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

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Abstract:	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 to remove salt ions from the saline soils and restore biodiversity. The practices differ but usually involve intercropping, crop rotation, and aquaponics. By using this biological approach, 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 to remediate saline soils by highlighting some experimental activities carried out at laboratory and field levels in the last few years.
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.

Dear Editor,

We would like to propose to this “Environmental and Experimental Botany” special issue, a review entitled “**Halophyte based Mediterranean agriculture in the contexts of food insecurity and global climate change**”. This paper will focus on the sustainable agricultural practices based on the cultivation of halophytes to remediate saline soils and to create new high added value products, by highlighting some experimental activities carried out at laboratory and field levels in the last few years. We think that this field of utilisation of halophytes in agriculture could be of interest for the readers of EEB and hope that the journal will be interested in this manuscript.

Best Regards
Karim Ben Hamed

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

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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 Mediterranean halophytes have traditional multipurpose uses.
- Halophytes may find niches in the demanding Mediterranean market.

Abstract

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 to remove salt ions from the saline soils and restore biodiversity. The practices differ but usually involve intercropping, crop rotation, and aquaponics. By using this biological approach, 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 to remediate saline soils by highlighting some experimental activities carried out at laboratory and field levels in the last few years.

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

1. Challenges of agriculture in the Mediterranean area

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

The Mediterranean region is one of the hotspots of the global biodiversity, with a remarkable richness in cultivated and wild species characterising this area. Its flora diversity has an outstanding from 15000 to 25000 species, 60% of which are unique to the region according to the International Union of Conservation of Nature IUCN (IUCN, 2008). Meanwhile, the Mediterranean basin is among the most threatened regions by climate change in the world (IUCN 2008). The Intergovernmental Panel on Climate Change (IPCC) predicts temperatures in the Mediterranean area will increase between 2 and 4°C, whereas rainfall will decrease between 4% and 30%, by 2050 (IPCC, 2013). This situation could be concomitant with the increasingly frequent events of drought, extreme climatic events and agro-biodiversity loss, with the northern side of the region experiencing similar conditions to those occurring today on the southern shores. Most Mediterranean soils are calcareous and therefore offer limiting availability for some nutrients such as iron leading to chlorosis in several crops. Moreover, approximately 18 million ha, corresponding to 25 % of total irrigated land in the Mediterranean area, are salt affected (FAO, 2011). In Italy, salinization affects almost all regions, accounting approximately for 3.2 Mha of soil (Dazzi and Lo Papa, 2013). In Spain, about 3% of the 3.5 million hectares of irrigated land are severely affected by salts and another 15% is at serious risk (Acosta et al., 2011). In Tunisia, salinity affects 10 % of the total surface area and 20 % of irrigated lands. Water is a scarce resource in most of the Mediterranean countries. Nowadays, many southern Mediterranean countries exhibit water availability below the benchmark threshold of 1000 m^3/person/year. In addition, lower water availability than this threshold is also reported for some Northern countries such as Spain, Greece and Italy, although on average they exceed the 1000 m^3/person/year threshold (Mancosu et al., 2015). Agriculture is the main water-consuming sector, being responsible for about 70.7% of freshwater withdrawals, accounting for 45% in the North and 82% in South and East and weighs heavily on fertilizer consumption, estimated at 141.3 kg/ha (FAO, 2015). Problems of sea water intrusion due to groundwater overexploitation are currently encountered in coastal areas of Italy, Spain, Greece and North Africa (Garcia-Caparrós et al., 2017; Payen et al., 2016). The decreasing availability of freshwater makes increasingly necessary the use of saline-sodic and/or of treated wastewaters for irrigation to sustain crop productivity, with the consequence of increasing the risk of soil and water salinization (Oron et al., 2002).

2. Improving crop productivity: Could halophytes be part of the solution?

The most effective solution to meet the growing demand for food is to increase the productivity of already cultivated lands (FAO, 2011). Nevertheless, this agricultural intensification is often associated with a high cost, a large consumption of water, energy and pesticides, in addition to soil depletion, loss of biodiversity and climate change. The current agricultural practices are increasing soil and water salinity, and unsustainable water use is leading to growing scarcity. As a result, many already dry and water-scarce regions have been hampered by more frequent droughts severely affecting agriculture. An average of 2,000 hectares of irrigated land in arid and semi-arid areas across 75 countries are degraded by salt every day and water scarcity already affects every continent (FAO, 2011). An alternative solution to palliate this environmental problematic may be the restoration of non-arable or marginal lands in the Mediterranean area in countries like France, Spain, Greece and Turkey and in areas such as North Africa and the Middle East.

Considered also as marginal lands, the salt affected agricultural soils in the Mediterranean region could be suitable for growing salt tolerant crops (Glenn et al., 1998). One of the key factors to improve salt tolerance of commercial crops cultivated in salt affected soils is to reduce the amount of salt transported from roots to shoots. This can be achieved by grafting a salt-sensitive cultivar onto a salt-tolerant one, and by conventional breeding. However, these approaches can have some limitations such as the reproductive barriers and the risk of undesirable traits transfer (Turan et al., 2012). Transcriptome sequencing may provide a functional view of the mechanisms to salinity tolerance. In addition, the use of transgenic plants to achieve information about the response of higher plants to salinity is a strategy widely addressed in numerous research groups (Hernández 2019). Nevertheless, success has not been achieved at field level (Panta et al., 2014). Alternatively, soil phytodesalination, based on the capacity of some halophytes to accumulate enormous sodium quantities in their shoots, is proposed as an innovative and cost-effective biological approach to desalinize the soil and to increase the productivity of salt sensitive crops (Koyro et al., 2014).

Arid and desert lands are also abundant in the Mediterranean area, which reservoirs of water contain too high salt levels for irrigation of conventional salt-sensitive crops. Many of these barren lands can become productive by growing selected crop halophytes and implementing appropriate cultural practices using this store of brackish water for irrigation. There are also extensive coastal areas and sand dunes where halophytes can be irrigated with seawater without the risk of salt build up in the rhizosphere (Atzori et al., 2019).

3. Responses of halophytes to salinity under Mediterranean environment

Salt stress is one of the most important abiotic stress challenges affecting plant growth and productivity, particularly in arid and semi-arid climates (Hernández et al., 2017). The presence of phytotoxic ions (especially Na^+ and Cl^-) in soils and irrigation water is a serious problem for agriculture practices in areas such as the Mediterranean basin (Acosta-Motos et al., 2017). According to the ability of plants to grow in saline environments, they can be classified in two main groups: glycophytes (salt-sensitive plants) and euhalophytes. The behaviour of both groups to the salinity challenge is quite different in terms of ion uptake, ion exclusion and/or compartmentalization, osmotic regulation, gas exchange responses, and photosynthetic performance, including chlorophyll contents and chlorophyll fluorescence, as well as antioxidant metabolism (Stepien and Johson 2009; Debez et al. 2013; Bose et al., 2014; Acosta-Motos et al., 2017). At the short-term, salinity impose an osmotic stress that can avoid water absorption by the roots, causing a water stress (Acosta-Motos et al., 2017). At the long-term, salinity also triggers a direct damage to the plant due to the accumulation of phytotoxic ions, which can lead to a number of harmful effects, including nutrient imbalance, enzymes inactivation and photosynthesis decline (Hernandez et al., 1999; Acosta-Motos et al., 2015). However, in addition to the osmotic and toxic effects, salt stress also induces an oxidative stress both at short and long terms (Hernández and Almansa 2002; Hernández et al., 2000; Acosta-Motos et al., 2015; Ellouzi et al., 2011). In order to optimal growth under high saline conditions, salt-tolerant plants, such as halophytes, have developed a series of adaptations, including morphologic, anatomical and biochemical adaptations, (Flowers and Colmer, 2008), the latter comprising ion homeostasis, regulation of osmolytes accumulation and, most importantly, up-regulation of antioxidative defences (Ozgur et al., 2013; Bose et al., 2014, Ben Hamed et al., 2020).

3.1. Morphological adaptations

Salinity treatment has an evident effect in plant morphology, anatomy and ultrastructure. The presence of high salt levels leads to a decline in plant growth, especially in the aerial part, with a reduction in leaf area. This response is considered as an avoidance mechanism in order to limit water loss by transpiration (Acosta-Motos et al. 2015). This growth decline implies an increase in root/shoot ratio, a response that can favour the accumulation of phytotoxic ions in roots, preventing their translocation to the aerial part (Acosta-Motos et al. 2015; 2017). Increased leaf thickness is a general response for both in glycophytes and halophytes plants. In *Eugenia myrtifolia* plants, 80 mM NaCl treatment for 30 days increased leaf thickness due to an increase in palisade parenchyma (Acosta-Motos et al. 2015). Similarly, an increase in leaf thickness was produced in *Crithmum maritimum*, *Cakile maritima*, *Atriplex halimus* and *Salicornia fruticosa* when grown in the presence of 100-300 mM NaCl (Ben Hamed et al., 2004; Debez et al., 2012; Yepes et al. 2018). Increased leaf thickness implies enhanced succulence and, as a consequence, leaf water content, which dilutes tissue-accumulated NaCl and, in turn, salt-induced damage (Debez et al., 2010; Rangani et al., 2016; Yepes et al. 2018). In the extreme halophyte *Salvadora persica* L., succulence was correlated with the degree of external NaCl levels. Thus, no succulence was observed at moderate or high salinity (250-750 mM), but under extreme salt concentration (1000 mM NaCl) increased succulence by 37%, in relation to control plants (Rangani et al. 2016). Likewise, salt treatment increased leaf succulence in *Atriplex halimus*, *Salicornia fruticosa* and *Cakile maritima*, a response that correlated with increased Na^+ contents in the leaf tissue (Yepes et al., 2018). However, a direct correlation between water relations and the salt-induced growth promotion in halophytic plants could not be established (Yepes et al., 2018). Another morphological adaptation of halophytes to salinity is based on the reduction of leaf canopy, number of branches and leaf area (Ranganni et al., 2016).

The chloroplast ultrastructure as well as the function of the photosynthetic machinery are affected by the presence of salts in the external media. However, the ultrastructure of other cell organelles, such as mitochondria and peroxisomes, are less affected. In the case of pea plants growth in the presence of NaCl, mitochondria displayed a lower number of cristae and lower electron density (Hernández et al., 1995). In addition, it has been reported that NaCl produced a disorganized and dilated thylakoids, and increased the number and size of plastoglobuli in pea, *Cistus* sp. and *Arbutus unedo* plants (Hernández et al., 1995; Sánchez-Blanco et al., 2004; Navarro et al., 2007). Concerning halophyte species, the chloroplast ultrastructure of *Arthronecmum macrostachyum* plants was affected in function of the external level of salinity;

at 510 mM NaCl, the optimal salt level for plant growth, chloroplasts showed the typical lenticular shape and thylakoidal structure (Trotta et al., 2012). However, when *A. macrostachyum* plants were grown at lower or higher external salt levels than the optimal one, chloroplasts showed ultrastructural alterations: at lower NaCl concentrations (0-80 mM NaCl), plants showed increased chloroplast size with thick grana and dilated thylakoids, whereas at higher NaCl levels (1030 mM), chloroplasts displayed an elongated shape with underdeveloped grana (Trotta et al., 2012).

3.2. Osmotic adjustment

Salt-treated plants have to overcome the lower osmotic soil potential due to the external salt accumulation. Osmotic adjustment occurs primarily with respect to the ions present in the soil (mainly Na^+ and Cl^-) (Flowers and Colmer 2015). Key to salt tolerance for halophytes is their capacity to regulate the uptake of Na^+ and Cl^- while preserving cytoplasmic Mg^{2+}, Ca^{2+}, and K^+ contents at levels necessary for maintaining essential enzyme activities. Halophyte plants display different mechanisms to avoid the toxic effects produced by the phytotoxic ions, including cellular dehydration, mineral imbalances, reduced gas exchange parameters and increased reactive oxygen species (ROS) generation, among other effects (Flowers and Colmer 2015). In that regards, ion transporters and membrane ATPases play key roles in numerous halophytes (Padan et al. 2001). The efficient Na^+ accumulation in vacuoles is considered as an important hallmark of halophytes (Song and Wang 2015), and Na^+/H^+ antiporters seems to contribute efficiently for the vacuolar Na^+ compartmentalization (Hasegawa 2013). The accumulation of Na^+ and Cl^- in the vacuole stimulates water uptake and therefore favour the increase of stem and leaf succulence. Moreover, Na^+ entry to the plant can be limited to the roots (Song and Wang, 2015). Importantly, activity of vacuolar membrane and plasma membrane ATPase contribute to maintaining pH and electrochemical differences across the membrane. In this sense, membrane ATPase activities significantly increased in *Suaeda salsa* under salinity conditions (Chen et al., 2010; Yang et al., 2010). Na^+ can be also excreted by using specialised leaf structures such as salt glands, salt bladders and salt hairs (Shabala, 2013). In addition, halophytic plants are able to regulate Na^+ and Cl^- uptake and transport. Na^+ efflux across leaf or root plasma membrane is carried out via Salt-Overly-Sensitive1 (SOS1) Na^+/H^+ antiporter (Song and Wang, 2015). Less information is available regarding Cl^- homeostasis in halophyte plants under conditions of high salinity, although it seems that the uptake of external Cl^- is due to an anion channel (Flowers and Colmer 2008; Bazihizina et al., 2019). Osmotic adjustment is also achieved by the accumulation of certain organic solutes, also known as osmolytes, in the cytosol. These include amino acids, mainly proline, quaternary ammonium compounds, tertiary sulphonium compounds, sugars and sugar alcohols (Flowers and Colmer, 2015). In addition, some osmolytes function as chemical chaperones as well as hydroxyl radical scavengers (Flower and Colmer, 2015).

3.3. Photosynthesis-related changes

It is well known that salt stress has a negative effect on gas exchange parameters, including net photosynthesis rate (P_N) and stomatal conductance (Acosta-Motos et al., 2017; Garcia-Caparros and Lao, 2018). However, the negative effect of salinity in the photosynthetic process is much more severe in salt-sensitive than in salt-tolerant species. In this regard, halophytes display different mechanisms to protect the photosynthetic machinery such as acquiring the Kranz anatomy to present chloroplast dimorphism or reducing stomata density (Rangani et al., 2016). Some halophytes are also able to change the CO_2 assimilation strategy from C_3 or C_4 to CAM, or from C_3 to C_4 photosynthesis in response to salinity, as described in *Atriplex lentiformis* (Meinzer and Zhu, 1999). The mentioned strategies can minimize ROS overgeneration during the saline challenge given that C_3 photosynthesis is more prone to oxidative damage by the activation of photorespiration (Bose et al., 2014).

At the biochemical level, the maintaining of chlorophyll contents in salinity conditions is another adaptation that protect the photosynthesis process in halophyte plants (Li et al. 2020; Stepien and Johnson, 2009; Acosta-Motos et al., 2015, 2017). In addition, an up-regulation of some photosynthesis-related proteins has been reported in the halophyte *Porteresia coarctata* when grows under high NaCl levels (Sengupta and Majumder, 2009). All these adaptations give rise to an effective photosynthetic system that allows halophytes to survive in saline soils.

Chlorophyll fluorescence is a useful tool to analyse the effect of environmental stresses in the photosynthetic process (Maxwell and Johnson, 2000). Fv/Fm (maximal quantum efficiency of photosystem II, PSII), Y(II) (PSII quantum yield), qN and qP (the coefficients of non-photochemical quenching and photochemical quenching, respectively) and NPQ (non-photochemical quenching) are good markers to analyse the effects on the PSII (Maxwell and Johnson, 2000) of environmental stressors such as salinity (Acosta-Motos et al 2015, 2017). In salt-sensitive plants, long-term NaCl treatment produced a decline in the photochemical quenching parameters (Fv/Fm, Y(II) and qP), whereas the non-photochemical quenching parameters (NPQ) remained unchanged or increased (Stepien and Johnson, 2009; Acosta-Motos et al., 2015; Cantabella et al., 2017). However, in most halophyte plants, the exposure to moderate or high NaCl levels did not alter chlorophyll fluorescence parameters, and even increased Fv/Fm and Y(II), whereas only extreme NaCl concentrations (up to 750 mM-1000 mN NaCl) decreased these parameters (Stepien and Johnson, 2009; Uzilday et al., 2015; Rangani et al., 2016).

3.4. Antioxidative metabolism

It is well known that salt stress induces an oxidative stress at the subcellular level mediated by the over-production of ROS (Hernández et al., 1993; Hernández et al., 1995). Likewise, extreme NaCl concentrations also induce an oxidative stress, which is reflected on increased levels of oxidative stress parameters such as lipid peroxidation, electrolyte leakage and ROS content (Ben Amor et al., 2006; Rangani et al., 2016). In order to face salt-induced oxidative stress, plants have developed a complex antioxidant defence machinery including enzymatic and non-enzymatic antioxidants (for more information please consult some revisions focus on halophyte plants, as Ozgur et al., 2013, Bose et al., 2014; Ben Hamed et al., 2021). Some authors have reported salt-induced activation of antioxidant defences as one of the mechanisms to confer salt tolerance (Hernández et al., 2000; Mittova et al., 2003). In contrast, others correlated salt tolerance trait with higher constitutive levels of antioxidant defences (Hernández et al., 2003; López-Gómez et al., 2007).

The levels of lipid peroxidation are a useful target for assessment of oxidative stress in plants, since hydroxyl radical is the most reactive form of ROS and may initiate lipid peroxidation by attacking polyunsaturated fatty acids (Hernández and Almansa, 2002). In the case of halophytes, lipid peroxidation has been mostly evaluated by measuring thiobarbituric reactive substances (TBARS) (Ozgur et al., 2013). In this sense, the damage produced by salinity varied with the species, the saline levels (from 150 to 1000 mM), and the duration of the treatment (from one week to 45 days) (Ozgur et al., 2013). In addition to lipid peroxidation, electrolyte leakage, direct evidence of membrane damage through increased permeability, is a complementary tool to determine ROS-caused damage to membranes (Ben Amor et al., 2006; Ben Hamed et al., 2007).

Several studies showed that halophytes had higher constitutive antioxidant activity than glycophyte species (Ozgur et al., 2013). Thus, halophytes are endowed with efficient antioxidant mechanisms that are even up-regulated when grow in saline environments. The existence of constitutively higher superoxide dismutase (SOD) levels in halophytes has been suggested as a key element in the adaptation of these plants to salinity (Bose et al., 2014). According to this concept, the rapid conversion of $O_2^{\cdot-}$ to H_2O_2 would rely in the role of the latter as a second messenger for early adaptive responses, while other enzymatic antioxidants may be involved in decreasing H_2O_2 levels once early signalling events have occurred (Miller et al. 2010; Bose et al., 2014). Extensive scientific literature reported changes on the main antioxidant enzymes under salinity conditions. For example, new catalase (CAT) and SOD isoforms were induced in *Suaeda maritima* in the presence of 255 mM NaCl (Mallik et al., 2011). In the halophyte *Eutrema parvulum*, 300 mM NaCl induced the expression of redox regulatory enzymes as well antioxidant enzymes such as Fe-SOD, Cu, Zn-SOD and the ascorbate-glutathione (ASC-GSH) cycle enzymes, which resulted in reduced H_2O_2 accumulation and lipid peroxidation, protecting the photosynthetic machinery (Uzilday et al., 2015). Thus, halophyte plants may cope with the salt-induced oxidative stress by displaying an efficient constitutive antioxidant machinery, the induction of new antioxidant isoforms or increased antioxidant enzyme activities (Ben Amor et al., 2006; Ozgur et al., 2013, Mallik et al., 2011; Rangani et al., 2016).

Moreover, non-enzymatic antioxidants are key factors preventing the deleterious effects of ROS. In general, halophytes contain higher basal levels of some non-enzymatic antioxidants than glycophytes such as α-tocopherol and polyphenols (Ellouzy et al., 2011; Ksouri et al., 2009). Proline, besides being a compatible solute, is also considered as a non-enzymatic antioxidant due to its capability to scavenge ·OH radicals (Bose et al., 2014). In that regards, increase in proline levels has been reported in different halophytes as a response to external salinity (Uzilday et al., 2015; Bose et al., 2014). Reduced ascorbate (ASC) and reduced glutathione (GSH) are redox-active compounds that have an important role in balancing cell redox state (Noctor and Foyer, 1988). The ascorbate redox state increased in *Cakile maritima* when grow at 100 mM NaCl, but suffered a strong decline at higher NaCl levels (400 mM), motivated by the increase in ascorbate peroxidase (APX) activity (Ben Amor et al., 2006). *Suaeda salsa* increased ASC, GSH, and the APX and GR (glutathione reductase) enzymatic activities to scavenge the H_2O_2 produced under saline conditions (Cai-Hong et al., 2005). In other cases, salinity increased GSH pool, as described in *C. maritima* and *Suaeda maritima* (Ben Amor et al., 2006; Alhdad et al., 2013), or had no effect on the glutathione metabolism, as observed in *Hordeum maritimum* (Hafsi et al., 2010).

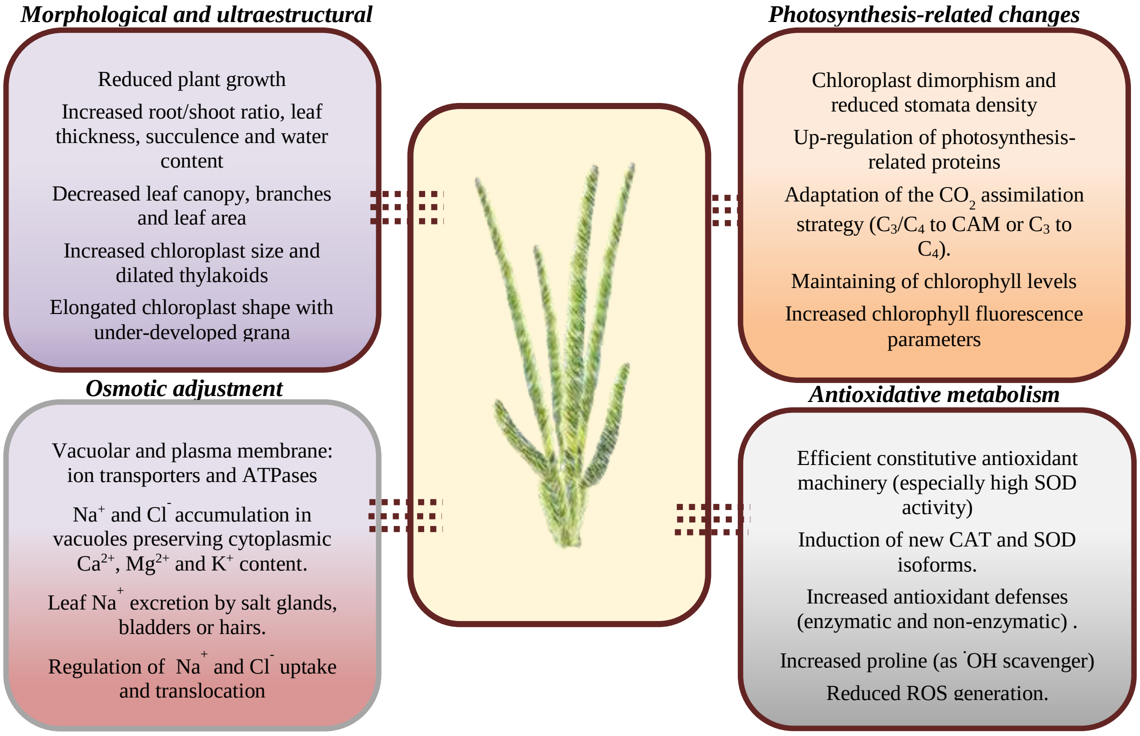

Figure 1. Adaptation of halophyte species under high external NaCl concentrations. Four components of the plant response to salinity conditions can be distinguished schematically: morphological/ultrastructural, photosynthesis, osmotic and antioxidative metabolism-related adaptations. CAT: catalase; SOD: superoxide dismutase; ROS: reactive oxygen species.

4. Alternative agricultural practices in salt-affected soils using halophytes

A promising strategy to allow cultivation of conventional crops in saline soils is the use of halophyte plants. Thanks to their ability to extract salts from the soil and to accumulate them in their tissues, to allow the osmotic adjustments needed for their survival, halophytes have the potential to improve the physico-chemical properties of the soil. The reduced salt levels in the crop rhizosphere would result in a better adaptation of the salt-sensitive plants to these extreme environments, allowing their cultivation in marginal underutilized lands or in salt-affected agricultural soils (Garcia-Caparros et al., 2020). Different strategies can be adopted to achieve this desirable outcome, such as halophytes integration in intercropping or rotation systems, which could require of domestication of some halophyte species or ecotypes particularly promising.

4.1. Intercropping halophytes and crop species

The use of intercropping systems in agriculture is a traditional practice diffused worldwide since long time, based on the evidence of reciprocal benefits and yield increase in comparison to the monoculture in a low input system (Glaze-Corcoran et al., 2020; Maitra et al. 2021). In intercropping systems, two (or more) crops are cultivated simultaneously in the same row, or in adjacent rows close enough for biological interaction, for an extensive proportion of their growth period (Figure 2). This cultivation method, that is still largely diffuse in developing countries, in the first world has been almost completely substituted by intensive monoculture systems, using high-yielding cultivars, mechanization, and massive application of chemicals (such as fertilizers and pesticides) (Machado, 2009, Ehrmann and Ritz, 2014, Maitra et al., 2021). Recently, however, the growing need of sustainable production systems, as well as the advances in the knowledge of the biochemical-physiological mechanisms at the basis of the success of intercropping cultivation, has attracted the interest of farmers towards the reintroduction of polycultures also in developed countries (Bracken, 2008; Gaudio et al., 2019; Glaze-Corcoran et al., 2020).

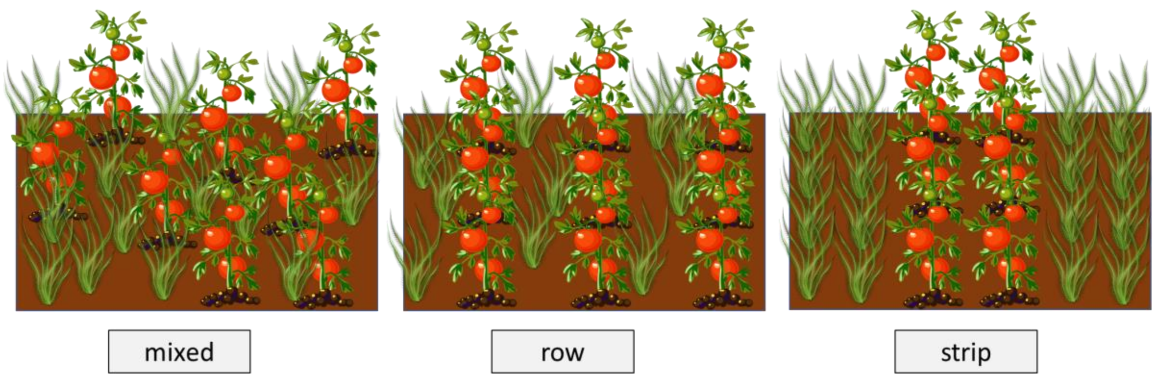

Figure 2. Examples of crop mixing/intercropping systems. In the mixed system the two crops are cultivated without any specific order or randomly. In the row system only one crop is planted in a row and the other one is present without a specific order. In the strip system both crops are grown in rows.

Particularly attracting is the use of halophytes as intercropping species to mitigate the salt stress for sensitive crops, thus overcoming the limits for their successful cultivation in marginal areas. Despite this increasing interest, few researches were conducted to validate the effectiveness of integrating halophytes in intercropping systems, and most of the published results were obtained in greenhouse experiments. A number of these researches used tomato (*Lycopersicon esculentum* Mill) as the cash crop species, being tomato one of the most cultivated species worldwide, particularly in the Mediterranean region. Albaho and Green (2000) tested the ability of *Suaeda salsa* L. to alleviate saline stress when intercropped with tomato in a closed insulated pallet. Despite a significant reduction of sodium levels both in the root medium (-50%) and in tomato leaves (-38%), the halophyte species did not prevent the growth reduction of tomato plants nor affected the tomato fruit yield. However, in the spring trials, incidence of blossom end rot (a physiological disorder caused by local Ca^{2+} deficiency) of tomato fruit was almost halved in the intercropped plants. Interestingly, Graifenberg et al. (2003) found an increased uptake of PO_4^{3-} and Ca^{2+} of tomato plants when cultivated with *Salsola soda* L. and *Portulaca oleracea* L. (purslane) in soil-filled benches of a greenhouse. The same authors observed a reduced Na accumulation in tomato leaves and a 22% and 33% increase in tomato yield by co-cultivation with *S. soda* and *P. oleracea*, respectively. However, a high sowing density of these two halophytes resulted in a negative effect on tomato growth and yield. This result highlights one possible limit of the intercropping systems, *i.e*. the competition among intercropped plants for light, nutrients and water, ultimately leading to a crop yield lower than in monoculture. Therefore, care must be given to the use of a balanced mix of the halophyte and cash crop plants to ensure low competition between species and an efficient utilization of the natural resources. The choice of the best performing intercropping species is also a determinant factor of a successful cultivation system. Indeed, another research on consociated cultivation of tomato and halophytes revealed a variable capacity to reduce salt levels and to increase fruit yield by *P. oleracea* L., *S. soda* L. and *Atriplex hortensis* L. (Zuccarini, 2008). Specifically, consociation with *P. oleracea* gave the best results, increasing tomato yield of about 44%, and enhancing K and N absorption, while *S. soda*, due to its fast growth, competed with the crop and nullified the benefits linked to the desalting activity. Differently, Karakas et al. (2019) reported a better performance of tomato plants grown in consociation with *S. soda* than with *P. oleracea*, and did not observe any competition between the consociated species, attributing this behaviour to the lower seed density of the halophytes used with respect to Zuccarini (2008). *S. soda* was also efficient when consociated with pepper (*Capsicum annuum*), which yield significantly increased under moderate (4 dS m^{-1}) but not under severe (7.8 dS m^{-1}) salinity levels (Colla et al., 2006).

The few examples reported above underline the need of a careful design of the mixed cultivation, not only in terms of choice of the best halophyte species, but also in the crop/halophyte seed (or plant) density, to reduce the competition for mineral nutrients, light and water.

The positive influence of halophytes in reducing the salt levels and alleviating stress symptoms (as reduced chlorophyll levels and photosynthesis rate) was verified in a mixed culture of cowpea (*Vigna unguiculata*) (salt sensitive species) and ice plant (*Mesembryanthemum crystallinum*) (salt accumulating halophyte), though a reduced growth of cowpea under moderate saline conditions was observed (Nanhapo et al., 2017).

Generally, the intercropping systems have been successful in ameliorating plant adaptation to salinity and in increasing crop yield under greenhouse conditions, while there is still the need to validate these results in field trials, because of the few studies conducted in open field and sometimes there is contradictory evidence. While all the examples reported above referred to experiments conducted in greenhouse, Simons et al. (2018) verified the feasibility of intercropping watermelon (*Citrullus lanatus* (Thunb.) cv. Matsum. and Nakai) with halophytes to mitigate the negative effects of saline irrigation water both in greenhouse and field experiments. The results indicated that, despite the good performance of *A. hortensis* L. (garden orache) and *P. oleracea* L. in greenhouse trials, these species were unable to reduce soil salinity in field conditions. Moreover, no influence was observed on plant water status and fruit quality of intercropped watermelon plants. However, intercropping with orache increased watermelon yield.

A three-year field experiment with cotton (*Gossypium hirsutum* L.)/*Suaeda salsa* and cotton/alfalfa (*Medicago sativa* L.) intercropping systems indicated the efficiency of this agronomic strategy in decreasing soil electrical conductivity, salt accumulation and pH, and in increasing soil porosity and organic carbon content (Liang and Shi, 2021). Cotton/*S. salsa* intercropping also led to increase in root mass density in cotton plants, and both intercropping systems resulted in increased cotton yield in two of the three years of trials as compared to the traditional cotton monoculture. Similarly, the rate of soil salt accumulation, a phenomenon that usually occurs following drip irrigation, was reduced when cotton was cultivated in intercropping with *S. salsa*, *M. sativa* L., or *Cuminum cyminum* L. (Guo et al. 2020). Such a result was related to the reduced soil surface evaporation due to the canopy cover of the halophytes, that intercepted a fraction of the solar radiation reaching the soil surface and reduced the wind speed. The presence of halophytes also reduced the salt level in the 0-40 cm and 0-100 cm deep soil layers but had no effect on cotton yield and biomass.

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

4.2. Crop rotation

To maximize the productivity of an intercropping system, crops with different nutrient requirements, rooting ability, canopy shape and height, must be chosen, also taking care to avoid the onset of competition between species. Moreover, it is undoubted that intercropping systems, despite of their many advantages, require more manpower, considering most modern farm machinery (both for planting and harvesting) designed to work on monocultures (Maitra et al., 2021). While intercropping is based on the co-cultivation of different plant species, crop rotation, or sequential cropping, is set up on temporal succession of two or more crops (Figure 3, Dury et al., 2012). Therefore, crop rotation can encompass some benefits of both intercropping and monoculture. The basic principle of crop rotation is the cultivation of one crop able to restore the nutrients taken up by the previous one, in order to limit the use of fertilizers, thus reducing the environmental impact of agriculture. One well-known example is nitrogen restoration operated by leguminous plants grown in succession of cereals or other crops (Stagnari et al., 2017). Of course, rotation should also be economically sustainable, so the plant species used for the sequential cropping are usually chosen among the cash crops or the forage species, to ensure a constant income over time (Dogliotti et al., 2004).

In the case of halophytes, the economic profitability must go hand in hand with their desalting ability, which is the main benefit brought by their use as rotating crop. Managing crop rotation in salt-affected soils needs to select suitable crops (species or cultivars) with varying degree of salt tolerance and high economic value to be grown after variable extent of soil reclamation achieved thanks to halophyte cultivation.

Figure 3. Crop rotation is based on temporal succession of two or more crops in the same field

A small-scale experiment carried out in soil-filled pots proved the ability of *Sesuvium portulacastrum* L. to desalting an experimentally salinized soil that, after plant removal, was used as substrate for barley (*Hordeum vulgare* L.) cultivation (Rabhi et al., 2010). This research demonstrated a better growth performance of the test culture in comparison to the control soil (without halophyte pre-cultivation), and lower Na^+ and higher K^+ levels in the barley shoots, suggesting the possibility of a successful employment of this halophyte to restore salt-affected fields for a subsequent cultivation of glycophyte crops. The desalination potential of *S. portulacastrum* was also demonstrated in larger scale field plots (Muchate et al., 2016). Another small-scale field experiment showed that the plantation of *Spinacia oleracea* in saline soil considerably decreased the electrical conductivity of the soil by 1.6 dS/m over 90 days of plantation. Subsequent to this growth period, the phytodesalinized soil supported the significant growth of rice (Muchate et al., 2018).

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

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

4.3. Halophyte domestication

Besides the use of halophytes in intercropping or rotation systems, two possible approaches to achieve a saline agriculture are: i) improving the salt-tolerance of cultivated crops, or ii) domestication of halophytes. This second approach is a needed step for profitable cultivation of halophytes. A major impediment to the massive use of halophyte plants in agriculture is the standardization of their performance, being halophytes mainly wild plants. Another constraint is the need to ensure the farmers the availability of a constant supply of the most suitable species. However, the main limit is probably related to the low growth rate, uneven seed germination, and the accumulation of toxic or bitter compounds in their tissues, characters that in cash crops species have been ameliorated by the long-term process of domestication (Gepts, 2004). Brown et al. (2014) discussed a strategy for domestication of wild halophytes for their employment as seawater-irrigated crops, based on the approached used for domestication of other wild species. One first aspect identified by these authors is the need to choose the wild species based on the location where the cultivation might be set up. In other words, latitude, environmental parameters, proximity to the coast, and other characteristics of the native place of the wild species must be as similar as possible to those of the agronomic fields where the crop might be grown. Also, a good knowledge of the life cycle of the wild species in their native environment is pivotal in driving the choice of the best candidate species. After this first step, several crop cycles must be operated until the occurrence of the so-called domestication syndrome, i.e. the modification of those traits indicative of the divergence of the cultivated species from its wild ancestor towards domestication, such as synchronization of flowering, fruit ripening, seed germination, loss of bitterness, reduced content of toxic compounds, increased fruit and seed size (Meyers et al., 2012). Another important objective of plant domestication is the shift of the metabolic resources towards aboveground, economically interesting, organs (leaves, fruit and seeds). Domestication via mass selection is time consuming and would allow fixing only few desirable traits. However, it allows selection of parent lines for selective breeding programs. An example of this approach in halophyte domestication is reported by Zerai et al. (2010), who adopted two breeding programs involving also hybridization and pedigree breeding, producing cultivars of *Salicornia bigelovii* Torr with a noteworthy phenotypic variability and higher seed yields or higher biomass yield, in the lines selected by Eritrea or Arizona breeding programs, respectively. Though none of these lines were tested in open field conditions and introduction of additional traits is desirable, the research proved the feasibility of developing a halophyte crop by conventional breeding methods. The improvement of crop characteristics by plant breeding (screening, recurrent selection, and interspecific hybridization) takes many generations of crosses and requires several experiments, sometimes unsuccessful and often lasting decades. This process is just at the beginning for halophytes, so many efforts are still to be done to achieve the desirable goal of making halophytes increasingly adaptable to sustainable farming systems. A possible difficulty in the domestication programs could derive from the limited availability of germplasm collections to sustain the breeding tests. Therefore, it is mandatory to collect and preserve valuable germplasm as a pre-requisite for research and breeding programs.

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

4.4. Halophyte aquaponics

The capacity of halophyte plants to uptake great amounts of salt ions and to adapt to extreme environments, hardly suitable for conventional crops, makes them optimal candidates for the design of marine aquaponics systems. Aquaponics is a multitrophic food production system integrating aquaculture, *i.e.* fish (or other aquatic animal species) farming, with hydroponic plant production (König et al., 2018). Traditional aquaculture has a heavy environmental impact, due to the release of high nutrient loadings into the water bodies and the great water consumption (Klinger and Naylor, 2012). In the light of the efficient use of water resource, the development of recirculating aquaculture systems (RAS) minimizes the water discharges to the environment by treating and reusing up to 90-99% of water (Badiola et al., 2012). However, a certain degree of freshwater exchange is still needed to avoid accumulation of organic wastes and inorganic nutrient residues (mainly nitrogen and phosphorus) over the threshold limits. The integration of plant cultivation in RAS has the potential to establish a zero-water discharge system. The effluents from aquaculture flow in fact into the hydroponic system where bacteria convert inorganic nitrogen into nitrites and nitrates that are absorbed by the plants as nutrients. The water is then recirculated back to the aquaculture system. In the case of marine aquaculture, halophytes are the most eligible species. A recent review by Custodio et al. (2017) evaluated the information deriving from published researches on halophyte ability to remediate effluents from aquaculture systems. The most studied species were *Aster tripolium* (5 studies), *Salicornia europaea* (4 studies), *Phragmites australis* (3 studies) and *Salicornia dolichostachya* (2 studies), and the experiments were set up in different geographic areas with diverse climates. The majority of these studies highlighted a good efficiency of nitrogen and phosphorus removal provided by halophytes, supporting the potential of profitable incorporation of these plants into integrated multi-trophic aquaculture (IMTA) systems.

Integration of plant production into aquaculture systems, besides the ecological benefits, in terms of water and energy saving and reduced waste release into the environment, may provide additional income if valuable plant species are used. Care must be addressed in the design of an efficient aquaponic system by selecting the most appropriate plant species, as well as the best ratio of fish feed to plant growing area, or, alternatively, the best ratio of hydroponic tank volume (or plant density) to fish production volume (Boxman et al., 2017). These authors observed a positive contribution of *Sesuvium portulacastrum* and *Batis maritima*, grown hydroponically in diluted sea water, in lowering the nitrate levels of water effluents deriving from the platy fish (*Xiphophorus* sp.) tank.

An efficient growth performance of whiteleg shrimp (*Litopenaeus vannamei*) and some halophytes (*Atriplex hortensis*, *Salsola komarovii* and *Plantago coronopus*) was achieved by Chu and Brown (2021) in a marine aquaponic system by adjusting salinity to a compromise level compatible for both the animal and the plant species.

Interestingly, Maciel et al. (2020) observed a modification of the lipidome of two halophytes (*Salicornia ramosissima* and *Halimione portulacoides*) cultivated in a marine aquaponic system in comparison to the wild populations. Specifically, both halophytes presented higher levels of glycolipids (and *H. portulacoides* also of phospholipids) bearing n-3 fatty acids, that undoubtedly increase the market value of these species, having the n-3 polyunsaturated fatty acids recognised healthy properties (Shahidi and Ambigaipalan, 2018).

In the light of the few examples reported above, it emerges that halophytes could be successfully integrated in marine aquaculture systems to meet the need to increase the production of fishes, crustaceans and molluscs in a sustainable and economically profitable way (Figure 4).

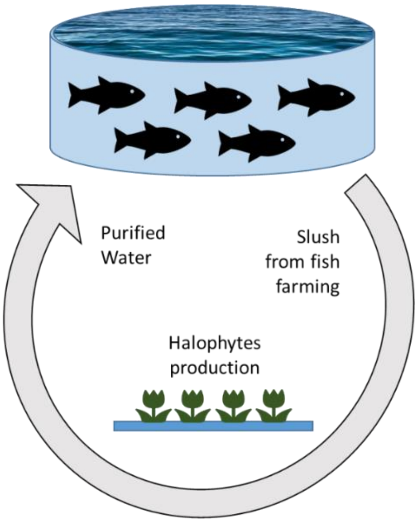

Figure 4. Integrated Multitrophic Aquaponic (IMTA) system for marine species and halophyte production.

5. Economic applications of halophytes and potential markets

Halophytes are abundant in Mediterranean coastal areas and can cope with adverse stressful conditions, such as high salinity and intense UV radiation, partially due to the synthesis of several bioactive secondary metabolites, as for example phenolic compounds and alkaloids. Besides their protective role for the plant, these molecules display important biological activities, including anti-oxidant, anti-inflammatory, antidiabetic and neuroprotective, which may explain the several ethnomedicinal and-veterinary uses of different halophyte species (Ksouri et al., 2012; Arya et al., 2019, Oliveira et al., 2021). For example, *Salicornia* L. species (sea asparagus) are used in traditional medicine against obesity and diabetes while *Crithmum maritimum* L. (sea fennel) and *Portulca olearacea* (common purslane) are used as diuretic and antiscorbutic (Pereira et al., 2017; Hwess et al., 2018). Being rich in mineral salts and having high water content, *P. olearacea* also has soothing properties for irritations of the bladder and urinary tract (Hwess et al., 2018). Another study shows that purslane vegetable contains high levels of omega-3 fatty acids for a land vegetable, as well as significant amounts of vitamin A, vitamin C, magnesium, potassium, calcium and iron (Simopoulos et al., 2004).

Halophyte's ethnomedicinal uses and chemical richness opens a cornucopia of naturally available bioactive products with a high added value in different commercial segments like the food, veterinary and pharmaceutical industries. Several Mediterranean species are edible and highly procured in the food industry due to their nutritional properties (Petroupoulos et al., 2018 a; b). This is the case of *Arthrocnemum macrostachyum* reported for its high commercial value and highly valued in gourmet cuisine (Barreira et al., 2017). *Helichrysum italicum* subsp.

picardii, *Crithmum maritimum*, and *Artemisia campestris* subsp. *maritima* are potential sources of herbal health-promoting beverages (Pereira et al., 2017a; b; Pereira et al., 2018). Other Mediterranean species like *Lithrum salicaria* and *Polygonum maritimum* are source of raw material for pharmaceutical and other related industries (Lopes et al., 2016; Rodrigues et al., 2018). A recent review by Oliveira et al. (2020) showed that essential oils in halophytes can be used as animal feed additives to improve ruminant health and productivity. Some anti-nutritional compounds like saponins, tannins and flavonoids can have anthelminthic and anti-bloat properties, besides their possible effects on the ruminal biohydrogenation and fermentation patterns and on the management of oxidative-related disorders (Oliveira et al., 2021). This novel line of research would deliver sustainable and integrative alternatives for veterinary practices.

From all the above referred it is easy to deduce that halophyte plants may find niches in the demanding market for novelties, as for example as herbs, vegetables, fresh gourmet products, and animal feed. One challenge that limits halophyte cultivation is the lack of knowledge about consumers' acceptance of halophyte products, which are fundamental to the commercialization of halophytes because farmers will start investing in the crop only if there is marketing potential (Centofanti and Banuelos, 2019). Halophytes are non-conventional crops and it would take a little to make people believe that they are good food for them, although some are used by certain communities for this purpose (Menzel and Leith, 1999). However, there are potentials to extract good quality oil from them (Weber et al. 2007), they could also serve as a source of feed, fiber and forage and this would not have any problem of acceptability.

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

Conclusion

The challenge posed to agriculture is not a question of quantities: it is a whole system that must be questioned at the same time as it is pushed to its limits. The past increase in yields has exhausted the soils whose fertility is now to be renewed. Agricultural activity contributes significantly to soil pollution, becoming its own victim of its excesses and must find more sustainable ways of farming. The climate is changing, and it becomes necessary to adapt to it.

Biodiversity has collapsed and it is essential to restore it. It will take new approaches, new methods, new technology - indeed, perhaps even new crops and new agricultural systems. Systems that integrate halophytes with or prior to crop cultivation in salt-affected soils is part of the answer. Besides, aquaponic halophytes production will be enhanced upon the reuse of nutrients originating from the marine aquaculture production. All these halophyte-based opportunities will enhance community sustainability and provide an increase in farmers' income while preserving agroecosystems' integrity and services. The design and large-scale implementation of halophyte-based farms in the Mediterranean arid and semi-arid regions will undoubtedly pose new research, engineering, monitoring, and regulatory challenges, with respect to food safety and ecological impacts as well as control of pests and pathogens. The successful adoption of sustainable halophyte farming in the context of competitive markets should also depend on business models that predict viable benefits of the new farming practices and products on human well-being and the local economy.

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