field levels in the last few years.

40

41 **Keywords:** Agriculture, aquaponics, biodiversity, crop rotation, domestication, halophytes,
42 Mediterranean climate, intercropping, phyto-desalination, salinity, sustainability.

43

44

45 **1. Challenges of agriculture in the Mediterranean area**

46 The major challenge of agriculture in the world is to feed about 9.8 billion of individuals in
47 2050 and 11.8 billion in 2100. The situation becomes more challenging when today 690 million
48 people are undernourished globally, with an additional 83 to 132 million people estimated in
49 2020 due to COVID -19 pandemic (FAO, 2020). Moreover, United Nations reports estimate
50 that in 2050, 68 % of the population will live in the cities (United Nations, 2018). This means
51 a decreasing number of farmers for a growing number of people to feed.

52 The Mediterranean region is one of the hotspots of the global biodiversity, with a remarkable
53 richness in cultivated and wild species characterising this area. Its flora diversity has an
54 outstanding from 15000 to 25000 species, 60% of which are unique to the region according to
55 the International Union of Conservation of Nature IUCN (IUCN, 2008). Meanwhile, the
56 Mediterranean basin is among the most threatened regions by climate change in the world
57 (IUCN 2008). The Intergovernmental Panel on Climate Change (IPCC) predicts temperatures
58 in the Mediterranean area will increase between 2 and 4°C, whereas rainfall will decrease
59 between 4% and 30%, by 2050 (IPCC, 2013). This situation could be concomitant with the
60 increasingly frequent events of drought, extreme climatic events and agro-biodiversity loss,
61 with the northern side of the region experiencing similar conditions to those occurring today
62 on the southern shores. The soils of the Mediterranean basin including European and African
63 areas are characterized to be shallow, with low organic carbon contents, high CaCO₃ contents
64 and therefore offer limiting availability for some nutrients such as iron leading to chlorosis in
65 several crops (Lagacherie et al., 2018). The recent study published by Hassani et al. (2020)
66 estimated that the area of salt-affected soils in Europe was 24 Mha being approximately 2.05%
67 of the total salt affected area at worldwide level (1,171.8 Mha). Moreover, approximately 18
68 million ha, corresponding to 25 % of total irrigated land in the Mediterranean area, are salt
69 affected (FAO, 2011). In Italy, salinization affects almost all regions, accounting
70 approximately for 3.2 Mha of soil (Dazzi and Lo Papa, 2013). In Spain, about 3% of the 3.5
71 million hectares of irrigated land are severely affected by salts and another 15% is at serious
72 risk (Acosta et al., 2011). In Tunisia, salinity affects 10 % of the total surface area and 20 % of
73 irrigated lands. Water is a scarce resource in most of the Mediterranean countries. Nowadays,
74 many southern Mediterranean countries exhibit water availability below the benchmark
75 threshold of 1000 m³/person/year. In addition, lower water availability than this threshold is
76 also reported for some Northern countries such as Spain, Greece and Italy, although on average
77 they exceed the 1000 m³/person/year threshold (Mancosu et al., 2015). Agriculture is the main

78 water-consuming sector, being responsible for about 70.7% of freshwater withdrawals,
79 accounting for 45% in the North and 82% in South and East and weighs heavily on fertilizer
80 consumption, estimated at 141.3 kg/ha (FAO and CIHEAM, 2015). Problems of sea water
81 intrusion due to groundwater overexploitation are currently encountered in coastal areas of
82 Italy, Spain, Greece and North Africa (Garcia-Caparrós et al., 2017; Payen et al., 2016). The
83 decreasing availability of freshwater makes increasingly necessary the use of saline-sodic
84 and/or of treated wastewaters for irrigation to sustain crop productivity, with the consequence
85 of increasing the risk of soil and water salinization (Oron et al., 2002).

86 **2. Improving crop productivity under salinity: Remediation effects of halophytes**

87 The most effective solution to meet the growing demand for food is to increase the productivity
88 of already cultivated lands (FAO, 2011). Nevertheless, this agricultural intensification is often
89 associated with a high cost, a large consumption of water, energy and pesticides, in addition to
90 soil depletion, loss of biodiversity and climate change. The current agricultural practices are
91 increasing soil and water salinity, and unsustainable water use is leading to growing scarcity.
92 As a result, many already dry and water-scarce regions have been hampered by more frequent
93 droughts severely affecting agriculture. An average of 2,000 hectares of irrigated land in arid
94 and semi-arid areas across 75 countries are degraded by salt every day and water scarcity
95 already affects every continent (FAO, 2011). An alternative solution to palliate this
96 environmental problematic may be the restoration of non-arable or marginal lands in the
97 Mediterranean area and in areas such as North Africa and the Middle East.
98 Considered also as marginal lands, the salt affected agricultural soils in the Mediterranean
99 region could be suitable for growing salt tolerant crops (Glenn et al., 1998). One of the key
100 factors to improve salt tolerance of commercial crops cultivated in salt affected soils is to
101 reduce the amount of salt transported from roots to shoots. This can be achieved by grafting a
102 salt-sensitive cultivar onto a salt-tolerant one, and by conventional breeding. However, these
103 approaches can have some limitations such as the reproductive barriers and the risk of
104 undesirable traits transfer (Turan et al., 2012). Transcriptome sequencing may provide a
105 functional view of the mechanisms to salinity tolerance. In addition, the use of transgenic plants
106 to achieve information about the response of higher plants to salinity is a strategy widely
107 addressed in numerous research groups (Hernández, 2019). Nevertheless, success has not been
108 achieved at field level (Panta et al., 2014). Alternatively, soil phytodesalination, based on the
109 capacity of some halophytes to accumulate enormous sodium quantities in their shoots, and
110 latter removal is proposed as an innovative and cost-effective biological approach to desalinize

111 the soil and to increase the productivity of salt sensitive crops (Debez et al., 2011; Koyro et al.,
112 2014; Panta et al., 2014).

113 Halophytes are able to adapt to saline environments by different mechanisms. Halophytes have
114 anatomical and physiological adaptations as well as an efficient metabolic responses to
115 promote osmotic and homeostasis adjustment (Flowers and Colmer, 2008; 2015; Hasegawa,
116 2013; Bose et al., 2014; Acosta-Motos et al., 2017; Hernandez, 2019; Ben Hamed et al., 2020).
117 From the point of view of phytoremediation, based on their salt tolerance, halophytes can use
118 distinct mechanisms such as salt accumulation, excretion and salt exclusion (Figure 1). Salt
119 accumulators are able to uptake and accumulate high total salts (more specifically sodium) in
120 their tissues and to produce high aerial biomass. Salt excreting halophytes, absorb salts and
121 excrete them by salt glands or bladders, conducting salts from the soil into the air. Salt
122 excluding halophytes prevent salts from entering their tissues; resulting in low rates of salt
123 translocation to shoots (Jesus et al., 2015). Since plant salt uptake in aerial biomass is key
124 element for efficient remediation, accumulating and excreting halophytes would be more
125 appropriate than excluding plants. Perennial accumulators would allow for a more prolonged
126 period of salt accumulation throughout the year than annual ones. The root architecture and the
127 growth rate of halophyte species represent key parameters for its suitability as phytoextractor.
128 Moreover, many halophyte species are able to exude from roots several compounds stimulating
129 soil microbial and enzyme activity favouring the decomposition of detritus to organic matter
130 (Jing et al., 2019; Figure 1).

131 The fate of halophyte biomass, i.e. harvesting or leaving in the fields, is another important
132 determinant of the success of desalting process. Plant, or at least shoot, harvesting would allow
133 the more efficient salt removal. This aspect is important mainly in crop rotation programs,
134 while in intercropping systems, because of the simultaneous growth with halophytes, crops are
135 expected to benefit of the salt absorption regardless of the halophyte removal from the site.
136 One major question in remediation programs is how to manage the salt-rich halophyte material.
137 Depending on the plant species (herbaceous, shrub, or tree), the salt concentration, the
138 harvested portion (i.e. stem-leaves or seeds), etc., the biomass may undergo different destinies,
139 such as fodder, feed, edible oil, timber, fibre, biofuel, energy production, essential oils, source
140 of bioactive compounds (Barreira et al., 2017; Agudelo et al., 2021; Turcios et al., 2021; Ozturk
141 et al., 2019; Ortiqova, 2019; Castañeda-Loaiza et al., 2020; Stevanovic et al., 2019).

142

143 **3. Alternative agricultural practices in salt-affected soils using halophytes**

144 The reduced salt levels in the crop rhizosphere under halophyte cultivation would result in a
145 better adaptation of the salt-sensitive plants to these extreme environments, allowing their
146 cultivation in marginal underutilized lands or in salt-affected agricultural soils (Garcia-
147 Caparros et al., 2020). Different strategies can be adopted to achieve this desirable outcome,
148 such as halophytes integration in intercropping or rotation systems, which could require of
149 domestication of some halophyte species or ecotypes particularly promising.

150 **3.1. Halophyte use in intercropping and crop rotation systems**

151 The use of intercropping systems in agriculture is a traditional practice diffused worldwide
152 since long time, based on the evidence of reciprocal benefits and yield increase in comparison
153 to the monoculture in a low input system (Glaze-Corcoran et al., 2020; Maitra et al. 2021). In
154 intercropping systems, two (or more) crops are cultivated simultaneously in the same row, or
155 in adjacent rows close enough for biological interaction, for an extensive proportion of their
156 growth period. This cultivation method, that is still largely diffuse in developing countries, in
157 the first world has been almost completely substituted by intensive monoculture systems, using
158 high-yielding cultivars, mechanization, and massive application of chemicals (such as
159 fertilizers and pesticides) (Machado, 2009, Ehrmann and Ritz, 2014, Maitra et al., 2021).
160 Recently, however, the growing need of sustainable production systems, as well as the
161 advances in the knowledge of the biochemical-physiological mechanisms at the basis of the
162 success of intercropping cultivation, has attracted the interest of farmers towards the
163 reintroduction of polycultures also in developed countries (Bracken, 2008; Gaudio et al., 2019;
164 Glaze-Corcoran et al., 2020).

165 Particularly attracting is the use of halophytes as intercropping species to mitigate the salt stress
166 for sensitive crops. By overcoming the limits for successful cultivation of cash crops in
167 marginal areas, halophytes have the potential to enable more sustainable and resilient
168 agriculture systems. Despite this increasing interest, few researches were conducted to validate
169 the effectiveness of integrating halophytes in intercropping systems, and most of the published
170 results were obtained in greenhouse experiments. Successful and unsuccessful responses
171 obtained in intercropping experiments are summarised in table 1. A number of these researches
172 used tomato (*Lycopersicon esculentum* Mill) as the cash crop species, being tomato one of the
173 most cultivated species worldwide, particularly in the Mediterranean region. Tabulated studies
174 mainly concentrated on the effects of *Suaeda salsa* L., *Salsola soda* L., *Portulaca olearacea*
175 L. and *Atriplex hortensis* cultivation to improve tomato performance. Graifenberg et al. (2003)

176 highlighted one possible limit of the intercropping systems, *i.e.* the competition among
177 intercropped plants for light, nutrients and water, ultimately leading to a crop yield lower than
178 in monoculture.

179 Generally, the intercropping systems have been successful in ameliorating plant adaptation to
180 salinity and in increasing crop yield under greenhouse conditions, while there is still the need
181 to validate these results in field trials, because of the few studies conducted in open field and
182 sometimes there is contradictory evidence (Table 1). Simpsons et al. (2018) reported that,
183 despite the good performance of *A. hortensis* L. and *P. oleracea* L. in greenhouse trials, these
184 species were unable to reduce soil salinity in field conditions and to ameliorate plant water
185 status and fruit quality of intercropped watermelon. Association of the two halophytes *Bacopa*
186 *monnieri* L. and *Sesuvium verrucosum* improved the chemical and physical characteristics of a
187 saline soil, allowing after 240-days desalting period, the co-cultivation of maize (*Zea mays*)
188 with a yield of 8.5 t ha⁻¹ (Lastiri-Hernández et al. 2020). In line with this, intercropping *S. salsa*
189 with cotton under three-year field conditions significantly decreased soil salinity and bulk
190 density, while increasing soil porosity, soil organic carbon, root growth, total aboveground
191 biomass and cotton yield, when compared with conventional monoculture system (Liang and
192 Shi, 2021). Similar results were obtained by intercropping cotton with *S. salsa*, *M. sativa* L., or
193 *Cuminum cyminum* L. (Guo et al., 2020).

194 The mixed cultivation was adopted, and is still practiced, as subsistence farming, because of
195 the reciprocal benefits between the two cultivated species in a low input system and the
196 possibility to harvest at least one product in the case of one crop failure. In the case of
197 halophytes intercropping, the latter benefit is less evident, though many halophytes are
198 traditionally eaten or used as feed (Panta et al., 2014; Petropoulos et al., 2018 a, b). Additional
199 uses and valorisation of halophyte biomass will be discussed in the next paragraph. In the case
200 of forage, mixed cultivation has the advantage to complement the characteristics of the two
201 species to obtain a product with better quality than a monoculture. An example of a successful
202 intercropping of forage plants is reported by Hedayati-Firoozabadi et al. (2020), who tested the
203 influence of irrigation with saline water on different planting ratios of sorghum (*Sorghum*
204 *bicolor*), a high-quality forage crop, and kochia (*Bassia indica*), a halophyte species with low
205 quality as forage. While under non saline irrigation the monoculture was the best choice, under
206 saline conditions the intercropping system, particularly with the 2/1 sorghum/kochia ratio,
207 resulted in a better quality in terms of reduced content of ash, neutral detergent fiber and acid
208 detergent fiber. Similarly, an intercropping cultivation of the halophyte *Kochia scoparia* with
209 two moderately salt tolerant fodder species (*Cyamopsis tetragonoloba* and *Sesbania aculeata*)

210 was effective in reducing the negative effects of salinity and increasing the forage yield
211 (Ghaffarian et al. 2020).

212 To maximize the productivity of an intercropping system, crops with different nutrient
213 requirements, rooting ability, canopy shape and height, must be chosen, also taking care to
214 avoid the onset of competition between species. In this context, it is important to highlight that
215 halophytes could even increase soil salinity, because of retention of high transpiration rates
216 under saline conditions, leading to drawing up of saline groundwater near coastal regions
217 (Wendelberger and Richards 2017), with progressive increasing disturbance of crop growth.

218 Moreover, it is undoubted that intercropping systems, despite of their many advantages, require
219 more manpower, considering most modern farm machinery (both for planting and harvesting)
220 designed to work on monocultures (Maitra et al., 2021). While intercropping is based on the
221 co-cultivation of different plant species, crop rotation, or sequential cropping, is set up on
222 temporal succession of two or more crops (Dury et al., 2012). Therefore, crop rotation can
223 encompass some benefits of both intercropping and monoculture. The basic principle of crop
224 rotation is the cultivation of one crop able to restore the nutrients taken up by the previous one,
225 in order to limit the use of fertilizers, thus reducing the environmental impact of agriculture.
226 One well-known example is nitrogen restoration operated by leguminous plants grown in
227 succession of cereals or other crops (Stagnari et al., 2017). Of course, rotation should also be
228 economically sustainable, so the plant species used for the sequential cropping are usually
229 chosen among the cash crops or the forage species, to ensure a constant income over time
230 (Dogliotti et al., 2004).

231 In the case of halophytes, the economic profitability must go hand in hand with their desalting
232 ability, which is the main benefit brought by their use as rotating crop. Halophyte-mediated
233 desalting and fertilization of soils can be in fact exploited to allow a better growth performance
234 of many cashcrops. Managing crop rotation in salt-affected soils needs to select suitable crops
235 (species or cultivars) with varying degree of salt tolerance and high economic value to be grown
236 after variable extent of soil reclamation achieved thanks to halophyte cultivation.

237 Ben Asher et al. (2012) demonstrated the effectiveness of SWAP (soil, water, atmosphere,
238 plant) model to simulate crop rotation in saline environments, by comparing modelled and
239 measured data derived from several experimental sites located in Israel, Turkey and Portugal,
240 using lettuce as salt-sensitive species, and *Tetragonia tetragonioides* and *P. oleracea* as
241 desalting species. These authors also highlighted the importance to know the maximum salinity
242 level that can be tolerated by the desalting species without experiencing yield reduction and
243 loss of economical income, in order to profitably include halophytes in crop rotation programs.

244 Examples of successful cultivation of crop species after desalting are reported in table 1. A
245 small-scale experiment carried out in soil-filled pots proved the ability of *Sesuvium*
246 *portulacastrum* L. to desalting an experimentally salinized soil that, after plant removal, was
247 used as substrate for barley (*Hordeum vulgare* L.) cultivation (Rabhi et al., 2010). This research
248 demonstrated a better growth performance of barley and lower Na⁺ and higher K⁺ levels in its
249 shoots, suggesting the possibility of a successful employment of this halophyte to restore salt-
250 affected fields for a subsequent cultivation of glycophyte crops. The desalination potential of
251 *S. portulacastrum* was also demonstrated in larger scale field plots (Muchate et al., 2016).
252 Another small-scale field experiment showed that the plantation of *Spinacia oleracea* in saline
253 soil considerably decreased the electrical conductivity of the soil over 90 days of plantation.
254 Subsequent to this growth period, the phytodesalinized soil supported the significant growth of
255 rice (Muchate et al., 2018).

256 Recently Barcia-Piedras et al. (2019) proved the effectiveness of *Arthrocnemum*
257 *macrostachyum* as desalting species in artificially salinized soil under non-leaching conditions.
258 Such a desalting activity resulted in earlier, faster and better emergence of barley, while wheat
259 (*Triticum durum*), which is more salt sensitive than barley, was unable to germinate unless it
260 was sown in remediated soils.

261 A successful remediation of saline areas was achieved thanks to a 4-year period of liquorice
262 (*Glycyrrhiza glabra*) cultivation, after which the soils were returned to a cotton/wheat crop
263 rotation (Kushiev et al., 2005). A noteworthy increase in the yield of both crops was achieved,
264 demonstrating the capacity of liquorice in restoring abandoned saline soils into productive
265 fields with a low-cost approach. Moreover, liquorice cultivation produced high quality forage
266 and roots for pharmaceutical and beverage production, providing potential additional income
267 to farmers.

268 Despite these encouraging reports, the massive literature on the desalting properties of the
269 halophytes and their ability to improve soil structure and fertility, very few studies have
270 validated such potential on the growth and yield of a glycophytic crop cultivated in succession
271 with halophyte. Accordingly, there is a need to additional tests, particularly under field
272 conditions, to confirm and optimize the sustainable use of halophytes in crop rotation systems
273 in marginal degraded lands.

274 **3.2. Potential uses of halophyte biomass, after remediation process**

275 Halophytes are abundant in Mediterranean coastal areas and can cope with adverse stressful
276 conditions, such as high salinity and intense UV radiation intense UV radiation (40-60 Wm⁻²

277 UV-A and 2-3 Wm⁻² UV-B), partially due to the synthesis of several bioactive secondary
278 metabolites, as for example phenolic compounds and alkaloids (Hupel et al., 2011). Besides
279 their protective role for the plant, these molecules display important biological activities,
280 including anti-oxidant, anti-inflammatory, antidiabetic and neuroprotective, which may
281 explain the several ethnomedicinal and-veterinary uses of different halophyte species (Ksouri
282 et al., 2012; Arya et al., 2019, Oliveira et al., 2021). For example, *Salicornia* L. species (sea
283 asparagus) are used in traditional medicine against obesity and diabetes while *Crithmum*
284 *maritimum* L. (sea fennel) and *Portulca olearacea* (common purslane) are used as diuretic and
285 antiscorbutic (Pereira et al., 2017; Hwess et al., 2018). Being rich in mineral salts and having
286 high water content, *P. olearacea* also has soothing properties for irritations of the bladder and
287 urinary tract (Hwess et al., 2018). Another study shows that purslane vegetable contains high
288 levels of omega-3 fatty acids for a land vegetable, as well as significant amounts of vitamin A,
289 vitamin C, magnesium, potassium, calcium and iron (Simopoulos et al., 2004).

290 Halophyte's ethnomedicinal uses and chemical richness opens a cornucopia of naturally
291 available bioactive products with a high added value in different commercial segments like the
292 food, veterinary and pharmaceutical industries. Several Mediterranean species are edible and
293 highly procured in the food industry due to their nutritional properties (Petropoulos et al., 2018
294 a; b). This is the case of *Arthrocnemum macrostachyum* reported for its high commercial value
295 and highly valued in gourmet cuisine (Barreira et al., 2017). *Helichrysum italicum* subsp.
296 *picardii*, *Crithmum maritimum*, and *Artemisia campestris* subsp. *maritima* are potential sources
297 of herbal health-promoting beverages (Pereira et al., 2017a; b; Pereira et al., 2018). Other
298 Mediterranean species like *Lithrum salicaria* and *Polygonum maritimum* are source of raw
299 material for pharmaceutical and other related industries (Lopes et al., 2016; Rodrigues et al.,
300 2018). A recent review by Oliveira et al. (2020) showed that essential oils in halophytes can be
301 used as animal feed additives to improve ruminant health and productivity. Some anti-
302 nutritional compounds like saponins, tannins and flavonoids can have anthelmintic and anti-
303 bloat properties, besides their possible effects on the ruminal biohydrogenation and fermentation
304 patterns and on the management of oxidative-related disorders (Oliveira et al., 2021). This novel
305 line of research would deliver sustainable and integrative alternatives for veterinary practices.

306 From all the above referred it is easy to deduce that halophyte plants may find niches in the
307 demanding market for novelties, as for example as herbs, vegetables, fresh gourmet products,
308 and animal feed. One challenge that limits halophyte cultivation is the lack of knowledge about
309 consumers' acceptance of halophyte products, which are fundamental to the commercialization
310 of halophytes because farmers will start investing in the crop only if there is marketing potential

311 (Centofanti and Banuelos, 2019). Halophyte's species will take a little to make people believe
312 that they are good food for them, although some are used by certain communities for this
313 purpose (Menzel and Leith, 1999). However, there are potentials to extract good quality oil
314 from them (Weber et al., 2007), they could also serve as a source of feed, fiber and forage and
315 this would not have any problem of acceptability.

316 To take halophytes from the laboratory to the farm and thus scale up its production, it is also
317 important to create a value chain, which allows for the production of fresh and processed
318 halophyte-based food products. To increase profitability of halophyte cultivation, there is a
319 need for a whole system to add more value to halophyte-based food products in addition to
320 practices that increase its yields. It is also necessary to build public awareness and increase
321 consumer knowledge about the nutritional and health benefits of halophyte-based food
322 products.

323 **4. Halophyte domestication**

324 Besides the use of halophytes in intercropping or rotation systems, two possible approaches to
325 achieve a saline agriculture are: i) improving the salt-tolerance of cultivated crops, or ii)
326 domestication of halophytes. An update on molecular strategies for the generation of salt-
327 tolerant crops using halophytes for interspecific hybridization or as donors of candidate genes
328 for glycophyte transformation is reported by Ferreira Barros et al. (2021). Moreover, evidence
329 is accumulating on the potential of halophyte root microbioma to improve the salt-tolerance of
330 non-host crops, as demonstrated, for example, in rice and cucumber seedlings colonised by
331 rhizospheric bacteria or endophytic fungi isolated from *S. soda* (Yuan et al., 2016).

332 Domestication of halophyte is a needed step for profitable cultivation of these species. A major
333 impediment to their massive use in agriculture is the standardization of their performance,
334 being halophytes mainly wild plants. Another constraint is the need to ensure the farmers the
335 availability of a constant supply of the most suitable species. However, the main limit is
336 probably related to the low growth rate, uneven seed germination, and the accumulation of
337 toxic or bitter compounds in their tissues, characters that in cash crops species have been
338 ameliorated by the long-term process of domestication (Gepts, 2004). Brown et al. (2014)
339 discussed a strategy for domestication of wild halophytes for their employment as seawater-
340 irrigated crops, based on the approaches used for domestication of other wild species. One first
341 aspect identified by these authors is the better performance of halophytes in environments
342 similar to those where they usually grow in nature. Accordingly, a prerequisite for their
343 successful domestication is the choice of the wild species based on the location where the

344 cultivation might be set up. In other words, latitude, environmental parameters, proximity to
345 the coast, and other characteristics of the native place of the wild species must be as similar as
346 possible to those of the agronomic fields where the crop might be grown. Also, a good
347 knowledge of the life cycle of the wild species in their native environment is pivotal in driving
348 the choice of the best candidate species. After this first step, several crop cycles must be
349 operated until the occurrence of the so-called domestication syndrome, i.e. the modification of
350 those traits indicative of the divergence of the cultivated species from its wild ancestor towards
351 domestication, such as synchronization of flowering, fruit ripening, seed germination, loss of
352 bitterness, reduced content of toxic compounds, increased fruit and seed size (Meyers et al.,
353 2012). Another important objective of plant domestication is the shift of the metabolic
354 resources towards aboveground, economically interesting, organs (leaves, fruit and seeds).
355 Domestication via mass selection takes many generations of crosses and requires several
356 experiments, sometimes unsuccessful and often lasting decades. Besides, it would allow fixing
357 only few desirable traits. However, it allows selection of parent lines for selective breeding
358 programs. An example of this approach in halophyte domestication is reported by Zerai et al.
359 (2010), who adopted two breeding programs involving also hybridization and pedigree
360 breeding, producing cultivars of *Salicornia bigelovii* Torr with a noteworthy phenotypic
361 variability and higher seed yields or higher biomass yield, in the lines selected by Eritrea or
362 Arizona breeding programs, respectively. The research proved the feasibility of developing a
363 halophyte crop by conventional breeding methods though none of these lines were tested in
364 open field conditions and introduction of additional traits such as lowering of toxic compounds
365 in the edible parts of the plant, resistance towards biotic stress, reduced plant size to cope with
366 lodging, synchronization of flowering and seed production, improved retention of seeds, rapid
367 germination, strong growth and vigor is desirable.

368 A successful example of halophyte domestication is represented by quinoa (*Chenopodium*
369 *quinoa* Wild.), a pseudocereal that has about 2500 accessions and a great agronomic potential.
370 Indeed, it is increasingly cultivated globally thank to its good nutritional value and high
371 tolerance to salinity and other environmental stresses (Zhou et al. 2017).

372 A prerequisite for a successful use of halophytes as crops is the genetic characterization of the
373 accessions collected from different sites, aimed to the development of well characterised lines
374 for breeding, together with the definition of the optimal conditions for seed germination and
375 plant cultivation. Singh et al. (2014) performed an extensive characterization of *Salicornia* and
376 *Sarcocornia* spp, followed by germination trials and cultivation of selected accessions in
377 hydroponics (with or without sand as a supporting medium) with different salinity levels up to

378 harvestable size, to evaluate the optimal growth conditions. This study allowed to detect high
379 physiological plasticity in *S. dolichostachya* and, accordingly, a potential cultivation under low-
380 to-high salinity conditions, both under flooded and drained environment, while *S. ramosissima*
381 was more suitable for dry areas. Moreover, seed dimorphism of *Salicornia* spp. did not affect
382 timing of germination, thus preventing the need for growers to separate seeds into small- and
383 large-size groups before sowing. To maximise biomass production, delaying flowering is
384 mandatory. The critical day length required to inhibit flowering depend on ecotypes and it is
385 generally higher for genotypes from northern latitudes. It is therefore important to select the
386 right genotype-light regimen combination to maximise vegetable production.

387 Ventura and Sagi (2013) highlighted the difficult to generalise the salt tolerance mechanisms
388 and the growing performance studied in small scale experiments to the real cultivation under
389 agricultural field conditions. However, in the case of *Salicornia* and *Sarcocornia*, many
390 greenhouse and field experiments were performed, and different cultivation systems have been
391 already tested, varying irrigation system, daylength, harvest regimen, making these plants a
392 sort of model for the development of other halophyte species whose commercial cultivation is
393 still at its beginning. These authors also suggest that investigating the halophyte behaviour
394 directly in filed studies and, even better, directly in the farmer's fields, would fasten the
395 domestication process and the profit generation.

396 The improvement of crop characteristics by plant breeding is just at the beginning for
397 halophytes, so many efforts are still to be done to achieve the desirable goal of making
398 halophytes increasingly adaptable to sustainable farming systems. A possible difficulty in the
399 domestication programs could derive from the limited availability of germplasm collections to
400 sustain the breeding tests. Therefore, it is mandatory to collect and preserve valuable
401 germplasm as a pre-requisite for research and breeding programs.

402 However, the recent advances in identification of the genetic traits associated with salinity
403 tolerance pave the way for an efficient and accelerated selection of the most promising parent
404 lines without the necessity of laborious and time-consuming screening procedures, and for the
405 improvement of the wild plant genetic resources, once demonstrated the inheritability of these
406 traits.

407 **5. Halophyte aquaponics**

408 The capacity of halophyte plants to uptake great amounts of salt ions and to adapt to extreme
409 environments, hardly suitable for conventional crops, makes them optimal candidates for the
410 design of marine aquaponics systems. Aquaponics is a multitrophic food production system

411 integrating aquaculture, *i.e.*, fish (or other aquatic animal species) farming, with hydroponic
412 plant production (König et al., 2018).

413 A recent review by Custodio et al. (2017) evaluated the information deriving from published
414 researches on halophyte ability to remediate effluents from aquaculture systems. The most
415 studied species were *Aster tripolium* (5 studies), *Salicornia europaea* (4 studies), *Phragmites*
416 *australis* (3 studies) and *Salicornia dolichostachya* (2 studies). The experiments were set up in
417 different geographic areas with diverse climates and generally reported significant removal of
418 nutrient loadings supporting the potential of profitable incorporation of these plants into
419 integrated multi-trophic aquaculture (IMTA) systems. Alternatively, constructed wetlands
420 (CWs) planted with halophytes demonstrated a good removal efficiency of total N and P,
421 sometimes approaching the total elimination (Buhmann and Papenbrock, 2013; Lymbery et al.,
422 2006, Webb et al., 2012).

423 Many studies on the integration of halophytes in aquaculture systems have been already
424 published; few of them were listed in Table 2. Several examples were successful in decreasing
425 many indexes of water pollution, among which the biological oxygen demand (BOD) and both
426 nitrate and nitrite N (Lin et al., 2003). However, they were very low efficient in phosphate
427 removal, probably due to the high hydraulic loading and/or the low phosphate uptake by some
428 halophyte species. Previous studies reported a more efficient phosphate removal, that was
429 inversely related to the hydraulic loading, by a combination of *Phragmites australis* with two
430 other halophyte species, *Ipomoea aquatica* and *Paspalum vaginatum* (Lin et al., 2002a, b).

431 Boxman et al. (2017) highlighted the need to optimize the conditions of the aquaponic system
432 that integrates the most appropriate halophytes. They observed a positive contribution of
433 *Sesuvium portulacastrum* and *Batis maritima*, grown hydroponically in diluted sea water, in
434 lowering the nitrate levels of water effluents deriving from the platy fish (*Xiphophorus* sp.)
435 tank. The same authors (Boxman et al., 2018) also proved the effectiveness of these halophyte
436 species to support red drum (*Sciaenops ocellatus*) farming in a prototype, commercial-scale
437 marine aquaponic system that included a moving bed bioreactor (MBBR) for nitrification and
438 a sand filter for solids removal and denitrification (Table 2). An efficient growth performance
439 of whiteleg shrimp (*Litopenaeus vannamei*) and some halophytes (*Atriplex hortensis*, *Salsola*
440 *komarovii* and *Plantago coronopus*) was achieved by Chu and Brown (2021) in a marine
441 aquaponic system by adjusting salinity to a compromise level compatible for both the animal
442 and the plant species (Table 2). The results obtained reported a better growth performance of
443 the shrimp (higher final weight and weight gain rate) under higher saline conditions, whereas
444 in the case of halophytes, the trend was the opposite with a lower growth under higher saline

445 conditions and also a reduction of nutrient uptake. Accordingly, the intermediate saline
446 condition (i.e., 15 ppt) was suggested as the optimal condition for the development of shrimp-
447 halophyte marine aquaponics (Table 2).

448 In the case of super intensive fish or shrimp farming, the nutrient load of the effluents may be
449 efficiently reduced by the combination of halophyte cultivation with polychaete-assisted sand
450 filters (Marques et al. 2017).

451 However, despite water effluents from aquaculture is a rich source for most macronutrients,
452 plants cultivated in aquaponic system could suffer micronutrient deficiency, that may reduce
453 the commercial production of halophyte biomass. The fast growth rate in a nutrient-rich
454 environment needs integration of the limiting nutrient, like molybdenum for *S. europaea*
455 (Ventura et al. 2010), iron for *Salicornia dolichostachya* (Singh et al., 2014), *Aster tripolium*
456 (Ventura et al., 2013) and *Apium graveolens* (Sbai and Haouala, 2018). However, species-
457 specific response to micronutrient supplementation in a saline aquaponic system was reported
458 by Doncato and Costa (2021), who observed increased growth and biomass production of
459 *Paspalum vaginatum* Sw. while *Salicornia neei* Lag. was unaffected by mineral
460 supplementation in water and even underwent an important reduction of shoot biomass
461 following foliar fertilization. Interestingly, Maciel et al. (2020) observed a modification of the
462 lipidome of two halophytes (*Salicornia ramosissima* and *Halimione portulacoides*) cultivated
463 in a marine aquaponic system in comparison to the wild populations. Specifically, both
464 halophytes presented higher levels of glycolipids (and *H. portulacoides* also of phospholipids)
465 bearing n-3 fatty acids, that undoubtedly increase the market value of these species, having the
466 n-3 polyunsaturated fatty acids recognised healthy properties (Shahidi and Ambigaipalan,
467 2018).

468 In the light of the few examples reported above, it emerges that halophytes could be
469 successfully integrated in marine aquaculture systems to meet the need to increase the
470 production of fishes, crustaceans and molluscs in a sustainable and economically profitable
471 way, promoting integration of green and blue revolution.

472 **Conclusion**

473 Nowadays, the use of the modern genetic engineering tools is allowing the development of
474 high salt tolerant cultivars but due to the long term required to obtain them and the high degree
475 of soil salinity in several parts of the world, the use of halophytes seems to be one of the most
476 feasible option to feed the population. These halophytes can be used for the restoration of saline
477 soils mainly due to the physiological and biochemical characteristics triggered by them over

478 the evolution compared to the glycophytes allowing them the survival under these harsh
479 conditions. Different alternative agronomic practices including halophytes such as
480 intercropping or rotation implemented at worldwide level are giving promising results level in
481 terms of yield and quality in cash crops species mainly related to the reduction of soil salinity
482 levels exerted by halophytes. This fact led us to continue with this research line conducting
483 different cropping systems for their establishment in the Mediterranean arid and semi-arid
484 regions. Not only at agronomic level halophytes can be of special interest since they can be
485 combined simultaneously with the production of animal aquatic species in marine aquaponics
486 systems offering to the population a dual system of feeding (crops and marine species) with
487 reduced environmental impact. Besides, halophytes are an invaluable source of nutraceutical
488 and medicinal compounds which many of them are still unknown. The successful adoption of
489 sustainable halophyte farming systems will offer to the worldwide population new sources of
490 food with interesting healthy properties as well as an environmental solution to restore the
491 biodiversity severely affected by the human action and climate changes.

492 **Credit author statement**

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506 **References**

507 Acosta, J.A., Fazb, A., Jansen, B., Kalbitz, K., Martínez-Martínez, S., 2011. Assessment of
508 salinity status in intensively cultivated soils under semiarid climate, Murcia, SE Spain. *J. Arid*
509 *Environ.* 75, 1056-1066.

510 Acosta-Motos, J.R., Ortuño, M.F., Bernal-Vicente, A., Díaz-Vivancos, P., Sánchez-Blanco,
511 M.J., Hernández, J.A., 2017. Plant Responses to Salt Stress: Adaptive Mechanisms.
512 *Agronomy-Basel* 7, 18.

513 Agudelo, A., Carvajal, M., Martínez-Ballesta, M.D.C., 2021. Halophytes of the Mediterranean
514 basin-Underutilized species with the potential to be nutritious crops in the scenario of the
515 climate change. *Foods*, 10, 119.

516 Albaho, M.S., Green, J.L., 2000. *Suaeda salsa*, A desalinating companion plant for greenhouse
517 tomato. *Hort. Sci.* 35, 620-623.

518 Arya, S.S., Devi, S., Ram, K., Kumar, S., Kumar, N., Mann, A., Kumar, A., Chand, G., 2019.
519 Halophytes: The plants of therapeutic medicine. In: Hasanuzzaman, M., Nahar, K., Öztürk, M.
520 (Eds.) *Ecophysiology, Abiotic Stress Responses and Utilization of Halophytes*. Springer,
521 Singapore, pp. 271-287.

522 Barcia-Piedras, J. M., Pérez-Romero, J. A., Mateos-Naranjo, E., Camacho, M., Redondo-
523 Gómez, S. 2019. Effect of prior salt experience on desalination capacity of the halophyte
524 *Arthrocnemum macrostachyum*. *Desalination*. 463, 50-54.

525 Barreira, L., Resek, E., Rodrigues, M.J., Rocha, M.I., Pereira, H., Bandarra, N., da Silva, M.M.,
526 Varela, J., Custódio, L., 2017. Halophytes: Gourmet food with nutritional health benefits?. *J.*
527 *Food Comp. Anal.* 59, 35-42.

528 Ben Asher, J., Beltrao, J., Aksoy, U., Anac, D., Anac, S., 2012. Modeling the effect of salt
529 removing species in crop rotation. *Int. J. Energy Environ.* 6, 350–359.

530 Ben Hamed, K., Dabbous, A., Soud, A., Abdelly, C., 2020. Antioxidant molecules and
531 enzymes and their relevance to the salt adaptation of halophytes. In: Grigore M.N. (Ed.)
532 *Handbook of Halophytes*. Springer, Switzerland.

533 Bose, J., Rodrigo-Moreno, A., Shabala, S., 2014. ROS homeostasis in halophytes in the context
534 of salinity stress tolerance, *J. Exp. Bot.* 6, 1241-1257.

535 Boxman, S.E., Nystrom, M., Capodice, J.C., Ergas, S.J., Main, K.L., Trotz, M.A., 2017. Effect
536 of support medium, hydraulic loading rate and plant density on water quality and growth of
537 halophytes in marine aquaponic systems. *Aquac. Res.* 48, 2463-2477.

538 Boxman, S.E., Nystrom, M., Ergas, S.J., Main, K.L., Trotz, M.A. 2018. Evaluation of water
539 treatment capacity, nutrient cycling, and biomass production in a marine aquaponic system.
540 *Ecol. Engin.* 120, 299-310, <https://doi.org/10.1016/j.ecoleng.2018.06.003>

541 Bracken, M.E.S., 2008. Monocultures versus Polycultures. In Jørgensen, S.E., Fath, B.D.
542 (Eds.), *General Ecology. Encyclopedia of Ecology* 3. Elsevier, Oxford, pp. 2446-2449.

543 Brown, J.J., Glenn, E.P., Smith S.E., 2014. Domestication for high-salinity agriculture. In:
544 Khan, M.A. et al. (Eds.), *Sabkha Ecosystems: Volume IV: Cash Crop Halophyte and*
545 *Biodiversity Conservation, Tasks for Vegetation Science 47*. Springer, Dordrecht, pp 73-80.

546 Buhmann, A., Papenbrock, J., 2013. Biofiltering of aquaculture effluents by halophytic plants:
547 Basic principles, current uses and future perspectives. *Environ. Exp. Bot.* 92, 122-133.

548 Castañeda-Loaiza, V., Oliveira, M., Santos, T., Schüller, L., Lima, A.R., Gama, F., Salazar, M.,
549 Neng, N.R., Nogueira, J.M.F., Varela, J., Barreira, L., 2020. Wild vs cultivated halophytes:
550 Nutritional and functional differences. *Food Chem.* 333, 127536.

551 Centofanti, T., Banuelos, G., 2019. Practical uses of halophytic plants as sources of food and
552 fodder. In: Hasanuzzaman, M., Shabala, S., Fujita M. (Eds.), *Halophytes and Climate Change:*
553 *Adaptive Mechanisms and Potential Uses*. CAB International, Wallingford, pp 324-342.

554 Chu, Y.T., Brown, P.B., 2021. Evaluation of pacific Whiteleg Shrimp and three halophytic
555 plants in marine aquaponic systems under three salinities. *Sustain.* 13, 269.

556 Colla, G., Rouphael, Y., Fallovo, C., Cardarelli, M., 2006. Use of *Salsola soda* as a companion
557 plant to improve greenhouse pepper (*Capsicum annuum*) performance under saline conditions.
558 *New Zeal. J. Crop Hort. Sci.* 34, 283-290.

559 Custodio, M., Villasante, S., Cremades, J., Calado, R., Lillebø, A.I., 2017. Unravelling the
560 potential of halophytes for marine integrated multi-trophic aquaculture (IMTA)- perspective
561 on performance, opportunities and challenges. *Aquacult. Environ. Interact.* 9, 445-460.

562 Dazzi, C., Lo Papa, G., 2013. Soil threats. In: Costantini, E.A.C., Dazzi, C. (Eds.), *The soils in*
563 *Italy*. Springer, Dordrecht, pp. 205-245.

564 Debez, A., Huchzermeyer, B., Abdelly C., Koyro, H.W., 2011. Current challenges and future
565 opportunities for a sustainable utilization of halophytes. In: Öztürk et al. (Eds.), *Africa and*
566 *Southern Europe, Tasks for Vegetation Science*. Springer, Dordrecht, Springer.

567 Dogliotti, S., Rossing, W.A.H., van Ittersum, M.K., 2004. Systematic design and evaluation of
568 crop rotations enhancing soil conservation, soil fertility and farm income: a case study for
569 vegetable farms in South Uruguay. *Agric. Syst.* 80, 277-302.

570 Doncato, K.B., Costa, C.S.B., 2021. Micronutrient supplementation needs for halophytes in
571 saline aquaponics with BFT system water, *Aquaculture*, 531, 735815.

572 Dury, J., Schaller, N., Garcia, F., Reynaud, A., Bergez, J.E., 2012. Models to support cropping
573 plan and crop rotation decisions. A review. *Agron. Sustain. Develop.* 32, 567-580.

574 Ehrmann, J., Ritz, K., 2014. Plant: soil interactions in temperate multi-cropping production
575 systems. *Plant Soil* 376, 1-29.

576 FAO, 2011. The State of the World's Land and Water Resources for Food and Agriculture
577 (SOLAW) – Managing Systems at Risk. Food and Agriculture Organization of the United
578 Nations, Rome and Earth scan, London.

579 FAO, CIHEAM (2015) “Mediterranean food consumption patterns Diet, environment, society,
580 economy and health”. Available online at: <http://www.fao.org/3/a-i4358e.pdf>.

581 FAO, IFAD, UNICEF, WFP, WHO. 2020. The State of Food Security and Nutrition in the
582 World 2020. Transforming food systems for affordable healthy diets. Rome, FAO.
583 <https://doi.org/10.4060/ca9692en>

584 Ferreira Barros, N. L., Novaes Marques, D., Araújo Tadaiesky, L. B., Batista de Souza, C. R.,
585 2021. Halophytes and other molecular strategies for the generation of salt-tolerant crops. *Plant*
586 *Physiol. Biochem.* 162, 581-59, doi:10.1016/j.plaphy.2021.03.028.

587 Flowers, T.J., Colmer, T.D., 2008. Salinity tolerance in halophytes. *New Phytol.* 179, 945-963.

588 Flowers, T.J., Colmer, T.D., 2015. Plant salt tolerance: adaptations in halophytes. *Annal Bot.*
589 115, 327-331.

590 García-Caparros, P., Lao, M.T., 2018. The effects of salt stress on ornamental plants and
591 integrative cultivation practices. *Sci. Hort.* 240, 430-439.

592 Garcia-Caparros, P., Contreras, J.I., Baeza, R., Segura, M.L., Lao, M.T., 2017. Integral
593 management of irrigation water in intensive horticultural systems of Almería. *Sustain.* 9, 2271.

594 García-Caparros, P.; Llanderal, A.; Lao, MT., 2020. Halophytes as an option for the restoration
595 of degraded areas and landscaping. 1-16. In: Grigore, M.N. (Ed.) *Handbook of Halophytes*.
596 Springer, Switzerland, pp. 1-16.

597 Gaudio, N., Escobar-Gutiérrez, A.J., Casadebaig, P., Evers, J.B., Gerard, F., Louran, G.,
598 Colbach, N., Munz, S., Launay, M., Marrou, H., Barillot, R., Hinsinger, P., Bergez, J-E.,
599 Combes, D., Durand, J-L., Frak, E., Pages, L., Pradal, C., Saint-Jean, S., van der Werf, W.,
600 Justes, E., 2019. Current knowledge and future research opportunities for modeling annual crop
601 mixtures. A review. *Agron. Sustain. Dev.* 39, 20.

602 Gepts, P., 2004. Crop domestication as a long-term selection experiment. *Plant Breed. Rev.* 24,
603 1-44.

604 Ghaffarian, M.R., Yadavi, A., Dehnavi, M.M., Mohammadi Nassab, A.D, Salehi, M., 2020.
605 Improvement of physiological indices and biological yield by intercropping of *Kochia* (*Kochia*
606 *scoparia*), *Sesbania* (*Sesbania aculeata*) and Guar (*Cyamopsis tetragonoloba*) under the salinity
607 stress of irrigation water. *Physiol. Mol. Biol. Plants* 26, 1319-1330.

608 Glaze-Corcoran, S., Hashemi, M., Sadeghpour, A., Jahanzad, E., Afshar, R.K., Liu, X.,
609 Herbert, S.J., 2020. Understanding intercropping to improve agricultural resiliency and
610 environmental sustainability. *Adv. Agron.* 162, 199-256.

611 Glenn, E.P., Brown, J.J., O'Leary, J.W., 1998. Irrigating crops with seawater. *Sci. Amer.* 279,
612 76-81.

613 Graifenberg, A., Botrini, L., Giustiniani, L., Filippi, F., Curadi, M., 2003. Tomato growing in
614 saline conditions with biodesalinating plants: *Salsola soda* L., and *Portulaca oleracea* L. *Acta*
615 *Hortic.* 609, 301-305.

616 Guo, J.Z., Shi, W.J., Li, J.K., 2020. Effects of intercropping different halophytes in bare strips
617 on soil water content, salt accumulation, and cotton (*Gossypium hirsutum*) yields in mulched
618 drip irrigation. *Appl. Ecol. Environ. Res.* 18, 5923-5937.

619 Hassani, A., Azapagic, A., Shokri, N., 2020. Predicting long-term dynamics of soil salinity and
620 sodicity on a global scale. *Proc. Natl. Acad. Sci.U.S.A.* 117, 33017-33027.

621 Hasegawa, P.M., 2013. Sodium (Na⁺) homeostasis and salt tolerance of plants. *Environ. Exp.*
622 *Bot.* 92, 19-31.

623 Hedayati-Firoozabadi, A., Kazemeini, S.A, Pirasteh-Anosheh, H., Ghadiri, H., Pessarakli, M.,
624 2020. Forage yield and quality as affected by salt stress in different ratios of *Sorghum bicolor*-
625 *Bassia indica* intercropping. *J. Plant Nutr.* 43, 2579-2589.

626 Hernández, J.A., 2019. Salinity tolerance in plants: trends and perspectives. *Int. J. Mol. Sci.*
627 20, 2408.

628 Hupel, M., Lecointre, C., Meudec, A., Poupart, N., Gall, E.A., 2011. Comparison of
629 photoprotective responses to UV radiation in the brown seaweed *Pelvetia canaliculata* and the
630 marine angiosperm *Salicornia ramosissima*. *J. Exp. Marin. Biol. Ecol.* 401, 36-47.

631 Hwess, H., Ayadi, R., Mahouachi, W., Rezgui, M., Balti, H., Hamrouni L., 2018.
632 Ethnobotanical and ethnopharmacological notes on *Portulaca oleracea* (L.). *Phytoth.* 16,
633 S215-S219.

634 IPCC (2013) The physical science basis. 5th Assessment report. Available online at:
635 <https://www.ipcc.ch/report/ar5/wg1/>

636 IUCN (2008) The Mediterranean: a biodiversity hotspot under threat. Available online at:
637 [https://cmsdata.iucn.org/downloads/the_mediterranean_a_biodiversity_hotspot_under_threat](https://cmsdata.iucn.org/downloads/the_mediterranean_a_biodiversity_hotspot_under_threat_factsheet_en.pdf)
638 [_factsheet_en.pdf](https://cmsdata.iucn.org/downloads/the_mediterranean_a_biodiversity_hotspot_under_threat_factsheet_en.pdf).

639 Jing, C., Xu, Z., Zou, P., Tang, Q., Li, Y., You, X., Zhang, C., 2019. Coastal halophytes alter
640 properties and microbial community structure of the saline soils in the Yellow River Delta,
641 China. *Appl. Soil Ecol.* 134, 1-7.

642 Karakas, S., Cullu, M.A., Kaya, C., Dikilitas, M., 2016. Halophytic companion plants improve
643 growth and physiological parameters of tomato plants grown under salinity. Pak. J. Bot. 48,
644 21-28.

645 König, B., Janker, J., Reinhardt, T., Villarroel, M., Junge, R., 2018. Analysis of aquaponics as
646 an emerging technological innovation system. J. Clean. Prod. 180, 232-243.

647 Koyro, H.W., Lieth, H., Gul, B., Ansari, R., Huchzermeyer, B., Abideen, Z., Hussain, T., Khan,
648 M.A., 2014. Importance of the diversity within the halophytes to agriculture and land
649 management in arid and semiarid countries. In: Khan, M.A. et al. (Eds.), Sabkha Ecosystems:
650 Volume IV: Cash Crop Halophyte and Biodiversity Conservation, Tasks for Vegetation
651 Science 47. Springer, Dordrecht, pp. 175-198.

652 Ksouri, R., Falleh, H., Megdiche, W., Trabelsi, N., Mhamdi, B., Chaieb, K., Bakrouf, A.,
653 Magné, C., Abdelly, C., 2009. Antioxidant and antimicrobial activities of the edible medicinal
654 halophyte *Tamarix gallica* L. and related polyphenolic constituents. Food Chem. Toxicol. 47,
655 2083-2091.

656 Kushiev, H., Noble, A.D., Abdullaev, I., Toshbekov, U., 2005. Remediation of abandoned
657 saline soils using *Glycyrrhiza glabra*: A Study from the Hungry steppes of central Asia. Inter.
658 J. Agri. Sustain. 3, 102-113.

659 Lagacherie, P., Álvaro-Fuentes, J., Annabi, M., Bernoux, M., Bouarfa, S., Douaoui, A.,
660 Grunberger, O., Hammani, A., Montanarella, L., Mrabet, R., Sabir, M., Raclot, D., 2018.
661 Managing Mediterranean soil resources under global change: expected trends and mitigation
662 strategies. Reg. Environ. Change 18, 663-675.

663 Lastiri-Hernández, M.A., Álvarez-Bernal, D., Ochoa-Estrada S., Contreras-Ramos S.M., 2020.
664 Potential of *Bacopa monnieri* (L.) Wettst and *Sesuvium verrucosum* Raf. as an agronomic
665 management alternative to recover the productivity of saline soils. Internat. J. Phytoremed.
666 22:4, 343-352.

667 Liang, J., Shi, W., 2021. Cotton/halophytes intercropping decreases salt accumulation and
668 improves soil physicochemical properties and crop productivity in saline-alkali soils under
669 mulched drip irrigation: A three-year field experiment. Field Crops Res. 262, 108027.

670 Lin, Y.F., Jing, S.-R., Lee, D.Y., Wang, T.W., 2002a. Removal of solids and oxygen demand
671 from aquaculture wastewater with a constructed wetland system in the start-up phase. Water
672 Environ. Res. 74, 136–141.

673 Lin, Y.F., Jing, S.R., Lee, D.Y., Wang, T.W., 2002b. Nutrient removal from aquaculture
674 wastewater using a constructed wetlands system. Aquaculture 209, 169–184.

675 Lin, Y.F., Jing, S.R., Lee, D.Y., 2003. The potential use of constructed wetlands in a
676 recirculating aquaculture system for shrimp culture. *Environ. Pollut.* 123, 107–113.

677 Lopes, A., Rodrigues, M.J., Pereira, C., Oliveira, M., Barreira, L., Varela, J., Trampetti, F.,
678 Custodio, L., 2016. Natural products from extreme marine environments: Searching for
679 potential industrial uses within extremophile plants. *Ind. Crops Prod.* 94, 299-307.

680 Lymbery, A.J., Doupé, R.G., Bennett, T., Starcevich, M.R., 2006. Efficacy of a subsurface-
681 flow wetland using the estuarine sedge *Juncus kraussii* to treat effluent from inland saline
682 aquaculture, *Aquac. Engin.*, 34, 1-7, <https://doi.org/10.1016/j.aquaeng.2005.03.004>.

683 Machado, S., 2009. Does intercropping have a role in modern agriculture? *J. Soil Water*
684 *Conserv.* 64, 55A-57A.

685 Maciel, E., Domingues, P., Domingues, M. R. M., Calado, R., Lillebø, A., 2020. Halophyte
686 plants from sustainable marine aquaponics are a valuable source of omega-3 polar lipids. *Food*
687 *Chem.*, 320, 126560.

688 Maitra, S., Hossain, A., Brestic, M., Skalicky, M., Ondrisik, P., Gitari, H., Brahmachari, K.,
689 Shankar, T., Bhadra, P., Palai, J.B., Jena, J., Bhattacharya, U., Duvvada, S.K., Lalichetti, S.,
690 Sairam, M., 2021. Intercropping - A low input agricultural strategy for food and environmental
691 security. *Agronomy* 11, 343.

692 Mancosu, N., Snyder, R.L., Kyriakakis, G., Sapno, D., 2015. Water scarcity and future
693 challenges for food production. *Water* 7, 975-992.

694 Marques, B., Calado, R., Lillebø, A.I., 2017. New species for the biomitigation of a super-
695 intensive marine fish farm effluent: Combined use of polychaete-assisted sand filters and
696 halophyte aquaponics. *Sci. Tot. Environ.* 599-600. 1922-1928.

697 Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence: a practical guide. *J. Exp. Bot.*
698 51, 659-668.

699 Menzel, U., Lieth, H., 1999. Halophyte Database Vers. 2.0. In: Lieth, H., Moschenko, M.,
700 Lohman, M., Koyro, H.W., Hamdy, A. (Eds.), *Halophyte Uses in different climates I:*
701 *Ecological and Ecophysiological Studies. Progress in Biometeriology*, Vol. 13. Backhuys
702 Publishers, The Netherlands, p. 77-88.

703 Meyer, R.S., DuVal, A.E., Jensen, H.R., 2012. Patterns and processes in crop domestication:
704 an historical review and quantitative analysis of 203 global food crops. *New Phytol.* 196, 29-
705 48.

706 Muchate, N.S., Nikalje, G.C., Rajurkar, N.S., Suprasanna, P., Nikam, T.D., 2016. Physiological
707 responses of the halophyte *Sesuvium portulacastrum* to salt stress and their relevance for saline
708 soil bio-reclamation. *Flora* 224, 96-105.

709 Muchate, N.S., Rajurkar, N.S., Suprasanna, P. Nikam, T.D., 2018. Evaluation of *Spinacia*
710 *oleracea* (L.) for phytodesalination and augmented production of bioactive metabolite, 20-
711 hydroxyecdysone. *Int. J. Phyto.* 20, 981-994.

712 Nanhapo, P.I., Yamane, K., Iijima, M., 2017. Mixed cropping with ice plant alleviates the
713 damage and the growth of cowpea under consecutive NaCl treatment and after the recovery
714 from high salinity. *Plant Prod. Sci.* 20, 111-125.

715 Oliveira, M., Hoste, H., Custódio, L., 2020. A systematic review on the ethnoveterinary uses
716 of Mediterranean salt-tolerant plants: exploring its potential use as fodder, nutraceuticals or
717 phytotherapeutics in ruminant production. *J. Ethnopharmacol.* 267, 113464.

718 Ortiqova, L.S., 2019. Fodder halophytes for saline lands of Kyzylkum desert. *Amer. J. Plant*
719 *Sci.* 10, 1517-1526.

720 Ozturk, M., Altay, V., Güvensen, A., 2019. Sustainable use of halophytic taxa as food and
721 fodder: an important genetic resource in Southwest Asia. In *Ecophysiology, abiotic stress*
722 *responses and utilization of halophytes* (pp. 235-257). Springer, Singapore.

723 Panta, S., Flowers, T., Lane, P., Doyle, R., Haros, G., Shabala, S., 2014. Halophyte agriculture:
724 success stories. *Environ. Exp. Bot.* 107, 71-83.

725 Payen, S., Basset-Mens, C., Núñez, M., Follain, S., Grünberger, O., Marlet, S., Perret, S., Roux,
726 P., 2016. Salinisation impacts in life cycle assessment: a review of challenges and options
727 towards their consistent integration. *Intern. J. Life Cycle Asses.* 21, 577-594.

728 Pereira, C.G., Barreira, L., da Rosa Neng, N., Nogueira, J.M.F., Marques, C., Santos, T.F.,
729 Varela, J., Custodio, L., 2017 a. Searching for new sources of innovative products for the food
730 industry within halophyte aromatic plants: *In vitro* antioxidant activity and phenolic and
731 mineral contents of infusions and decoctions of *Crithmum maritimum* L. *Food Chem. Toxicol.*
732 107, 581-589.

733 Pereira, C.G., Barreira, L., Bijttebier, S., Pieters, L., Neves, V., Rodrigues, M.J., Rivas, R.,
734 Varela, J., Custodio L., 2017 b. Chemical profiling of infusions and decoctions of *Helichrysum*
735 *italicum* subsp. *picardii* by UHPLC-PDA-MS and in vitro biological activities comparatively
736 with green tea (*Camellia sinensis*) and rooibos tisane (*Aspalathus linearis*). *J. Pharm. Biomed.*
737 *Anal.* 145, 593-603.

738 Pereira, C.G., Barreira, L., Bijttebier, S., Pieters, L., Marques, C., Santos, T.F., Rodrigues, M.J.,
739 Varela, J., Custódio, L., 2018. Health promoting potential of herbal teas and tinctures from
740 *Artemisia campestris* subsp. *maritima*: from traditional remedies to prospective products. *Sci.*
741 *Rep.* 8, 4689.

742 Petropoulos, S.A., Karkanis, A., Martins, N., Ferreira, I.C., 2018 a. Edible halophytes of the
743 Mediterranean basin: Potential candidates for novel food products. Trends Food Sci. Tech. 74,
744 69-84.

745 Petropoulos, S.A., Karkanis, A., Martins, N., Ferreira, I.C., 2018 b. Halophytic herbs of the
746 Mediterranean basin: An alternative approach to health. Food Chem. Tox. 114, 155-169.

747 Rabhi, M., Ferchichi, S., Jouini, J., Hamrouni, M.H., Koyro, H.W., Ranieri A., Abdelly, C.,
748 Smaoui, A., 2010. Phytodesalination of a salt-affected soil with the halophyte *Sesuvium*
749 *portulacastrum* L. to arrange in advance the requirements for the successful growth of a
750 glycophytic crop. Biores. Technol. 101, 6822-6828.

751 Rodrigues, M.J., Slusarczyk, S., Pecio, L., Matkowski, A., Salmas, R.E., Durdagi, S., Pereira,
752 C., Varela, J., Barreira, L., Custodio, L., 2018. In vitro and in silico approaches to appraise
753 *Polygonum maritimum* L. as a source of innovative products with anti-ageing potential. Ind.
754 Crops Prod. 111, 391-399.

755 Sbai, H., Haouala, R., 2018. Responses of two Apiaceae species to direct iron deficiency. Int.
756 J. Photochem. Photobiol 2, 16–21.

757 Shahidi, F., Ambigaipalan, P., 2018. Omega-3 polyunsaturated fatty acids and their health
758 benefits. Ann. Rev. Food Sci. Technol. 9, 345-381.

759 Simopoulos, A.P., 2004. Omega-3 fatty acids and antioxidants in edible wild plants. Biol. Res.
760 37, 263-277.

761 Simpson, C.R., Franco, J.G., King, S.R., Volder, A., 2018. Intercropping halophytes to mitigate
762 salinity stress in watermelon. Sustain. 10, 681.

763 Singh, D., Buhmann, A.K., Flowers, T.J., Seal, C.E., Papenbrock, J., 2014. *Salicornia* as a crop
764 plant in temperate regions: selection of genetically characterized ecotypes and optimization of
765 their cultivation conditions. AoB PLANTS 6: plu071.

766 Stagnari, F., Maggio, A., Galieni, A., Pisante, M., 2017. Multiple benefits of legumes for
767 agriculture sustainability: an overview. Chem. Biol. Tech. Agric. 4, 1-13.

768 Stevanovic, Z., Stankovic, M.S., Stankovic, J., Janackovic, P., Stankovic, M., 2019. Use of
769 halophytes as medicinal plants: Phytochemical diversity and biological activity. Halophytes
770 and Climate Change: Adaptive Mechanisms and Potential Uses, 343.

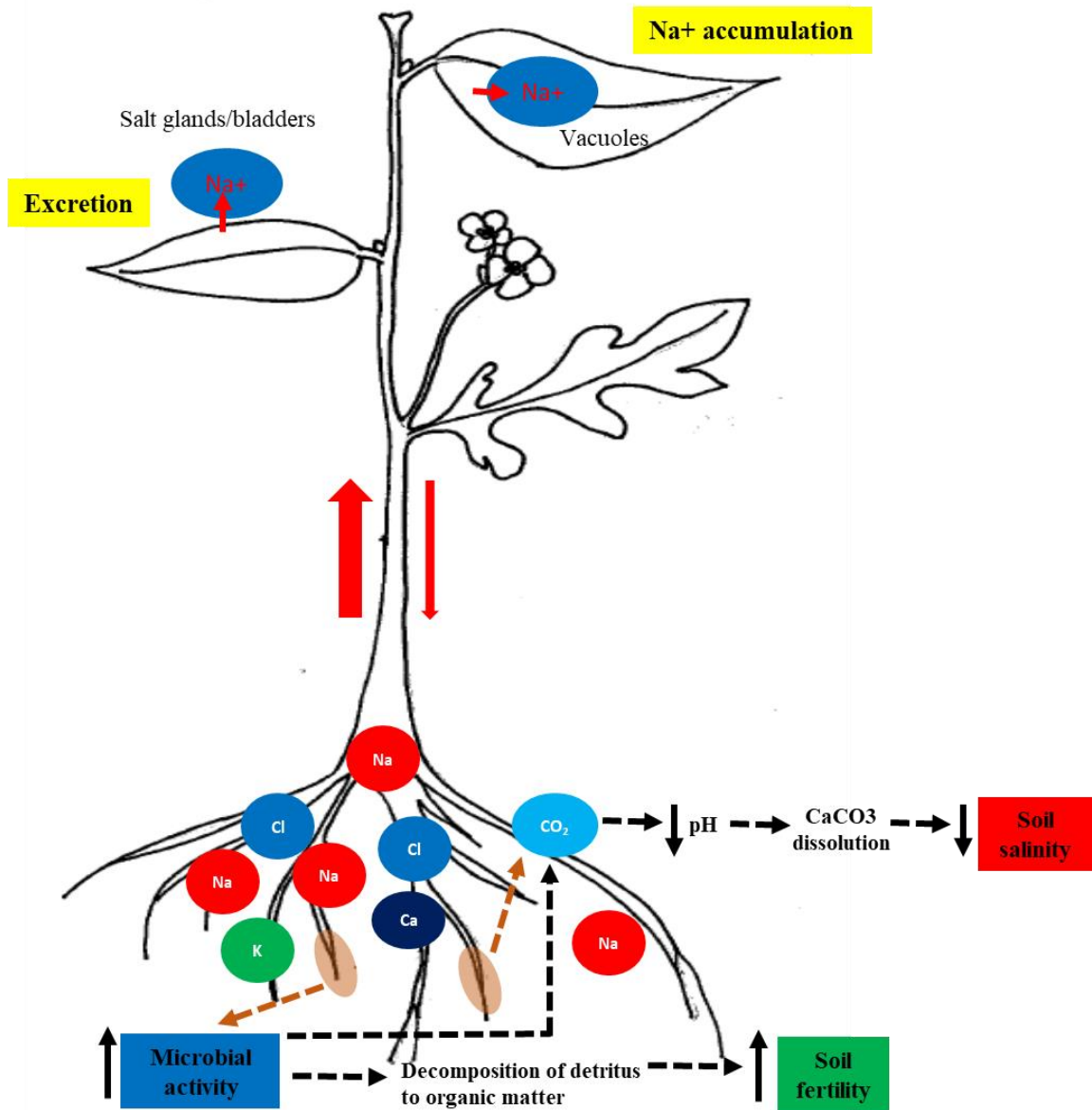
771 Turan, S., Cornish, K., Kumar, S., 2012. Salinity tolerance in plants: Breeding and genetic
772 engineering. Aust. J. Crop Sci. 6, 1337-1348.

773 Turcios, A.E., Cayenne, A., Uellendahl, H., Papenbrock, J., 2021. Halophyte plants and their
774 residues as feedstock for biogas production-Chances and challenges. Appl. Sci. 11, 2746.

775 United Nations (2018) 2018 Revision of World Urbanization Prospects.
776 [https://www.un.org/development/desa/publications/2018-revision-of-world-urbanization-
778 prospects.html](https://www.un.org/development/desa/publications/2018-revision-of-world-urbanization-

777 prospects.html).
778 Ventura, Y., Myrzabayeva, M., Alikulov, Z., Cohen, S., Shemer, Z., Sagi, M., 2013. The
779 importance of iron supply during repetitive harvesting of *Aster tripolium*. *Funct. Plant Biol.* 40,
780 968–976.
781 Ventura, Y., Sagi, M., 2013. Halophyte crop cultivation: The case for *Salicornia* and
782 *Sarcocornia*. *Environ. Exp. Bot.* 92, 144– 153.
783 Ventura, Y., Wuddineh, W.A., Ephrath, Y., Shpigel, M., Sagi, M., 2010. Molybdenum as an
784 essential element for improving total yield in seawater-grown *Salicornia europaea* L. *Sci.*
785 *Hortic.* 126, 395–401.
786 Uzilday, B., Ozgur, R., Sekmen, A.H., Yildiztugay, E., Turkan, I., 2015. Changes in the
787 alternative electron sinks and antioxidant defence in chloroplasts of the extreme halophyte
788 *Eutrema parvulum* (*Thellungiella parvula*) under salinity. *Ann. Bot.* 115, 449-463.
789 Weber, D.J., Ansari, R., Gul, B., Khan, M.A., 2007. Potential halophytes as source of edible
790 oil. *J. Arid Environ.* 68, 315-321.
791 Webb, J.M., Quintā, R., Papadimitriou, S., Norman, L., Rigby, M., Thomas, D.N., Le Vay, L.,
792 2012. Halophyte filter beds for treatment of saline wastewater from aquaculture. *Water Res.*
793 46, 5102-5114.
794 Wendelberger, K.S., Richards, J.H. 2017. Halophytes can salinize soil when competing with
795 glycophytes, intensifying effects of sea level rise in coastal communities. *Oecologia* 184, 729–
796 737. <https://doi.org/10.1007/s00442-017-3896-2>
797 Yuan, Z., Druzhinina, I., Labbé, J., Redman, R., Qin, Y., Rodriguez, R., Zhang, C., Tuskan, G.
798 A., Lin, F., 2016. Specialized microbiome of a halophyte and its role in helping non-host plants
799 to withstand salinity. *Sci. Rep.* 6, 32467.
800 Zerai, D.B., Glenn, E.P., Chattervedi, R., Lu, Z., Mamood, A.N., Nelson, S.G., Rat, D.T., 2010.
801 Potential for the improvement of *Salicornia bigelovii* through selective breeding. *Ecol. Eng.*
802 36, 730-739.
803 Zou, C., Chen, A., Xiao, L., Muller, H.M., Ache, P., Haberer, G., Zhang, M., Jia, W., Deng,
804 P., Huang, R., Lang, D., Li, F., Zhan, D., Wu, X., Zhang, H., Bohm, J., Liu, R., Shabala, S.,
805 Hedrich, R., Zhu, J.K., Zhang, H., 2017. A high-quality genome assembly of quinoa provides
806 insights into the molecular basis of salt bladder-based salinity tolerance and the exceptional
807 nutritional value. *Cell Res.* 27, 1327–1340.

808 Zuccarini, P., 2008. Ion uptake by halophytic plants to mitigate saline stress in *Solanum*
809 *lycopersicon* L., and different effect of soil and water salinity. *Soil Water Res.* 3, 62-73.
810



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813 **Figure 1.** Remediation effects of halophytes on saline soils.

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Table 1. Examples of successful and unsuccessful use of halophytes in intercropping (IC) and crop rotation (CR) systems, carried out under greenhouse conditions (G) or in field experiments (F)

Halophyte species	Crop species	Cultivation system	Experimental conditions	Successful responses	Unsuccessful responses	References
<i>Suaeda salsa</i> L.	<i>Lycopersicon esculentum</i> Mill	IC	G, closed insulated pallet	lower Na levels in the root medium and tomato leaves lower incidence of blossom end rot of tomato fruit	no effect on tomato growth reduction no effect on reduced tomato yield	Albaho and Green (2000)
<i>Salsola soda</i> L. <i>Portulaca oleracea</i> L.	<i>Lycopersicon esculentum</i> Mill	IC	G, soil-filled benches	higher PO ₄ ³⁻ and Ca ²⁺ uptake by tomato plants reduced Na level in tomato leaves higher tomato yield	lower tomato growth and yield by high sowing density of the halophytes	Graifenberg et al. (2003)
<i>Portulaca oleracea</i> L.	<i>Lycopersicon esculentum</i> Mill	IC	G, sandy soil-filled benches	higher tomato yield higher K absorption		Zuccarini (2008)
<i>Salsola soda</i> L.	<i>Lycopersicon esculentum</i> Mill	IC	G, sandy soil-filled benches		lower tomato plant biomass and lower fruit yield halophyte competition	Zuccarini (2008)
<i>Atriplex hortensis</i> L.	<i>Lycopersicon esculentum</i> Mill	IC	G, sandy soil-filled benches	higher tomato yield		Zuccarini (2008)
<i>Portulaca oleracea</i> L.	<i>Lycopersicon esculentum</i> Mill	IC	G, soil-filled pots	lower Na levels in tomato leaves and roots higher Ca and Mg levels in tomato leaves and roots higher K in tomato leaves	no effect on reduced fruit weight	Karakas et al. (2019)
<i>Salsola soda</i> L.	<i>Lycopersicon esculentum</i> Mill	IC	G, soil-filled pots	higher fruit weight under high salinity lower Na levels in tomato leaves and roots higher Ca and Mg levels in tomato leaves and roots higher K in tomato leaves		Karakas et al. (2019)
<i>Salsola soda</i> L.	<i>Capsicum annuum</i>	IC	G, hydroponics	higher fruit yield under moderate salinity	no effect on reduced fruit yield under severe salinity	Colla et al. (2006)
<i>Mesembryanthemum crystallinum</i>	<i>Vigna unguiculata</i>	IC	G, soil-filled plastic trays plus hydroponics	lower Na levels in soil and cowpea leaves lower chlorophyll loss lower decrease of photosynthesis rate		Nanhapo et al. (2017)
<i>Atriplex hortensis</i> L.	<i>Citrullus lanatus</i> (Thunb.)	IC	F, saline irrigation	higher watermelon yield	no reduction of soil salinity no effect on plant water status and fruit quality	Simpsons et al. (2018)
<i>Portulaca oleracea</i> L.	<i>Citrullus lanatus</i> (Thunb.)	IC	F, saline irrigation		no reduction of soil salinity no effect on plant water status and fruit quality lower watermelon yield (possible competition)	Simpsons et al. (2018)
<i>Bacopa monnieri</i> (L.) Wettst <i>Sesuvium verrucosum</i> Raf	<i>Zea mays</i>	IC	F	lower soil EC and pH higher soil porosity maize cultivation with high yield		Lastiri-Hernández et al. (2020)
<i>Suaeda salsa</i> <i>Medicago sativa</i> L.	<i>Gossypium hirsutum</i> L.	IC	F	lower soil EC, salt accumulation and pH higher soil porosity and organic carbon content higher root mass density and cotton yield		Liang and Shi (2021)

<i>Suaeda salsa</i> L. <i>Medicago sativa</i> L. <i>Cuminum cyminum</i> L.	<i>Gossypium hirsutum</i> L.	IC	F	lower soil salt accumulation	no effect on cotton yield and biomass	Guo et al. (2020)
<i>Bassia indica</i>	<i>Sorghum bicolor</i>	IC	F, different planting ratios	better quality, particularly with the 2/1 sorghum/bassia ratio	lower sorghum yield with 1/2 sorghum/bassia ratio due to halophyte competition	Hedayati-Firoozabadi et al. (2020)
<i>Kochia scoparia</i>	<i>Cyamopsis tetragonoloba</i> <i>Sesbania aculeata</i>	IC	F	higher leaf K levels, water content and chlorophyll higher forage yield in simultaneous intercropping with <i>C. tetragonoloba</i> and <i>. aculeate</i>		Ghaffarian et al. (2020)
<i>Sesuvium portulacastrum</i> L.	<i>Hordeum vulgare</i> L.	CR	G, Soil-filled pots	lower shoot Na levels higher shoot K levels and higher biomass production		Rabhi et al. (2010)
<i>Spinacia oleracea</i>	<i>Oryza sativa</i>	CR		Lower soil EC significant growth of rice		Muchate et al. (2018)
<i>Arthrocnemum macrostachyum</i>	<i>Hordeum vulgare</i> L. <i>Triticum durum</i>	CR	G, artificially salinized soil	lower Na levels in soil earlier, faster and better emergence of barley wheat germination		Barcia-Piedras et al. (2019)
<i>Glycyrrhiza glabra</i>	<i>Gossypium hirsutum</i> L./ <i>Triticum aestivum</i> L.	CR	F	lower Na levels in soil higher soil organic matter higher percentage of seed germination and yield		Kushiev et al. (2005)

Table 2. Examples of successful and unsuccessful use of halophytes in aquaponic systems. CW, constructed wetland; FWS, free water surface; SF, subsurface flow; RAS, recirculating aquaculture system; MBBR, moving bed bioreactor; BOD, biological oxygen demand; SS, suspended solids; TAN, total ammonium; DIN, dissolved inorganic nitrogen, DIP, dissolved inorganic phosphorus, TDN, total dissolved nitrogen.

Halophyte species	Aquatic animal species	Aquaponic system	Successful responses	Unsuccessful responses	References
<i>Salicornia europaea</i> L.	shrimp, sole and turbot	CW pilot filter beds integrated into a RAS	lower DIN under ambient nitrogen loading lower DIP	no significant removal of DIN under high TDN loading	Webb et al. (2012)
<i>Juncus kraussii</i>	rainbow trout (<i>Oncorhynchus mykiss</i>)	pilot-scale CW, SF	lower nitrogen and phosphorus active uptake by the soil-plant ecosystem increase with high nutrient levels. no effect of salinity on N removal	reduced P removal by salinity reduced growth of <i>J. kraussii</i> by salinity	Lymbery et al. (2006)
<i>Phragmites australis</i>	Pacific white shrimp (<i>Litopenaeus vannamei</i>)	pilot-scale CW unit: FWS and SF CWs arranged in series, integrated into an outdoor RAS	lower BOD ₅ , SS, TAN, nitrates and nitrites	scarce phosphate removal	Lin et al. (2003)
<i>Sesuvium portulacastrum</i> <i>Batis maritima</i>	platy fish (<i>Xiphophorus</i> sp.)	bench-scale marine aquaponic systems	lower nitrate and nitrite levels in water effluents		Boxman et al. (2017)
<i>Sesuvium portulacastrum</i> <i>Batis maritima</i>	red drum (<i>Sciaenops ocellatus</i>)	prototype, commercial-scale marine aquaponic system with MBBR and sand filter	efficient removal of N load prevention of nitrate accumulation production of organic fertilizer support of a high fish biomass density production of edible halophyte biomass		Boxman et al. (2018)
<i>Atriplex hortensis</i> <i>Salsola komarovii</i> <i>Plantago coronopus</i>	whiteleg shrimp (<i>Litopenaeus vannamei</i>)	marine aquaponic system	higher salinity: better growth performance of the shrimp lower salinity: better growth performance of the halophytes intermediate saline condition: optimal condition for the integrated shrimp-halophyte marine aquaponics	higher salinity: lower growth of halophytes and reduced nutrient uptake lower salinity: lower growth of the shrimps	Chu and Brown (2021)
<i>Halimione portulacoides</i>	flatfish (<i>Solea senegalensis</i> Kaup)	land-based aquaponic system with sand filter hosting the polychaete <i>Hediste diversicolor</i>	lower organic matter and DIN		Marques et al. (2017)
<i>Salicornia neei</i> Lag. <i>Paspalum vaginatum</i> Sw <i>Apium graveolens</i> L	Pacific white shrimp (<i>Litopenaeus vannamei</i>)	saline aquaponic system integrated or not with micronutrient supplementation in water or as foliar spraying	higher growth and biomass production of <i>P. vaginatum</i> with micronutrient supplementation in water	scarce development of <i>A. graveolens</i> plants in this aquaponic system no effect on <i>S. neei</i> growth by micronutrient supply in water lower shoot biomass of <i>S. neei</i> by foliar fertilization lack of knowledge on the toxicity of water supplemented with micronutrients to animals	Doncato and Costa (2021)

Conflict of Interest

The authors declare that they have no conflict of interest.

Credit author Statement

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