

## Review

# Sustainable agricultural management of saline soils in arid and semi-arid Mediterranean regions through halophytes, microbial and soil-based technologies

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## ABSTRACT

Soil salinization is an important global issue since marginal salt-affected soils have harmful consequences in agriculture and ecosystems. This article reviews different sustainable strategies adopted for marginal soil reclamation in Mediterranean climates. An innovative approach to soil salinity management includes a wide range of technologies, such as: phytoremediation, phytodesalination, vegetative bioremediation, amendments application and Technosols as well as inoculation with beneficial microorganisms like plant growth promoting bacteria and arbuscular mycorrhizal fungi. Besides that, the role of Mediterranean halophyte crops in accelerating salt-affected area's recovery while providing food and feed, and beneficial halophilic microorganisms for new bioinoculant production, are discussed. We conclude that the combined use of plant, soil- and microbial-based technologies is a valuable option to relieve saline stress exposure and improve crops growth and yield in saline conditions.

## 1. Introduction

Salt stress is one of the most dangerous threats for crop production limiting globally the agricultural productivity (Morton et al., 2019). Land salinisation is particularly prevalent in semi-arid and arid climates and its origin can be natural, namely in coastal regions of low-lying countries, or can be the result of anthropic activities (Corwin, 2021; Stavi et al., 2021). The area of salt-affected soils in Europe is estimated at 24 Mha, being approximately 2.05 % of the total salt affected area worldwide (1171.8 Mha) (Hassani et al., 2020). This area is expanding due to the global climate change, which is exacerbating the increase in temperature and the intensity of droughts (Cook et al., 2014). The salt affected areas in Europe are mainly located in the Mediterranean region along with Eastern Europe. These areas are characterized by lowlands along the coastal lines and are highly sensitive to desertification due to salinization (Allen et al., 2014; Daliakopoulos, 2016). Moreover, the degradation of soil and water resources in these areas has increased in

the last twenty years due to the intrusion of seawater into the aquifers near the coast, sea level rise generated by global warming, and improper use and management of irrigation water and drainage (Daliakopoulos et al., 2016). Further, irrigation of crops with saline waters raises agricultural and environmental risks due to soil salinization and water quality degradation (Pulido-Bosch et al., 2018; Minhas et al., 2020). In the Mediterranean region, 25 % of irrigated cropland is affected by moderate-to-high salinization, leading to moderate soil degradation (Mateo-Sagasta et al., 2015). Soil salinization has severe effects on soil quality through changes in soil structure and chemistry, soil biology, crop productivity and yield (Osman et al., 2019). The world's human population is expected to reach 9.7 billion by 2050, and global food production will need to produce 40–54 % more than in 2012 to match this growth (FAO, 2021). In the future, food production will rely in 428 farmed species, of which 29 dominant and 116 relevant, that is, responsible for 99 % of annual production (FAO, 2021). Most of these species are salt sensitive (non-halophytes, generally referred as

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glycophytes) that under moderate salinity conditions (electrical conductivity – EC = 4–8 dS m<sup>-1</sup>) display severe reductions in yield quality and quantity (50–80 %). While halophytic (salt tolerant or halophytes) species can survive under 200 mM NaCl or approximately 20 dS m<sup>-1</sup> (Flowers and Colmer, 2008), and plant's growth can be stimulated within a salinity range from 15 to 25 dS m<sup>-1</sup> (Rozema and Schats, 2013).

Saline soils are ecological niches characterized by the presence of extremophilic bacterial and fungal communities showing specific adaptation strategies. Halophytic microorganisms play crucial roles in plants survival, since they can degrade toxic compounds and improve salt tolerance in plants under such conditions (Yadav, 2020; Jain et al., 2021). Hence, these microorganisms represent a cost-effective solution for salinized soils, enhancing plant's ability to live in saline conditions and crop yield (Soldan et al., 2019).

This review highlights our current understanding on the following aspects: (i) soil salinization processes and the consequences of soil salinization in agriculture and environment; (ii) differences in salt tolerance among species and halophytes' uses in saline agriculture; and (iii) microbial and soil technologies employed in plant cultivation and saline soils' environmental reclamation, with a special focus in the arid and semi-arid Mediterranean regions.

## 2. Salt-affected soils: Origins and impacts in agriculture and environment

Soil salinization is the increasing concentration of readily soluble salts in the soil circulating water, containing chloride, sulfate, carbonate, hydrogen carbonate, nitrate, Ca, Mg, Na and K either due to natural processes (primary salinization) or anthropic actions (secondary salinization) (Richards, 1954; Nachshon, 2018; Stavi et al., 2021). The primary drivers of soil salinization are mineralogical and chemical characteristics of the parent materials, topography, type of climate (especially arid and semi-arid climate), chemical composition of the groundwater, sea/tidal water level, windblown salt particles, and flood/runoff from salt-affected areas.

The secondary drivers (human-inducers) as unsustainable soil management (e.g., change of land use or plant cover in some edaphoclimatic conditions, improper irrigation or poor-quality water (saline or brackish water) or irrigation practices, deforestation and deep-rooted vegetation loss, fertilization through high application rate and/or amendments (e.g., manure, gypsum, or elemental sulfur) are all factors impacting soil salinization (Datta and de Jong, 2002; Daliakopoulos et al., 2016; Omuto et al., 2020; Ondrasek and Rengel, 2021; Stavi et al., 2021; FAO, 2022). The over pumping of water from coastal aquifers also leads to seawater intrusion in coastal areas that increases the amount of salt affected land (FAO, 2022).

Salt-affected soils are classified as saline, saline-sodic and sodic according to the soil pH, electrical conductivity (EC), and exchangeable sodium percentage (ESP), which indicates the degree to which soil exchange complex is saturated with Na or sodium adsorption ratio (SAR) that gives information on the comparative concentrations of Na, Ca, and Mg in soil solution (Weil and Brady, 2017). The soils commonly designed as Saline are classified, according to the International Soil Classification from FAO (WRB, 2015), as Solonchaks. This soil type shows a high concentration of soluble salts at some periods of the year presenting a salic horizon (WRB, 2015). Nonetheless, other soil types can present significant salinity due, for instance, to their location in low-lying areas influenced by marine tides (Fluvisols; WRB, 2015). Another case is the soils classified as Solonetz (WRB, 2015) with an exchangeable complex dominated by Na forming a natric horizon.

Saline soils present pH < 8.5, EC of the solution extracted from a water-saturated soil paste > 4 dS m<sup>-1</sup>, sodium adsorption ratio (SAR) < 13 and/or ESP < 15, and the dominant anions are chloride and sulfate (Weil and Brady, 2017; Omuto et al., 2020). Sodic soils have relatively high Na contents on the exchange complex (ESP and SAR > 15 and 13, respectively) but soluble salt content is low (EC < 4 dS m<sup>-1</sup>) and soil pH

ranges from 8.5 to 10.5. In these soils, the dominant anions are carbonate and hydrogen carbonate (Richards, 1954). Saline-sodic soils have intermediate characteristics between saline and sodic soils, pH > 8.5, high proportion of Na (ESP > 15 or SAR > 13) and EC > 4 dS m<sup>-1</sup> (Weil and Brady, 2017).

Soil salinization is the main responsible for changes in soil physico-chemical properties (Fig. 1), soil biology and plant growth disturbances (Bui, 2013). High amounts of Na in soils' solution displace exchangeable Ca and Mg on exchangeable complex of the soil mineral/organic colloidal components. The high amount of Na in the soil complex contributes to clays and organic matter dispersion and rupture of aggregates. Therefore, these soils have poor structure dominated by microporosity and low hydraulic conductivity (infiltration and percolation), and aeration (Rengasamy, 2016). Thus, sodic soils may be more prone to erosion or, after rainfall or irrigation, remain waterlogged for prolonged periods (FAO, 2021). The dispersed solid phases eluviation form dense crusts in depth leading to porosity decrease and consequently alteration of hydrodynamic behavior (percolation, ascension by capillarity). In natural saline soils (Solonchaks), these salt crusts are included in the salic horizon, and soil volume used by root system development can be confined (WRB, 2015). Other changes in soil conditions occur, such as the redox potential, which may affect nutrient cycle dynamics and lead to plants' nutritional imbalance (Purwanto and Alam, 2020).

The irrigation of soils with waters (superficial or ground waters) or effluents (e.g., domestic wastewaters) with EC values higher than 0.6 dS m<sup>-1</sup> (slightly brackish) can be a source for degradation at physico-chemical and biological levels, reducing development and productivity of most plant species (García-Caparrós and Lao, 2018; Ondrasek and Rengel, 2021; Omuto et al., 2020).

Concerning soil fertilization, if available elements input exceeded plant uptake and/or there is not an adequate leaching of the elements, the soil solution tends to enrich itself and, after water evaporation, elements crystallize as solid phases with, usually, high solubility. In agriculture soils, although K is important for plant nutrition its increase in soil solution can cause soil clay dispersion, but to a lesser extent than Na, negatively affecting hydraulic conductivity and aggregate stability (Arienzo et al., 2012; Marchuk et al., 2014). The use of irrigation wastewater with a high K concentration should be done with caution due to its potential negative impacts on soil structural stability, although K effects depends on soil type, especially soil clay mineralogy (Marchuk and Marchuk, 2018).

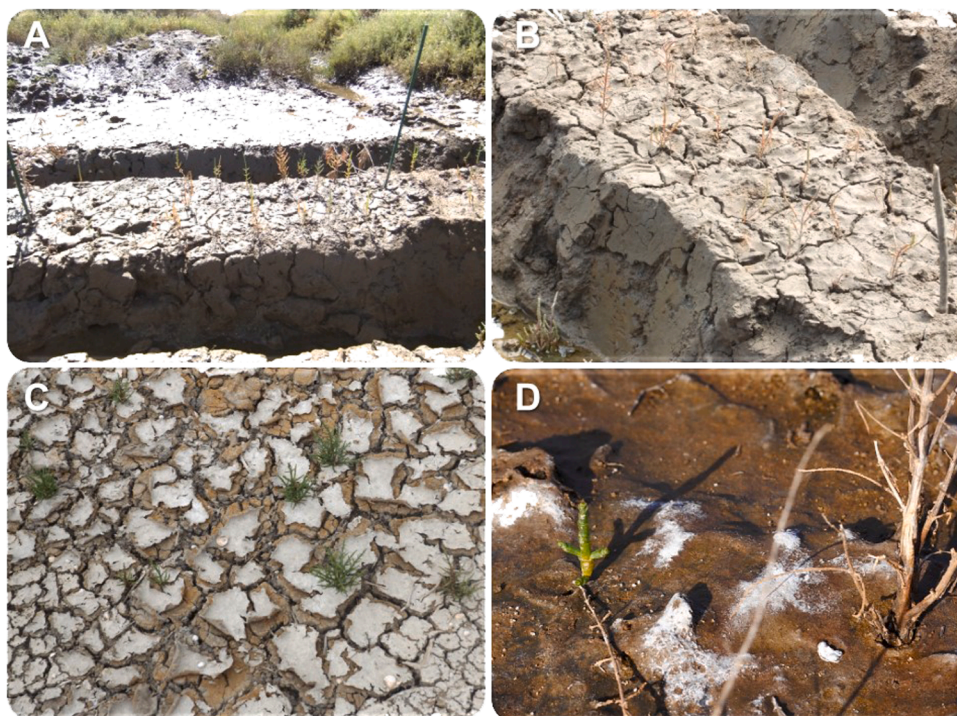
At biological level, soil salinization affects considerably several ecological soil functions like respiration, overall microbial activity such as specific processes as organic matter decomposition, nitrification, and denitrification (Singh, 2021). Furthermore, soil organic carbon content can be negatively affected leading to a concomitant reduced microbial activities (Dong et al., 2022).

Plant growth is negatively affected by salt stress because of the disruption of certain physiological processes leading to reductions in yield and/or quality (Morton et al., 2019). These harmful effects on plants are associated to imbalance in the ratios of macronutrients, nutritional deficiency, and Na phytotoxicity (in case of sodic soils). In addition, the osmotic potential between soil solution and plant root cells decreases due to the high amounts of cations and anions in solution as reflected by high EC (Hasanuzzaman and Fujita, 2022).

## 3. The response of plants to salt stress

### 3.1. Glycophytes

In general, salinity stress affects photosynthesis, respiration, distribution of photoassimilates causing plant growth inhibition, wilting, drying, and death of entire organs of most plants and vegetable crops (generally, glycophytic species), because of salt toxicity (Cheeseman, 2015; Zörb et al., 2019). If grown under saline conditions, these species



**Fig. 1.** Salt-affected soils with solid phases (efflorescences), usually with high solubility, on the soil surface. Poor structure along the soil profile (A-B) contributes to low hydraulic conductivity and waterlogging (C-D). The dense salt crust crusts of solid phases from these soils can crack in dry conditions whereas in wet conditions these may not fully dissolve as in Tagus and Guadiana estuaries (southwest Europe, Portugal, and Spain) (C-D). Halophytes, as *Salicornia ramosissima* J. Woods and *Sarcocornia* sp. have high salinity tolerance and can grow naturally in salt-affected soils from lower salt marshes (A-D).

suffer several damages caused by the osmotic and toxic effect of Na and Cl uptakes resulting in decline of several physiological parameters and yield (Soundararajan et al., 2019). Salt sensitivity can change during plant growth stages being seedling establishment more sensitive than plants at later stages (Läuchli and Grattan, 2007).

In vegetable crops and fleshy fruits with low salinity tolerance, salinity stress may cause decline of biomass and yield (Zörb et al., 2019). Several examples are given in Table 1. Regarding vegetables, *Pisum sativum* L. (Pandolfi et al., 2012) and *Phaseolus vulgaris* L. (Bolton and Simon, 2019) interact against salt stress showing impairments in the photosynthetic apparatus and yield reduction associated to osmotic and ionic effects. Salt stress reduced plant growth as in *Raphanus sativus* L. (Sanoubar et al., 2020) and *Spinacia oleracea* L. (Ors and Suarez, 2016), although this decrease was lower compared to salt stress sensitive species. Many of the fleshy fruits are characterized by low salt sensitivity as *Pyrus communis* L. (Yousefi et al., 2019) and *Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa*; the latter one shows reduction in the number and length of new shoots (Zhong et al., 2019). In *Citrus sinensis* (L.) Osbeck. besides to a marked decline in biomass, stomatal aperture and chlorophyll content were severely affected in salinity conditions (Simpson et al., 2015). Staple foods as potatoes, rice, wheat, and corn are also damaged by soil salinization. Wheat and corn cultivated under increasing NaCl concentrations had a clear reduction in the aerial part biomass leading to a respective yield decline (Tufail et al., 2013; Zafar et al., 2015).

Mediterranean crops are characterized to tolerate moderate saline conditions (4–8 dS m<sup>-1</sup>), but there are also species well adapted to drought conditions though sensitive to salt stress (De Ollas et al., 2019). For instance, *Ficus carica* L. that is moderately salt tolerant (Table 1), growth under saline conditions did not result in high biomass decrease, and plants showed reduced relative water and chlorophyll contents (Sadder et al., 2021). *Beta vulgaris* L. and *Sacharum officinarum* L. growth was enhanced under moderate saline conditions but with restricted photosynthetic activity and nutrient uptake (Pirhadi et al., 2016; Hosain et al., 2017). Furthermore, the reproductive growth of some Mediterranean crops such as chickpea and grapevines also had a reduction in flower and seed numbers under salinity conditions (Abdullah et al.,

2001; Sulpice et al., 2003; Sohrabi et al., 2008; Flowers et al., 2010; Khan et al., 2015; Baby et al., 2016).

Salinity triggered different responses depending on ornamental crop species (Table 1). For example, the shrubs *Viburnum lucidum* L. and *Callistemon citrinus* (Curtis) Stapf. presented a clear decrease in shoot and root biomass under high level of NaCl concentration (200 mM) (Cirillo et al., 2016; Sifola et al., 2017). Whereas, ornamental shrubs as *Cestrum aurantiacum* Lindl., *Cotoneaster lacteus* W. W. Sm., *Eugenia myrtifolia* Roxb., *Pyracantha fortuneana* (Maxim.) H. L. Li ‘Harlequin’ and *Teucrium fruticans* L. exposed to increasing EC levels (1.8, 4.8 and 7.8 dS m<sup>-1</sup>) showed that *C. lacteus* was the most salt sensitive species as revealed by leaf necrosis. While *C. aurantiacum* and *P. fortuneana* exhibited a reduced growth in salinity conditions having only slight necrosis on their foliage, *T. fruticans* and *E. myrtifolia* were able to cope with salt stress (Cassaniti et al., 2012). *Kalanchoe blossfeldiana* Poelln and *Gazania splendens* Lem plants grown under high EC (7.5 dS m<sup>-1</sup>) in the nutrient solution presented a similar decrease on total biomass and nutrient content in roots and leaves. While *K. blossfeldiana* plants avoided Na accumulation by shedding leaves, *G. splendens* plants triggered Cl and Na accumulation at root level, salt secretion through leaves, shedding of old leaves and increases in leaf succulence (García-Caparrós et al., 2016).

In salt sensitive crops, ion homeostasis can be disturbed when there are excessive amounts of salt ions in soil solution, resulting in ionic imbalance. The ion disturbance generates antagonistic cation-cation and anion-anion uptake interactions that may have diverse consequences, such as induction of senescence and reduced nutrients availability (Zörb et al., 2019). Excessive Na can induce decreases in K uptake reducing shoot growth (Zörb et al., 2014) and Ca deficiency symptoms like lesions and reduced dry weights of leaf blades (Maas, 2019). Excess of Cl can influence NO<sub>3</sub> uptake (Cerezo et al., 1999; Abdelgadir et al., 2005) decreasing wheat growth and yield in wheat (Hu and Schmidhalter, 1998). The photosynthetic capacity can also be affected by salinity stress inducing reduction in chlorophyll and carotenoid contents and plant growth (Munns and Tester, 2008; Chaves et al., 2009) associated to pigments degradation (Abdallah et al., 2016; Leiva-Ampuero et al., 2020). Salt stress moreover leads superoxide radicals (O<sub>2</sub>) and hydrogen

Table 1

Degree of salt tolerance, salinity thresholds and salt damages in several species sorted by groups. EC: electrical conductivity.

|                            | Species                        | Degree of salt tolerance | EC or NaCl concentration thresholds | References                         |
|----------------------------|--------------------------------|--------------------------|-------------------------------------|------------------------------------|
| <b>Vegetables</b>          | <i>Solanum lycopersicum</i>    | Salt sensitive           | 0–40 mM NaCl                        | Di Gioia et al. (2013)             |
|                            | <i>Cucumis sativus</i>         | Moderately salt tolerant | 0–100 mM NaCl                       | Elsheery et al. (2020)             |
|                            | <i>Lactuca sativa</i>          | Salt sensitive           | 0–100 mM NaCl                       | Leyva et al. (2011)                |
|                            | <i>Raphanus sativus</i>        | Salt tolerant            | 0–200 mM NaCl                       | Sanoubar et al. (2020)             |
|                            | <i>Spinacia oleracea</i>       | Moderately salt tolerant | 0–15 dS m <sup>-1</sup>             | Ors and Suarez (2016)              |
|                            | <i>Daucus carota</i>           | Moderately salt tolerant | 0–250 mM NaCl                       | Bolton and Simon (2019)            |
|                            | <i>Phaseolus vulgaris</i>      | Salt sensitive           | 0–75 mM NaCl                        | Assimakopoulou et al. (2015)       |
|                            | <i>Capsicum annuum</i>         | Salt sensitive           | 0–100 mM NaCl                       | Kaya et al. (2020)                 |
|                            | <i>Pisum sativum</i>           | Salt sensitive           | 0–80 mM NaCl                        | Pandolfi et al. (2012)             |
|                            | <i>Solanum melongena</i>       | Salt sensitive           | 0–160 mM NaCl                       | Hannachi and Van Labeke (2018)     |
| <b>Freshly fruits</b>      | <i>Pyrus communis</i>          | Salt sensitive           | 0–150 mM NaCl                       | Yousefi et al. (2019)              |
|                            | <i>Malus domestica</i>         | Salt sensitive           | 0–100 mM NaCl                       | Sales et al. (2017)                |
|                            | <i>Diospyros kaki</i>          | Salt sensitive           | 0–40 mM NaCl                        | Gil-Muñoz et al. (2020)            |
|                            | <i>Actinidia deliciosa</i>     | Moderately salt tolerant | 0–1.2 g L <sup>-1</sup> NaCl        | Zhong et al. (2019)                |
|                            | <i>Ananas comosus</i>          | Salt sensitive           | 0–10 dS m <sup>-1</sup>             | Quintana et al. (2012)             |
|                            | <i>Fragaria ananassa</i>       | Salt sensitive           | 0–40 mM NaCl                        | Orsini et al. (2012)               |
|                            | <i>Persea americana</i>        | Salt sensitive           | 0–1.5 dS m <sup>-1</sup>            | Acosta-Rangel et al. (2019)        |
|                            | <i>Mangifera indica</i>        | Salt sensitive           | 0–50 mM NaCl                        | Mahouachi (2018)                   |
|                            | <i>Mussa paradisiaca</i>       | Salt sensitive           | 0–60 mM NaCl                        | Ji et al. (2019)                   |
|                            | <i>Eriobotrya japonica</i>     | Moderately salt tolerant | 0–8 dS m <sup>-1</sup>              | Sadeghi and Shekafandeh (2014)     |
| <b>Staple foods</b>        | <i>Solanum tuberosum</i>       | Salt sensitive           | 0–60 mM NaCl                        | Jaarsma and de Boer (2018)         |
|                            | <i>Triticum aestivum</i>       | Salt sensitive           | 0–150 mM NaCl                       | Zafar et al. (2015)                |
|                            | <i>Oryza sativa</i>            | Salt sensitive           | 0–60 mM NaCl                        | Kibria et al. (2017)               |
|                            | <i>Zea mays</i>                | Salt sensitive           | 0–120 mM NaCl                       | Tufail et al. (2013)               |
|                            | <i>Sorghum bicolor</i>         | Salt sensitive           | 0–150 mM NaCl                       | Maswada et al. (2018)              |
|                            | <i>Beta vulgaris</i>           | Salt tolerant            | 0–300 mM NaCl                       | Hossain et al. (2017)              |
|                            | <i>Saccharum officinarum</i>   | Salt tolerant            | 0–600 mM NaCl                       | Pirhadi et al. (2016)              |
|                            | <i>Manihot esculenta</i>       | Moderately salt tolerant | 0–150 mM NaCl                       | Gleadow et al. (2016)              |
|                            | <i>Glycine max</i>             | Salt sensitive           | 0–150 mM NaCl                       | Pi et al. (2016)                   |
|                            | <i>Hordeum vulgare</i>         | Salt sensitive           | 0–100 mM NaCl                       | Zeeshan et al. (2020)              |
| <b>Ornamental plants</b>   | <i>Callistemon laevis</i>      | Salt sensitive           | 0–4 dS m <sup>-1</sup>              | Álvarez, and Sanchez Blanco (2015) |
|                            | <i>Viburnum lucidum</i>        | Moderately salt tolerant | 0–200 mM NaCl                       | Sifola et al. (2017)               |
|                            | <i>Petunia hybrida</i>         | Salt sensitive           | 0–125 mM NaCl                       | Arun et al. (2016)                 |
|                            | <i>Euonymus japonicus</i>      | Moderately salt tolerant | 0–9 dS m <sup>-1</sup>              | Miralles et al. (2016)             |
|                            | <i>Kalanchoe blossfeldiana</i> | Salt sensitive           | 0–7.5 dS m <sup>-1</sup>            | García-Caparrós et al. (2016)      |
|                            | <i>Eugenia myrtifolia</i>      | Moderately salt tolerant | 0–12 dS m <sup>-1</sup>             | Acosta-Motos et al. (2015)         |
|                            | <i>Viburnum tinus</i>          | Salt sensitive           | 0–4 dS m <sup>-1</sup>              | Gómez-Bellot et al. (2015)         |
|                            | <i>Calendula officinalis</i>   | Salt sensitive           | 0–100 mM NaCl                       | Lacramioara et al. (2015)          |
|                            | <i>Nerium oleander</i>         | Salt tolerant            | 0–800 mM NaCl                       | Kumar et al. (2017)                |
|                            | <i>Lavandula multifida</i>     | Moderately salt tolerant | 0–200 mM NaCl                       | García-Caparrós et al. (2017)      |
| <b>Mediterranean crops</b> | <i>Ficus carica</i>            | Moderately salt tolerant | 0–150 mM NaCl                       | Sadder et al. (2021)               |
|                            | <i>Olea europaea</i>           | Salt sensitive           | 0–60 mM NaCl                        | Moretti et al. (2018)              |
|                            | <i>Punica granatum</i>         | Moderately salt tolerant | 0–200 mM NaCl                       | Liu et al. (2020b)                 |
|                            | <i>Prunus amygdalus</i>        | Salt sensitive           | 0–75 mM NaCl                        | Aazami et al. (2021)               |
|                            | <i>Vitis vinifera</i>          | Moderately salt tolerant | 0–150 mM NaCl                       | Oraei et al. (2019)                |
|                            | <i>Phoenix dactylifera</i>     | Moderately salt tolerant | 0–240 mM NaCl                       | Al Kharusi et al. (2017)           |
|                            | <i>Citrus sinensis</i>         | Salt sensitive           | 0–10 dS m <sup>-1</sup>             | Simpson et al. (2015)              |
|                            | <i>Citrus latifolia</i>        | Salt sensitive           | 0–75 mM NaCl                        | Aparicio-Durán et al. (2021)       |
|                            | <i>Laurus nobilis</i>          | Salt sensitive           | 0–40 mM NaCl                        | Maatallah et al. (2015)            |
|                            | <i>Ceratonia siliqua</i>       | Moderately salt tolerant | 0–240 mM NaCl                       | Correia et al. (2010)              |

peroxide (H<sub>2</sub>O<sub>2</sub>) accumulation in different cell compartments, including chloroplasts, mitochondria and apoplasmic space, which increases oxidative stress and in reactive oxygen species (ROS) accumulation (Hasanuzzaman et al., 2021).

### 3.2. Halophytes

Extremophile plants as halophytes can survive and complete their life cycle in the presence of significant concentrations of soluble salts containing Na in the medium in which they grow (Aronson, 1989, ~80 mM NaCl; Flowers and Colmer, 2008, ~200 mM NaCl). Fewer than 1500 species of flowering plants have evolved the ability (<https://ehalo.ph.uc.pt/>) to grow and develop in these harsh environments, usually with high salinity and UV radiation (Santos et al., 2016). These species have adaptive mechanisms to cope with saline stress, including

combined biochemical, physiological, anatomical, and morphological characteristics to survive in saline environments (Flowers and Colmer, 2015; Yuan et al., 2019; Rahman et al., 2021). Some species also have adaptive defense strategies, such as seed heteromorphisms (e.g., *Suaeda* sp. - seeds with different sizes, colors, etc.) and seed dormancy that allow plant survival (Liu et al., 2018). The latter strategy has an ecological function by permitting seeds to remain un-germinated on saline soils until a rain event(s) increases soil water potential allowing favorable conditions for seed germination and seedling establishment (e.g., *Eutrema* (*Thellungiella*) *salsugineum* (Pall.) Al-Shehbaz & Warwick, *Halocnemum strobilaceum* (Pall.) M. Bieb., *Haloxylon ammodendron* (C. A. Mey.) Bunge ex Fenzl, *Haloxylon persicum* Bunge, *Suaeda corniculata* (C. A. Mey.) Bunge and *Suaeda physophora* Pall.) (Ungar, 1978; Gulzar and Khan, 2001; Song et al., 2005; Qu et al., 2008; Cao et al., 2012; Kazachkova et al., 2016). Depending on species, halophytes (e.g., *Cakile*

*maritima* Scop., *Limonium algarvense* Erben, *Plantago crassifolia* Forssk., *Suaeda salsa* (L.) Pall) often show increased flower number, decreased sterility, and high seed quality under salinity conditions (Debez et al., 2004; Vicente et al., 2004; Guo et al., 2015; Cortinhas et al., 2020). However, halophytes vegetative and reproductive growth can be affected by salt treatments as in non-halophytes being the seed germination-seedling transition stage the most salt sensitive (Kazachkova et al., 2016; González-Orenga et al., 2019; Cortinhas et al., 2021).

Other adaptive mechanisms include succulence, leaf salt excretion, Na and Cl exclusion at root level, Na and Cl compartmentalization in vacuoles while maintaining Ca and K uptakes, and synthesis of osmolyte compounds, enabling halophytes to grow for long periods of time under high salinity (Acosta et al., 2017; Dassanayake and Larkin, 2017; Caperta et al., 2020). Ion's compartmentation in the vacuoles is required for osmotic balance because any excess of ions may cause damage in the plant tissues (Flowers and Colmer, 2015). The influx and efflux of Na ions to cell vacuoles is performed by a variety of transporters that contribute to keep Na away from the metabolic machinery in the cytoplasm (Flowers and Colmer, 2015).

When grown at elevated NaCl concentration succulent halophytes can enhance succulence by increasing leaf thickness as in *Crithmum maritimum* L., *Cakile maritima* Scop., and *Salicornia fruticosa* (L.) A. J. Scott (Debez et al., 2004; Debez et al., 2012; Yepes et al., 2018). The improvement in leaf thickness enhanced leaf water content, which may dilute tissue-accumulated NaCl by avoiding salt-induced damage (Debez et al., 2010; Rangani et al., 2016; Yepes et al., 2018). Some halophytes present peculiar epidermal structures as salt-secreting structures, with anatomical and structural dissimilarities (Dassanayake and Larkin, 2017; Caperta et al., 2020). Salt glands are found in just 12 of the 111 families that contain halophytes, with five families containing approximately 90 % of the species (Plumbaginaceae, 28 %; Poaceae, 21 %; Amaranthaceae, 20 %; Tamaricaceae, 15 % and Frankeniaceae, 6 %), with seven families containing the remaining 10 % (Caperta et al., 2020). *Limonium algarvense* that possesses salt glands, saline water irrigation decreases stomatal density and stomatal indexes but not changes saline glands distribution nor leaf anatomy (Cortinhas et al., 2020). *Tamarix africana* Poiret which is well adapted to contaminated saline soils, stored the contaminants in the roots and shoots and excrete salt and hazardous elements by saline glands (Santos et al., 2017a).

Biochemical mechanisms are also important to achieve osmotic adjustment via the accumulation of compatible solutes (osmolytes) in halophytic species (Munns and Tester, 2008; Szabados and Savoré, 2010; Slama et al., 2015). These osmolytes can directly have a role as chemical chaperones to protect macromolecular structures and can act as ROS scavengers or as signaling molecules that help to avoid ROS toxicity (Slama et al., 2015; Acosta et al., 2017). In *Kochia sieversiana* (Pall.) C. A. Mey. (Yang et al., 2008) and *S. fruticosa* (Hameed et al., 2012), proline and sugars concentrations increased at salinities above the optimal for plant growth.

#### 4. Saline agriculture with halophytes and possible utilizations

The limited availability of arable land and freshwater, along with sea rising level, triggered the development of saline agriculture. This alternative form of farming uses soil and water unsuitable for conventional crops (having lower salt tolerance), but appropriate for crops tolerating saline irrigation water or even halophytes (Ventura et al., 2015; García-Caparrós et al., 2020; Hussain et al., 2020).

Saline agriculture based on growing halophytes offers feasible alternatives for food, fodder, bioenergy, ornamental, and pharmaceutical uses (Cassaniti et al., 2013; Koyro et al., 2014; Panta et al., 2014; Álvarez and Sánchez-Blanco, 2015; Ventura et al., 2015; Sharma et al., 2016a; Petropoulos et al., 2018; Cortinhas et al., 2019; Elouafi et al., 2020; Rodrigues et al., 2020; Corrêa et al., 2021; Duarte and Caçador, 2021). Several halophytes may provide an economically sound and environmentally suited source of products for a wide range of purposes.

However, relevant issues related to their cultivation in arid and semi-arid conditions remain to be defined in the Mediterranean area.

Edible halophytes belonging to the genera *Atriplex*, *Bassia*, *Beta*, *Cakile*, *Chenopodium*, *Crithmum*, *Plantago*, *Portulaca*, *Salicornia*, *Salsola*, and *Suaeda* have received attention as potential food sources due to their beneficial effects as food (Barreira et al., 2017; Agudelo et al., 2021; Lombardi et al., 2022). For instance, the green leafy vegetables halophytes *Salicornia* and *Sarcocornia* spp. have been farmed on a commercial scale for gourmet cuisine (Antunes et al., 2021; Lima et al., 2022). The sea fennel or *C. maritimum*, well known for its high content of antioxidant compounds and that has been consumed for many years (Atia et al., 2011; Cortinhas et al., 2019; Agudelo et al., 2021), is also proposed as an alternative cash crop in the context of saline agriculture (Ventura et al., 2014). The juvenile edible leaves' biomass of succulent plants of *Mesembryanthemum crystallinum* (L.) Rothm. (ice plant) are consumed as a vegetable crop due to its functional value in terms of nutrients and antioxidants (Atzori et al., 2017).

Halophytes can be used as part of the ruminants' diet where the animals graze on native vegetation or planted halophytes (Al-Azzawi and Flowers, 2022). For instance, El-Hack et al. (2018) reviewed the feasibility of halophytes as animal feeding stating that *Atriplex* sp., *Kochia* sp., and *Acacia* sp. can be considered of crucial importance. Similarly, Altay and Ozturk (2020) reported the feasibility of growing *Salsola* sp. as animal fodder in different arid regions of the world. On the same line, Kewan et al. (2019) reported several halophytes as possible alternatives for animal feeding, including *Kochia indica* Wight and *Atriplex lentiformis* (Torr.) S. Watson, among others.

The use of halophytes for biofuel generation is an environmentally friendly alternative especially in terms of gas emissions. Biofuels are gaining importance due to the high price of the crude oil and the high energy demands (Ali et al., 2021). An experiment with four halophytic species (*Avicennia marina*, *Tamarix nilotica*, *Zygophyllum album*, and *Zygophyllum coccineum*) showed that *A. marina* had the highest capacity of biogas generation (Kamel et al., 2019). The facultative halophyte *Chenopodium quinoa* Willd. (quinoa) is able to produce high methane yields using its biomass. In this sense, Turcios et al. (2016) reported a value of 2888 mL CH<sub>4</sub> g<sup>-1</sup> of volatile solids in plants grown under 20 ppt ~ 342 mM of NaCl. Similarly, Cayenne et al. (2022) investigated the biomethane potential of *Salicornia europaea* L. and *Salicornia ramosissima* J. Woods resulting that *S. europaea* showed the highest biomethane yield (250 mL CH<sub>4</sub> g<sup>-1</sup> of volatile solids) when grown under ~ 342 mM of NaCl.

Halophytes have long been used for pharmaceutical purposes and currently researchers are mainly focused on discerning the bioactive compounds responsible for these medical properties (Giordano et al., 2021; Ferreira et al., 2022). For instance, Mohammed et al. (2021) showed anti-inflammatory and analgesic properties of an ethanolic extract of the aerial part of *Salsola cyclophylla* Baker. These properties were ascribed to the presence of 52 compounds belonging to phenols, flavonoids, coumarins, and aliphatics classes. Halophyte *Limonium spathulatum* (Desf.) Kuntze has a high content of antioxidant compounds (phenolic) responsible for the anti-diabetic and anti-inflammatory activities (Mazouz et al., 2020). Regarding anticarcinogenic properties, an ethyl acetate extract from the whole *C. maritimum* plant reduced Huh7 and HepG2 cell lines proliferation (hepatocellular carcinoma) by interfering with the cell cycle (Gnocchi et al., 2020).

Due to halophytes ability to uptake significant amounts of elements associated to salinity, they can also be used as NaCl removing crops, particularly as an intercrop, or including them in rotation programs as in the context of an environmentally friendly alternative (Hamed et al., 2021). For instance, the facultative halophytic, pseudo-cereal crop quinoa (Adolf et al., 2013; Ruiz et al., 2016) is a minor crop with high nutritious value (Ruiz-Carrasco et al., 2011). This crop has been utilized in the cropping system of salt-affected areas in the Mediterranean area (Pulvento et al., 2012; Yazar et al., 2015). It could be an alternative crop to cereals and food legumes in this region, since these latter crops are

less tolerant to high levels of salinity in the irrigation water (Arslan et al., 2016). Many halophytes are used in ornamental horticulture, particularly from families Chenopodiaceae (e.g., *Atriplex*, *Bassia*, *Halocnemum*, *Suaeda*) and Plumbaginaceae (*Armeria* and *Limonium* spp.) as well as other halophyte species that have been reported as feasible options for ornamental purposes in Mediterranean saline areas (Cassaniti et al., 2013; García-Caparrós et al., 2020). In the Mediterranean context there are very few cases where biosaline agriculture has been accomplished in field trials. For instance, Zenobi et al. (2021, 2022) noted that the growing of *Crithmum maritimum* in Italy in an organic farm resulted in an enhancement of biomass and total yield.

## 5. Microbial symbiotic interactions with plants

Plants interact with microorganisms present in the rhizosphere, which is the nearest soil to roots with high microbial activity, in the phyllosphere and endosphere (i.e. inside the tissues) (Carvalhais et al., 2015). Plant-associated microorganisms, which live outside their host tissues are known as epiphytes, while those living in the endosphere are known as endophytes (Kuklinsky-Sobral et al., 2004). These microbial communities including bacteria, fungi, protists, nematodes, and viruses, form the plant microbiome and are essential for proper plant growth and nutrient uptake as well as to improve tolerance to biotic and abiotic stresses, including salinity stress (Trivedi et al., 2020).

### 5.1. Plant growth promoting bacteria (PGPB)

Within plant microbiome, the mutualistic epiphytic and endophytic bacteria presenting properties that assist plants are known as Plant Growth Promoting Bacteria (PGPB). These bacteria can improve plant growth and development by several mechanisms like improving nutrient uptake (e.g., N, P, Fe) and protecting against phytopathogens and abiotic stress factors (Wani et al., 2007; Navarro-Torre et al., 2020a; Trivedi et al., 2020) (Figs. 2 and 3). Moreover, most of these bacteria produce siderophores that act as ligands with Fe (III) ions making them available to plants (Alori and Babalola, 2018). Many PGPB can also produce phytohormones (e.g., auxins, gibberellins, abscisic acid) (Jha and Saraf, 2015) which modify plant morphology and physiology, including root architecture and elongation, allowing by this means a better nutrient access (Turan et al., 2016). These bacteria can also

contribute to reduce plants' stress by decreasing ethylene production due to activity of the 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase enzyme, which degrades the ACC, an ethylene precursor (Glick, 2014). Altogether, these properties can support plant growth and development not only in non-stressful conditions but also in degraded environments where plants are subjected to various stress factors like soil contamination with metals, drought, and/or salinity (Navarro-Torre et al., 2020a; Glick and Gamalero, 2021). Therefore, their use as inoculants for crop development promotion has increased in the last years (Kumar et al., 2021; Teo et al., 2022).

Some PGPB are halotolerant bacteria or halophiles, depending on whether they grow in presence of NaCl or need NaCl to grow, respectively (Ventosa et al., 1998). These mechanisms include changes in cell wall and/or plasmatic membrane to avoid salt entry, like Na and K pumps and antiporter channels, osmoprotectant accumulation such as low molecular weight organic molecules that balance the osmotic pressure in cells (e.g., ectoine, betaine, trehalose); proteins and enzyme modifications making them active in presence of NaCl; secretion of exopolysaccharides (EPS) to help biofilm formation, and DNA modifications (e.g., increase in guanine and cytosine contents) (Etesami and Beattie, 2018). A great diversity of halophilic bacterial species has been isolated from the halophytes' rhizospheres and phyllospheres (Table 2; Fig. 2). Among them, *Aeluropus* Trin. (Wang et al., 2020), *A. macrostachyum* (Navarro-Torre et al., 2016; 2017b), *A. tripolium* (Szymanska et al., 2016), *Atriplex* spp. (Mukhtar et al., 2019; Genitsaris et al., 2020), *Chritum* sp. (Genitsaris et al., 2020), *Glaux maritima* L. (Yamamoto et al., 2020), *H. portulacoides* (Mesa-Marín et al., 2019), *Limonium sinense* Girard Kuntze (Qin et al., 2018), *Messerschmidia sibirica* L. (Tian and Zhang, 2017), *Salicornia* spp. (Shi et al., 2015; Szymanska et al., 2016; Furtado et al., 2019; Mesa-Marín et al., 2019; Genitsaris et al., 2020; Yamamoto et al., 2020), *Salsola stocksii* Boiss. (Mukhtar et al., 2019), *Sesbania cannabina* (Retz.) Poir. (Zheng et al., 2020) and *Suaeda* spp. (Shi et al., 2015; Wang et al., 2020).

#### 5.1.1. The use of halophilic PGPB as a strategy to cope with soil salinity in crops

Halotolerant and halophilic PGPB isolated from halophytes can improve growth and alleviate the stress of different crops cultivated in saline conditions (Table 3). Despite that studies in the Mediterranean context are very scarce, Tolba et al. (2019) demonstrated the positive

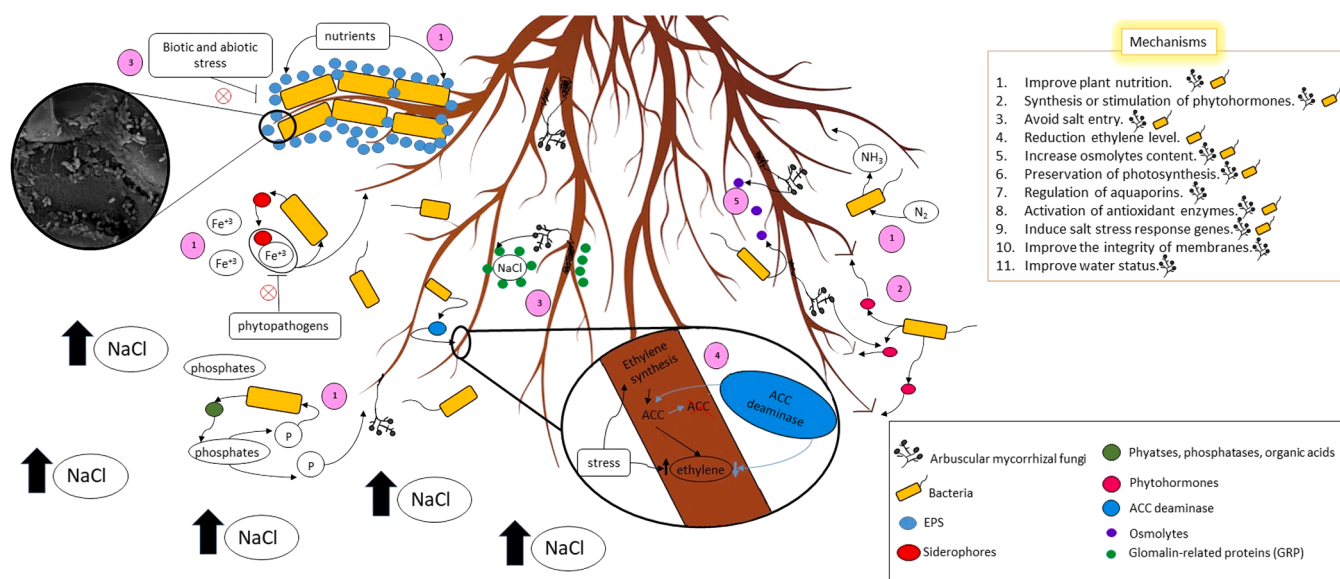


Fig. 2. Microbial benefits to plants against saline conditions. Principal plant growth promoting properties showed by plant growth promoting bacteria and arbuscular mycorrhiza fungi. The scanning electron microscopy photography shows the biofilm formed in roots of germinating seeds of *Arthrocnemum macrostachyum* by *Pantoea agglomerans* RSO7, isolated from *Spartina maritima* in Paredes-Páliz et al. (2016).

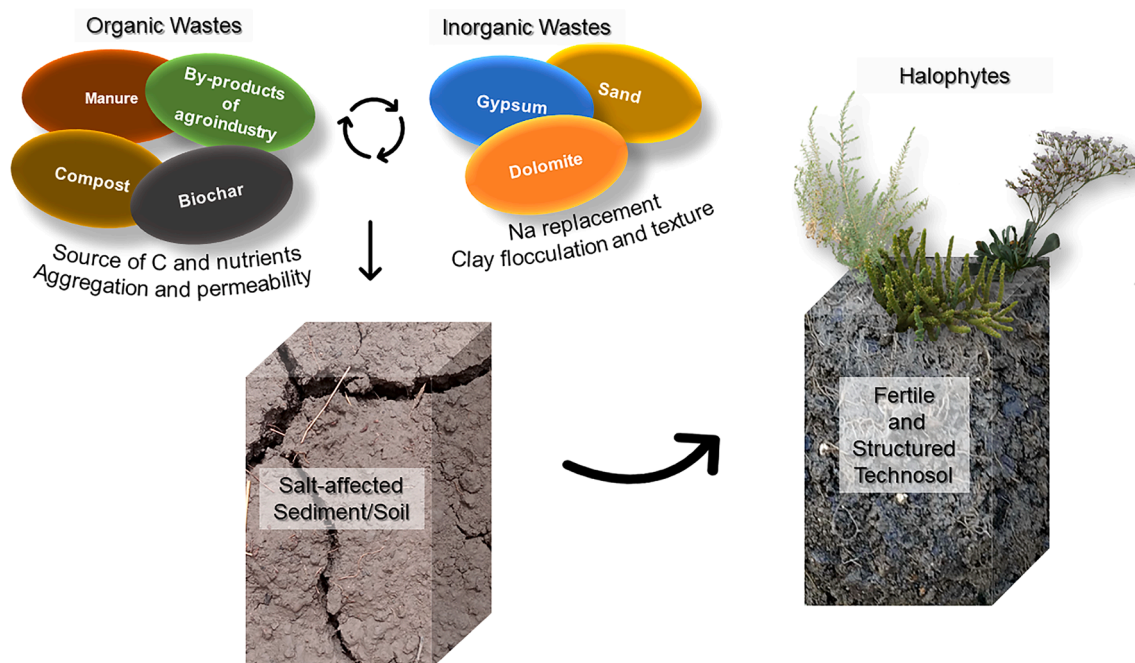


Fig. 3. Example of organic and inorganic residues used in Technosol elaboration. These residues improve fertility and structure properties of salt-affected sediments/soils and cultivation of add-value halophytes.

effects of stevia crops' inoculation with halophilic PGPB isolated from halophyte under saline conditions (in Egypt). Bacterial inoculation improved plant growth and photosynthesis as well as RuBisCO accumulation. Plant growth promotion was also observed in durum wheat crops inoculated with *Bacillus atropheus* strains isolated from halophytes (Kerbab et al., 2021). The bacterial inoculation enhanced photosynthetic pigments content and reduced plants' stress level. Rhizospheric bacteria isolated from halophytes growing in Andalusian marshes also promoted development of Swiss chard and strawberry crops under saline conditions (Redondo-Gómez et al., 2022a; b). In other regions, other studies showed similar effects in different crops, such as peanut, sugar beet, soybean, barley, tomato, rice, etc (Table 3).

According to the mechanisms used by PGPB to assist plant growth (Fig. 2) under saline conditions, nutrient uptake and biomass increase was always improved when plants were inoculated with bacteria in contrast with non-inoculated ones (Table 3). In saline conditions bacterial inoculation also improved photosynthetic parameters in sugar beet (Zhou et al., 2017; Redondo-Gómez et al., 2022a), and similar results were also found in tomato, rice, and wheat (Taj and Challabathula, 2021; Babar et al., 2021). Concomitantly, an increase in different osmolytes content such as glycine and betaine were observed after peanut, tomato, rice, and maize bacterial inoculation in plants exposed to saline stress (Shukla et al., 2012; Ullah and Bano, 2015; Taj and Challabathula, 2021). The water content was another parameter that was benefited with bacterial inoculation in such crop plants suggesting that bacteria regulate aquaporin expressions under saline conditions to increase water accumulation and maintain ion homeostasis (Shukla et al., 2012; Sharma et al., 2016b; Taj and Challabathula, 2021; Babar et al., 2021). PGPB can modulate genes related to salt tolerance in soybean like *GmFLD19* and *GmNARK*, which were upregulated under salt stress, and *GmFLD19* and *GmNARK* that were downregulated, respectively (Khan et al., 2021). Finally, plants inoculated with PGPB showed a decrease in stress level due to activation of antioxidant enzymes that reduce the ROS (Ullah and Bano, 2015; Sharma et al., 2016b; Taj and Challabathula, 2021; Redondo-Gómez et al., 2022b), and/or reduction of ethylene levels (Zhou et al., 2017).

## 5.2. Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) are important soil inhabitants belonging to phylum Glomeromycota that form mutualistic symbiosis with circa 70 % of the terrestrial plants (van der Heijden et al., 2015). These fungi are obligate symbionts relying on the plant host for their growth and survival. Up to 20 % of photosynthetic products can be diverted from the plant to the maintenance of mycorrhizal structures (Jakobsen and Rosendahl, 1990; Bryla and Eissenstat, 2005). In exchange for carbon compounds, the AMF provide the host plant with nutrients (especially P) and water improving their tolerance to a variety of biotic and abiotic stresses, including salinity (Smith and Read, 2008).

Under saline conditions, the AMF can promote activation of several mechanisms and pathways in their hosts to help them cope with salinity stress (Fig. 2) (Evelin et al., 2019; Dastogeer et al., 2020). The AMF can enhance soil nutrient uptake, therefore improving plant nutritional status and growth (Tian et al., 2004; Porcel et al., 2012) and stability and integrity of cellular membranes under saline conditions, which enables a higher membrane permeability, and consequently a more efficient P uptake than non-mycorrhizal plants (Hameed et al., 2014; Pan et al., 2020). Mycorrhizal fungi enhance chlorophyll synthesis, photosynthesis, and water use efficiencies (Porcel et al., 2012; Hameed et al., 2014), compensating by this means the effects of the negative water potentials commonly found in saline soils. This is due to a higher root development that can explore more soil volume in search of water (Ruiz-Lozano and Azcón, 2000), stimulation of phytohormone production (e.g., ABA) (Jahromi et al., 2008; Ren et al., 2018; Hashem et al., 2019) and upregulation of aquaporin expression (Ouziad et al., 2006). Furthermore, AMF prevent or diminish osmotic stress caused by salinity through osmotic adjustment that is achieved through osmolytes accumulation (e.g., proline, glycine betaine and soluble sugars) (Porcel et al., 2012; Chun et al., 2018), and by K and Ca uptake increase that serve as osmotic equivalents to Na (Porcel et al., 2012; Estrada et al., 2013a; Chun et al., 2018). On the other hand, AMF can also prevent element toxicity by ion entry restriction, exclusion or immobilization in different plant, soil, or fungal compartments (Estrada et al., 2013a; Kapoor et al., 2013), and by the excretion of glomalin-related proteins (GRP) into the soil under moderately saline conditions (Hammer and Rillig, 2011;

**Table 2**  
New species of bacteria isolated from halophytes microbiome.

| Plant host species                | Species  | References  |
|-----------------------------------|--|---|
| <i>Arthrocnemum macrostachyum</i> | <i>Halomonas radialis</i> ; <i>Kokuria salina</i> ; <i>Kushneria phyllosphaerae</i> and <i>Kushneria endophytica</i> ; <i>Labrenzia salina</i> ; <i>Microbulbifer rhizosphaerae</i> ; <i>Pseudoalteromonas rhizosphaerae</i> ;   | Navarro-Torre et al. (2020b); Navarro-Torre et al. (2018); Camacho et al. (2016); Navarro-Torre et al. (2021); Lucena et al. (2017)   |
| <i>Carex scabrifolia</i>          | <i>Rosellomorea arthrocnemi</i> ; <i>Vibrio palustris Gynuella sunshinyii</i> ; <i>Hahyoungchilella caricis</i> ; <i>Marteella caricis</i> ; <i>Pedobacter endophyticus</i>  | Chung et al. (2015); Kim and Lee (2019); Lee (2019); Peng et al. (2021)   |
| <i>Halimione portulacoides</i>    | <i>Saccharospirillum correiae</i> ; <i>Salinicola aestuarinus</i> , <i>Salinicola endophyticus</i> , <i>Salinicola halimionae</i> , <i>Salinicola halophyticus</i> and <i>Salinicola lusitanus</i> ;   | Fidalgo et al., (2017, 2019)  |
| <i>Kalidium cuspidatum</i>        | <i>Corynebacterium kalidii</i> ; <i>Marinilactibacillus kalidii</i> ; <i>Sinomicrobium kalidii</i>   | Feng et al. (2022); Huang et al. (2022); Li et al. (2022)   |
| <i>Karelinea</i> sp.              | <i>Microbacterium karelineae</i>   | Zhu et al. (2021)   |
| <i>Limonium tetragonum</i>        | <i>Marteella limonii</i>   | Chung et al. (2016)   |
| <i>Salicornia</i> sp.             | <i>Zhihengliuella somnathii</i> ; <i>Zunongwangia flava</i>  | Jha et al. (2015); Cho et al. (2018)  |
| <i>Salsola affinis</i>            | <i>Arthrobacter endophyticus</i>   | Wang et al. (2015)  |
| <i>Spartina maritima</i>          | <i>Marinomonas spartinae</i> ; <i>Vibrio spartinae</i>   | Lucena et al. (2016); Lucena et al. (2017)  |
| <i>Suaeda</i> sp.                 | <i>Actinotalea suaedae</i> ; <i>Aurantiacibacter rhizosphaerae</i> ; <i>Bacillus suaedae</i> , <i>Cytobacillus suaedae</i> and <i>Paenalkalicoccus suaedae</i> ; <i>Erythrobacter suaedae</i> ; <i>Hoyosella suaedae</i> ; <i>Larsenimonas suaedae</i> ; <i>Marteella suaedae</i> ; <i>Microbacterium suaedae</i> ; <i>Ruania rhizosphaerae</i> ; <i>Sanguibacter suaedae</i> ; <i>Sphingobacterium endophyticum</i> | Zhao et al. (2015); Lee and Kim (2020); Xu et al. (2022); Lee et al. (2019); Liu et al. (2021); Chung et al. (2016); Lu et al. (2021); Ma et al. (2021); Liu et al. (2020a) |
| <i>Tamarix chinensis</i>          | <i>Salinicola tamaricis</i>  | Zhao et al. (2017)  |



**Table 3**

Halotolerant and halophilic plant growth promoting bacteria isolated from halophytes used as biofertilizers in crops grown under saline conditions.

| Crop species   | PGPB species   | Halophyte species from which bacteria were isolated   | Improvements  | References                   |
|--|--|---|---|------------------------------|
| <i>Arachis hypogaea</i> (peanut)                                       | <i>Brachy bacterium saurashtrense</i> JG-06, <i>Brevibacterium casei</i> JG-08, and <i>Haerero halobacter</i> JG-11  | <i>Salicornia brachiata</i>   | Improve seed germination and plant biomass, increase water content and osmolytes' contents, and decrease lipidic peroxidation   | Shukla et al. (2012)         |
| <i>Arachis hypogaea</i> (peanut)                                       | <i>Agrobacterium tumefaciens</i> MBE01, <i>Klebsiella</i> sp. MBE02, <i>Ochrobactrum anthropi</i> MBE03, <i>Pseudomonas</i> sp. MBE05 and <i>Pseudomonas. stutzeri</i> MBE04,  | <i>Arthrocnemum indicum</i> .   | Maintain ion homeostasis, decrease ROS level, and improve plant growth  | Sharma et al. (2016b)        |
| <i>Beta vulgaris</i> (sugar beet)                                      | <i>Micrococcus yunnanensis</i> TGT-R7, <i>Planococcus rifteoensis</i> LH-T4 and <i>Variovorax paradoxus</i> NG-T6  | <i>Nitraria tangutorum</i> , <i>Kalidium capsicum</i> and <i>Suaeda physophora</i>  | Improve seed germination, plant biomass, photosynthetic parameters, and decrease ethylene level   | Zhou et al. (2017)           |
| <i>Beta vulgaris</i> (sugar beet)                                      | <i>Bacillus zhangzhouensis</i> HPJ40 and <i>Pseudarthrobacter oxydans</i> SRT15  | <i>Atriplex portulacoides</i> and <i>Salicornia ramosissima</i>   | Plant growth stimulation, improve salt tolerance, reduce electrolyte leakage and Na <sup>+</sup> uptake, and improve photosynthetic parameters and antioxidant capacity | Redondo-Gómez et al. (2022a) |
| <i>Fragaria vesca</i> (strawberry)                                     | Biofertilizer 1 ( <i>Aeromonas aquariorum</i> SDT13, <i>Bacillus thuringiensis</i> SDT14 and <i>Pseudomonas composti</i> SDT3), Biofertilizer 2 ( <i>Pseudoalteromonas prydzensis</i> RA15, <i>Staphylococcus warneri</i> RA18 and <i>Vibrio kanaloae</i> RA1), Biofertilizer 3 (strains: <i>Bacillus aryabhattai</i> SMT48, <i>Bacillus licheniformis</i> SMT51 and <i>Bacillus methylotrophicus</i> SMT38), Biofertilizer 4 ( <i>Marinobacter sediminum</i> HPJ15, <i>Vibrio parahaemolyticus</i> HPJ50 and <i>Vibrio spartinae</i> HPJ2), Biofertilizer 5 ( <i>Pseudarthrobacter oxydans</i> SRT15, <i>Thalassospira australica</i> SRT8 and <i>Vibrio neocaledonicus</i> SRT1) | <i>Sporobolus montevidensis</i> , <i>Allenrolfea occidentali</i> , <i>Sporobolus maritimus</i> , <i>Atriplex portulacoides</i> and <i>Salicornia europaea</i> | Improve plant growth and flowering  | Redondo-Gómez et al. (2022b) |
| <i>Glycine max</i> (soybean)   | <i>Arthrobacter woltuwensis</i> ALT43 and <i>Bacillus aryabhattai</i> ALT29  | sand dune halophytes  | Increase biomass, photosynthetic pigments, and glutathione. Reduce stress level and modulate genes involved in salt tolerance   | Khan et al. (2021)           |
| <i>Hordeum vulgare</i> (barley) and <i>O. sativa</i> (rice)            | <i>Gordonia terrae</i> KMP456-M40  | <i>Avicennia marina</i>   | Improve ear biomass in barley and seed germination in rice  | Soldan et al. (2019)         |
| <i>Lycopersicon esculentum</i> (tomato)                                | <i>Arthrobacter</i> sp. and <i>Bacillus megaterium</i>   | <i>Tamarix chinensis</i> , <i>Suaeda salsa</i> and <i>Zoysia sinica</i>   | Decrease salt stress level  | Fan et al. (2016)            |
| <i>Lycopersicon esculentum</i> (tomato) and <i>Oryza sativa</i> (rice) | <i>Staphylococcus sciuri</i> ET101   | <i>Salicornia europaea</i>  | Increase growth rate, improve photosynthesis, increase water content, glycine and betaine contents, decrease ROS accumulation   | Taj and Challabathula (2021) |
| <i>Medicago sativa</i> (alfalfa)                                       | <i>Bacillus</i> sp. Su1–1 and <i>Halomonas</i> sp. A07–1   | <i>Salicornia rubra</i> , <i>Sarcocornia utahensis</i> , and <i>Allenrolfea occidentalis</i>  | Stimulate plant growth  | Kearl et al. (2019)          |
| <i>Oryza sativa</i> (rice) and <i>Cucumis sativus</i> (cucumber)       | <i>Pseudomonas</i> sp. RS1   | <i>Suaeda salsa</i>   | Increase plant biomass  | Yuan et al. (2016)           |
| <i>Solanum lycopersicum</i> (tomato)                                   | <i>Bacillus pumilus</i> AM11 and <i>Exiguobacterium</i> sp. AM25   | <i>Avicennia marina</i>   | Increase biomass, photosynthetic pigments, and photosynthetic rate, and increase antioxidant enzymes' level   | Ali et al. (2017)            |
| <i>Stevia rebaudiana</i>   | <i>Streptomyces fradiae</i> 8PK and <i>Streptomyces variabilis</i> 4NC   | <i>Cucumis sativus</i> and <i>Salicornia europaea</i>   | Enhance plant growth and increase RuBisCO accumulation  | Tolba et al. (2019)          |
| <i>Triticum aestivum</i> (wheat)                                       | <i>Arthrobacter aurescens</i> , <i>Bacillus atrophaeus</i> , <i>Enterobacter asburiae</i> , and <i>Pseudomonas fluorescens</i>   | <i>Salicornia</i> spp., <i>Echinochloa stagnina</i> , and <i>Tamarix</i> spp.   | Increase biomass, regulate Na <sup>+</sup> /K <sup>+</sup> balance, decrease ethylene emissions, and overexpress genes involved in antioxidant mechanisms               | Safdarian et al. (2020)      |
| <i>Triticum aestivum</i> (wheat)                                       | <i>Enterobacter</i> sp. Y7   | <i>Psoralea corylifolia</i>   | Improve seed germination  | Sorty et al. (2016)          |
| <i>Triticum aestivum</i> (wheat)                                       | <i>Alcaligenes faecalis</i> SBN01 and <i>A. faecalis</i> SBN02   | <i>Sesbania aculeata</i> and <i>Atriplex lentiformis</i>  | Increase plant biomass, osmolytes, and photosynthetic pigments. Reduce stress level and improve PSII efficiency   | Babar et al. (2021)          |
| <i>Triticum durum</i> (durum wheat)                                    | <i>Bacillus atropheus</i> BR5; <i>B. atropheus</i> OR15, and <i>B. atropheus</i> RB13  | <i>Suaeda mollis</i> and <i>Salsola tetrandra</i>   | Improved growth parameters and photosynthetic pigments, and reduce stress level   | Kerbab et al. (2021)         |
| <i>Zea mays</i> (maize)  | <i>Arthrobacter pascens</i> and <i>Bacillus</i> sp.  | <i>Atriplex leucoclada</i> and <i>Suaeda fruticosa</i>  | Enhance plant biomass, increase osmolytes accumulation and antioxidant enzymes activity   | Ullah and Bano (2015)        |

Krishnamoorthy et al., 2014). These glycoproteins can improve soil aggregation and therefore contribute to improve soil structure. Antioxidant enzyme activities such as catalase (CAT), superoxide dismutase (SOD), peroxidase and ascorbate peroxidase are also enhanced in mycorrhizal plants, enabling them to reduce ROS levels in their hosts,

thus preventing oxidative damage induced by salinity (Porcel et al., 2012; Hashem et al., 2015, 2018; Ait-El-Mokhtar et al., 2019; Evelin et al., 2019).

### 5.2.1. Arbuscular mycorrhizal fungi in saline soils

Elevated NaCl concentrations in soils can have a negative impact in several AMF characteristics, probably derived from Na toxicity and/or osmotic stress. However, some AMF can adapt to different salinity conditions, as demonstrated by the presence of spores in a wide range of saline environments, including coastal sand dunes (Rodríguez-Echeverría and Freitas, 2006; Campubri et al., 2011, 2012; Sridhar, 2016), salt marshes (Sengupta and Chaudhuri, 1990; Hoefnagels et al., 1993; Carvalho et al., 2001; Hildebrandt et al., 2001; Wilde et al., 2009), arid oases (Lumini et al., 2020) and other arid regions like deserts (Mathur et al., 2007). Some species can inhabit even in soils with very high EC (Aliasgharzadeh et al., 2001).

In saline soils from the Mediterranean basin, the most common mycorrhizal species belong to Glomeraceae family. For example, in Portuguese coastal dunes *Glomus intraradices* (syn. *Rhizophagus intraradices*), *G. fasciculatum* (syn. *R. fasciculatus*), *G. hoi*, *G. constrictum* (syn. *Septoglomus constrictum*) and *Glomus globiferum* have been observed, although members from other families were also present, such as *Scutellospora persica* and *Diversispora spurcum* (Rodríguez-Echeverría and Freitas, 2006). In East Spanish coastal dunes, besides *G. intraradices* and *S. persica*, and other Glomeraceae (*G. ambisporum*, *G. diaphanum* /*R. diaphanus*, *G. clarum*/*R. clarus*, and *G. microaggregatum*) and non-Glomeraceae species (*Gigaspora margarita*) were also found (Camprubi et al., 2011, 2012). On the other hand, in Portuguese salt marshes, as well as in other European salt marsh environments, *G. etunicatum* (syn. *Claroideoglomus etunicatum*) is dominant (Hildebrandt et al., 2001; Landwehr et al., 2002). In Tunisian Sahara oases, *R. irregularis*, *Funnelliformis coronatus*, *Albahypha drummondii* and *Dominikia disticha* are the species most frequently found (Chebaane et al., 2020) whereas in Algerian natural wetlands, members of Glomeraceae and Acaulosporaceae families dominate, including species of *Acaulospora*, *Rhizoglomus* or *Funnelliformis* as well as AMF from other families (e.g., Ambisporaceae, Archaeosporaceae, Diversisporaceae, Claroideoglomeraceae and Paraglomeraceae (Sidhoum et al., 2020).

Many halophytes belong to plant families that do not establish mycorrhizal symbioses, such as Amaranthaceae or Chenopodiaceae (Becerra et al., 2019). However, halophytes from Asteraceae and Plantaginaceae families can be highly mycotrophic and benefit from the mutualistic association with AMF (Dashtebani et al., 2014; Becerra et al., 2019). This association not only improves plant nutrition and water uptake but also help plants to cope with salinity, improving ion homeostasis and eventually plant survival, growth, and reproduction (Al-Garni, 2006; Estrada et al., 2013b; Liu et al., 2018; Pan et al., 2020; Diao et al., 2021). Therefore, these plants' mycorrhizal condition can be determinant for some species survival in these environments, which apart from salt stress may also present additional concomitant stress factors such as high UV radiation, low water availability, or waterlogging.

### 5.2.2. Mycorrhizal inoculations as a strategy to increase plant tolerance in salt-affected soils

In the Mediterranean region, an improvement in plant salinity tolerance by different commercial or collection AMF species has been demonstrated in a variety of hosts, including halophytes and glyco-phytes. The most widely tested AMF species have been *R. irregularis*, *R. intraradices*, *R. iranicum*, *F. mosseae*, *C. claroideum* and *G. macrocarpium*, being the inoculated crops tomato, pepper, lettuce, soybean, maize, and olive trees (Al-Karaki et al., 2001; Jahromi et al., 2008; Porras-Soriano et al., 2009; Aroca et al., 2013; Kapoulas et al., 2019; Abdelhameid and El-Shazly, 2020; Moreira et al., 2020) (Table 4).

Regardless AMF benefits that can bring to their hosts, there is a high variability on the functionality of mycorrhizal symbioses under soil salinity conditions. For instance, in the study of Porras-Soriano et al. (2009), among the three studied AMF species (*G. mosseae* syn. *F. mosseae*, *G. intraradices* syn. *R. intraradices*, *G. claroideum* syn. *C. claroideum*), *G. mosseae* provided the highest salinity tolerance to the

host (olive tree). However, other works showed little effect to AMF inoculation on plant salt tolerance as in tomato plants (Gómez-Bellot et al., 2020).

Halophytic AMF were used to inoculate crop and non-crop plants as a strategy to increase their performance under salinity conditions. This was the case for an *G. geosporum* (syn. *F. geosporum*) isolate native inoculated in fleabane (*Conyza bilbaoana* J. Rémy) producing a remarkable improvement in plant growth and P concentration under salinity-induced stress (Oliveira et al., 2006). A positive response in inoculated plants using a consortium of native AMF (composed by *G. mosseae*, *G. intraradices* and *G. etunicatum*) isolated from a salt marsh in soybean was observed when irrigated with saline water. Plants presented higher auxin concentrations and lower thiobarbituric acid reactive substances (TBARS), H<sub>2</sub>O<sub>2</sub> and malondialdehyde (MDA) than non-inoculated plants (Hashem et al., 2019). In maize, differences were found in plant performance when a collection-*R. irregularis* isolate was inoculated and when indigenous isolates of *R. intraradices*, *S. constrictum*, *C. etunicatum* were inoculated at three salinity conditions (Estrada et al., 2013a). In all conditions native *R. intraradices* and *C. etunicatum* improved plant growth, increased K and decreased Na in plant tissues compared to non-inoculated plants, while the AMF collection did not show significant differences or led to even lower growth (Estrada et al., 2013a). In halophyte *Asteriscus maritimus* (L.) Less., the native consortium was more efficient than AMF collection in promoting salinity tolerance, since plants presented higher growth, efficiency of photosystem II, stomatal conductance, and glutathione accumulation than those inoculated with *R. irregularis* (Estrada et al., 2013b).

Halotolerant AMF may also show variability in their effects on the host. In palm trees inoculated with two consortia of halotolerant AMF or two halotolerant AMF single species, plant growth improvement under saline stress was not always significant for all the inoculants and depended on the salt (NaCl) concentration and on the type of inoculum used (consortium or single species, or the original location; Outamamat et al., 2021). In all AMF-inoculated plants P concentration was higher at 10 g L<sup>-1</sup> NaCl, but at 20 g L<sup>-1</sup> only plants inoculated with the single-species inoculum showed a significant P concentration increase. Moreover, the K was higher than Na content in seedlings inoculated with single species in saline soils (Outamamat et al., 2021). Other studies show that AMF isolated from saline soils are not always able to promote a higher salt stress tolerance in their hosts when compared to AMF from non-saline environments. Camprubi et al. (2011) demonstrated that when a consortium of native halophile AMF isolates and a non-native collection AMF were inoculated in psamophyllic plant species in dune sandy soils, six out of 15 species responded positively in terms of growth to the inoculation with both native and non-native inocula. However, in two of the species (*Ononis natrix* L., *Armeria maritima* Willd.) only the AMF collection promoted plant biomass, and in another species (*Elymus farctus* (Viv.) Runemark ex Melderis) the consortium with native AMF improved plant growth. Similar results were found when lettuce plants were inoculated with *Glomus* sp. isolated from a saline soil and a collection *Septoglomus deserticola* (Ruiz-Lozano and Azcón, 2000). Although both AMF increased plant tolerance to salinity, the latter promoted a higher shoot biomass and P and N accumulation in plant tissues than the AMF from the saline soil, and *Glomus* sp. promoted higher root biomass.

## 6. Soil technologies to recover saline soils and sediments

The type, characteristics, and soils' properties, as well as their edaphic and biogeochemical processes can be specific of each geographic and geological area. Salt-affected areas can present other soil constraints as low concentration of nutrients, alkaline pH and poor structure, and consequent lack of drainage that can limit the success of soil recovery. Therefore, it is essential to understand the source of salinization (and sodicity) and its spatial variability as well as its effects under the edaphoclimatic conditions to design a successful remediation

Table 4

Arbuscular mycorrhizal fungi isolated from saline and non-saline environments used for plant growth and salinity tolerance stimulation.

| Crop species   | Mycorrhizal species   | Experimental conditions  | Location | Effects on the host   | Authors                      |
|--|---|--|----------|---|------------------------------|
| <i>Acacia saligna</i>  | Consortium of AMF of the genera <i>Glomus</i> , <i>Gigaspora</i> and <i>Acaulospora</i>   | Irrigation with saline water at concentrations of 6.25, 12.50 or 25 dS m <sup>-1</sup> . | Egypt    | Under saline conditions improved shoot and root growth, promoted osmotic adjustment and proline content, improved chlorophyll, N and P contents in leaves, reduced Na and increased K.  | Soliman et al. (2012)        |
| <i>Asteriscus maritimus</i>  | <i>R. irregulare</i> from a collection, and indigenous isolates of <i>Rhizogloium intraradices</i> , <i>Septogloium constrictum</i> , <i>Claroideogloium etunicatum</i>   | Salinized soil with final concentration of 0, 100, and 175 mM NaCl                       | Spain    | The native consortia were more efficient than AMF collection in promoting tolerance to salinity, since plants presented higher growth, efficiency of photosystem II, stomatal conductance and glutathione accumulation than the ones inoculated with <i>R. irregulare</i> . Survival at the highest salinity level was also significantly higher. | Estrada et al. (2013b)       |
| <i>Arundo donax</i>  | Commercial inoculum with <i>Rhizophagus intraradices</i> and <i>Funneliformis mosseae</i>   | 1, 75 and 150 mM NaCl  | Spain    | At all NaCl concentrations, inoculated plants had lower Na <sup>+</sup> uptake, Na <sup>+</sup> root-to-shoot translocation, Na <sup>+</sup> /K <sup>+</sup> ratio, and higher P and K use efficiencies. 75 mM NaCl, inoculated plants showed increased growth.   | Romero-Munar et al. (2019)   |
| <i>Capsicum annuum</i> (two pepper genotypes)  | <i>Rhizophagus intraradices</i>   | Plant transplantation to a soil with enhanced P and salinity                             | Greece   | In saline soil AMF stimulated growth, fruit yield and number of fruits per plant in one of the cultivars when pre-inoculated in the greenhouse, but in the other cultivar inoculation did not have a significant effect.  | Kapoulas et al. (2019)       |
| <i>Glycine max</i> (salt tolerant and sensitive genotypes of soybean)  | Consortium of native <i>Funneliformis mosseae</i> (syn. <i>Glomus mosseae</i> ), <i>Rhizophagus intraradices</i> (syn. <i>Glomus intraradices</i> ) and <i>Claroideogloium etunicatum</i> (syn. <i>Glomus etunicatum</i> ) isolated from a salt marsh | Irrigated with 200 mM NaCl   | Egypt    | In saline conditions, higher levels of IAA and IBA, and lower thiobarbituric acid reactive substances (TBARS) and H <sub>2</sub> O <sub>2</sub> content.  | Hashem et al. (2019)         |
| <i>Medicago sativa</i> (alfalfa)   | A mixture of indigenous species <i>Glomus</i> sp., <i>Sclerocystis</i> sp. and <i>Acaulospora</i> sp.   | Plants grown in non-saline or salinized soil (0 and 120 mM NaCl)                         | Morocco  | Inoculation reduced the deleterious effects of salinity on plant growth and leaf water potential. Electrolyte leakage, malondialdehyde (MDA) content decreased, production of compatible osmolytes (sugar) and antioxidant enzymes increased.   | Ben Laouane et al. (2019)    |
| <i>Lactuca sativa</i> (lettuce)  | <i>Glomus</i> sp. isolated from saline soils and <i>Glomus deserticola</i> (syn. <i>Septogloium deserticola</i> ) from nonsaline soils  | Soil with three salt concentrations: 0.25, 0.50 or 0.75 g NaCl Kg <sup>-1</sup>          | Spain    | AMF differed in their symbiotic efficiencies, especially at highest salinity. <i>Septogloium deserticola</i> was more infective and led to higher shoot growth, N and P accumulation, while <i>Glomus</i> promoted higher root growth.  | Ruiz-Lozano and Azcón (2000) |
| <i>Lactuca sativa</i> (lettuce)  | <i>G. intraradices</i> DAOM 197198  | Watering with 0, 50, 100 mM of NaCl  | Spain    | Improved shoot dry weight, relative water content and ABA content. Proline content was lower in inoculated plants at 50 mM, but there were no differences between inoculated and non-inoculated plants at 100 mM.   | Jahromi et al. (2008)        |
| <i>Lactuca sativa</i> (lettuce)  | <i>Glomus intraradices</i>  | 0, 40 and 80 mM of NaCl  | Spain    | Under salt stress, inoculated plants had higher growth, stomatal conductance and photosystem II efficiency, and had lower ABA levels.   | Aroca et al. (2013)          |
| <i>Lotus creticus</i> , <i>Glaucium flavum</i> , <i>Pancretium maritimum</i> , <i>Elymus farctus</i> , <i>Thymbra capitata</i> , <i>Ammophila arenaria</i> , <i>Dorycnium pentaphyllum</i> , <i>Halimium halimifolium</i> , <i>Ononis natrix</i> . | <i>Glomus intraradices</i> (reclassified as <i>Rhizophagus irregulare</i> )   | Irrigation once per week with diluted and undiluted sea water                            | Spain    | Mycorrhizal inoculation reduced plant mortality, except in <i>D. pentaphyllum</i> .   | Camprubi et al. (2012)       |
| <i>Olea europaea</i> (olive tree)  | Collection AMF: <i>Glomus mosseae</i> , <i>Glomus intraradices</i> , <i>Glomus claroideum</i>   | Substrate with 6 g NaCl Kg <sup>-1</sup>   | Spain    | AMF inoculation alleviated the negative effects of salinity in stem diameter, number of shoots, shoot length and nutrient content, which was attributed to increase in K acquisition. <i>G. mosseae</i> was the AMF with the best results.  | Porrás-Soriano et al. (2009) |

(continued on next page)

Table 4 (continued)

| Crop species   | Mycorrhizal species  | Experimental conditions   | Location | Effects on the host  | Authors                         |
|--|--|---|----------|--|---------------------------------|
| <i>Phaseolus vulgaris</i>  | <i>Glomus intraradices</i>   | Plants watered with NaCl. The soil final electrical conductivities: 0.12 and 3.06 dS m <sup>-1</sup> in control and salinity pots | Spain    | Under salinity conditions leaf relative water content was higher and transpiration lower in inoculated plants. Root hydraulic conductance tended to be higher too.   | Aroca et al. (2007)             |
| <i>Phoenix dactylifera</i> (palm tree)                                     | A mixture of indigenous species <i>Glomus</i> sp., <i>Sclerocystis</i> sp. and <i>Acaulospora</i> sp.  | Plants grown in non-saline or salinized soil (0 and 240 mM NaCl)  | Morocco  | Root colonization decreased by salinity. Inoculation reduced the negative impact of salinity in growth and physiological parameters, on plant nutrition and on lipid peroxidation and H <sub>2</sub> O <sub>2</sub> content. However, superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase increased in inoculated plants under saline conditions.   | Ait-El-Mokhtar et al. (2019)    |
| <i>Phoenix dactylifera</i> (palm tree)                                     | Two consortia of halotolerant AMF (isolated from a Palm grove and from a date palm rhizosphere, both with saline soils), and mono-species AMF inocula isolated from the same two locations | 0, 10 and 20 g L <sup>-1</sup> NaCl   | Morocco  | Under saline conditions inoculation with different native and non-native consortia and mono-species inocula tended to improve plant growth, although it was not statistically significant in all cases. P, K improved by inoculation at 10 g L <sup>-1</sup> but differences were less significant at 20 g L <sup>-1</sup> . Na content was significantly lower and Mg higher in plant inoculated with the mono-species inoculum. Catalase, SOD and PPO were higher in plants inoculated with mono-species inoculum. | Outamat et al. (2021)           |
| <i>Solanum lycopersicum</i> (salt tolerant and sensitive tomato cultivars) | <i>Glomus mosseae</i> (syn. <i>F. mosseae</i> )  | Salt was applied at saturation extract (ECe) values of 1.4 (control), 4.9 (medium) and 7.1 dS m <sup>-1</sup> (high salt stress)  | Jordan   | Under medium salinity conditions, in both cultivars, inoculated plants had higher P, K, Zn, Cu, and Fe concentrations than non-inoculated plants, and nutrient uptake was higher in Marriha (salt-sensitive) than in Pello cultivar (salt-tolerant).   | Al-Karaki et al. (2001)         |
| <i>Solanum lycopersicum</i> (tomato)                                       | <i>Glomus mosseae</i> (syn. <i>F. mosseae</i> )  | Irrigation with saline water (2.4 dS m <sup>-1</sup> )  | Jordan   | Plants pre-inoculated with AMF under saline conditions had higher biomass growth, fruit fresh yield and P, K, Zn, Cu, and Fe concentration in shoots than non-inoculated plants, but lower Na concentrations.  | Al-Karaki (2006)                |
| <i>Solanum lycopersicum</i> (tomato)                                       | <i>Glomus macrocarpium</i>   | Irrigation with saline water (2800 mg L <sup>-1</sup> and 3800 mg L <sup>-1</sup> )   | Egypt    | Inoculation reduced the negative impact of salinity in growth parameters, nutrient content, and yield.   | Abdelhameid and El-Shazy (2020) |
| <i>Solanum lycopersicum</i> (tomato)                                       | <i>Glomus iranicum</i> var <i>tenuipharum</i>  | Irrigation with saline reclaimed water  | Spain    | By the end of the experiment, in soils irrigated with reclaimed water relative the chlorophyll content (RCC) was lower in inoculated plants. No differences in photosynthesis rate and stomatal conductance. Leaf water relations and leaf mineral content were not affected by AMF, Ca/Na and K/Na.   | Gómez-Bellot et al. (2020)      |
| <i>Triticum aestivum</i> (wheat)   | Consortium of collection AMF: <i>Funnelformis geosporum</i> , <i>F. mosseae</i> , <i>Rhizophagus clarus</i> and <i>Scutellospora persica</i> .   | Plants grown in non-saline or salinized soil 75 or 150 mM NaCl  | Egypt    | Inoculation reduced the deleterious effects of salinity on plant growth, grain yield, P, N, chlorophyll and carotenoid contents, reduced proline levels, reduction of the relative permeability and MDA in leaves.   | Elgharably and Nafady (2021)    |
| <i>Zea mays</i> (maize)  | <i>R. irregulare</i> from a collection, and indigenous isolates of <i>Rhizoglyphus intraradices</i> , <i>Septoglyphus constrictum</i> , <i>Claroideoglyphus etunicatum</i>                 | Plants grown in non-saline or salinized soil 66 or 100 mM NaCl  | Spain    | At all salinity conditions the native <i>R. intraradices</i> and <i>C. etunicatum</i> improved plant growth compared to non-inoculated plants, while AMF collection did not show significant differences or led to even lower growth. Native isolates increased K <sup>+</sup> and decreased Na <sup>+</sup> in their host compared to the non-inoculated plants.  | Estrada et al. (2013a)          |
| <i>Zea mays</i> (maize)  | Commercial <i>Rhizophagus irregulare</i>   | 0–5 g NaCl kg <sup>-1</sup> soil  | Portugal | Under saline conditions, inoculated plants tended to increase growth in respect to the non-inoculated ones. No effect on P content in roots and shoots. AMF induced an increase in N in roots.   | Moreira et al. (2020)           |

and/or management plan.

Although some techniques are indicated for the remediation of salt-affected soils, their response may vary over time and space, in relation to the initial soil characteristics, climatic conditions and severity of salinity and/or sodicity (FAO, 2022). Some of these techniques act directly on reducing the effects of salinity and/or sodicity (e.g., leaching of soluble salts or exchange of Na from the exchangeable complex by divalent cations) while others (e.g., phytoremediation, amendments application, designed Technosols) may improve soils physic-chemical and biological characteristics (Aguilar-Garrido et al., 2022; FAO, 2022). The application rate of irrigation water or amendments is based on EC or SAR; however, its variability at the soil surface and along the soil profile is not usually considered, which limits the efficiency of the remediation strategy (Günel, 2021). The application of several types of mulch or rubble barrier within the soil can also reduce the effect of the salinization at soil surface due to decrease in evaporation, salt accumulation or break in continuity of saline water ascent by capillarity (Saifullah et al., 2018; Ondrasek and Rengel, 2021; FAO, 2022).

The most common practice for salt-affected soils remediation is a higher irrigation volume, especially by flooding to dissolve soluble salts and leaching elements to deeper layers outside the roots system (FAO, 2018; Stavi et al., 2021). The depth of to which the soil must be leached depends on crop species, and the most advisable period for the application of this technique is the season of the year with the lowest evaporation, when the saline groundwater is deep. Nonetheless, its efficiency always depends on water quality, amounts applied, and soil physical parameters like structure and porosity. A disadvantage of this process is that it increases the risk of groundwater salinization and may also contributes to leaching of nutrients needed to plants (Devkota et al., 2015; FAO, 2018).

Amendments application, namely from traditional sources, as organic and inorganic Ca-containing, or biochar can be used in soil rehabilitation. Organic amendments (e.g., manure, compost, by-products of agroindustry) and biochar can improve soil physical properties (e.g., macro-aggregation processes, aggregates stability and structure) and hydraulic conductivity thereby enhancing water drainage and leaching of soluble salts (Nachshon, 2018; Saifullah et al., 2018; Ondrasek and Rengel, 2021; Stavi et al., 2021). Moreover, the above referred authors reported that organic amendments and biochar can also be a source of exchangeable Ca and Mg, increasing soil cation exchange capacity, Na immobilization, organic matter and available nutrients supplies, and soil pH decrease. A prior chemical characterization of amendments is a key point since some organic amendments (e.g., manure) present significant salinity (Stavi et al., 2021) and high potential hazardous elements concentration.

Inorganic amendments containing high amounts of Ca and Mg (e.g., gypsum and dolomite) are specially used in the rehabilitation of sodic soils. The application of these amendments followed by irrigation leads to Na replacement in the soil exchangeable complex by Ca (or Mg), followed by some Na leaching to deeper layers (WRB, 2015; Günel, 2021; Stavi et al., 2021). Moreover, the presence of significant amounts of Ca can promote clay flocculation and particle aggregation, improving soil structure, hydraulic conductivity, and aeration (Omuto et al., 2020; Ondrasek and Rengel, 2021). The application of amendments with  $\text{NH}_4$  and K cations can have similar effect but Na replacement by Ca and Mg appears to be relevant (Stavi et al., 2021). In sodic soils, the combined application of organic and inorganic amendments can be more effective than the single application of inorganic amendments (Gonçalo et al., 2019).

In saline soils containing calcium carbonate, the recovery strategy can include acid solutions or acid amendments application (e.g., acid drainage generating materials – sulfide minerals) for carbonates dissolution and release of Ca to further Na replacement (Bresler et al., 1982; Qadir et al., 2001; WRB, 2015; FAO, 2018; Ondrasek and Rengel, 2021). However, acid amendments as pyrite or other sulfide minerals combined with irrigation can present extreme environmental risk due to the

release of potentially hazardous elements (e.g., Pb, As, Sb, Cu, Zn depending on the sulfide solid phases type), together with hydrogen ions. After organic and inorganic amendments application, a significant soil irrigation or precipitation is mandatory for their efficiency (Günel, 2021). Nonetheless, the availability of amendments and irrigation water with chemical quality and in high amounts is limited in some regions affected by salinization (FAO, 2022), and thus other techniques need to be explored.

An environmentally friendly remediation technique is via elaboration of Technosols (Fig. 3), man-made tailored soils, whose properties and pedogenesis are dominated by their technical origin (WRB, 2015). These soils may be elaborated from wastes and applied for subsequent recovery of salt-affected soils (Cortinhas et al., 2020, 2021), or other type of degraded soils, improving their physic-chemical and biological properties (Macía et al., 2014), while contributing to circular economy (Breure et al., 2018). Halophytes and other plants with salinity tolerance can be cultivated in such ameliorated salt-affected soils, being an alternative with significant relevance (Hasanuzzaman et al., 2014; Santos et al., 2017b; FAO, 2018; Cortinhas et al., 2020, 2021; Ondrasek and Rengel, 2021 and references herein).

The combination of plant-based techniques with the application of amendments or Technosols can be a valuable option to accelerate the salt-affected areas recovery (Cortinhas et al., 2020, 2021; Aguilar-Garrido et al., 2022). Technosols constructed with a mixture of organic and inorganic wastes and aquaculture sediments from earthen coastal ponds, or a saline Fluvisol from a saltmarsh area improved soil physic-chemical characteristics and fertility allowing cultivation of different halophyte species irrigated with estuarine water (Cortinhas et al., 2020, 2021). Also, glycophytic plants such as a biodiverse pasture composed of leguminous plants (*Trifolium* sp. and *Medicago* sp.) and gramineous plants (*Lolium* sp.) can also be cultivated in Technosols built with a saline Fluvisol and wastes (Aguilar-Garrido et al., 2022).

Moreover, the use of autochthonous species from saline environments may have advantages due to their better tolerance to edaphoclimatic conditions, besides having several uses (Hasanuzzaman et al., 2014; Santos et al., 2017b; Cortinhas et al., 2019, 2020, 2021). For phytodesalinization purposes the species used include among others *Atriplex halimus* L. (Gharaibeh et al., 2011), *Arthrocnemum indicum* (Rabhi, 2008, 2009), *Limonium bicolor* (Bunge) Kuntze (Sakai et al., 2012), *M. crystallinum* (Abdelly et al., 2006), *Salicornia persica* Akhani (Ebadi et al., 2018) *Suaeda fruticosa* (Zorrig et al., 2012) (Table 5). In *S. soda* and *P. oleracea* pot experiments in soils with different levels of salinity and Na in exchangeable fraction and irrigated with tap water, it was observed a decrease of EC, between 2 and 4-fold depending on salinity level and species, compared to the initial values (Karakas et al., 2017). *Salsola soda* and *P. oleracea* can remove 709 kg Na ha<sup>-1</sup> and 286 kg Na ha<sup>-1</sup>, respectively, from these soils in a period of 100 days (Karakas et al., 2017). Although, under in non-Mediterranean context other studies using halophytes species also reported a decrease in soil available Na concentration, and consequently EC (Ramaswamy et al., 2021). In a mesocosm assay where a soil was enriched with 3.8 g NaCl kg<sup>-1</sup> (7.1 dS m<sup>-1</sup> and 20.9 SAR) and irrigated with tap water, *Sesuvium portulacastrum* decreased progressively EC and SAR reaching, after 90 days, 4.9 dS m<sup>-1</sup> and SAR 13.5 (Muchate et al., 2016). *Suaeda aegyptiaca* (Hasselq.) Zohary and *Distichlis spicata* (L.) Greene plants growing in a soil mixture (2:1 clay loam: sand) and irrigated with aqueous solutions with NaCl with increasing values of EC had a progressive increase in Na concentration in both shoots and roots. The potential of *S. aegyptiaca* shoots to remove Na under all tested salinity levels was higher than *D. spicata* (Sabzalian et al., 2018). Field studies combining halophytes growth in various environmental conditions reported a high accumulation of Na (and other elements) in plants' tissues (Miranda et al., 2021; de Souza et al., 2014; Asghar et al., 2023; Ayyappan et al., 2013; Shaygan et al., 2018). These plant-based technologies have additional advantages by contributing to soil fertility, structure, drainage, and biological activity (Qadir and Oster, 2002; Jesus et al., 2015; Santos

**Table 5**

Halophytes species used for salt-affected soils rehabilitation.

| Halophytes species                   | References                  |
|--------------------------------------|-----------------------------|
| <i>Sesuvium portulacastrum</i>       | Abdelly et al. (2006)       |
| <i>Batis maritima</i>                |                             |
| <i>Mesembryanthemum crystallinum</i> |                             |
| <i>Salsola baryosma</i>              | Shekhawat et al. (2006)     |
| <i>Haloxylon recurvum</i>            |                             |
| <i>Suaeda nudiflora</i>              |                             |
| <i>Suaeda maritima</i>               | Ravindran et al. (2007)     |
| <i>Sesuvium portulacastrum</i>       |                             |
| <i>Arthrocnemum indicum</i>          | Rabhi et al. (2008)         |
| <i>Suaeda fruticosa</i>              |                             |
| <i>Sesuvium portulacastrum</i>       |                             |
| <i>Sesuvium portulacastrum</i>       | Rabhi et al. (2009)         |
| <i>Arthrocnemum indicum</i>          |                             |
| <i>Sesuvium portulacastrum</i>       | Rabhi et al. (2010)         |
| <i>Atriplex halimus</i>              | Gharaibeh et al. (2011)     |
| <i>Typha angustifolia</i>            | Boonsaner and Hawker (2012) |
| <i>Artemisia argyi</i>               | Sakai et al. (2012)         |
| <i>Limonium bicolor</i>              |                             |
| <i>Melilotus suaveolens</i>          |                             |
| <i>Salsola collina</i>               |                             |
| <i>Tecticornia indica</i>            | Zorrig et al. (2012)        |
| <i>Suaeda fruticosa</i>              |                             |
| <i>Sesuvium portulacastrum</i>       |                             |
| <i>Sulla carnosa</i>                 | Jlassi et al. (2013)        |
| <i>Salicornia persica</i>            | Ebadi et al. (2018)         |
| <i>Tecticornia pergranulata</i>      | Shaygan et al. (2018)       |
| <i>Scleroalaena longicuspis</i>      |                             |
| <i>Frankenia serpyllifolia</i>       |                             |
| <i>Sesuvium portulacastrum</i>       | Ramaswamy et al. (2021)     |
| <i>Salsola soda</i>                  | Karakaş et al. (2017)       |
| <i>Sesuvium portulacastrum</i>       |                             |
| <i>Suaeda vera</i>                   | Asghar et al. (2023)        |
| <i>Distichlis spicata</i>            | Sabzalian et al. (2018)     |
| <i>Suaeda aegyptiaca</i>             |                             |
| <i>Suaeda monoica</i>                | Ayyappan et al. (2013)      |
| <i>Atriplex nummularia</i>           | de Souza et al. (2014)      |
| <i>Sesuvium portulacastrum</i>       | Muchate et al. (2016)       |
| <i>Atriplex nummularia</i>           | Miranda et al. (2021)       |

et al., 2017b; Cortinhas et al., 2020, 2021).

## 7. Conclusions

This review summarizes successes and failures of plant-based, microbial and soil technologies approaches used in salt affected soils, with a focus in the Mediterranean region. The soils in the Mediterranean region are highly affected by salinization due to a high degree of desertification and non-correct land management. Despite studies in this context are relatively few, some works show that halophytes can successfully be used as alternative species for cultivation in salt-affected soils using saline water unsuitable for conventional crops. Alongside, extremophilic halophilic bacterial and arbuscular mycorrhiza isolates can also be utilized with positive impacts alleviating plant stress and increasing plant productivity. However, the establishment of the inoculated microbial strains in the target soil conditions may not always be successful, due to the complex interactions between non-native microorganisms and the native ones, the host genotype, and saline soil environment. Most studies on soil and plant-based technologies applied to salt-affected soils have been conducted under greenhouse conditions and have not made field trials for results validation. Field studies are required combining Technosols application and microbial inoculations and plant salinity tolerance assessment in both non-halophilic crops and halophytes.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

## Data availability

The authors are unable or have chosen not to specify which data has been used.

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