Soil Biology

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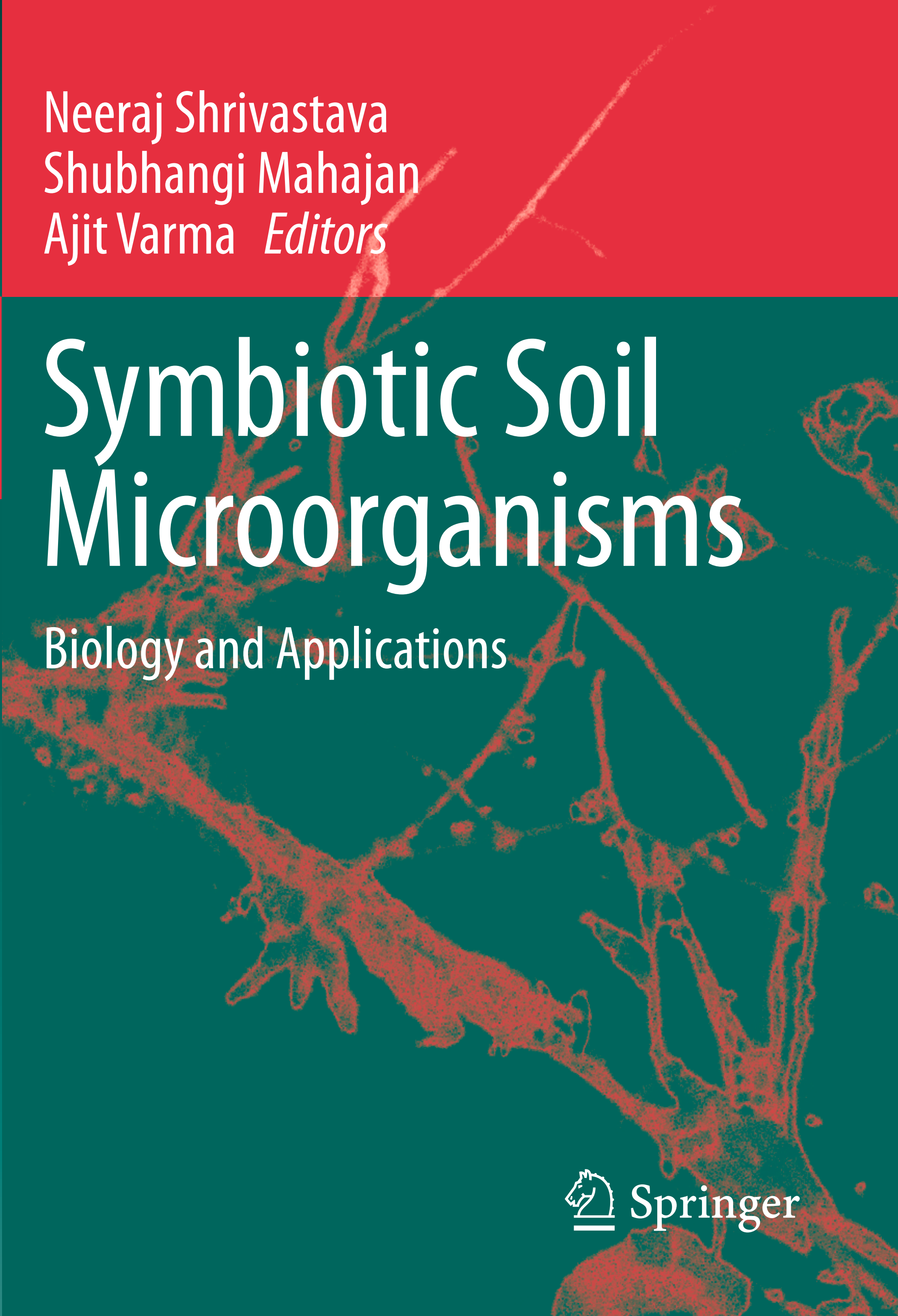

Symbiotic Soil Microorganisms

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Chapter 23
Do Mycorrhizal Fungi Enable Plants to Cope with Abiotic Stresses by Overcoming the Detrimental Effects of Salinity and Improving Drought Tolerance?

I. Ortas, M. Rafique, and F. Ö. Çekiç

Abstract Soil salinization and drought are major and growing ecological problems. They limit the productivity of crop plants cultivated on more than 20% of total agricultural lands worldwide. Global climate changes and sequences of agriculture-related management practices would induce salinity to more than 50% of the arable land by 2050. Excess salt in soil impedes plant photosynthetic processes, seed germination, and root uptake of water and nutrients such as K^+. Under the same soil and climate conditions, water deficiency is also one of the serious limiting factors for plant growth and food security. Application of biological processes such as mycorrhizal fungi as inoculants provide a cost-effective long-term solution for coping with saline and drought conditions. Inoculation of mycorrhizal fungi along with certain microbial strains in salt and drought-affected soils increase root infection. Arbuscular mycorrhizal fungi (AMF) are renowned for effective scavengers of free radicals in soil thereby increasing soil parameters optimal for plant growth. The mechanism to cope with drought stress involves in AMF-enhance drought and salt tolerance through direct water and nutrient uptake via extraradical hyphae, better root system architecture, enhancement of antioxidant defense systems, and greater osmotic adjustment. Mycorrhizal colonization upregulates the expression of chloroplast genes in leaves, and genes encoding membrane transport

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proteins involved in K^+/Na^+ homeostasis in roots. Mycorrhizal inoculated seedlings exhibit high root salicylic acid concentrations and lower leaf and root jasmonic acid concentrations under salt stress. The AMF improve root hydraulic conductivity as well as the plant water status and tolerance under drought stress. Essential nutrients are also taken up through mycorrhizal hyphae and differences in P and K acquisition, transpiration, and stomatal conductance are related to mycorrhizal efficiencies of different fungi. Indigenous microorganisms may be a promising biological technology to improve plant performance and development and to alleviate salt stress damage.

Keywords Salinity · Drought · Mycorrhizal fungi · Genes · Root architecture · Abiotic stress

23.1 Introduction

Abiotic stresses such as salinity and drought seriously threat the agricultural productivity and food security (Wang et al. 2003). Especially under semiarid and arid climatic conditions climate change increases soil salinization. Currently, over 7% of the Earth's land area is estimated to have saline soils (Ruiz-Lozano et al. 2001). Nearly 20% of the cultivated world's land and half of the irrigated land are affected by high salt concentrations Sudhir and Murthy (2004). Wang et al. (2003) and Porcel et al. (2012) reported that increased salinization of arable land is expected to have devastating global effects, resulting in up to 50% soil salinization by the year of 2050. At present, nearly 5% (77 million hectares) of total cultivated arable land is affected by salinity (Sheng et al. 2008). In the same climatic regions, water scarcity as well as salinity problem poses a serious threat to food security. Especially under arid and semiarid regions, water stress has limited crop productivity (Maggio et al. 2000). Under such semiarid and arid soil regions, salinity problem leads to major constraints on agricultural production. The salt tolerance of a plant is affected by soil, water, plant, and environmental conditions. Plant roots, soil nutrients availability, nutrient absorption capacity, and soil microbial activity especially mycorrhizal fungi significantly affect the plant tolerance to salt and drought stresses.

Arbuscular mycorrhizal fungi (AMF) are present in all kind of ecosystems, regardless of soil type, vegetation, or growing conditions (Mosse et al. 1981). This may lead to indirect effects of the AM association on the plant nutrients availability and uptake (Smith and Read 2008). Their early establishment in the growth process of plants is important. Mycorrhizae have a significant contribution on soil stabilization, as well. If soil erosion is pronounced, the scarcity of microbial propagules in such ecosystems may be a serious handicap to plant establishment and survival. In such cases it may be necessary to inoculate with indigenous fungal species or augment the natural AMF already present within the rhizosphere of leguminous plants.

According to Chitarra et al. (2016), Ruíz-Sánchez et al. (2011) mycorrhizal fungi play an instrumental role in the protection against abiotic stresses such as drought and salt stresses (Naher et al. 2013). Since salt and drought stress factors are serious for food security and sustainable agriculture; it is sound to use plant rhizosphere mechanisms to address the problems. Soil and environmental stress factors affect the efficiency and establishment of mycorrhizae. Mycorrhizae also have many advantages on stress tolerance (Barea et al. 1996) and abiotic stress factors (Swaty et al. 2004). For example, salinity suppressed the growth of AM. Salinity stress significantly reduced the root, stem and leaf dry matter and leaf area due to the direct effects of ion toxicity on plant. However, it has been shown that mycorrhizal colonization significantly improved plant chlorophyll concentration in comparison to the non-salinized and salinized plants (Latef and Chaoxing 2011).

The hyphal networks of AM fungi improve soil particle aggregation thereby they improve the resistance of plant to stress factors, as well. Lehnert et al. (2018) indicated that worldwide in the majority of wheat-growing areas, the incidence of drought stress has increased significantly resulting in a negative impact on plant development and grain yield. In several pot cultures, it has been tested the effects of AM symbiosis on the improvement of drought stress tolerance of wheat plants (Lehnert et al. 2018; Al-Karaki et al. 2004; Al-Karaki 1998; Al-Karaki and Clark 1999). Mycorrhizae can be a strong supporter to help symbiosis needed plantlets. Mycorrhizal fungi seem to act in three ways:

1. Help the plants to attain its best performance
2. Buffering the stress during acclimatization
3. Improve overall plant and soil health

It has been indicated that AMF can promote many aspects of plant life such as plant growth improvement, nutrients uptake, and stress tolerance (Chen et al. 2018). Also, AMF inoculation can increase resistance potential of plant against salt and drought stresses. Mycorrhizal association increases plant tolerance to drought stress as well (Wu et al. 2013). The work of Latef and He (2011) has shown that under several levels of salt application, concentrations of P and K were higher in *Rhizophagus mosseae* inoculated tomato (*Lycopersicon esculentum* L. cv. Zhongzha105) plants when compared with non-AM plants grown under non-saline and saline soil conditions. Usually, under salt stress conditions, AM inoculation reduces the tissue Na^+ concentration. Previously it has been shown that mycorrhizal inoculation significantly affects plant biochemical defense system by enhancement of antioxidant enzyme activities such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and ascorbate peroxidase (APX) in leaves of both salt-affected and non-affected plants. The results of Latef and Chaoxing (2011) have shown that AMF may protect tomato plants against salinity by alleviating salt-induced oxidative stress. Fan and Liu (2011)'s results also have shown that under drought, *G. mosseae* inoculated *Poncirus trifoliata* seedlings exhibited higher level of proline and activities of two antioxidant enzymes, superoxide dismutase (SOD) and peroxidase (POD) as compared to non-inoculated plants. Several studies showed that mycorrhizal inoculation can protect plants against salinity by alleviating the salt-induced oxidative stress. Lower oxidative damage in the mycorrhizal colonized plants may help plants to survive and grow properly. Wu et al. (2010) have shown that *R. mosseae* inoculated trifoliate orange seedlings significantly alleviated the growth reduction of salinity. It seems that mycorrhizae-inoculated citrus seedlings exhibited a more efficient antioxidant defense system, which may provide better protection against salt damage.

Salinity and AMF also had a significant effect on the concentration of phenols and ascorbic acid in the fruits (Grimaldo-Pantoja et al. 2017). Phenols and ascorbic acid may have direct and/or indirect effects on P nutrition (Smith and Read 2008). It has been estimated that approximately 90% of the land plant species roots have symbiosis with mycorrhizal fungi (Gadkar et al. 2001). Despite the low mycorrhizal affinity of the halophytes (Brundrett 1991) mycorrhizae occur under natural saline environmental conditions (Yamato et al. 2008).

It has been found that AMF inoculation improved water relations and alleviated the salt stress of many plants. Also, AMF inoculation provide high resistance to drought through enhanced water uptake (Ruiz-Lozano et al. 2001; Ruiz-Lozano et al. 2006). Under water deficiency since AMF associated plant roots enhanced mineral nutrients especially P, crop productivity is high (Al-Karaki et al. 1998; Marschner and Dell 1994). Also, mycorrhizae-inoculated plants have higher water uptake due to hyphal extraction of soil water and higher root hydraulic conductivity than non-mycorrhizal plants (Auge 2004; Ortuno et al. 2018). All such results suggest that mycorrhization brought biochemical changes helpful in mitigating different stresses experienced by drought and salt factors. The AMF (Smith and Read 2008) and rhizosphere organisms colonization may alleviate drought, salt, and metal stress of plants showing capability in binding heavy metals and mitigate the stress tension.

23.2 Effects of Mycorrhizal Inoculation on Salt and Drought Tolerance

Since the increase in human population has negative effects on land use for food security, soils are under stress. Recently poor soil quality and crop management have negative impact on salt stress, nutrient deficiency, and heavy metal pollution. Many researchers reported that mycorrhizae-inoculated plant species are more tolerant to stress factors such as nutrients concentrations (Zrnic and Siric 2017). Soil and environmental stress factors affect the efficiency and establishment of mycorrhizae. For example, salinity suppressed the growth of AMF. Salinity stress significantly reduced the root, stem and leaf dry matter and leaf area due to direct effects of ion toxicity on plant. However, it has been shown that mycorrhizal colonization significantly improved plant chlorophyll concentration in comparison to the non-salinized and salinized plants (Latef and Chaoxing 2011). The AM fungi also decrease nutrient leaching from the soil, consequently contributing to the retention of nutrients in the soil for saving the chemical fertilizers.

Various ecological approaches such as AM fungi, PGPR, and entophytic bacteria have been conducted. It is well known that a wide range of soil microbes including AM fungi and interaction with endophytic bacteria are able to alleviate soil stresses by (1) enhancing the availability of soil nutrients and water, (2) production of plant hormones, (3) controlling pathogens by producing antibiotics, (4) adjusting and regulating the concentrations of toxic ions, and (5) production of different biochemical compounds to increase plant defense systems (Miransari 2016; Hamilton III and Frank 2001; Miransari 2014). Miransari (2016) indicates that especially under stress, the right combination of AM fungi and the host plant may result in the highest level of efficiency. It is possible under stress conditions that the growth and activity of both AM fungi, other microorganism, and the plant can be adversely affected. It is well known that salt has detrimental effects on spore germination of AMF. For better management of stress factors such as salt on plant growth and plant health, it is possible to isolate the tolerant species of mycorrhizal fungi from the saline soils. Rivero et al. (2018) reported that AMF isolated from the stressful environment was the most effective approach in improving plant tolerance to salt stress. In many Central European soils, AMF spores were isolated from different sodic soils and results showed that up to 80% of all spores from different sites gave single PCR-pattern which closely matched to *R. geosporum* (Bothe 2012).

23.3 Effects of Salinity and Water Stress on Soil Properties and Plant Growth

It is estimated that more than 33% world's irrigated arable land is affected by salinity. Salt stress causes decrease in plant productivity by disrupting the photosynthesis mechanism. Hokmabadi et al. (2005) indicated that relative growth rate (RGR), net assimilation rate (NARw) decreased with increasing salinity level with time for all treatments and rootstocks of pistachio. In general, salt stress is due to accumulation of Na^+ of The intracellular accumulation of Na^+ ions under salt stress conditions alters the ratio of K: Na, which affect the bioenergetic processes of photosynthesis (Sudhir and Murthy 2004). High concentrations of Na^+ and Cl^- accumulation in the root and root cells produce extreme rations of Na^+/Ca^{2+}, Na^+/K^+, $Ca^{2+/}Mg^{2+}$, and $Cl^-/NO_3{}^-$ which are depressed nutrient–ion activities (Grattan and Grieve 1998). As a result, of nutritional disorders, plants undergo stress conditions. Since mycorrhizae have affected the absorption of other nutrients, they may dilute the effect of Na^+ and Cl^- ions in the root medium. In a screened work with 29 different citrus genotypes and rootstocks, it has been postulated that high concentration of Cl^- and/or Na^+ in the leaves of citrus has been related to disturbances in mineral nutrients, CO_2 gas exchange and water relations (Cimen and Yesiloglu 2016). Navarro et al. (2014) result indicated that response of mycorrhizal inoculation to salt stress was related to the nutritional status and their findings confirm that AM fungi can alter host responses to salinity stress, improving P, K, Fe, and Cu plant nutrition in Cleopatra mandarin plant. Under saline treatments, mycorrhizal inoculation increased root Mg concentration. More Mg concentration may dilute Na^+ concentration in the root medium. The results of Latef and Chaoxing (2011) under nonsaline and saline conditions, Na^+ concentration was lower in AM than non-AM tomato plants. Also, the concentrations of P and K were higher in AM when compared with non-AM tomato plants. According to results of Porras-Soriano et al. (2009a) *R. mosseae* was the most efficient inoculum in reducing the detrimental effects of salinity; it increased shoot growth by 163% and root growth by 295% in the nonsaline medium, and by 239% (shoot) and by 468% (root) under the saline conditions in olive plantlets. Porras-Soriano et al. (2009a) have shown that K content was enhanced under salt conditions by 6.4-fold with *R. mosseae*, 3.4-fold with *R. intraradices*, and 3.7-fold with *R. claroideum* inoculated olive plantlets under nursery conditions.

Mycorrhizal inoculation also decreased the plant shoot/root dry weight ratio as well (Porras-Soriano et al. 2009a). The results of Yang et al. (2014) show that mycorrhizal inoculation significantly increased the root length colonization of mycorrhizal apple plants under high degrees of salinity levels as compared to non-mycorrhizal plants. The work of Al-Khaliel (2010) has shown that under salinity and P deficient soil conditions, mycorrhiza inoculated peanut plants chlorophyll content and leaf water content increased significantly and also salinity tolerance significantly increased. In another pot experiment, Al-Karaki (1998) used two durum wheat genotypes (drought-sensitive and drought-tolerant) under water-stressed and well-watered conditions and the results showed that AM inoculated plants had high shoot and root dry matters under water stress than non-inoculated plants.

23.3.1 Mycorrhizal Fungi: Role in Soil Property Improvement Under Stress Conditions

In order to rehabilitate land sources suffering from soil salinization, useful reclamation programs are undertaken. The AM fungi is suggested as a useful strategy for saline soils (Zhang et al. 2019a). Mycorrhizae can influence soil aggregation by improving structure of the soil (Rillig and Mummey 2006), and they have a direct impact on soil aggregation (Ji et al. 2019). The AM fungi can enhance soil stability by producing hyphal network and glycoproteins (Trouvelot et al. 2014). They can provide a direct link between soil and roots (Lenoir et al. 2016). Therefore, the relationship and feedback between soil structure and mycorrhizae are of special interest. The AM fungi can affect N metabolism of the soil by enhancing the proportion of soil macroaggregate in saline soil. The increase in soil NH_4^+-N by AM fungi can regulate the hyphal growth and AM fungal hyphae can cause a decrease in salt concentration in the hyphosphere (Zhang et al. 2019a). Therefore, AM fungi can be suggested as an important bioindicator for soil quality or soil pollution and a potential application for restoring the degraded ecosystems (Lenoir et al. 2016).

The AM fungi regulate glomalin-related soil protein which is produced by spores and hyphae of AM fungi (Chi et al. 2018; Lovelock et al. 2004). Glomalin and glomalin-related soil protein (GRSP) can lead to an interesting response between soil structure and fungal growth. In poorly aggregated soil, GRSP can be produced in considerable concentrations (Rillig and Mummey 2006; Jones et al. 1997). In a previous study, it was mentioned that spore density, GRSP content, and hyphal length were significantly enhanced by AM fungi under both drought and well-watered conditions, and they strongly suggest dominant role of AM fungi in the management of soil water-stable aggregates by improving soil aggregate stability especially under drought stress (Ji et al. 2019). Likewise, AM fungi can display strongly positive feedback to the conditions by stimulating aggregated soils (Rillig and Mummey 2006).

The GRSP released from mycorrhiza influences the properties of rhizosphere. Previous studies indicate that exogenously applied GRSP could strongly stimulate root morphology and plant growth under drought stress. The GRSP can also modulate the phytohormones especially auxin (IAA), abscisic acid (ABA), and methyl jasmonate (MeJA) concentrations under drought stress. Therefore, the exogenous treatment of GRSPs is suggested as a plant growth regulator for improving drought tolerance (Chi et al. 2018). However, sodic soil can cause a decrease in GRSP concentration. It can be related to the adaptation of the plant-fungi interaction to various environmental conditions (Zhang et al. 2017). The AM fungi symbiosis can be used as an adaptation strategy by enhancing water use efficiency of the plant and it can eliminate the deleterious effects of water stress (Pavithra and Yapa 2018). Moreover, different species of mycorrhizae can stimulate the aggregation of soil to different degrees (Rillig and Mummey 2006). In addition, the physical and chemical properties of the soil effect AM fungi colonization such as low nutrients level and clay concentration are the key factors for colonization (Coutinho et al. 2019). Pesticide residues such as glyphosate in the soil or the plant can cause an inhibition in the mycorrhizal colonization, and a reduction in mycorrhizal symbiosis can be strongly dependent on the soil history (Helander et al. 2018). Therefore, the interaction between AM fungi and plant species should be well evaluated to improve success.

23.3.2 *Effects of Salt and Drought Condition on Arbuscular Mycorrhiza Development*

The interaction between plants and AM fungi is strongly correlated with the soil properties, and it depends on environmental and atmospheric conditions (Bitterlich et al. 2018; Mirzaei and Moradi 2017). Drought and salinity affect mycorrhizal symbiosis (Füzy et al. 2008). Spore production and hyphal development of AM fungi are negatively affected by water availability. Le Pioufle and Declerck (2018) reported that polyethylene glycol which stimulates osmotic stress in plants decreased AM fungi development. Hyphal growth and spore germination of AM fungi can be reduced in saline environments (Evelin et al. 2009; Juniper and Abbott 2006). The colonization of some AM fungal species is reduced because NaCl impacts directly on AM fungi. The extension of hyphae and spore germination can be inhibited in the presence of NaCl. However, various AM fungal species have different germination abilities under salinity. Spores of some AM fungal species can germinate even under 300 mM NaCl (Juniper and Abbott 2006). Bencherif et al. (2015) demonstrated that number of spores of some AM fungal species isolated from various saline soils could increase under salinity, and this adaptation of AM fungi could be used to restore saline arid lands. Carvalho et al. (2004) mentioned that some AM fungal species could adapt to salt marsh soils. The AM fungi diversity and fungal spore density are also strongly affected by soil nutrient availability and land use practices and agricultural soils (Soka and Ritchie 2018). Therefore, environmental conditions should be well evaluated before the application of AM fungi.

23.3.3 Mycorrhizal Fungi for Salinity Stress Remediation

Mycorrhizae remediation is an important on-site remediation strategy which uses microorganisms and plants for cleaning heavy metals from contaminated environments. As mycorrhizae remediation is a relative low-cost, natural method, it is suggested as a solution for environmental problems. In the mycorrhizae remediation process fungi can sequester or degrade the contaminants because of their mycelium morphology supplying highly extensive and reactive surface (Aroca et al. 2017; Barun Kumar Manjhi et al. 2016). The AM fungi can reduce the transport of heavy metals from roots to shoots (Zhang et al. 2005). Khan (2006) mentioned that AM fungi can act as a bioprotectant, biofertilizer, and biodegrader. The AM fungi can have a significant role in phytoremediation (Wang et al. 2005) and in contaminated soils, phytoremediation can be enhanced by AM fungi inoculation to crops (Khan et al. 2014). The AM fungi have also beneficial role in phytoremediation under drought and salt stresses (Liu et al. 2018a).

Cadmium (Cd) and Nickel (Ni) are important heavy metals, which can enter to food chain via contaminated agricultural products or drinking water. These metals have deleterious effects on human health (Barun Kumar Manjhi et al. 2016). Several studies indicate that heavy metals such as Zn, Cd, As, and Se can be taken up by AM fungi from the environment (Aroca et al. 2017; Giasson et al. 2006). The AM fungi can help to immobilize heavy metals such as Cu, Pb, Zn, and Cd in the roots and alleviate the toxicity of heavy metals (Zhang et al. 2005). The useful effects of AM fungal colonization under metal toxicity are the improved P uptake and decreased Cd, As and Cu concentrations in the shoots. In another study, it was reported that

AM fungi could induce the expression of metallothionein genes under Ni stress and help to alleviate the negative effects of Ni stress (Shabani and Sabzalian 2016). Therefore, AM fungi could have a beneficial impact on the ecological restoration of metalliferous mine areas (Chen et al. 2007).

Basidiomycetes can also degrade persistent organic pollutants, recalcitrant hydrocarbons, such as polyaromatic hydrocarbons (PAHs), aromatic hydrocarbons, halogenated hydrocarbons, and phenols, explosives and dyes. Basidiomycete species can degrade various kinds of hydrocarbons by their essential enzymes (Treu and Falandysz 2017). Boldt-Burisch et al. (2018) mentioned that AM fungal colonization in the roots are not affected by soil hydrocarbons. Therefore; the use of AM fungi symbiosis is suggested in contaminated soils with high efficiency (Zaefarian et al. 2013). However, heavy metal translocation can be affected by the interaction between host plants and different AM fungi isolates (Liang et al. 2009) and the interaction of heavy metal with other metals (Giasson et al. 2006). Therefore, the selection of the species used for bioremediation and the potential interactions with other soil organisms should be well evaluated (Treu and Falandysz 2017).

Barun Kumar Manjhi (Barun Kumar Manjhi et al. 2016) mentioned that AM fungi can be suggested as a filter and AM fungi can inhibit the transport of heavy metals to the plants. The AM fungi can protect the host plants from heavy metals such as Zn, Cd, and Pb toxicity in contaminated soils. The AM fungi can inhibit heavy metals uptake in high concentrations, therefore; they could enhance the plant growth (Liang et al. 2009). In addition, AM fungi can induce heavy metal accumulation in some plant species. The AM fungi may enhance stress tolerance in the contaminated soils via trapping heavy metals in their extraradical hyphae and plant root systems (Carvalho et al. 2006). Roy et al. (2018) reported that AM fungi could be used in the remediation of toxic fly ash by phyto-bio-rhizo-mycoremediation application. The AM fungal species such as *R. tenue*, *R. mosseae,* and *Gigaspora* spp. can defend plants against the deleterious effects of heavy metals (Lal 2002). Giasson et al. (2006) mentioned that plants infected with *R. intradices* can sequester Cd, Zn, As, and Se more than non-mycorrhizal plants. In another study, it was mentioned that *R. mosseae* could lead to high tolerance to heavy metal toxicity (Zhang et al. 2005).

Gai et al. (2018) reported that some species such as *Claroideoglomus claroideum* and *R. etunicatum* tolerated Cd in soil. *R. claroideum* was identified as more tolerant to the toxicity of Cd by measuring root colonization and total extraradical mycelium length. In another study, it was mentioned that *R. intraradices* increased plant growth in Cd contaminated areas (Redon et al. 2008). The AM fungi can also increase As uptake via active arsenite-translocating ATPase. However, the translocation can be altered via AM fungi (Giasson et al. 2006). Glomalin has an important impact on the achievement of mycorrhizoremediation in heavy metal tolerance. Glomalin can isolate heavy metals (Khan 2005). The AM fungi can have an important impact on the accumulation of glomalin-related soil protein, soil organic matter and soil organic carbon and influence the particle-size distribution and aggregate formation in heavy metal contaminated areas (Li et al. 2017). Therefore, the AM fungi are suggested for the recovery of contaminated soils (Abu-Elsaoud et al. 2017; Yang et al. 2017). (Loha et al. 2018) mentioned that a cyclin (SiPHO80) in the protein family could play important roles in homeostasis of inorganic phosphate and regulate the tolerance to heavy metal stress in *Serendipita indica* an osmotolerant AM fungal specie. Therefore, *S. indica* is suggested as a potential biofertilizer. We can also benefit from AM fungi by their role on heavy metal phytoextraction (Wang et al. 2005). Among other metals, Se can be extracted more easily by AM fungi inoculated plants (Giasson et al. 2006). In another study, *R. intraradices* caused an increase in available Cd and reduced Cd contents in leachates. Therefore, AM fungi were suggested as a good approach for the phytoextraction process (Redon et al. 2008).

23.4 Mycorrhizal Inoculation: Effects on Plant Shoot and Root Growth Under Salt Conditions

Salinity affects the plant root and shoot growth. Number of studies have been conducted to evaluate the counter-effect of AM fungi in salinity tolerance implacable to plant growth attributes which include root and shoot growth, chlorophyll content, stomatal conductance, inter and intracellular CO_2 concentration in the plant leaves. Elhindi et al. (2017) conducted a study in sweet basil (*Ocimum basilicum*) plants at three salinity levels which were nonsaline ($EC = 0.64$ dS m^{-1}), low saline ($EC = 5$ dS m^{-1}), and highly saline ($EC = 10$ dS m^{-1}). The AM fungi used in the study were *R. deserticola*. Observed data showed that AM fungi significantly increased dry biomass of plant as a whole but shoot height and their branches were not enhanced significantly. Similarly, another study was conducted on rice plants under salinity stress in the presence of AM fungi (*C. etunicatum*) by Porcel et al. (2016). The study was performed at two salinity levels (75 mM and 150 mM NaCl) where results showed that plants inoculated with AM fungi had more growth and shoot dry weight was increased by 40–62% under nonsaline (75 mM NaCl) conditions. Only increase of 51% was observed under 150 mM NaCl in the presence of AM fungi. It was decreased only by 10% in AM fungi inoculated plants at 150 mM NaCl. Besides that, a 17% reduction in dry weight was observed at 75 mM NaCl non-AM fungi inoculated plants.

In another study, Garg and Bhandari (2016) used silicon nutrition and AM fungi (*F. mosseae*) inoculation to evaluate plant biomass, root to shoot ratio and yield of *Cicer arietinum* L. genotypes under saline (0, 60, 80, and 100 mM NaCl) conditions. Observations showed that salinity significantly reduced the plant dry matter and declined the plant growth in all genotypes. Roots were observed more prone to salinity than leaves resulted in decrease of R/S ratio. Study also concluded that individual application of Si and AM fungi mitigate salinity effects on plant and induce significantly positive changes in plant growth. Moreover, when Si was applied with *F. mosseae*, in saline conditions, plant biomass significantly increased in comparison to Si fertilization only. Additionally, AM fungi directly facilitate in root biomass development and it enhances in comparison to Si application only.

23.5 Mycorrhizal Symbiosis and Mineral Uptake Under Salt and Drought Stress Factors

Several studies have been performed to evaluate the contribution of AM fungi in mitigating salinity and drought effect for better nutrient uptake and plant growth (Hammer et al. 2011; Ruiz-Lozano et al. 2012; Evelin et al. 2012). Studies suggest the mechanism of selective nutrients uptake through AM fungal hyphae into the plant roots which eliminate toxic effects of salt. Moreover, studies showed an increase in K^+ and a decrease in Na^+ concentrations in AM fungi inoculated plants (Evelin et al. 2012; Garg and Manchanda 2009).

Elhindi et al. (2017) grew sweet basil plants in nonsaline ($EC = 0.64$ dS m^{-1}), low saline ($EC = 5$ dS m^{-1}), and high saline soils ($EC = 10$ dS m^{-1}) where observed the mineral nutrients concentration in plant leaves. Results showed that K^+, P, and Ca^{2+} were higher in *G. deserticola* inoculated plants under non-stressed conditions. The content of Na^+ and Cl^- were exceptionally low in sweet basil. Similarly, significantly high amount of K^+, P, and Ca^{2+} was recorded in the sweet basil leaves of AM fungi inoculated plants either NaCl treatment was there or not. Overall increase in NaCl concentration decreased the nutrient content with exception for Na^+ and Cl^- content. The AM fungi significantly enhance leaf-K^+, P, and Ca^{2+} content under salinity stress conditions and reduce Na^+ and Cl^- content. Salinity had significant reducing effect on the ratio between K^+ and Na^+ and between Ca^{2+} and Na^+. There was a significant difference between K^+/Na^+ ratio and Ca^{2+} and Na^+ in AM fungi inoculated plants. In comparison to non-AM fungi inoculated plants, K^+/Na^+ ratio was higher regardless of the salinity strength. Therefore, AM fungi have the capability to reduce the imbalance of ions and their ratios such as Na^+ and Ca^{2+} uptake and K^+/Na^+, Ca^{2+}/Na^+ ratios in saline soil (Kaya et al. 2009).

Contribution of AM fungi in coping with abiotic stress to the associated plant is related to the alterations in hormonal homeostasis where ABA signaling is thoroughly studied (Ruiz-Lozano et al. 2012; Osakabe et al. 2014) (Fig. 23.1). The ABA is a stress hormone, and its production is triggered during environmental stresses such as salinity and drought (Osakabe et al. 2014). Plants adjust their ABA level according to physiological changes, environmental stress, and symbiotic relation. Aroca et al. (2013) endorsed the increase in ABA content when the plant is under stress condition. İn presence of AM fungi, stress is mitigated and ABA level decreases which may suggest that AM fungi inoculated plants are less stressed than non-AM fungi inoculated plants. Moreover, plant growth parameters and plant yield also prove plant fitness.

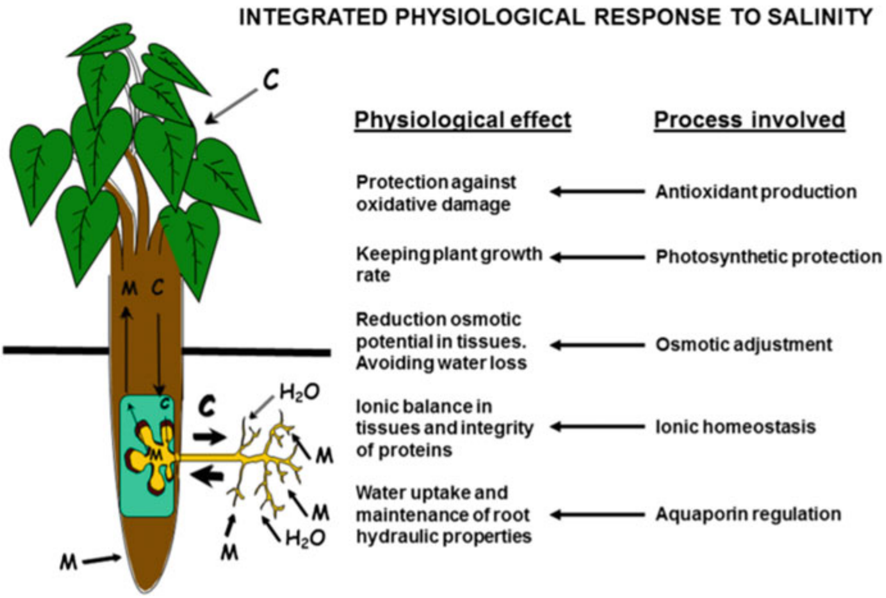

Fig. 23.1 Summary of the main processes by which AM fungi symbiosis can regulate the integrated physiological plant response in order to improve tolerance to salinity. The exchange flux of water, minerals (M), and carbon compounds (C) between the plant and the fungus is also represented. Minerals include nutrients and salt ions present in the soil solution. Adapted from Ruiz-Lozano et al. (2012)

23.5.1 Phosphate Uptake Assisted by the AM Symbiosis Under Salt Stress Conditions

Phosphorus (P) is a major nutrient of interest in symbiotic relationship of plant-AM fungi. It derives basic cellular functions in bioenergetics, metabolites activation, and enzymes regulation during structural formation as nucleic acids (Bucher 2007). Besides that, P is a limiting nutrient for plant productivity because of its immobile nature in soil. Porcel et al. (2016) conducted a study to evaluate the salinity effect on rice plant with non-AM fungi and AM fungi (*C. etunicatum*) application. Results revealed that P concentration was high in root and shoot of AM fungi inoculated plants regardless of the salt concentration. In roots, 175% increase in P concentration on average was recorded, whereas in the shoots, it approached 460% under nonsaline conditions and 190% in highly saline conditions. Indeed, the shoot P concentration decreased in AM plants due to salinity applied, although these plants always maintained higher shoot P concentration than non-AM plants.

23.5.2 Nitrogen Uptake and Transfer at the Mycorrhizal Interface Under Salt Stress Conditions

Nitrogen is a major nutrient required to the plants for their biomass (1–5% of dry weight), biochemical processes, and plant yield. As a significant amount of N requirement to the plant, it is available in the soil as two inorganic forms such as NO_3^- in upland soil and NH_4^+ in flooded soil (Bücking and Kafle 2015). İn AM fungi inoculated soils, N is taken up by three forms such as NH_4^+ (Frey and Schüepp 1993), NO_3^- (Tobar et al. 1994a), and amino acids (Cliquet et al. 1997). Besides that, AM fungi prefer to uptake NH_4^+ for the plant as it need extra energy to reduce NO_3^- into NH_4^+ before conversion into organic compounds (Courty et al. 2015; Nakano et al. 2001) (Fig. 23.2). This mechanism was further supported molecularly, and three mycorrhizal fungal ammonium transporter (AMT) genes such as *GintAMT1*, *2,* and *3* have been identified in *R. irregularis* (Pérez-Tienda et al. 2011; Calabrese et al. 2016). Among them, *GintAMT1* has high affinity for NH_4^+ transporter expressed in cortical cells with arbuscules and extraradical mycelium (ERM). The transcripts of *GintAMT1* could up-regulate in low supply of NH_4^+ particularly in acidic soils (López-Pedrosa et al. 2006). *GintAMT2* expresses in high-P soils and it suggests that more NH_4^+ is transferred (Calabrese et al. 2016). In anaerobic soils, NO_3^- uptake to the plant root is supported by mycorrhizal hyphae coupled to H^+-symport dependent process (Bago et al. 1996). Molecular evidence of NO_3^- absorption was confirmed as NO_3^- transporter, GiNT, from *R. irregularis* was found which is usually present in ERM (Koegel et al. 2015). The fungal GiNT represses in surplus supply of NH_4^+ which shows that upregulation of GiNT and *GintAMT* is dependent on NH_4^+ to NO_3^- ratio in soil.

Besides inorganic form of N, AM fungi can take up certain organic forms of N. Several studies have been conducted with labeled ^{13}C and ^{15}N from organic sources (amino acids) to evaluate the uptake capability of AM fungi. Results showed that only ^{15}N was taken up (Atul-Nayyar et al. 2009; Hodge 2001). Hodge, Campbell (Hodge et al. 2001) noticed 72% capturing from glycine source. An amino acid permease, *GmosAAP1*, involved in transporting amino acid across fungal membrane has been identified in the AM fungus *Funnelliformis mosseae* (Cappellazzo et al. 2008). Multiple transporters are involved in the uptake of amino acids through ERM. Another transporter *RiPTR2* has been identified in *R. irregularis* which is responsible for the transportation of dipeptides (Belmondo et al. 2014).

23.5.3 Water and Potassium Relationship in AM Colonized Plant Under Salt and Drought Conditions

The AM fungi are widely distributed in saline environment. In the presence of NaCl, AM fungi inoculated plant leaves showed high relative water content, moreover, high efficiency of water usage, and reduced water saturation (Sheng et al. 2008). The

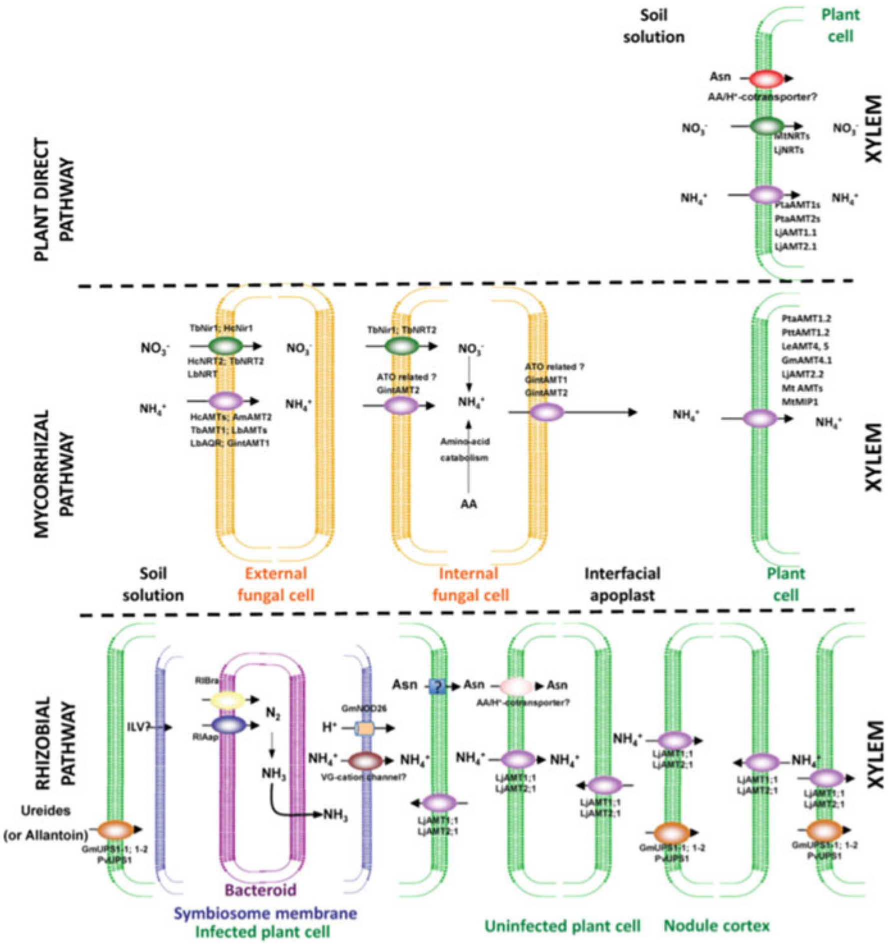

Fig. 23.2 Current knowledge about inorganic N transfer mechanisms in arbuscular and ectomycorrhiza and the rhizobium-legume symbiosis. Ammonium and nitrate are exchanged across the different compartments (soil, fungal/bacterial cells, apoplast, plant cells) by several membrane transporters that are not yet fully characterized. The different abbreviations are: NRT, nitrate transporter; AMT, ammonium transporter; LIV, leucine, isoleucine, valine; AA; amino acid; Asn, Asparagine; UPS, ureide permease; VG, voltage gated; Am, *Amanita muscaria*; Gint, *Glomus intraradices* (recently renamed *Rhizophagus irregularis*); Gm, *Glycine max*; Hc, *Hebeloma cylindrosporum*; Lb: *Laccaria bicolor*; Le, *Lycopersicum esculentum*; Lj, *Lotus japonicus*; Mt, *Medicago truncatula*; Pta, *Populus tremula* x alba; Ptt, *Populus trichocarpa*; Pp, *Pinus pinaster*; Pv, *Phaseolus vulgaris*; Rl, *Rhizobium leguminosarum*; Tb, *Tuber borchii*. Adapted from Courty et al. (2015)

improvement in water status through AM fungi linked to enhanced water uptake mainly because of AM fungal hyphae penetration (Jiang and Huang 2003). As water status is severely disturbed by the salinity stress, key role of AM fungi is to save the host plant from dehydration and thus aid the host plant to enable maximum absorption of water via deep fungal hyphal network system (Porcel et al. 2012). But the K concentration and its accumulation in plant under the saline environment did not affect significantly the AM fungi colonization. Minimum uptake of K was reported in tomato plant by AM fungi root colonization under salt stress (Al-Karaki 2000). Reports showed that maximum salt stress-tolerant mycorrhizal plants showed the highest concentration of K in their shoot which is correlated with the stomatal K regulation (Porras-Soriano et al. 2009b). The root colonizing fungi *R. intraradices* in olive plants under the medium saline condition showed the K acquisition by 3.4 fold as compared to nonmycorrhizal root colonized plants, and in turn reaching up to 6.4 fold in plants colonized by *R. mosseae* (Thomas et al. 2003). Under salt stress conditions, maximum effect on the K uptake was only noted upon the inoculation of AM fungi and thus both shoot and root accumulated more K in AM fungi inoculated plant in comparison to uninoculated plant under salt stress condition. In this way, *A. nilotica* inoculated with mycorrhiza showed high amount of K in shoot and root under all of the salt treatments (Giri et al. 2007). Some previous reports showed similar increase in K concentration and hence noted that high K^+:Na^+ was maintained by the mycorrhizal plant under the salinity stress condition by accumulating more K^+ (Mohammad et al. 2003). Furthermore, at medium and high levels of salinity stress; there is a minor effect of AM fungi root colonization on shoot K concentration (Mardukhi et al. 2011). Similarly, AM fungi symbiotic association has the potential to improve the plant tolerance against water deficit condition thereby maintaining the plant water relation (Stevens et al. 2011).

Both under water stress and well water conditions the water relations were prominent for mycorrhizal plants (Asrar et al. 2012). The adaptation of AM fungi to drought stress condition is quick and hence deliberate the fruitful effects on the host plant under water deficit stress conditions (Nasim 2010). The uptake and transportation of water and nutrients from the soil to host plant roots is among the key functions of extraradical hyphae of AM fungi (Peterson and Massicotte 2004). As compared to saturated soil conditions, the hyphal network transport more water under the dried soils. Similarly, the leaf water potential also enhanced by symbiotic association under drought stress condition (Gholamhoseini et al. 2013). The uptake of water is due to hydrophilic nature of hyphal tips, which absorb water from soil and transport via either cytoplasmic pathway or inner layer of wall from a single soil pore, alongside the AM hypha toward the cells of cortex (Allen 2007). When the soil dehydrates severely, the extraradical AM hyphae with a diameter of 2–5 m penetrate through soil pores and provide the mycorrhizal root more access to water zone (Wu et al. 2013). Some previous reports also showed that AM fungal colonization improved plant water relationship (Zhang et al. 2011). The AM symbiosis improved K tissue concentration which is an important physiological attribute to regulate the root water uptake potential of plant (Benlloch-González et al. 2009). The high potassium uptake by mycorrhizal application under drought stress conditions showed that AM symbiosis has the potential of reducing drought stress and reconstruction of ecosystems (Wu et al. 2011).

23.5.4 Mycorrhizal Fungi: Effects on Macro and Micronutrients Uptake Under Salt and Drought Stress Conditions

Generally, under salinity stress conditions, due to imbalance in nutrient composition such as excessive Na^+ and Cl^- ions uptake caused the excessive toxicity thereby leading to a reduction in osmotic potential of plants, disruption of cell organelles and their metabolism and ultimately salt affect plant growth and reduce the yield. The nutrient imbalance in the plant cells caused by nutrient uptake and/or transport to the shoot leading to ion deficiencies (Adiku et al. 2001). The AM fungi inoculation significantly increased the content of P and ascorbic acid of the pepper plant and also salinity and AM fungi had a significant effect on the concentration of phenols and ascorbic acid in the fruit (Grimaldo-Pantoja et al. 2017).

The AM fungi have the potential to assist plant for nutrients uptake under different stresses including salinity and drought (Al-Karaki 2000). The performance of mycorrhizal resistant species under salinity condition is determined by the uptake of nutrients (Daei et al. 2009). In mycorrhizal plants, the uptake of N, P, K, Ca, and Mg was significantly enhanced as compared to non-mycorrhizal plants (Heidari and Karami 2014; Ortaş and Rafique 2017). The prominent species of AM fungi such as *R. mosseae* and *R. intraradices* increased Zn and Mn concentration significantly in pistachio plants, regardless of the soil moisture conditions (Bagheri et al. 2012). Similarly Al-Karaki et al. (2001) demonstrated that the uptake of Cu, Fe, and Zn significantly increased for mycorrhizal plants with respect to non-mycorrhizal plants under salinity stress (Al-Karaki et al. 2001). According to Daei et al. (2009), mycorrhizae absorbed maximum amount of Zn and produced high quantity of root and yield under saline stress condition. Various nutrients such as N, Ca, Mg, Fe, Cu, and Mn were absorbed by different cultivars of wheat under saline soil inoculated with AM fungi species including *R. etunicatum*, *R. mosseae*, and *R. intraradices* (Mardukhi et al. 2011). Plants inoculated with AM fungi showed significant uptake of micronutrients as compared to uninoculated control in lettuce plant whereas other studies showed that rhizospheric bacteria with AM fungi inoculated wheat plants had more efficiency against Se (Durán et al. 2016). The study of Mohammad et al. (2003) showed that under salinity stress conditions, the uptake of micronutrients improved upon the inoculation of AM fungi, similarly the indigenouos AM fungi inoculation enhanced the uptake of Fe, Mn, and Cu. While the Zn uptake was promoted by AM fungi under all the treatment of salinity stress.

There is an increase in AM fungi response by decreasing fertility of soil and furthermore along with increasing the severity of drought stress (García et al. 2008). Reports showed that AM fungi application significantly reduced the drought stress and drought-induced deficient nutrients such as Fe and Zn (Gholamhoseini et al. 2013). The drought stress was reduced in pistachio cultivars assisted by the inoculation of AM fungi which improve the uptake of slowly diffusing mineral ions, i.e., PO_4^{2-} and Zn^{2+} (Bagheri et al. 2012). The higher mineral nutrients content such as Fe and Zn were observed in plants inoculated with AM fungi as compared to non-mycorrhizal plants under drought and well water conditions (Amiri et al. 2017). Furthermore, the inoculation of *F. mosseae* and *R. intraradices* incremented the Zn content under severe drought conditions (Shirani et al. 2018). The inoculation of AM fungi species such as *R. mosseae* and *R. intraradices* enhanced the Zn uptake up to 4.14% and 3.95%, Cu concentration up to 12.72% and 11.72% with respect to uninoculated treatment under drought stress (Askari et al. 2018).

23.6 Effects of Mycorrhizal Inoculation and Biochar Application to Reduce the Salt Effects on Nutrient Uptake and Plant Growth

Conversion of the barren saline land into cultivated field is a solution to meet current challenges of world global food security (Biswas and Biswas 2014). The emerging knowledge of biochar addition has shown that it improves the physiochemical and biological properties of salt-affected soils (Dahlawi et al. 2018; Rafique et al. 2017). The increased uptake of P in salt-affected soil by biochar is due to its direct action of P source facility and indirectly biochar promotes the growth medium condition particularly soil organic carbon (Lashari et al. 2013). The higher K concentration in salt-affected soil induced by biochar addition is considered as one of the most significant mechanisms for biochar to enhanced the growth of plants under salt stress (Abbas et al. 2018). The nutrient status of plants affected by biochar ability of increasing nutrient retention, decreased leaching, and gaseous losses through improving surface properties of soil (Mukherjee and Zimmerman 2013). By promoting the root biochar interaction, the application of biochar increment nutrients procurement potential of plants in saline soils (Olmo et al. 2016). The addition of biochar in field and Laboratory condition in saline soil might mitigate its adverse effects and plant growth is augmented by releasing essential macro- and micronutrients including Ca, K, N, P, and Zn (Kim et al. 2016). The combined application of biochar and AM fungi improve plant yield under saline soil with respect to individual application of AM fungi and biochar. The enhanced yield was credited by increasing P and Mn and moreover the Na^+/K^+ ratio in plant grown under salt stress condition inoculated with AM fungi and biochar (Hammer et al. 2015). The green house study showed a significant synergistic application of biochar and AM fungi on the growth parameters and nutrient uptake in seedlings (Budi and Setyaningsih 2013). A generally better plant nutrition status may help to overcome salinity stress. Not only Na^+ levels were reduced, but also K and Mg concentrations and total K and Mg uptake were clearly increased in plants that received biochar and/or AM fungi addition (Hammer et al. 2015).

23.7 Effects of Mycorrhizal Inoculation on Water Uptake

The influence of AM fungi mainly depends on the uptake and transportation of water and nutrients, which enhances the hydration of plant tissue for securing physiological sustainability and improvement in growth (Abdel-Salam et al. 2018). The AM fungi inoculation significantly enhanced plant water relation under drought stress conditions (Borde et al. 2012). Therefore, improved water relation in plant inoculated with mycorrhiza also augmented the nutrient status which in turn exclusively extract the moisture contents of soil (Subramanian et al. 2006). The application of AM fungi regulates activity and expression of aquaporin both in fungal species and host plant in order to tolerate the drought stress conditions (Li et al. 2013). By activating the antioxidant defense system and stabilizing water table of soil aggravates the AM fungi boost the plant tolerance to water deficit conditions (Bedini et al. 2009). The AM fungi symbiosis significantly influenced the water uptake from soil. Regarding water uptake from the soil, effectiveness of different fungal species vary among themselves. This effectiveness in plant water uptake by AM fungi is mainly related to the external mycelium produced by individual AM fungi species and also related with the root colonization rate for alive and active structure (Baum et al. 2015). The increase in water and several macro- and micronutrients uptake was due to AM fungal hyphae that can extend to explorable surface area almost up to 50 times (Berruti et al. 2014). Therefore the host plant along with AM fungal species inoculation showed positive impact on water use efficiency (Bernardo et al. 2019). The AM fungal species alter the rate of translocation of water, hydration of tissue, and thus improved the physiological and water status of host plants (Liu et al. 2015). Through the plant symbiosis with AM fungi, the plant can be beneficial for transportation of water and thus helping the plant to possess stomata opening (Zhu et al. 2012). Mycorrhizal seedling enhanced more uptake of water than non-mycorrhizal seedling under water deficit conditions (Gong et al. 2013). This is due to the expansion of fungal hyphae in the absorption region in host plant thereby enhancing the water absorption through root (Liu et al. 2015).

23.8 Mechanisms of Mycorrhizae on Salt Tolerance in Soil and Inside the Host Plant

Salinity is a major problem for plant growth and yield (Porcel et al. 2012). The toxicity of Na^+ and Cl^- ions causes an imbalance in the nutrient composition and a decrease in plants osmotic potential, therefore salt stress induces physiological drought in plants (Evelin et al. 2009). Under salinity, AM fungi can improve water content and enhance beneficial nutrient uptake such as P, N, Mg, and Ca. The AM fungi lead various biochemical, physiological, and molecular changes in plants. The AM fungi induce photosynthetic efficiency, nitrogen fixation, and the accumulation of various osmolytes, polyamines, prolines, betaines, and carbohydrates and enhance leaf, stem, and root biomass and K^+:Na^+ ratios in leaves. It is also strongly mentioned that antioxidant system is enhanced by AM fungi (Porcel et al. 2012; Evelin et al. 2009; Cekic et al. 2012; Chang et al. 2018). Therefore, AM fungi symbiosis is suggested as a promising method for utilization of salt-alkaline lands (Chang et al. 2018). And mycorrhizal inoculation could be used in order to develop salt-tolerant crop plants (Porcel et al. 2012; Evelin et al. 2009).

The AM fungi can induce the expression of aquaporin and stress-related genes like absciisic acid (*Lsnced*), late embryogenesis abundant protein (*LsLea*), Δ1-pyrroline-carboxylate synthetase (*LsP5CS*) and PIP, Na^+/H^+ antiporters. The expression of these genes protects mycorrhizal plants from the detrimental effects of salt stress(Porcel et al. 2012; Evelin et al. 2009). The AM fungi can also maintain water use efficiency and stomatal behavior by regulating the key genes in the ABA pathway (14-3-3 genes), therefore AM fungi can improve drought tolerance (Xu et al. 2018). Under water deficiency it was reported that AM fungi and N-fixing bacteria could cause an increase in grain protein content and benefits to agricultural production (Oliveira et al. 2017).

Mycorrhizal fungi enhance plant growth, nutrition acquisition, antioxidant system, and siderophore production under adverse conditions. Therefore, they are suggested instead of the use of pesticides and inorganic fertilizers in agricultural applications and for developing sustainable and safer agricultural productions. As it is a biological process, it is essential for sustainable agriculture and it can be replaced by conventional agriculture applications (Kumar and Verma 2018). Hence, AM symbiosis can be a potential answer for conservation of some plant species in their natural ecosystems (Zarik et al. 2016). However, further studies should be done focusing on AM fungal salt-tolerant strains, cyclic nucleotide-gated channels, and cation proton antiporters to develop of salt-tolerant inoculums and for successful environmental and agricultural managements (Kumar et al. 2015).

23.8.1 Mycorrhizal Effectiveness for Hormonal Process and Signaling Under Salt Stress

The symbiosis is older than 450 million years, and it is environmentally friendly. The alleviation of detrimental effects of stress conditions is known to be related to phytohormones, secondary metabolites, and signaling molecules (Lopez-Raez 2016). Phytohormones have vital roles in plant metabolism. They act as stimulators in plant defense response under various environmental stresses. Phytohormones can also be produced by AM fungi which can be used for inducing the host tolerance under various conditions such as salinity, drought, heavy metal stress, and nutrient deficiency (Egamberdieva et al. 2017). The AM fungi can mediate with the phytohormone balance in the host plants, therefore AM fungi have important impact on the plant development by influencing as bioregulator and enhancing tolerance against environmental stresses as bio protector. By selecting the appropriate combinations of plant and fungus, maximum benefits can be achieved for farming. In addition, AM fungi can lead to a reduction in biocides and chemical fertilizers (Rouphael et al. 2015). Therefore, identification of interactions between host, microbe, and stress should be well evaluated (Egamberdieva et al. 2017).

Plant-associated microbes have beneficial impacts on the stimulation of phytohormones such as cytokinins, gibberellins, auxins, ABA, and salicylic acid in plant tissues (Lopez-Raez 2016). Among the phytohormones, AM fungi and salicylic acid mediate carbohydrate metabolism and ion homeostasis in crop plants and they can eliminate the deleterious effects of salt stress. Salicylic acid can enhance number of arbuscules and vesicles and cause an increase in the root colonization under salt stress. Therefore, seed priming with salicylic acid improves AM symbiosis and it is suggested as a potential approach in sustainable agriculture production under salinity (Liu et al. 2018b). Salicylic acid can also modulate water conductivity by regulating the root aquaporins. In addition, there is a strong network between aquaporins and phytohormones, especially salicylic acid, abscisic acid, and jasmonic acid in the controlling of the water transport in the roots (Quiroga et al. 2018). In addition, AM fungi can induce auxin synthesis and lead to high root hair growth under drought stress, therefore AM fungi can help to stimulate the deleterious effects of osmotic stress (Liu et al. 2018b).

The ABA normally regulates stomatal closure under drought stress, however in mycorrhizal plants (Ouledali et al. 2019) demonstrated that ABA was not the key factor in controlling the stomata behavior, AM fungi also control the stomata regulation. The AM fungi can also cause an increase in expressing the jasmonic acid gene in the roots under drought stress and this increase could help to respond to water stress (Duc et al. 2018). Under nutrient deficiency strigolactones (SLs), a plant hormone which modulates the coordinated plant development, can act as signals for the establishment of AM fungal symbiosis. The SLs can help host plant to alleviate the symptoms of stresses. Because of the beneficial effects of strigolactones, they are suggested as sustainable and innovative strategy for modern agricultural processes (Lopez-Raez 2016). The AM symbiosis can mediate various plant hormones and plant growth regulators; therefore, this symbiosis can have beneficial effects on plant metabolism under normal and stress conditions.

23.9 Alleviation of Salt and Drought Stresses by Arbuscular Mycorrhizal (AM) Fungi

Soil salinity and drought are among the most harmful stresses which affect the plant growth by reducing water uptake and cause osmotic stress (Santander et al. 2017). Both salinity and drought effect negatively on the distribution of mineral nutrients balance. Salinity causes imbalances of nutrients because of the deficiencies or the competitions of Na^+ and Cl^- ions with the essential nutrients. In this response, K^+ concentration is important in order to maintain turgor pressure under stress conditions. It is mentioned that high ratios of K^+:Na^+ is important for the improvement of the plant resistance to salinity. The Ca^{2+} can also regulate the plant resistance as a signal under salinity and drought (Hu and Schmidhalter 2005). Sun et al. (2017) mentioned that AM fungi formation could alleviate the deleterious effects of drought stress and eliminate growth retardation, therefore AM fungi increase plants yield in semiarid and/or arid environments. In a previous study, it was reported that AM fungi caused an increase of P uptake in dry soil (Neumann and George 2004). The AM fungal species such as *Septoglomus constrictum* can have a positive effect on the plant tolerance to drought stress by expression of some genes in the roots and it was mentioned that inoculation with *S. constrictum* could have higher stress tolerance to drought than non-mycorrhizal plants (Duc et al. 2018). In another study, it was reported that AM fungi improved photosynthetic efficiency, and proline, protein concentrations, and leaf gas exchanges. The symbiosis enhanced C sequestration in drought and salinization affected regions and increased the resistance of plants to drought and salinity (Zhang et al. 2018). Combination of AM fungal species could also increase the tolerance to drought stress in addition to abiotic stress tolerance (Oyewole et al. 2017). Therefore, AM fungi can be suggested as a promising biological application for the alleviation of salt and drought stresses (Zhang et al. 2018).

23.9.1 Arbuscular Mycorrhizal Fungi Increase Tolerance to Salinity in Plant Species

The AM fungi can make symbiosis with various vegetable crops. This symbiosis can lead to profitable and commercial agricultural and horticultural products. The success of the inoculation is strongly related to the properties of soil and genotypes of AM fungi and host plants. Moreover, environmental conditions such as water supply and nutrient content affect significantly AM fungi efficiency on their host plants. Optimum combinations of AM fungi and crop plants should be well evaluated according to soil properties and inoculation methods (Baum et al. 2015). The AM fungi can have a potential to enhance sustainability and profitability of salt tolerance of plants (Ashok Aggarwal et al. 2012). Hashem et al. (2018) indicated that AM fungi inoculation could ameliorate the deleterious effects of salt stress by enhancing biomass and pigment, phenols, proline contents, jasmonic acid, salicylic acid contents and antioxidant enzyme activities (Ashok Aggarwal et al. 2012).

Some families such as Apiaceae, Amaryllidaceae, Cucurbitaceae, Asteraceae, Solanaceae, and Fabaceae have high mycorrhizal dependency. The AM fungi can induce growth promotion and product quality of these host plants (Baum et al. 2015). The AM fungi affect secondary metabolites and enhance the nutraceutical compounds in the host plants. In order to supply the global food demand, high sustainable horticultural products should be well developed. In this response, the AM fungi is a promising environment friendly strategy (Garg and Bharti 2018). In addition to the applications of biofertilizers and biopesticides, AM fungi inoculation is a promising strategy for future applications (Baum et al. 2015). Amanifar et al. (2019) mentioned that AM fungi induced genes expression which have important role in triterpene saponin glycyrrhizin biosynthesis and pharmaceutical contents quality under salt stress and also enhanced growth, P and K uptake, higher K^+/Na^+ ratio, proline content, and membrane integrity. Therefore, AM fungi can eliminate the deleterious effects of salt stress, and it can be used as a practical application for exploiting the salinity in soils.

23.9.2 Crop Tolerance to Salinity and Drought and Relation with Mycorrhizal Dependency

Drought and salt stress are usually developed at the same time and in the same area. It is well known that plants use some root-rhizosphere mechanisms against drought and salt stress. For instance, mycorrhizal fungi cooperation with the plant roots to reduce the severity of salt and drought stresses. Especially plant genotypes which depend on mycorrhizae have more tolerance than other genotypes. Under pot culture, soil culture 94 bread wheat genotypes tolerance to water stress was tested and it has been shown that drought stress tolerance of wheat was significantly increased in the presence of mycorrhizae compared to drought stress tolerance in the absence of mycorrhizae (Lehnert et al. 2018). Zrnic and Siric (2017) reported that mycorrhiza inoculated plants are more tolerant to nutrients and water stress, soil salinity, and heavy metals concentrations. It has been indicated that plant drought tolerance is under the genes control. Fan and Liu (2011) reported that mRNA abundance of four genes involved in reactive oxygen species homeostasis and oxidative stress battling was higher in the AM plants when compared with the non-AM plants. They indicated that possible drought-induced genes may enhance the tolerance of AM plants to water deficit (Fan and Liu 2011).

23.9.2.1 Selective Interactions Between Different Species of Mycorrhizal Fungi and Plant for Salt and Drought Tolerance

Salinity stress also causes water deficiency of plant tissue, and under low water potential reduces growth by inhibiting cell division and cell expansion (Hasegawa et al. 2000a). Under salinity stress plants can develop several mechanisms such as (1) increasing the plant membrane thickness and enhancing the cell wall thickness (Miransari 2016). (2) increasing the number of vesicles in plant cells. (3) mycorrhizal infected unit can increase against salt damage to reduce the deleterious effects. (4) Plant roots and mycorrhizae increase water efficiency and uptake. Miransari (2016) indicates that especially under stress, the right combination of AM fungi and the host plant may result in the highest level of efficiency. The AM fungi can alleviate salt stress in mycorrhizal inoculated plant species through several mechanisms. Evelin et al. (2009) indicated the mechanisms of AM fungi which can employ to enhance the salt tolerance of host plants such as enhanced nutrient acquisition (P, N, Mg, and Ca), maintenance of the K^+:Na^+ ratio, biochemical changes (accumulation of proline, betaines, polyamines, carbohydrates, and antioxidants), physiological changes (photosynthetic efficiency, relative permeability, water status, ABA accumulation, nodulation, and nitrogen fixation), molecular changes (the expression of genes: PIP, Na^+/H^+ antiporters, Lsnced, Lslea, and LsP5CS) and ultrastructural changes. Mycorrhizal infection seems that significantly control many plant physiological and biochemical mechanisms. Under water stress conditions Wu and Xia (2006) shown that *Citrus tangerine* leaves and root parts have higher K^+ and Ca^{2+} than non-inoculated plants. Ortuno et al. (2018) reported that when the substrate (silt and compost) was well-watered mycorrhizal inoculation reduced the Na and increased phosphorus uptake of *Cistus albidus* plants.

It seems that mycorrhiza species have different effects on reducing salt effects on plant growth. Estrada et al. (2013) treated three native AM fungi inoculation on maize plant and the results showed a significant increase of K^+ and reduced Na^+ accumulation as compared to non-mycorrhizal plants, concomitantly with higher K^+/Na^+ ratios in their tissues. The work of Estrada et al. (2013) has shown that when native AM fungi isolates are used mycorrhizal benefits could be enhanced. One pot experiment was conducted under drought stress conditions by Liu et al. (2018c) and their results indicated that mycorrhizal inoculation stimulated greater root hair growth of trifoliate orange that is independent on AM fungi species related with mycorrhiza-modulated auxin synthesis and transport, which benefits the host plant to enhance drought tolerance.

The study of (2006) suggests that *R. versiforme* mycorrhizal inoculation helps in increments of enzymatic and non-enzymatic antioxidant productions which in turn help plants to enhance drought tolerance. The AM fungi inoculated plants activities of SOD, guaiacol peroxidase (G-POD) and glutathione reductase (GR), catalase (CAT) and ascorbate peroxidase (APX) were significantly higher than in non-AM roots and those higher enzymatic and non-enzymatic antioxidant productions would partly alleviate oxidative damage (Wu et al. 2006). In another work, Lehnert et al. (2018) have shown that genotypes differed in their response to mycorrhizae under drought stress conditions. In many work AM fungi and PGPB dual inoculation have a significant role in stimulation of plants growth, induce tolerance to drought, and salinity (Tobar et al. 1994b). The PGPB (*Pseudomonas aurantiaca*, *P. extremorientalis*) and *R. irregularis* inoculated wheat seed germination is better, seedling growth and root elongation is better, salinity tolerance is high (Egamberdieva and Kucharova 2009). Ruiz-Lozano et al. (2018) reported that a symbiotic association with AM fungi resulted in salinity tolerance, CO_2 utilization, and enhanced growth in rice. Elhindi et al. (2017) have also documented the role of AM fungi in reducing salt stress in sweet basil.

The AM fungi inoculation help pistachio growth in several ways such as growth, success of grifting and water and nutrient uptake (Abbaspour et al. 2012). Also Abbaspour et al. (2012)'results have shown that AM formation enhanced the drought tolerance of pistachio plants. On the other hand, the results of Bagheri et al. (2011) have shown that the adverse effects of water stress were significantly reduced by AM inoculation. Ferguson et al. (1998) indicated that mycorrhizal growth promotion is generally observed in more stressful conditions. The results of Shamshiri and Fattahi (2016) showed the depressing effect of salt stress on mycorrhization extent and showed that the effect of salinity on colonization rate is completely under the influence of host plant of pistachio (*Pistacia vera*) rootstocks.

Mycorrhiza species especially indigenous species have significant effects on salt tolerance. The results of Paymaneh et al. (2019) shown that one of the indigenous AMF communities from low-salinity soils conferred a significant tolerance of pistachio to salinity in terms of maintaining its phosphorus acquisition upon the stress.

23.9.3 Effects of AMF-Colonization on Survival Rate of Horticultural Plants After Transplantation to the Field Conditions

According to Rouphael et al. (2015) the AM fungi interfere with the phytohormone balance of host plants, thereby influencing plant development (bioregulators) and inducing tolerance to soil and environmental stresses (bioprotector) factors. In general, under salinity and water stress conditions plant photosynthesis rate decreases. Salinity also indirectly affect plant growth by affecting photosynthesis, turgor, and enzyme activities of plant (Hasegawa et al. 2000b). Mycorrhizal inoculation is expected to stimulate the photosynthesis. Irrigation with saline water and mycorrhizal inoculation in cucumber plants increased fresh and dry weight, proline, electrolyte leakage, photosynthesis, and stomatal conductance (Haghighi et al. 2017). In many works, it has been shown that mycorrhiza inoculation increases citrus, pistachio, maize, tomato, wheat, clover, lettuce plants tolerances to salinity stress (Al-Karaki et al. 1998; Al-Khaliel 2010; Paymaneh et al. 2019; Feng et al. 2002; Satir et al. 2016). Mycorrhizal inoculated trifoliate orange seedlings displayed significantly lower polyamine oxidase activity and diamine oxidase activity in leaves and roots, irrespective of NaCl concentration (Wang et al. 2016). Also, in that work, they have reported that mycorrhizal inoculated seedlings showed significantly higher soluble protein concentration, ornithine decarboxylase, arginine decarboxylase, and superoxide dismutase activity in leaves and roots.

23.9.4 Effect of Biochar and Mycorrhizae on Alleviation of Salt and Drought

Biochar is an important multifunctional carbon material that can have effect biological, chemical, and physical properties of soil and improve the soil quality (Yu et al. 2019). Biochar is a pyrolyzed organic material as a soil amendment. The effects of biochar on soil properties mainly depend on feedstock and pyrolysis conditions, pH, nutrient contents, and ion exchange capacities of biochar (Hammer et al. 2015). The longevity of biochar in the soil presents can act as bioremediation in comparison to other organic materials such as compost and animal manure that more quickly break down. It has shown that the application of biochar has a potential improvement on the soil's physical and chemical properties and also on plant growth under abiotic stress factors such as heat, drought, and salinity. Under salt-affected and water-stressed soil conditions biochar addition usually ameliorated the soil physicochemical and biological properties and also enhanced the plant physiological performance as well as plant growth, yield, and nutrients uptake (Ali et al. 2017). Through this way plants' growth is better than non-biochar amendment control treatments (Farhangi-Abriz and Torabian 2017). Farhangi-Abriz and Torabian (2017) conducted, a pot experiment, under salt added soil conditions biochar amendment reduced osmotic substances and oxidative stress of common bean plant.

It is a potential source of nutrient especially P recycling from the agricultural wastes to enrich the soil fertility and quality. Biochar production and its soil application as an amendment achieved promising results for crop production (Dickinson et al. 2015; Ortas 2016), soil chemical and physical properties improvement and biochemical properties enhancement to facilitate soil biota (Puga et al. 2015), mitigation of climate change effects in a long-term experiment (Smith 2016) and disposal of large scale waste biomass such as sludge wastes (Jeffery et al. 2015). Also, biochar can be used for reducing the abiotic factors such as salt effects. Biochar addition widely increases soil porosity and accordingly which can enhance the potential of soil to boost plant growth (Mollinedo et al. 2016). Co-application of biochar and mycorrhizae that promote plant growth and reduce the salt and drought stress. In a pot experiment it has been demonstrated that biochar application together with AM fungal inoculation resulted in an additional yield increase in *Lactuca sativa* compared to each alone under nonsaline conditions (Hammer et al. 2015). A field experiment was conducted by Thomas et al. (2013) that their results showed that hardwood sawdust biochar addition significantly adsorbed great amounts of added salt from the soil. And they reported that biochar application alone increased biomass of *P. vulgaris*, with a ~50% increase relative to untreated control plants. And their results also indicated that biochar can ameliorate salt stress effects on plants through salt absorption. Through biochar large surface and mycorrhizal hyphae can be novel dual applications to mitigate the effects of salinization in agricultural, urban, and contaminated soils.

Drought stress can cause a decline in colonization of AM fungi; however, biochar amendment can enhance nutrient uptake, chlorophyll content, and photosynthesis efficiency and ameliorate significantly the deleterious effects of drought stress by enhancing mycelium, arbuscule, and spore numbers, therefore the colonization can increase under water deficiency (Hashem et al. 2019). Biochar treatments in the soils can increase AM fungi colonization and improve the interaction between roots and AM fungi (Yu et al. 2019). Biochar application can have beneficial effects on the nutrient especially P uptake and enhance plant growth (Shen et al. 2016). In saline soils biochar treatment may have benefits, the application can cause an increase in AM fungi growth and inhibit the negative effects of salt stress (Hammer et al. 2015). Zhang et al. (2019b) reported that combination of biochar amendment and AM fungi inoculation could have positive effects on both nutrient uptake and decrease the deleterious effects of heavy metal stress in polluted soils. The AM fungal spores were isolated from different sodic soils in Central Europe results are indicating that up to 80 % of all spores from the different sites gave one single PCR-pattern which closely matched that of *R. geosporum* (Bothe 2012).

23.10 Conclusion

All literature records show that AM colonization may alleviate and compensate the growth limitations imposed by salt and water deficiency stress conditions. It seems that AM symbiosis improve plant nutrition by allowing the cells to regulate ions more effectively. Also, inoculation can improve mineral nutrient uptake by availability or transport of mycorrhizal hyphae, thus enhancing salt tolerance. Under AM inoculation conditions higher absorption of P, Zn, Cu, K, Ca, and Mg in plants under saline conditions may improve growth rate, salt tolerance and suppress the adverse effects of the salinity stress. Under saline conditions, there may be a displacement of membrane-associated Ca by Na in roots membranes. Potassium also can have a similar displacement with excess Na. Since AM inoculated plants have high Ca and Mg, Ca may help to keep membrane integrity and protect host plants against salt damage (Läuchli and Epstein 1990). Under salinity conditions, lower Na uptake and the higher Mg absorption by mycorrhizal inoculation might be an important salt-alleviation mechanism for salt tolerance of plant species. In salinity affected soils, AM inoculation may also alleviate some of physiological mechanisms of plants. Mycorrhiza inoculated plants may exudate more carbohydrate like cytokinin to rhizosphere to enhance chloroplast development and increase the chlorophyll levels in order to increase the photosynthesis values.

PNW 601-E • November 2007. D.A. Horneck, J.W. Ellsworth, B.G. Hopkins, D.M. Sullivan, and R.G. Stevens. Managing salt-affected soils for crop production (Horneck et al. 2007)

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