Sanjay Arora · Atul K. Singh
Y.P. Singh   *Editors*

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Foreword

Salinity and sodicity of soil is a global problem that extends across all continents in more than 100 countries of the world, presenting a major threat to farm agricultural production, leading to adverse implications for food security, environmental health, and economic welfare. The remediation of salt-affected lands and their management will go a long way in meeting the desired 57% increase in global food production by the year 2050. Amelioration of saline and sodic soils has been predominantly achieved through the application of chemical amendments. However, amendment costs have increased prohibitively over the past two decades due to competing demands from industry and reductions in government subsidies for their agricultural use in several developing countries. Also, the availability of chemical amendments, such as gypsum, that come from minerals is a problem. Saline soil improvement needs excessive amounts of good quality water to wash salts as an ameliorative measure. In many countries in arid and semiarid regions where rainfall is scanty and the availability of good quality waters is a problem, this method of reclamation does not seem to be feasible. However, alternate biological methods such as planting the soil with salt-tolerant plants where salts are taken up by these plants and removed from the soil or exchanged through biological processes can be used. Bioremediation is considered as a promising option as it requires low initial investments and improves the soil quality and the crop produce. Halophilic microorganisms are organisms that grow optimally in the presence of high salt concentrations. These have high potential for bioremediation applications and have been reported by several workers. The applications of halophilic bacteria trigger recovery of salt-affected soils by directly supporting the establishment and growth of vegetation in soils stressed with salts.

The biotic approach ("plant-microbe interaction") for overcoming salinity/sodicity problems has recently received considerable attention throughout the world. Bacteria are most commonly used in the bioremediation of soils. Vesicular-arbuscular mycorrhiza or VAM fungi is also found to be effective in alleviating salt stress and increasing availability of nutrients to the plants. Bioremediation, including phytoremediation approaches for management of saline, sodic and coastal

saline, and waterlogged soils, seems needed. Bioremediation and management of vast areas of salt-affected soils involve considerations of economic viability, environmental sustainability, and social acceptability of different approaches. Phytoremediation strategies can be economically beneficial if there is market demand for the selected crops, grasses, or trees, or if they are useful locally at the farm level. However, in any economic analysis of sodic soil amelioration, it is also important to consider the long-term benefits of improvements made to the soil and the environment. This all will help in bioremediation of saline soil and improvement of crop yields, and in turn will help in uplifting the socioeconomic status of the farming community. However, there are several opportunities and challenges for the future of bioremediation techniques for the effective reclamation of salt-affected soils. In this book, the information and technologies developed for bioremediation and management of salt-affected soils are compiled with an emphasis on characterization, reclamation, microbial and vegetative bioremediation, and management technologies for salt-affected and waterlogged sodic soils.

In this book, attempts have been made to address a wide range of issues related to principles and practices for rehabilitation of inland and coastal salt-affected soils as well as waterlogged saline and sodic soils. Several site-specific case studies typical to the saline and sodic environment, including coastal ecologies, sustaining productivity, rendering environmental services, conserving biodiversity, and mitigating climate change, are included and described in detail. Written by leading researchers and experts of their specialized fields, this book, though in an Indian context, will serve as a knowledge center for experts in management of salt-affected soils but also for researchers, policy makers, environmentalists, students, and academics from all parts of the world. Further, it will also help reverse salinity development to ensure the livelihoods of resource-poor farming families living in harsh ecologies including coastal areas which are more vulnerable to climate change.

I congratulate and extend my appreciation to the editors for conceptualizing and developing the framework of this publication, and the authors for summarizing their wealth of knowledge and experiences. I sincerely hope and believe that the information contained in this book will provide new insight to researchers, extension workers, field officers, and others involved in reclamation and management of salt-affected soils.

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Preface

In the past, the increasing needs of a growing population for food, fuel and fiber were met by cultivating progressively larger areas of land and by intensifying the use of existing cultivated land. Under circumstances with diminishing good-quality lands and stagnating crop yields, the food demands of an increasing population must be met through the reclamation and management of degraded lands, including salt affected lands. Salt-affected soils cover about 6 % of the world's lands, which is mainly due to either natural causes or human-induced causes that affect about 2 % (32 million ha) of dryland farmed areas and 20 % (45 million ha) of irrigated lands globally. In India, about 6.73 million ha of land are affected by salts. To overcome this problem, several researchers have advocated the biological approach to improve these lands for cultivation. Innovative technologies in managing marginal salt affected lands merit immediate attention in view of climate change and its impact on crop productivity and the environment. The management of degraded land on a sustainable basis offers an opportunity for the horizontal expansion of agricultural areas in the India. During the last three decades, a number of strategies to ameliorate different kinds of marginal lands, including salt affected areas, have been developed. Adequate knowledge in diagnosis and management technologies for saline and alkali lands is essential to obtain maximum crop production from these resources. Bioremediation is one of the eco-friendly approaches for improving the productivity of salt affected soils.

This book attempts to gather and discuss the information and technologies developed for the bioremediation and management of salt affected soils. The emphasis in this endeavour was on characterization, reclamation, microbial and vegetative bioremediation and management technologies for salt affected and waterlogged sodic soils. This book contains 14 chapters that highlight the significant environmental and social impacts of different ameliorative techniques for salt affected soils. Bioremediation, including phytoremediation approaches for managing saline, sodic and coastal waterlogged soils, is the major emphasis. Agronomic practices, including agroforestry at different scales, with case studies in India are also part of the book. The book summarizes and updates information about the distribution,

reactions, changes in bio-chemical properties and microbial ecology of salt affected soils in India that can be useful globally. Furthermore, it addresses the environmental and socio-economic impacts of reclamation programs with particular emphasis on the impacts on agricultural production and rehabilitation of degraded lands, vis-a-vis the economics of farmers. The decision-making process related to the reclamation and management of vast areas of salt affected soils involves considerations of the economic viability, environmental sustainability, and social acceptability of different approaches. The book contains the latest case studies and applied techniques of bioremediation of salt affected soils.

Overall, we hope the book facilitates future examinations of large scale adoptions of effective techniques by providing summaries of existing data and research related to the restoration of degraded lands through halophyte plant species, diversification of crops, and introduction of microbes for remediation of salt affected soils, and offering a framework for better understanding and identifying the future challenges.

We are thankful to the authors who are experts in their respective fields, and have written a comprehensive and valuable resource for researchers, academicians and students interested in the fields of soil science, environmental science, microbiology, remediation technology, and plant and soil stresses.

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Contents

Arbuscular Mycorrhizal Fungi (AMF) for Sustainable Soil and Plant Health in Salt-Affected Soils

R.S. Yadav, M.K. Mahatma, P.P. Thirumalaisamy, H.N. Meena, D. Bhaduri, Sanjay Arora, and J. Panwar

1   Introduction

Soil salinity is a serious problem for crop growth and productivity and is increasing day by day throughout the world particularly in arid and semiarid areas. The extent of salt-affected soils is highest in Asia Pacific region including Australia. Countries like Argentina, Australia, China, Egypt, India, Iran, Iraq, Pakistan, Thailand, former Soviet Union and USA are predominantly affected by soil salinization. Salt-affected soils are occupying about 7 % of the earth's land surface (Ruiz-Lozano and Azcón 2000) and about 5 % of the total cultivated land around the world, i.e. 1.5 billion hectares (Sheng et al. 2008). It is anticipated that the increased salinization of arable land will result in to 50 % land loss by the middle of the twenty-first century (Wang et al. 2003). Consequently, the total salt-affected area (6.74 mha) is likely to increase to 16.2 mha by 2050. Secondary salinization, dry land salinity, coastal salinity and sea water ingress are the major cause of concern in salt-affected regions in different continents. Since the nature and properties of the problem soils are diverse, specific approaches are needed to reclaim and manage these soils to maintain their long-term productivity. Continuous utilization of good quality land and water resources in the domestic and industrial sectors has already generated enhanced interest in the utilization of salt-affected soils and poor quality waters. Excessive seepage, ingress of sea water, aridity, excessive water use, faulty irrigation practices, pedogenic sources,

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saline water irrigation, wind-blown salt, capillary rise from shallow water table, etc., are the probable reasons for saline soils. In general, three categories of salinity effects have been considered for low plant productivity: (1) general growth suppression due to a low osmotic potential especially during germination, emergence and early seedling growth (Maas and Hoffman 1977; Maas et al. 1983; Marschner 1995), (2) growth suppression caused by toxicity of specific ions (Maas 1986) and (3) growth suppression due to nutritional imbalance of essential ions (Munns and Termant 1986). Often, these different effects are indistinguishable and, in fact, the primary cause of salinity damage is not known. The effects of salinity/sodicity on plants are thus quite complicated and inseparable in some cases. Overall, salinity leads to many detrimental effects on plants and that at different life stages. Many strategies were proposed to overcome salt detrimental effects such as development of new salt-tolerant crops trough breeding or genetic engineering (Tang et al. 2005; Wu et al. 2005; Wei-Feng et al. 2008), removing excessive salt accumulation in groundwater and desalinizing water for irrigation (Ashraf and Harris 2004; Flowers 2004; Zhang and Blumwald 2001). Although these strategies appear efficient, yet they are costly and out of reach for developing countries that are the most affected. Hence, a new alternative attempt has taken up to tackle the deleterious effects of saline soils which involve inoculation of salt-tolerant arbuscular mycorrhizal fungi (AMF) in agricultural crop.

These specialized fungi colonize plant roots and extend far into the soil. More than 90 % of plant species in natural areas form a symbiotic relationship with the beneficial mycorrhizal fungi. The plant supplies carbohydrate to the fungi, while the mycorrhizal fungi extend the surface area of the plant's roots and thus increase their ability to absorb more nutrients and water from the soil.

AMF maintain physiological and biochemical processes of the host plant (Augé 2000; Ruiz-Lozano 2003). In salt-stressed soil, phosphate ions usually precipitate along with Ca^{2+}, Mg^{2+} and Zn^{2+} and are less available to plants (Azcón-Aguilar et al. 1979). But, AMF symbiosis in plants enhances the uptake of less mobile phosphorus by extending their external hyphal network beyond nutrient depletion zone. In mitigation of salt stress, AMF also improve plant growth and hormonal status, increase nutrient acquisition, maintain osmotic balance, reduce ion toxicity, etc. (Juniper and Abbott 1993; Lindermann 1994; Ruiz-Lozano 2003). It also provides a stable soil for plant growth via production of glomalin—a substance that binds soil aggregates (Wright and Upadhyaya 1998). In this chapter we have discussed the role of AMF in amelioration of salt-affected soils and the mechanism of salt tolerance in AMF-plant symbiosis.

2   Effects of Salt Stress on Plant Growth and Nutrient Uptake

Salinity causes both ionic and osmotic imbalance on plants and most of the known responses to salinity are linked to these effects. The general response of plants to salinity is reduction in growth (Romero-Aranda et al. 2001; Ghoulam and Foursy

2002). The initial and primary salinity, especially at low to moderate salt concentrations, is due to osmotic effects (Munns and Termant 1986). Osmotic effects of salts on plants are as a result of lowering water potential due to increased solute concentration in the root zone. Thus, in some species salt stress may resemble drought stress. However, at low or moderate salt concentration, plants adjust osmotically and maintain a potential for the influx of water (Günes et al. 1996; Ghoulam and Foursy 2002). At high salinity, some specific symptoms of plant damage may be recognized, such as necrosis and leaf-tip burn due to Na^+ or Cl^- ions. High ionic concentrations may disturb membrane integrity and function and interfere with internal solute balance and nutrient uptake, causing nutritional deficiency symptoms similar to those of drought (Grattan and Grieve 1999). The degree to which growth is reduced varies with species and to a lesser extent with varieties (Bolarin et al. 1991; Ghoulam and Foursy 2002). Salt accumulation in leaves causes premature senescence, reducing the supply of assimilates to the growing regions and thus decreasing plant growth (Munns 1993). Romero-Aranda et al. (2001) suggested that induced water stress occurs as a result of salt accumulation at the soil/root interface. This accumulation results in a lower total water potential (Ψp), bringing about substantial difficulties in water uptake by plants. As the concentration of the external solution becomes hypertonic, the plasma membrane separates from the cell wall and shrinkage of the protoplast occurs. The space between the plasma membrane and the cell wall is filled with the extracellular solution. The outcome of this stress is a decrease in water content. There are many evidences which indicate that primary effects of salinity take place in roots, and it is water deficit rather than specific ion toxicity (Munns and Termant 1986). According to Sohan et al. (1999) and Romero-Aranda et al. (2001), increase of salt in the root-zone medium can lead to a decrease in leaf water potential and may affect many plant processes. At very low soil water potential, this condition can interfere with plant's ability to extract water from the soil and maintain turgor (Sohan et al. 1999). Many authors reported that water and osmotic potential of plants became more negative with an increase in salinity, whereas turgor pressure increased (Meloni et al. 2001; Romero-Aranda et al. 2001; Gulzar et al. 2003). Most of the rapid responses in leaf elongation rate to substrate salinity are attributable to changes in leaf water status. The quantity of ions delivered to the shoot per root mass and time are a real measure of the plant's ability to adjust, and in *Suaeda maritima*, the rate of Na^+ transport was much greater than in some non-halophytes even at moderately high external concentrations.

High NaCl uptake competes with the uptake of other nutrient ions, such as K^+, Ca^{2+}, N and P, resulting in nutritional disorders and eventual reduction in yield and quality (Grattan and Grieve 1999). A number of studies have shown that salinity can reduce N accumulation in plants (Feigin et al. 1991; Pardossi et al. 1999; Silveira et al. 2001). In most cases, salinity decreased the concentration of P in plant tissues (Kaya et al. 2001), but in some studies, salinity either increased or had no effect on P uptake (Ansari 1990).

Salinity stress can cause an imbalance in the uptake of mineral nutrients and their accumulation within the plants (Grattan and Grieve 1994). Osmotic stress, ion imbalances, particularly with Ca^{2+} and K^+, and direct toxic effects of Na^+ and Cl^- ions on the metabolic processes are the most important and widely studied

physiological impairments caused by salt stress (Munns 2002). Research revealed that salinity inhibits the growth of plants by affecting both water absorption and biochemical processes such as N and CO_2 assimilation and protein biosynthesis (Cusido et al. 1987). Under saline conditions plants fail to maintain the required balance of organic and inorganic constituents leading to suppressed growth and yield (Günes et al. 1996). Plant performance, usually expressed as a crop yield, plant biomass or crop quality (both of vegetative and reproductive organs), may be adversely affected by salinity-induced nutritional disorders. These disorders may be a result of the effect of salinity on nutrient availability, competitive uptake, transport or partitioning within the plant (Grattan and Grieve 1999; Zhu 2003; Ali et al. 2008; Nasim et al. 2008).

3 Effect of AMF on Plant Growth and Nutrient Uptake Under Salinity

"Mycor"-"rrhiza" literally means "fungus"-"root" and describes the mutually beneficial relationship between fungi and the roots of vascular plants. These specialized fungi, belong to the order Glomales, colonize plant roots and extend far into the soil. More than 90 % of plant species in natural areas form a symbiotic relationship with the beneficial mycorrhizal fungi. AMF associations are composed of three main structures. First, hyphae work as external filamentous arms searching for nutrients around the root zone (Hodge 2000). Second, there are specialized vesicles within the root, which are thought to be storage organs, especially for lipids (Hirsch and Kapulnik 1998). Arbuscules are the third important part of the AM association. They are branched intercellular structures, resembling trees, and are the main functional site of phosphorus and other nutrient exchange in the root system (Smith et al. 2000).

The plant supplies carbohydrate to the fungi, while the mycorrhizal fungi establish symbioses with roots. Thus it extends the surface area of the plant's roots and contributes to improving water use and uptake of less mobile nutrients like phosphorus, zinc and copper. Besides, these AMF also alter hormonal status of plants and increase plant tolerance to various biotic and abiotic factors (Smith and Read 1997). Thus, AMF can promote plant growth (Hirrel and Gerdemann 1980; Copeman et al. 1996) through improvement of plant nutrition and production of osmoregulators (Ojala et al. 1983; Duke et al. 1986; Ruiz-Lozano and Azcón 2000).

AMF that widely exist in salt-affected soils (Juniper and Abbott 1993) are considered as tolerant isolates. These AMF may have a higher ability to improve the survival and growth of host plants than species or isolates from normal edaphic condition. Many studies have demonstrated that inoculation with AMF improves growth of plants under a variety of salinity stress conditions (Ruiz-Lozano et al. 1996; Al-Karaki et al. 2001). To some extent, these fungi have been considered as bio-ameliorators of saline soils (Azcón-Aguilar et al. 1979; Singh et al. 1997; Rao

1998). Several researchers reported that inoculation with AMF improves growth of crops and plants under salt stress (Jindal et al. 1993; Yano-Melo et al. 2003; Giri and Mukerji 2004; Tian et al. 2004; Cho et al. 2006; Ghazi and Al-Karaki 2006; Sharifi et al. 2007; Beltrano et al. 2013). Higher plant growth rate was observed in AMF-inoculated banana (Yano-Melo et al. 2003), cotton (Tian et al. 2004), soybean (Sharifi et al. 2007), lettuce (Aroca et al. 2013), strawberry (Sinclair et al. 2014) and tomato (Latef and Chaoxing 2011; Balliu et al. 2015) than that of controls under saline condition. When AMF are inoculated in saline soils, there is high demand of energy for fungal survival and establishment, and once the fungus becomes effective, increasing nutrient uptake and host plant tolerance occur.

The improved growth of AMF inoculated plants has been attributed to enhanced acquisition of mineral nutrients such as P, Zn, Cu and Fe (Nelson and Safir 1982; Al-Karaki et al. 2001; Ghazi and Al-Karaki 2006). Mycorrhizal colonization improves plant growth under salinity that may be due to enhanced P uptake by AMF plants (Poss et al. 1985; Duke et al. 1986).

AMF-inoculated control plants also increased the uptake of phosphorous (P). The enhancement of plant P uptake by AMF has been considered one of the main reasons for amelioration of growth in salt-affected plants (Ruiz-Lozano and Azcón 2000; Giri et al. 2007). However, in some cases Plant tolerance to salt was not related to P concentration (Danneberg et al. 1992; Ruiz-Lozano et al. 1996). Under salinity conditions plants accumulate less potassium (K^+). But inoculation of AMF significantly improves concentration of K^+ in salinity condition. Higher K^+ accumulation by mycorrhizal plants in saline soil maintains high K^+/Na^+ ratio and ionic balance of the cytoplasm by influencing Na efflux from plants. The replacement of K^+ by Na^+ allows osmotic adjustment which may be the responsible factor. AMF lowers the Na^+ concentration than that of nonmycorrhizal plants regardless of salinity level (Giri et al. 2007). Increased salt tolerance in AMF-colonized plants is also influenced by the internal transport or storage of Na^+ or Cl^- ion (Al-Karaki 2000; Baker et al. 1995).

Potassium plays an important role in processes such as water balance, cell extension and solute transport in the xylem. Cell extension is the consequence of K^+ accumulation. Potassium is required for stabilizing pH in the cytoplasm and for increasing the osmotic potential in the vacuole of plant cells. Stomatal regulation is a major mechanism controlling the water regime in the plant which is also governed by K^+. In addition, potassium as osmotic solute is able to maintain a high tissue water level even under conditions of osmotic deficiency. In higher plants, K^+ affects photosynthesis at various levels. The role of K^+ in CO_2 fixation has been demonstrated, and an increase in the leaf potassium content is accompanied by increased rates of photosynthesis, photorespiration and RuBP carboxylase activity and a concomitant decrease in dark respiration. Enhanced respiration rates are a common feature of potassium deficiency (Bottrill et al. 1970). The degree of salt tolerance of mycorrhizal plants largely depends on K^+. The highest salt tolerance of mycorrhizal plants has the greatest K shoot concentration (Porras-Soriano et al. 2009).

4 AMF for Soil Health

Quality soil is critical for any sustainable development which is continuously decreasing due to rapid civilization and industrialization. The quality of soil depends not only on its physical or chemical properties but also on the diversity and activity of soil biota (Doran and Linn 1994).

AMF are major components of the soil microfauna and obviously interact with other microorganisms in the rhizosphere (Bowen and Rovira 1999). AMF develop intensively inside roots of plant and within the soil by forming an extensive extraradical network, and this improves mineral and water uptake capacity of plants from the soil. Thus, AMF symbiosis changes plant physiology as well as nutritional and physical properties of the rhizosphere soil. This, in turn, affects colonization patterns of this region by soil microorganisms by the so called mycorrhizosphere effect (Gryndler 2000). In the mycorrhizosphere, AMF interact with natural and introduced microorganisms and affect soil properties and quality (Fig. 1).

The extraradical hyphae of AMF act as a direct conduit for host C into the soil and contribute directly to its C pools, bypassing the decomposition process. As a consequence of this, the amount and activity of other soil biota are stimulated; however, this seems to be a selective phenomenon, since it stimulates in particular the microbes having antagonistic activity against soilborne pathogens (Linderman 2000). The reason for this phenomenon is unknown, but this observation clearly indicates that AMF could be useful biological tools for maintaining healthy soil systems.

Another important role of mycorrhizal fungal mycelium is in the formation of water-stable soil aggregates (Andrade et al. 1998; Bethlenfalvay et al. 1999; Miller and Jastrow 2000). Indeed, AMF produce a very stable hydrophobic glycoprotein, glomalin, which is deposited on the outer hyphal walls of the extraradical mycelium and on adjacent soil particles and which appears to act as a long-term soil-binding agent (Wright and Upadhyaya 1998, 1999). As a consequence, the extraradical
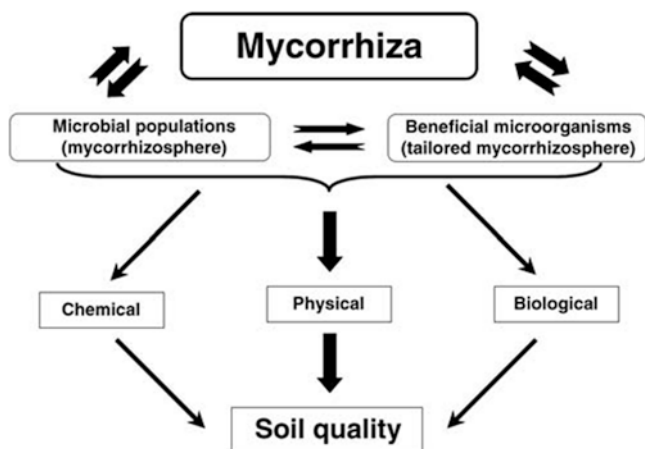
Fig. 1 Arbuscular mycorrhizal fungi interact with natural and introduced microorganisms in the mycorrhizosphere, thus affecting soil properties and quality (Source: Jeffries et al. 2003)

hyphae, together with the fibrous roots, can form a "sticky-string bag that contributes to the entanglement of soil particles to form macroaggregates," (Miller and Jastrow 2000) a basic building block of soil structure. Thus, AMF are essential components for maintaining soil structure in agricultural soils.

5 Mechanisms of Amelioration of Salt Stress in AMF-Plant Symbiosis

5.1 Morpho-physiological Alterations

Morphological and physiological characteristics of plants are keys to address any abiotic (salt) stress management, hence most integral part of such experiments. There are number of studies carried out to assess the role of AMF for alleviating the salt stress in crop plants, and most of them reported a positive outcome. Association of AMF showed beneficial effect on root morphology of *Citrus tangerina* seedlings and enhanced the characters like root length, root-projected area, root surface area and root volume under salinity (Wu et al. 2010). Mycorrhizal colonization also caused improvement in fruit fresh weight, fruit number and fruit yield of salt-stressed tomato plants (Al-Karaki 2000; Latef and Chaoxing 2011). Improved growth, yield and quality of fruits of *Cucurbita pepo* plants was also noticed when colonized by *Glomus intraradices* in salinity stress (Colla et al. 2008). Olive plants inoculated with *Glomus mosseae* helped to survive the plants better in salt-stressed condition in terms of enhanced root and shoot growth and lesser biomass reduction (Porras-Soriano et al. 2009). Among field crops, AMF-inoculated maize plants showed to have better root morphology (length, mass, surface area, diameter and volume) under imposition of salt treatments (Sheng et al. 2009).

5.2 Biochemical and Physiological Changes

Various studies have investigated to understand mechanisms for enhanced salt tolerance of AMF plants. These mechanisms include better ability for nutrient and water uptake due to an extended explored soil surface by fungal hyphae, greater root hydraulic conductivity and osmotic adjustment, maintenance of enhanced K^+/Na^+ ratios and lower accumulation of sodium in the shoots of the host plants (Fig. 2). Thus salt-stress alleviation by AMF results from a combination of nutritional, biochemical and physiological effects. In this section, we discuss our current knowledge of the regulation by AMF symbiosis of plant responses to salt stress and propose new perspectives for physiological and molecular studies, which should shed further light on the intimate tolerance mechanisms induced by AMF symbiosis.

Plant tolerance to salt itself is a complex trait to which many different factors may contribute. Plants have evolved biochemical and molecular mechanisms, which may act in a concerted manner and constitute the integrated physiological response to soil
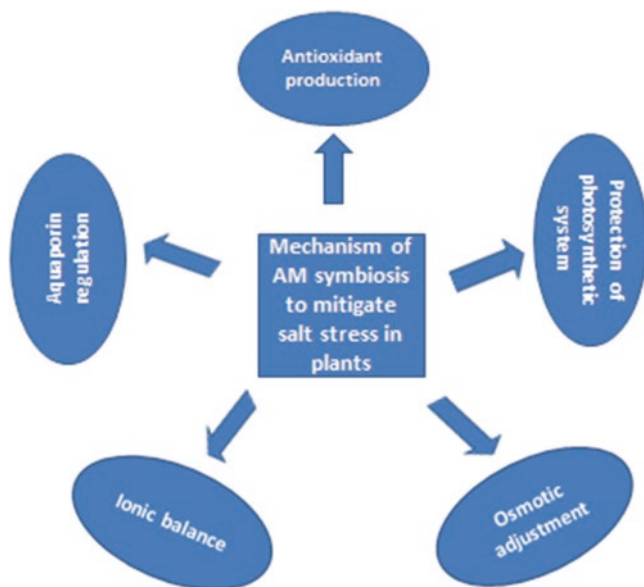
Fig. 2 Mechanisms of the AMF symbiosis which regulate the physiological plant responses in order to improve tolerance to salinity. The exchange flux of water, minerals (M) and carbon compounds (C) between the plant and AMF is also shown. Minerals include nutrients and salt ions present in the soil solution

salinity. The most important plant strategies are (1) synthesis and accumulation of compatible solutes; (2) control of ion uptake by roots, compartmentation and transport into plant tissues, which constitutes the ion homeostasis strategy; (3) fine regulation of water uptake and distribution to plant tissues by the action of aquaporins; and (4) reduction of oxidative damage through improved antioxidant capacity. Additional plant responses can include selective build-up or exclusion of salt ions, maintenance of photosynthesis at values adequate for plant growth, changes in membrane structure and synthesis of phytohormones (Turkan and Demiral 2009).

5.2.1 Osmotic Adjustment

Water potential of salt-accumulated soil becomes more negative. Thus, to avoid cell dehydration, plants must respond by decreasing their water potential in order to maintain a favourable gradient for water flow from the soil into the roots. Accumulation of some inorganic ions such as Na^+ and K^+ and compatible organic solutes, known as osmotic adjustment or osmoregulation is the most important mechanism to reduce plant osmotic potential (Morgan 1984; Hoekstra et al. 2001). The most important organic solutes include amino acids (proline), amide and proteins, quaternary ammonium compounds (glycine betaines) and polyamines, soluble sugars, pinitol and mannitol (reviewed by Ruiz-Lozano et al. 2012). Osmotic adjustment allows cells to maintain turgor and related processes, such as cellular expansion and growth, stomatal opening and photosynthesis, while keeping a

gradient of water potential favourable to water entering the plant. Proline, glycine betaine, pinitol and mannitol are important osmoprotectant osmolytes that are synthesized by many plants in response to dehydration stresses, including salinity. Proline plays roles in stabilizing subcellular structures, in buffering cellular redox potential under stresses and in scavenging free radicals (Chen and Dickman 2005). Betaines can stabilize protein complexes and the structures and activities of enzymes, as well as maintaining the integrity of membranes against the damaging effects of salt stress (Evelin et al. 2009). The effects of salinity on various biochemicals on AMF plants are listed in Table 1.

Table 1 Biochemical compounds increased/decreased in various crops/plants under AMF symbiosis during salinity stress

Compound	Crop/plant	Fungus	Effect	References
Proline	*Glycine max* *Cyamopsis tetragonoloba* *Zea mays* *Lactuca sativa*	*Glomus mosseae* and *Glomus fasciculatum* *Glomus mosseae* *Glomus* spp.	Increase Decrease Decrease	Datta and Kulkarni (2014) Sheng et al. (2011) Ruiz-Lozano et al. (1996)
Glycine betaine	*Phragmites australis*	*Glomus fasciculatum*	Increase	Al-Garni (2006)
Polyamines	Lotus glaber	*Glomus intraradices*	Increase	Sannazzaro et al. (2007)
Carbohydrates	*Glycine max* *Cyamopsis tetragonoloba* *Vigna radiata*	*Glomus mosseae* and *Glomus fasciculatum* *Glomus clarum*	Increase Increase	Datta and Kulkarni (2014) Rabie (2005)
Chlorophyll	*Capsicum annuum* *Glycine max* *Cyamopsis tetragonoloba* *Zea mays*	*Glomus intraradices* *Glomus mosseae* and *Glomus fasciculatum* *Glomus mosseae*	Increase Increase Increase	Beltrano et al. (2013) Datta and Kulkarni (2014)
Abscisic acid	*Solanum lycopersicum* *Lactuca sativa*	*Glomus mosseae*, *Glomus intraradices* *Glomus etunicatum* *Glomus intraradices*	Reduce salt-induced increase Reduce	Abeer et al. (2015b) Aroca et al. (2013)
Auxin	*Solanum lycopersicum*	*Glomus mosseae*, *Glomus intraradices* *Glomus etunicatum*	Enhance salt-induced decrease	Abeer et al. (2015b)
Antioxidant enzymes	*Solanum lycopersicum* *Malus hupehensis* *Vigna unguiculata*	*Glomus mosseae* *Glomus versiforme* *Glomus mosseae*, *Glomus intraradices* and *Glomus etunicatum*	Increase Increase Increase	He et al. (2007) Yang et al. (2014) Abeer et al. (2015a)

So far, investigations carried out on osmoregulation in AMF symbiosis are scarce and somewhat contradictory. Several studies have reported a higher concentration of osmolytes in AMF plants than in non-AMF plants at different salinity levels (Jindal et al. 1993; Al-Garni 2006; Sharifi et al. 2007; Talaat and Shawky 2011), while, in contrast, other studies have reported that non-AMF plants accumulate more osmolytes than AMF plants under salt stress (Wang et al. 2004; Rabie and Almadini 2005; Jahromi et al. 2008; Sheng et al. 2011). These studies involve different plant species such as soybean, wheat, bean, lettuce and maize and different plant parts and also different AMF such as *Glomus intraradices*, *Glomus mosseae* or a mixture of *Glomus* spp. and even different treatments such as salt pretreated mycorrhizal fungi (Sharifi et al. 2007; Ruiz-Lozano et al. 2011), which may explain the contrasting results obtained. Thus results suggest that proline accumulation in plants may be due to salinity and not necessarily the result of mycorrhizal colonization or that proline accumulation may be a symptom of stress in less-salt-tolerant species.

5.2.2 Polyamines

Free polyamines are small organic cations that are necessary for eukaryotic cell growth. Putrescine (Put), spermidine (Spd) and spermine (Spm) are three main polyamines in plants. These cations are thought to play an important role in plant responses to a wide array of environmental stressors such as salinity (Delauney and Verma 1993; Krishnamurthy and Bhagwat 1989), high osmolarity (Besford et al. 1993) and antioxidative stress (Kurepa et al. 1998). They have been proposed as candidates for regulation of root development under saline situations (Couee et al. 2004). Polyamine-enhanced membrane stability has been shown to have a significant effect on both H^+/ATPase and Ca^{2+}/ATPase transporters during salinity stress (Roy et al. 2005; Pottosin and Shabala 2014). Inoculation of host plants with AMF increases free polyamine concentrations in plants under saline conditions. Free polyamine concentrations in plants generally reduced under saline conditions.

5.2.3 Antioxidants

Reactive oxygen species (ROS) such as singlet oxygen, superoxide anion (O_2-), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH) are unavoidable byproducts of the interaction between oxygen and electrons leaked from the electron transport chains in chloroplast and mitochondria during normal aerobic metabolism (Scandalios 1993; Asada 1999). These radicals and their derivatives are among the most reactive species known to chemistry, capable of reacting indiscriminately to cause oxidative damage to biomolecules such as lipid peroxidation, denaturation of proteins and mutation of DNA (Bowler et al. 1992), and in the absence of the protective mechanism, they can damage cell structure and function (Alguacil

et al. 2003). Plant cells have protective and repair mechanism to minimize the occurrence of oxidative damage, which include non-enzymatic molecules that act as ROS scavengers such as ascorbate, glutathione, a-tocopherol, flavonoids, anthocyanines and carotenoids, and specific ROS-scavenging antioxidative enzymes consist of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APOX), glutathione reductase, dehydroascorbate reductase, monodehydroascorbate reductase, guaiacol peroxidase, oxidized glutathione, glutathione peroxidase and the enzymes involved in the ascorbate–glutathione cycle (Alguacil et al. 2003; Wu et al. 2006).

A correlation between antioxidant capacity and salinity tolerance has been documented in several plant species (Benavides et al. 2000; Núñez et al. 2003; Turkan and Demiral 2009). Further, several studies have suggested that AMF symbiosis helps plants to alleviate salt- or water-deficit stresses by enhancing the activities of antioxidant enzymes (Porcel et al. 2003; Ghorbanli et al. 2004; Zhong et al. 2007; Garg and Manchanda 2009; Talaat and Shawky 2011). Thus, mycorrhizal plants possess enhanced activity of several antioxidant enzymes.

5.2.4 Abscisic Acid Content

Abscisic acid (ABA) is a phytohormone well known for its signalling role in the regulation of plant growth and development and also plays an important role in the response of the plant to abiotic stress, including salinity stress. ABA promotes stomatal closure to reduce water loss and induces the expression of stress-related genes, diminishing the damage it has caused (Evelin et al. 2009). It has been documented that mycorrhization can alter the ABA levels in the host plant (Duan et al. 1996; Estrada-Luna and Davies 2003). The effects of AMF species on ABA content also varied with the host plants (Evelin et al. 2009).

5.3 Physiological Changes

Salt stress can affect several physiological mechanisms in the plant such as photosynthetic efficiency, membrane disruption, gas exchange and induce physiological drought by altering water status. Various investigations demonstrated that AMF symbiosis can alleviate such effects by employing various mechanisms which are discussed below.

A higher chlorophyll content in leaves of mycorrhizal plants under saline conditions has been observed by various authors (Colla et al. 2008; Selvakumar and Thamizhiniyan 2011). This suggests that salt interferes less with chlorophyll synthesis in mycorrhizal than in non-mycorrhizal plants (Giri and Mukerji 2004). The antagonistic effect of Na^{2+} on Mg^{2+} uptake is counterbalanced and suppressed in the presence of mycorrhiza, thereby increase chlorophyll synthesis (Giri et al. 2003).

AMF-colonized plants exhibited higher chlorophyll fluorescence which is a measure of photosynthetic efficiency of photosystem II, as well as an enhanced stomatal conductance rate both under non-saline and under saline conditions. These two positive effects may also have accounted for the enhanced plant growth of AMF-colonized plants, most probably by enhancing CO_2 fixation under salt stress. In this sense, several studies have shown a correlation between tolerance to abiotic stresses and maintenance of efficiency of photosystem II, which also sustained plant productivity (Loggini et al. 1999; Ruiz-Sánchez et al. 2010; Aroca et al. 2013). The higher values of photosynthetic efficiency in mycorrhizal plants indicate that the photosynthetic apparatus of these plants is less damaged by the salt stress imposed (Germ et al. 2005; Redondo-Gómez et al. 2010). Mycorrhiza-inoculated plants also showed higher non-photochemical quenching than the uninoculated plants which protect the leaf from light-induced damage (Maxwell and Johnson 2000; Sheng et al. 2008). The higher performance of photosystem II and the enhanced stomatal conductance in mycorrhizal plants could have contributed to decreased photorespiration, leading to a lower production of reactive oxygen species in these plants (Cadenas 1989; Ruiz-Sánchez et al. 2010), thus contributing to an enhanced salinity tolerance and growth.

Some studies have shown that colonization of plant roots by the AM fungus *G. intraradices* prevented leaf dehydration caused by salinity (Aroca et al. 2006; Porcel et al. 2006). Lower water saturation deficit and higher turgor potential in AMF plants also improve the water status of the plant (Al-Garni 2006; Sheng et al. 2008). AMF colonization induces an increase in root hydraulic conductivity of the host plants under osmotic stress conditions (Sánchez-Blanco et al. 2004; Aroca et al. 2007). AMF-colonized plants are able to fix more CO_2 than non-inoculated plants and hence their growth is improved (Querejeta et al. 2007).

AMF-inoculated plants maintain a higher electrolyte concentration than that of non-mycorrhizal plants by maintaining membrane integrity and stability (Garg and Manchanda 2008; Kaya et al. 2009). Consequently, higher electrical conductivity of mycorrhizal roots was observed than the non-mycorrhizal roots (Garg and Manchanda 2008). This suggests that mycorrhizal plants had a much lower root plasma membrane electrolyte permeability than the non-mycorrhizal plants. The increased membrane stability has been attributed to mycorrhiza-mediated enhanced P uptake and increased antioxidant production (Feng et al. 2002).

5.4 Molecular Changes

A few studies are available on molecular mechanism of AMF symbiosis to alleviate salinity stress in plants. The expression studies and/or overexpression of a few proteins, including cation channels and transporters, Δ1-pyrroline-5-carboxylate synthetase (P5CS), late embryogenesis abundant protein (Lea), ABA and aquaporins, is documented in AMF symbiosis during salinity.

5.4.1 Aquaporins

Aquaporins belong to the major intrinsic protein (MIP) family of transmembrane channels that facilitate and regulate the passive movement of water molecules but not of H^+ and other ions following a water potential gradient (Hill et al. 2004; Kruse et al. 2006). In plants, aquaporins are subdivided into five evolutionarily distinct subfamilies: the plasma membrane intrinsic proteins (PIPs), the tonoplast intrinsic proteins (TIPs), the small basic intrinsic proteins (SIPs), the nodulin-like intrinsic proteins (NIPs) (Chaumont et al. 2001; Johanson et al. 2001) and the uncharacterized X intrinsic proteins (XIPs) (Gupta and Sankararamakrishnan 2009), which have been shown recently to transport a variety of uncharged substrates (Bienert et al. 2011). The role of aquaporins in water uptake was confirmed by inhibition of root water transport by the general aquaporin blocker mercury ions (Maggio and Joly 1995).

Expression analysis of aquaporin genes in salt-stressed AMF plants revealed contrasting results. A significantly downregulated expression of LeTIP and LePIP1 was observed in non-treated controls and salt-stressed roots of *Lycopersicon esculentum*, but LePIP2 transcripts level did not alter. Moreover, the expression of aquaporin was drastically reduced after AMF colonization than salinity (Ouziad et al. 2006). In contrary to these results, a higher expression of all PvPIP genes is observed in AMF *Phaseolus vulgaris* roots than non-AMF plants (Aroca et al. 2007). Similarly, Jahromi et al. (2008) reported that under salt-stress conditions (0–100 mM NaCl), mycorrhizal *Lactuca sativa* plants maintained the expression of the LsPIP2 gene and upregulation of LsPIP1 gene, while in the absence of salinity, the expression of lettuce PIP1 and PIP2 genes was inhibited by mycorrhization. Thus, under salinity, AMF symbiosis enhanced the expression of PIP genes, and its protein could contribute to regulating root water permeability to better tolerate the osmotic stress generated by salinity (Aroca et al. 2007; Jahromi et al. 2008). These results point to the possibility that AMF differentially exert control on the expression of different members of the large family of aquaporins (Ouziad et al. 2006) and that each PIP gene analysed may have a different function and regulation in AMF symbiosis. How much this contrasting result reflects biological or technical differences remains to be evaluated. Further analyses should focus on those aquaporins with a proven capacity for water transport such as PIPs (mainly the PIP2 subgroup) and TIPs. These analyses should be correlated with measures of root and leaf hydraulic conductivities and water status in order to determine the final influence of the regulated aquaporins on the tissue water permeability and content.

5.4.2 Δ1-Pyrroline-5-carboxylate Synthetase, Late Embryogenesis Abundant Protein and ABA

The expression of genes encoding Δ1-pyrroline5-carboxylate synthetase (LsP5CS), late embryogenesis abundant protein (LsLea) and ABA (Lsnced) was determined following varied salt treatments (0–100 mM NaCl) on *L. sativa* plants colonized by

Glomus intraradices (Jahromi et al. 2008). The PC5S enzyme catalyses the rate-limiting step in the biosynthesis of proline. Late embryogenesis abundant proteins act as stress markers. They also possess chaperone-like activity, thus having a protective role during osmotic stress. Lsnced encodes for 9-cis-epoxycarotenoid dioxygenase, a key enzyme in the biosynthesis of the stress hormone ABA. ABA promotes stomatal closure to minimize transpirational water loss. It also mitigates stress damage through the activation of many stress-responsive genes, which collectively increases plant-stress tolerance (Bray 2002). They reported a higher expression of genes LsP5CS and Lsnced in non-AMF plants than AMF plants at 50 mM NaCl, though at 100 mM, the levels were similar. The LsLea gene was found to express under conditions of salt stress, and the induction of this gene was found to be lower in AMF plants than non-AMF plants. The lower expression of these genes under AMF symbiosis suggests that AMF plants were less strained than non-AMF plants by salinity stress imposed, which may be due to a primary salt avoidance mechanism such as Na^+ and Cl^+ accumulation (Giri et al. 2003; Al-Karaki 2006).

5.4.3   Cation Channels and Transporters

Ouziad et al. (2006) analysed the expression of two antiporters (LeNHX1 and LeNHX2) in tomato-AM symbiosis during salinity stress. They reported that AMF symbiosis did not alter the expression of these genes under salinity. Zhongqun and Huang (2013) reported that mycorrhizal colonization significantly reduced the amount of LeNHX1transcript under salt stress. These results could not clear the mechanism of LeNHX1 and LeNHX2 genes in tomato-AM symbiosis during salinity stress. Under salinity conditions Na^+ can be exported either into the apoplast by a plasma membrane-associated Na^+/H^+ antiporter or into vacuoles by a tonoplast-associated Na^+/H^+ antiporter (Blumwald et al. 2000). In tomato, there are at least four LeNHX-type genes. LeNHX1, 3 and 4 are tonoplast Na^+/H^+ antiporter (Pardo et al. 2006) and LeNHX2 has been shown to be a K^+/H^+ transporter (Venema et al. 2003). Thus study of all genes during salinity and AM symbiosis is required to know the role of LeNHX genes in salt tolerance.

The cyclic nucleotide-gated ion channel (CNGC) family is composed of non-selective cation channels that enable the uptake of Na^+, K^+ and Ca^{2+} (Kaplan et al. 2007). It has been suggested that CNGCs contribute to sodium reallocation within the plant tissues, assisting the plant in coping with salinity stress (Porcel et al. 2012).

Kugler et al. (2009) have reported that both AtCNGC19 and AtCNGC20 were upregulated in the shoot of *Arabidopsis* in response to elevated NaCl. While in the root, CNGC19 did not respond to changes in the salt concentration, in the shoot, it was strongly upregulated. To demonstrate the function of CNGCs in tomato under salt stress, the SlCNGC virus-induced gene-silenced tomato plants were examined for their role in salt tolerance. SlCNGC6-silenced plants exhibited more severe symptoms than that of SlCNGC1-, SlCNGC7-, SlCNGC8-, SlCNGC11- and SlCNGC14-silenced plants under salinity. At 3 days after 0.4 M NaCl supply, SlCNGC6-silenced plants completely wilted with all leaves desiccated. Moreover,

the RWC in SlCNGC6-silenced plant leaves (49.4) was significantly lower than in control (58.3 %). This RWC data correlated well with the severity of wilting symptoms in the silenced plants. These results demonstrated that SlCNGC6-silenced plants are more sensitive, while SlCNGC1-, SlCNGC8- and SlCNGC14-silenced plants are more tolerant to high concentration of salt stress, and indicated that SlCNGC6 may play a positive role, while SlCNGC1, SlCNGC8 and SlCNGC14 may play a negative role in salt tolerance in tomato (Saand et al. 2015). These results imply that different CNGC genes may play a role in salt stress.

There are several studies showing that AMF plants have better $K^+:Na^+$ ratios than non-AMF plants. However, the molecular mechanisms involved in such an effect are almost completely unknown. Thus, studying the possible regulation of genes encoding known ion transporters, such as high-affinity K^+ transporter (HKT), potassium channel (AKT), salt overly sensitive (SOS) and Na^+/H^+ exchanger (NHX), and probably also CNGCs, during the response of AMF symbiosis to salinity is a promising field. These studies should be accomplished in combination with measurements of sodium and potassium content and their ratios in the different plant tissues. Together, this should allow a better understanding of whether AMF symbiosis affects Na^+ and K^+ uptake, distribution and compartmentation within the plant cell and should shed further light on new mechanisms involved in the enhanced tolerance of AMF plants to salt stress.

5.5 *Enhanced Nutrient Uptake*

Facilitating the nutrient uptake for plants by the use of mycorrhiza has repeatedly been highlighted by the researchers throughout the world. Apart from primary soil nutrients (N, P, K), AMF proved its efficiency to absorb Mg, Ca, Cu, Zn, Fe, Ni and Cd through plant roots. It is often been considered that uptake and transport of nutrients from soil is the primary function of mycorrhizal fungi associated with plant roots (reviewed in Quilambo 2003).

Phosphorus absorption has often been easier under mycorrhizal inoculation; even under saline soil, the P uptake was found higher (Tian et al. 2004; Sharifi et al. 2007; Al-Khaliel 2010). Phosphorus being a poorly mobile nutrient as PO_4^{-3}, when show a positive influence in the presence of AMF towards absorption in plant roots, and that also under problem (saline) soil, demands a special mention. Despite P, N and K uptake was also found to improve by association of AMF (Rabie and Almadini 2005; Al-Khaliel 2010). Garg and Manchanda (2008) and Giri and Mukerji (2004) reported a higher N uptake under soil salinity by *Cajanus cajan* and *Sesbania* sp., respectively, in the presence of *Glomus* spp. Enhancement of potassium uptake under salt-stressed soil was also found for soybean plants (Sharifi et al. 2007).

A selective uptake of nutrients is also sometimes mentioned by AMF. Balancing the K^+/Na^+ ratio in plant tissues is a major concern to avoid the deleterious effects of soil salinity. AMF was also found to interfere in the increased uptake of K with concomitant decreased uptake of Na by plant roots (Zuccarini and Okurowska 2008).

Ca^{+2} and Mg^{+2} were also found to be absorbed more by plant roots with myccorrhizal association despite of soil salinity (Yano-Melo et al. 2003; Sharifi et al. 2007; Giri and Mukerji 2004).

This sort of beneficial activities by AMF often enhances the nutrient use efficiency of plants in marginal or degraded soils depleted in essential nutrients. This may further aggravate the fertility and productivity of these soils.

6   Conclusions

AMF have the potential to ameliorate salt stress and improve plant growth. AMF-mediated amelioration is attributed due to accumulation of different solutes and higher uptake of water and nutrients under salinity conditions. AMF symbiosis also regulates various plant physiological and biochemical processes such as water potential, ionic balance, stomata conductance, maintenance of photosynthesis, reduction of oxidative damage through antioxidant production and hormone-mediated signal transduction. However, the ultimate mechanisms that allow AMF plants a higher tolerance to salinity are still in infancy. Molecular bases of regulation of ionic homeostatis, cation to proton antiporter and cyclic nucleotide-gated channels under AMF symbiosis are largely unknown. Thus investigation on these aspects on arbuscular mycorrhizal symbiosis under salinity is a promising field that should shed further light on new mechanisms involved in the enhanced tolerance of AM plants to salt stress. Further, transcriptomic analysis of some AMF is a promising tool that could provide new data regarding fungal genes that may also participate in the response of AMF symbiosis to salinity stress.

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