The Interactions of Soil Microbes Affecting Stress Alleviation in Agroecosystems

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Abstract

Crop plants are subjected to different kinds of stresses, and as a result, their growth is adversely affected. Different mechanisms may be used by crop plants to tolerate the stress including the morphological and physiological ones. However, the efficiency of such mechanisms differs in sensitive and tolerant crop species, and the tolerant species can utilize such mechanisms more efficiently. The other important aspect of stress tolerance in crop plants is related to their interactions with the soil microbes. A wide range of soil microbes including arbuscular mycorrhizal (AM) fungi, plant growth-promoting rhizobacteria (PGPR), and endophytic bacteria as well as their interactions can affect stress tolerance in crop plants. Such a topic is among the most important research subjects and can greatly affect the efficiency of crop plants under stress. Mycorrhizal fungi are soil fungi, developing a symbiotic association with their nonspecific host plants, and increase their growth by enhancing the uptake of water and nutrients. PGPR are soil bacteria, which can enhance the growth of their host plant by different mechanisms through developing a nonsymbiotic association. The endophytic microbes are able to colonize the inner parts of their host plant and affect its growth under different conditions including stress. The interactions of soil microbes in most cases can positively affect the growth of the host plant under different conditions including stress. The important point, which deserves investigation, is the interaction of mycorrhizal fungi, PGPR, and the endophytic bacteria, which reside in plant roots affecting plant growth and yield production. Such details will be useful for the production of more tolerant microbial inoculums, which are more efficient under different conditions including stress. Some

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of the most important and recent findings related to the growth of crop plants under stress, as affected by the interactions of soil microbes, along with the future perspectives are presented, reviewed, and analyzed.

2.1 Introduction

Crop plants are subjected to different kinds of stresses, and as a result, their growth is adversely affected. Under stress, crop plants use different morphological and physiological mechanisms to alleviate the stress. However, the level of stress tolerance is different in sensitive and tolerant crop plants. Depending on the level of stress, crop response in sensitive and tolerant species is different, and accordingly they can tolerate the stress up to some level (Ramegowda and Senthil-Kumar 2015).

Crop plants interact with a wide range of microbes in the soil; however, the combination of soil microbes in the bulk soil and in the rhizosphere is different indicating that the crop plants are able to determine their combination of microbes in the microbiome (Bisseling et al. 2009; Zamioudis and Pieterse 2012). A wide range of beneficial soil microbes including mycorrhizal fungi, plant growth-promoting rhizobacteria (PGPR), and the endophytic bacteria and fungi are able to develop a symbiotic or nonsymbiotic association with their host plants and enhance the growth of their host plant. High rate of recognition and coordination between the host plant and the soil microbes are essential for the development of an intimate symbiosis association (Giovannetti et al. 2006; Berg 2009; Newton et al. 2010).

The important issue related to the growth of crop plants under stress is to provide them with their essential nutrients. Although chemical fertilizer can quickly provide crop plants with the nutrients necessary for their growth, due to the environmental and economic consequences, the single use of such method of fertilization is not recommendable. Accordingly, a suitable method of fertilization is the integrated use of chemical and biological fertilization (Miransari 2011a, b; Hoseinzade et al. 2016). According to FAO (2015), the world demand for N fertilizer has been equal to 141 682000 T, P_2O_5 at 51940000 T, and K_2O at 36367000 T, and the total value of fertilizer demand in 2015 has been equal to 223,064,000 T. The highest fertilizer use has been related to China, India, and the USA.

Interestingly, the soil microbes are able to determine the structure of plant community and plant traits. Accordingly, plant growth and yield production, nutrient uptake, and the functioning of ecosystem are affected by soil microbes (Degens 1998; Marschner and Rumberger 2004; Bell et al. 2005; Bonkowski and Roy 2005; Lau and Lennon 2011; Huang et al. 2014). This is an important approach toward the alleviation of soil stresses by soil microbes and development of tolerant plant and microbial species.

There has been a great and growing research on the use of biological fertilization including mycorrhizal fungi and PGPR integrated with chemical fertilization during the recent years, mainly for increasing the efficiency use of fertilization. In the past time, the use of microbial inoculants has been mostly for plant growth promotion and biological control. However, it has been just recently that biological fertilization has been used for the increased uptake of crop plants. More than 50% of N fertilizer is lost due to leaching and volatilization with long-time environmental consequences including the production of greenhouse gases, depletion of ozone, global warming, and acid rain (Flessa et al. 2002; Ma et al. 2007; Miransari and Mackenzie 2015).

The important role of soil microbes in the alleviation of stresses has been indicated by different research works. For example, the biochemical effects of soil microbes on the alleviation of soil stresses are by the production of (1) biofilm and exopolysaccharides affecting the properties of soil and (2) different organic products such as osmolytes, stress proteins, etc. A set of interactions between the soil, the microbes, and the plant affects the biological, the physical, and the chemical properties of soil (Flemming and Wingender 2010; Singh et al. 2011).

The production of microbial polysaccharides by the soil microbes results in the binding of soil particles and as a result improves the structure of the soil and plant tolerance under stress. The growth of the mycrorrhizal hyphae into the soil pores can stabilize the structure of the soil and increase the uptake of water and nutrients by the host plant under different conditions including stress (Sandhya et al. 2009a, b). The soil microbes can be used as models for understanding how soil stresses can affect crop growth and hence can be genetically modified for a more efficient use under stress conditions (Mantelin and Touraine 2004; Grover et al. 2011; Schenk et al. 2012; Bashan et al. 2014).

PGPR can affect crop growth and the environment by the following mechanisms: (1) the production of plant hormones, phosphorus (P)-solubilizing products, and siderophores; (2) biological N fixation; and (3) controlling pathogens. The PGPR can hence decrease the use of chemical fertilization, herbicides and pesticides, which is of environmental and economic significance (Yasmin et al. 2004; Yu et al. 2011). Such beneficial effects have resulted in the wide use of soil microbes including PGPR and arbuscular mycorrhizal fungi as important sources of fertilization, namely, biological fertilization (Adesemoye et al. 2009; Berg 2009; Miransari 2011a, b).

PGPR are also able to alleviate stress by the production of plant hormones such as cytokinin and antioxidants, which can scavenge the production of reactive oxygen species under stress. The PGPR are also able to alleviate the stress in the host plant by the induction of the stress genes and the production of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which is able to degrade the prerequisite for ethylene production and decrease the adverse effects of the stress hormone, ethylene, which its level increases under stress. The enzyme is able to increase root growth under drought stress and increases water uptake and water efficiency by the host plant (Berg 2009; Grover et al. 2011).

Although mycorrhizal fungi are able to develop an intimate symbiotic association with their host plant, at high concentration of P (greater than 100 mg/kg) such a symbiosis decreases significantly (Amijee et al. 1989; Koide 1991). Accordingly, at high fertile soils, the use of mycorrhizal fungi may not be beneficial, as the host plant is able to receive its essential P from the soil (Koide and Li 1990; Stewart et al. 2005).

The use of plant biostimulants such as soil microbes is an effective method to alleviate the adverse effect of stress on plant growth. Microbial inoculums including arbuscular mycorrhizal fungi, plant growth-promoting rhizobacteria, and N-fixing rhizobium can significantly alleviate the negative effects of stress on plant growth. The interactions between the soil microbes and between the plant and the soil microbes affect the efficiency of stress alleviation by the soil microbes (Calvo et al. 2014; Kalita et al. 2015; Mabrouk and Belhadj 2016).

Among the most studied PGPR strains is *Azospirillum* spp., which is able to develop a nonsymbiotic association with their host plant and reside on the root surface or inside the plant tissues (Hartmann and Bashan 2009; Bashan et al. 2014). The N-fixing ability of *Azospirillum* spp. has been indicated by different research works. For example, the rate of fixed N in wheat by *Azospirillum lipoferum* was in the range of 7–12%; however, in sugarcane, *Azospirillum diazotrophicus* was able to fix 60–80% of the plant total N (Saubidet et al. 2000; Calvo et al. 2014).

Different PGPR strains including *Bacillus subtilis* (Arkhipova et al. 2005), *Pseudomonas* spp. (Park et al. 2005), *Streptomyces* spp. (Glick 2015), *Micrococcus* spp. (Dastager et al. 2010), *Achromobacter* spp. (Pereg and McMillan 2015), *Flavobacterium* spp. (Glick 2015), *Azospirillum* spp. (Arzanesh et al. 2011; Miransari 2014), and *Erwinia* spp. (Hsieh et al. 2010) are able to increase the availability of P in the soil.

The PGPR are able to enhance the availability of P by the production of phosphatases and organic acids. The hydroxyl and carboxyl present in the organic acids are able to enhance the solubility of P by the following mechanisms: (1) chelating the P anions and (2) decreasing the pH of rhizosphere resulting in the release of P anion (Kpomblekou and Tabatabai 1994; Singh et al. 2011). The PGPR strains determine the types of organic acids, produced in the rhizosphere. For example, the organic acids including acetic, lactic, isobutyric, and isovaleric acids are produced by *Bacillus amyloliquefaciens* and *Bacillus licheniformis*. However, *Azospirillum* spp., *Pseudomonas* spp., and *Erwinia* spp. are able to produce gluconic acid (Martínez et al. 2011; Zhang et al. 2014).

The Gram-negative PGPR including *Enterobacter*, *Pseudomonas*, *Citrobacter*, etc. can increase P solubility by producing acid phosphatases. Using the organic source of phytate and by the production of phytase, the PGPR including *Bacillus* spp. and *Pseudomonas* spp. are able to increase the availability of P, for plant use (Martínez et al. 2011; Singh and Satyanarayana 2011).

The soil beneficial microbes are able to increase the growth of the host plant by the following mechanisms: (1) increased uptake of water and nutrients, (2) the fixation of nutrients such as nitrogen (N) by PGPR including rhizobium (symbiosis) and other microbes (nonsymbiosis), (3) production of different plant hormones, (4) controlling pathogens, (5) alleviating stress, and (6) interaction among soil microbes (Pozo and Azcon-Aguilar 2007; De Vleesschauwer and Höfte 2009; Lugtenberg and Kamilova 2009; Zamioudis and Pieterse 2012; Miransari et al. 2013).

The important point about the performance of soil microbes under stress is how the soil microbes are affected by the stress. Under stress different microbial genes are activated making the microbes tolerate the stress. However, if the soil microbes are isolated from stressed soils, they can be used more efficiently for the alleviation of stresses. Different osmoregulators are produced by PGPR under stress including K+, proline glutamate, trehalose, betaine, glycine, etc., which are able to regulate the osmotic potential of cytoplasm. The important role of trehalose, in rhizobium during the signaling with the host plant, and its effects on plant growth and yield under stress has been indicated. It has also been shown that the genetic modification of trehalose-signaling pathway in rhizobium can significantly affect the performance of legumes (Suarez et al. 2008).

The availability of potassium (K^+) as the other important nutrient is also affected by the activity of PGPR. Such PGPR are able to solubilize the K^+ in the minerals including illite, micas, and orthoclases by the production of organic acids. Accordingly, by dissolving K^+ or chelating silicon, the solubility of K+ increases (Miransari 2013; Ahmed et al. 2014). Singh et al. (2010) indicated that the strains of PGPR such as *Rhizobium* spp. and *Azotobacter chroococcum* are able to increase the availability of potassium (increased solubility) from mica for maize and wheat use. Accordingly, plant growth, K content, chlorophyll, and crude protein rate in plant increased. The authors accordingly indicated that it is possible to provide the plant with K using PGPR and mica.

Sheng and He (2006) found that the increased solubility of K by *Bacillus edaphicus* is due to the production of organic acids including oxalic, citric, α-ketogluconic, tartaric, and succinic by PGPR resulting in dissolving K and chelating silicon ions. The bacterial inoculants are able to enhance the availability and the uptake of different nutrients by the host plant, although more research work will have to be conducted to illustrate the related details.

With respect to the abovementioned details and importance of interactions among different soil microbes mainly PGPR, mycorrhizal fungi, and endophytic bacteria, in this chapter, the effects of soil microbes and their interactions on the growth of crop plants are presented, reviewed, and analyzed. Such kind of analyses can be useful for the development of methods and techniques, which can be used for the production of tolerant crop plants and efficient microbial inoculums under stress.

2.2 Crop and Stress

Stress significantly decreases plant growth by adversely affecting plant morphology and physiology. Plant by itself can tolerate the stress through the modification of its morphology and physiology. Plant roots are among the most important parts affecting plant response under stress. Several important functions, indicated in the following, are fulfilled by the roots, making the plant grow under different conditions including stress: (1) maintaining the plant in the soil, (2) absorbing water and nutrients for plant growth and yield production, (3) affecting the properties of the soil specifically the rhizosphere, (4) interacting with the other plant roots, (5) interacting with the soil microbes, and (6) production of different biochemicals.

Accordingly, if the root traits including root architecture and functioning are modified using molecular techniques, it is possible to enhance the root potentials including its interaction with the soil microbes affecting plant tolerance under stress. The following indicates how the modification of plant roots may affect root properties including its interaction with the soil microbial activities such as the process of symbiosis: (1) modifying rhizosphere pH affecting root functioning; (2) enhancing root interactions with soil microbes, which affects root functionality; (3) proliferation of roots enhancing nutrient uptake; (4) modifying the root exudates, which results in the increased uptake of nutrients (Haichar et al. 2014); and (5) the increased number and length of lateral roots improving nutrient uptake and its symbiosis with soil microbes (Meister et al. 2014).

The following mechanisms, which are the results of signaling communications between the host plant and the soil microbes, resulting in the subsequent colonization of plant roots by the microbes, indicate how the two symbionts may interact under stress: (1) the production of volatiles by bacteria affects the translocation of Na^+ and its uptake by plant; (2) the production of ACC deaminase by bacteria decreases the level of ethylene in plant; (3) the bacteria produces cytokinin, resulting in the increased production of ABA in plant; (4) bacterial production of antioxidants scavenges the production of reactive oxygen species in plant; (5) the production of exopolysaccharides by bacteria improves the properties of soil; and (6) the bacteria are able to produce IAA and some unknown growth substances, which increase root growth under different conditions including stress (Grover et al. 2011).

Production of tolerant crop plants under stress can increase crop growth and yield. Different methods have been used so far including the breeding techniques and the use of soil microbes, both of which have been indicated to be effective on the growth of crop plants under stress. The use of soil microbes has also been indicated to be useful for the growth of crop plants under stress. A wide range of soil microbes have been tested under stress; however, more research is essential on the production and use of microbial inoculums under different conditions including stress.

2.3 Arbuscular Mycorrhizal Fungi and Stress

The symbiotic mycorrhizal fungi are able to increase plant growth under different conditions including stress. In such a symbiotic association, the fungi provide the host plant with water and nutrients for carbon, which is utilized by the fungi for their growth and activities. The fungi can increase plant growth under stress by the following mechanisms: (1) the extensive hyphal network, (2) production of plant hormones, (3) interaction with the other soil microbes, (4) improving the root growth of the host plant, and (5) increased uptake of different nutrients mainly P.

Different research works have indicated the alleviating effects of mycorrhizal fungi under salt stress in different crop plants mainly due to the improved production of proline, resulting in osmoregulation. However, other processes such as the increased uptake of P and higher concentration of sugar can also improve the host plant tolerance under salinity stress (Ben Khaled et al. 2003; Daei et al. 2009; Talaat and Shawky 2014; López-Ráez 2015; Garg and Singla 2016).

Numerous research works have indicated the positive effects of mycorrhizal fungi on plant growth and yield production under different types of stresses including salinity, drought, acidity, compaction, flooding, heavy metals, cool temperature, etc. according to the following details. Among the most important potentials of mycorrhizal fungi under stress is their extensive network of hyphal, which is able to enhance plant host tolerance by significantly increasing the uptake of water and nutrients. The fungal hyphae are able to grow even in the finest soil micropores where the root hairs are not able to grow and absorb water and nutrients for the host plant use. Such ability is important for affecting plant growth under compaction stress (Miransari 2010; Garg and Chandel 2010).

The alleviating effects of mycorrhizal fungi on different stresses including salinity (Al-Karaki 2000; Colla et al. 2008; Daei et al. 2009), drought (Subramanian et al. 2006; Wu et al. 2008), acidity (Raju et al. 1988; Vosatka et al. 1999; Muthukumar et al. 2014), compaction (Miransari et al. 2008, 2009), heavy metals (Audet and Charest 2007; Miransari 2011c), flooding (Rutto et al. 2002; Carvalho et al. 2003), temperature (Bunn et al. 2009; Zhu et al. 2010), and nutrient deficiency (Miransari 2010; Smith et al. 2010) have been indicated.

For example, the improving effects of mycorrhizal fungi on the growth of plant under osmotic and drought stress have been indicated by the following mechanisms: (1) enhanced activities of antioxidants such as catalase, peroxidase, and superoxide dismutases; (2) decreased production of soluble protein and malondialdehyde; (3) the increased levels of nonstructural carbohydrate; and (4) the increased rate of K^+, $Ca2^+$, and Mg^{2+} (Wu and Xia 2006).

2.4 Plant Growth-Promoting Rhizobacteria and Stress

Research work has indicated the enhancing effects of PGPR on plant growth under stress. The mechanisms, which PGPR use under stress to alleviate the stress and increase plant growth, are (1) the modification of plant morphology and physiology; (2) the production of plant hormones; (3) the increased rate of proline; (4) the increased uptake of nutrients by the host plant; (5) the decreased production of the stress hormone, ethylene, by the production of ACC deaminase; and (6) the interactions with the other soil microbes (Kaymak 2010; Miransari 2014). The promoting effects of *Rhizobium* spp. and *Azospirillum* spp. on the growth of plant under drought and saline conditions have been indicated (Hamaoui et al. 2001, Arzanesh et al. 2011). The rhizobium and PGPR strains have been isolated from stress conditions. The adaptation of soil microbes under stress is a function of gene regulation, resulting in the survival of the microbes (Ali et al. 2009). For example, the use of *Pseudomonas* spp. strain AMK-P6 increased the thermotolerance of sorghum seedlings under heat stress by the following: (1) the production of high molecular weight protein in plant leaf, (2) increased plant biomass, and (3) enhanced production of amino acid, sugar, proline, and chlorophyll II content (Ali et al. 2009).

Under stress PGPR use different mechanisms to handle the stress. For example, in a saline environment, the bacterial cells lose their water and as a result the dehydration of the cytoplasm decreases. Microbes also utilize the following mechanisms to alleviate the adverse effects of stress on their growth and activities including:

1. The increased ionic strength, which increases the salt concentration of cytoplasm equal to the surrounding environment.
2. The increased uptake of K^+ as well as the enhanced accumulation of the compatible solutes including amino acids, sugars, polyols, and betaines by the microbial cells. Such solutes are synthesized by the bacterial cells or taken up from the environment (Street et al. 2006; Paul and Nair 2008). The authors indicated that under salt stress the PGPR *Pseudomonas fluorescens* MSP-393 was able to tolerate the stress by the production of different solutes including glycine, alanine, serine, glutamic acid, asparatic acid, and threonine. Such solutes can also stabilize the structure of proteins under stress (Street et al. 2006; Paul and Nair 2008).
3. The alteration of cellular composition under stress, which modifies the structure of proteins, saccharides, and glucans, is also another mechanism used by the microbes to alleviate stress. The production of exopolysaccharides, which are able to stabilize the water content and regulate the carbon diffusion into the surrounding environment of the cell by *Pseudomonas* under stress, increased the bacterial tolerance to survive the stress (Sandhya et al. 2009a).
4. The expression of salt-responsive genes in the microbes under salinity stress can regulate the microbial response under stress (Paul and Lade 2014; Chakraborty et al. 2015).

PGPR are also able to increase the growth of the host plant by increasing the availability of iron (Fe III) in the rhizosphere where the concentration of Fe III is little. The Fe-binding chelators (siderophores) can bind FE III under little concentration of FE and transfer it to the cell (Sayyed et al. 2005; Dimkpa et al. 2009; Marschner et al. 2011). For example, the enhancing effects of PGPR such as *Streptomyces* and *Bacillus* on the growth of different plants, due to the production of siderophores, have been indicated (Imbert et al. 1995; Fiedler et al. 2001; Temirov et al. 2003). The production of siderophores by PGPR is also of environmental significance as they can chelate different heavy metals and hence can be used for the bioremediation of contaminated sites.

2.5 PGPR and Plant Hormones

The soil microbes not only develop the suitable mechanisms for their survival under stress, they are also able to enhance the host plant tolerance under stress. For example, the production of different plant hormones by PGPR increases the growth of plant roots including root length, the number of root tips, and root surface area. Accordingly, the uptake of water and nutrients and hence plant growth increases by the host plant (Adesemoye et al. 2009; Egamberdieva and Kucharova 2009).

Production of plant hormones such as auxins, cytokinins, ethylene, and gibberellins is another important mechanism by PGPR affecting the growth of the host plant. PGPR are able to modify the production of hormones by the host plant. The growth of different plant parts including the roots (root length, root initiation, and formation of root hairs) is regulated by plant hormones. A high number of research works have indicated the production of auxin by PGPR; the hormone is able to affect plant growth by (1) affecting cellular growth and division, (2) root growth, (3) differentiation of vesicular bundles, (4) apical dominance, (5) ethylene production, and (6) expression of different plant genes (Döbbelaere et al. 1999; Spaepen et al. 2008).

The production of plant hormones by PGPR is regulated by different mechanisms. For example, the root exudates can modify the production of plant hormones by *A. brasilense*; if the production of root exudates decreases and is not at a suitable rate for bacterial growth, the production of IAA by PGPR increases resulting in the production of root hairs and lateral roots. The production of IAA by *A. brasilense* Sp245 increased leaf length and the growth of the aerial part in spring wheat, related to the control treatment (Spaepen et al. 2008).

The other important plant hormone, which is produced by PGPR, is cytokinin inducing plant cellular activities specifically cell division, as well as leaf growth and senescence. The production of cytokinin by *Bacillus subtilis* increased the rate of cytokinin production and the subsequent plant growth in lettuce. The cytokinin-producing PGPR can also increase plant growth under drought stress (Arkhipova et al. 2005).

Gibberellins can affect plant growth by affecting the cellular activities and growth (Eichmann and Schäfer 2015). The hormone can affect different stages of plant growth including the floral, the fruit, the aerial part, and the root growth as well as the seed germination. Similar to the other plant hormones, such as auxin and cytokinins, gibberellins can also act in combination and cross talk with the other plant hormones. Different species of *Azospirillum* can produce gibberellins affecting plant growth and yield production (Piccoli et al. 1997; Spaepen et al. 2009). The production of gibberellins has also been indicated in the other bacterial strains such as *Bacillus* spp., *Herbaspirillum seropedicae*, and *Acetobacter diazotrophicus*. Although the exact mechanism, which promotes plant growth by gibberellins, has not been indicated, the increased root growth, specifically the density of root hairs by the hormone, enhances the uptake of water and nutrients by plant (Gutiérrez-Mañero et al. 2001; Kang et al. 2012; Cassán et al. 2014).

The other plant hormone, ethylene, regulates different plant activities such as fruit ripening, cell growth, the germination of seeds, and the senescence of leaf and flower. The production of the hormone also increases under stress, and as a result, it is called the stress hormone (Spaepen et al. 2009) adversely affecting plant growth, specifically the root growth. The production of the hormone is regulated by ACC synthase. Research work has indicated that PGPR are able to decrease the production of the stress hormone ethylene in plant by the production of 1-aminocycloprop ane-1-carboxylate (ACC) deaminase, which is able to degrade ACC synthase into α-ketobutyrate and ammonia. Accordingly, the level of stress hormone in plant decreases, and as a result, plant growth increases. The production of ACC synthase by plant roots results in the degradation of the enzyme by soil PGPR and due to the decreased concentration of enzyme in the rhizosphere plant exudates more enzyme into the soil, and as a result, the level of enzyme deceases in plant, and hence plant biomass increases (Jalili et al. 2009; Glick 2015).

2.6 Endophytic Microbes and Stress

The endophytic microbes colonize the endosphere and the rhizosphere. Such soil microbes are able to enhance plant growth under different conditions including stress. The endophytic microbes including bacteria and fungi are able to enter plant tissues, establish a systemic nonpathogenic and intercellular association with the host plant, and complete their life cycle. A wide range of endophytic microbes are found in a single plant affecting plant growth and yield production (Naveed et al. 2014a).

The endophytic microbes are able to alleviate the adverse effects of stress on plant growth by morphological, biochemical, and physiological adaptation. The microbes are also able to affect the host plant growth by affecting the availability of different soil nutrients by the following mechanisms: (1) the reduction of the root diameter, (2) enhancing the length of root hairs, and (3) the production of different biochemicals including the phenolic products. Such compounds are also able to affect root growth under acidic conditions by the sequestration of aluminum on the root surfaces (Malinowski and Belesky 2000; Barac et al. 2004; Bauer and Mathesius 2004). The alleviating effects of endophytic fungi on plant growth are by the following activities: (1) inducing systemic resistance in the host plant, (2) activation of stress enzymes, and (3) production of different metabolites (Yuan et al. 2010).

Naveed et al. (2014a) investigated the microbial strains, which may enhance maize growth under biotic and abiotic stresses. The five endophytic strains of bacteria were isolated from the maize roots. All strains were able to increase maize growth under nonstressed and stressed conditions; however, *Enterobacter* sp. was among the most efficient strain under control and stress conditions. The bacteria were able to enhance maize morphology and physiology and were able to colonize plant roots and stems as well as the rhizosphere.

In another experiment Naveed et al. (2014b) evaluated the effects of *Burkholderia phytofirmans* and *Enterobacter* sp. on the growth, photosynthetic activity, and water content of two maize genotypes grown under drought stress. The plants were subjected to drought stress 45 days after planting during the vegetative growth stage by withholding irrigation. The bacterial inoculants were able to inoculate maize seedlings efficiently and be isolated from different plant parts under control and stress conditions. The bacteria were able to enhance plant growth under stress by improving plant morphology, physiology, and water content compared with uninoculated plants. Strain *B. phytofirmans* was the more efficient strain than *Enterobacter* sp. under the stress. The authors accordingly indicated that it is possible to alleviate drought stress on maize growth although such a potential is a function of plant genotype and bacterial strains.

Waqas et al. (2014) investigated how soybean growth and yield are affected by the combined effects of biochar and endophytic fungi producing plant hormones under heavy metal stress. The endophytic fungi were isolated from a wetland area polluted with zinc. According to the results, the combined or the single use of the endophytic fungi and biochar (15% w/w) significantly increased soybean growth under nonstressed and stressed conditions (Zn at 5253.6 mg/kg). The treatments decreased the uptake of Zn by plant tissues. The fungi were able to inoculate the plant roots in the presence of biochar under nonstressed and stressed conditions. The treatments induced plant systemic resistance by significantly increasing the production of jasmonic acid. The authors accordingly indicated that the combined use of the endophytic fungi and biochar is recommendable under the stress of heavy metal for soybean production.

The alleviating effects of *Enterobacter* sp. EJ01 isolated from sea china pink (*Dianthus japonicus* Thunb) in salty areas of South Korea were shown by Kim et al. (2014). The bacteria were used for the inoculation of tomato and *Arabidopsis* under salty conditions and were able to alleviate the stress by the production of ACC deaminase and indole-3-acetic acid (IAA). The growth parameters of plants including fresh and dry weight and plant height were increased by the bacteria under the stress conditions. The effects of the bacteria on plant growth at the molecular level were by the enhanced expression of the *Arabidopsis* genes, which are responsive under salt stress including RAB18, DREB2b, RD29A, and RD29B.

The bacteria were also able to upregulate the expression of genes, which results in the production of proline such as P5CS1 and P5CS2 and in priming such as MPK3 and MPK6 under stress. The bacteria also increased the scavenging process of reactive oxygen species in tomato plants subjected to the stress conditions. In conclusion, the authors indicated that the newly isolated bacteria are able to alleviate the stress of salinity on tomato and *Arabidopsis* growth by activating a set of different mechanisms, most importantly the related salt stress signaling pathway.

2.7 Interactions of Soil Microbes Affecting Soil Stresses

Although the single use of soil microbes has been proved to be effective on the alleviation of soil stresses, their combined use has also indicated to be a great tool for plant growth under stress. However, more research work in this respect is essential. This is because, if the possible interactions between the soil microbes are illustrated under different conditions including stress, it is possible to recognize and select the most efficient microbial consortium for inoculum production. However, it has also to be mentioned that the interactions between the soil microbes may be positive or negative, and for the production of effective inoculums under stress, the microbes with positive interactions must be selected (Miransari 2011a, b). The following examples show how the soil microbes may interact under different conditions including stress.

The coinoculation of corn plants with *Rhizobium* and *Pseudomonas* enhanced corn tolerance under salt stress by the following mechanisms: (1) decreased electrolyte leakage, (2) increased production of proline, (3) maintaining leaf water content, and (4) selective uptake of K^+ (Bano and Fatima 2009; Paul and Lade 2014). Alami et al. (2000) found that rhizobium enhanced sunflower tolerance under drought stress by improving the structure of soil due to the production of exopolysaccharide.

According to Chen et al. (2007), there is a correlation between the production of proline under drought and salinity stresses. Accordingly, the authors inserted the *pro*BA gene from *Bacillus subtilis* into *Arabidopsis thaliana*, which resulted in the increased production of proline in the plant and enhanced plant growth under stress. Proline is also able to neutralize the cellular redox potential. The coinoculation of corn (*Zea mays* L.) plants with *Rhizobium* and *Pseudomonas* enhanced the salt tolerance of the plant by (1) the increased production of proline, (2) decreased electrolyte leakage, and (3) increased uptake of K^+. Under salinity and temperature stresses, the positive effects of proline on the cell growth are by the protection of cellular membranes and the proteins resulted from the adverse effects of the stress. Proline is also able to act as a protein like molecule and scavenge the hydroxyl radical molecules produced under stress (Bano and Fatima 2009).

The coinoculation of lettuce plants with PGPR (*Pseudomonas* spp.) and mycorrhizal fungi (*Glomus* sp.) increased the production of catalase under severe drought stress indicating that the combined use of such soil microbes can be used for the alleviation of drought stress. However, interestingly the alleviating effects of mycorrhizal fungi under salinity stress have been more evident and constant than under drought stress (Kohler et al. 2008).

Research work has indicated that a wide range of PGPR strains in combination with mycorrhizal fungi are able to increase plant growth and yield production significantly. The related PGPR are *Azospirillum* spp., *Pseudomonas* spp., *Acinetobacter* spp., and *Bacillus* spp., which in combination with AM fungi increased the uptake of different nutrients including Ca, Mg, S, Mn, Fe, Zn, and Cu in different crop plants (Liu et al. 2000; Khan 2005; Kohler et al. 2008).

Kohler et al. (2010) investigated the single and the combined use of *Glomus mosseae* and *Pseudomonas mendocina* on the structural properties of lettuce (*Lactuca sativa* L.) soil under salt stress. The PGPR significantly increased the plant growth compared with the control treatment under control and saline conditions; however, mycorrhizal fungi just increased plant growth under the moderate level of salinity. With increasing the level of salinity, even in the presence of microbial inoculation, the aggregate stability of soil decreased, compared with the control treatment. The high level of salinity decreased the concentration of glomalin-related soil protein, although the highest level was related to the inoculated soil.

The authors accordingly indicated that the use of mycorrhizal fungi and PGPR may be restricted under salinity stress due to the adverse effects of salinity on the structure of the soil, which is due to the increased concentration of sodium and the less concentration of glomalin-related soil protein, compared with control conditions. Under adverse conditions such as drought, the production of exopolysaccharides by the soil bacteria enhances the aggregate stability of soil, and as a result, the water retention of soil increases (Kohler et al. 2010).

Franzini et al. (2010) investigated the tripartite symbiosis of mycorrhizal fungi and rhizobium in four different genotypes of bean (*Phaseolus vulgaris*) under moderate drought stress. Surprisingly, most of the microbial treatments including one species of fungi and one strain of rhizobium adversely affected the growth of bean plants under moderate drought conditions. However, such a deleterious effect was a function of plant genotype and microbial species. Mycorrhizal fungi decreased plant growth by inhibiting nodule development and N_2-fixation. At the moderate level of drought stress, the combined use of AM fungi and rhizobium negatively affected bean growth, indicating the importance of selecting the right combination of bean genotype and microbial species.

The interactions between soil microbes have been reviewed by different researchers. For example, Gopal et al. (2012) reviewed the interactions between mycorrhizal fungi and soil bacteria and the interactions between mycorrhizal fungi and spore-associated bacteria. The authors accordingly indicated that a more clear understating on the interaction among mycorrhizal fungi, spore-associated bacteria, and PGPR can enhance the quality of inoculums. Franzini et al. (2013) suggested that although the interactions between mycorrhizal fungi and PGPR are usually positive enhancing the legume growth and yield, under drought stress such kind of interactions may negatively affect legume growth and yield. Accordingly, in their experiment they evaluated the combined effects of six rhizobium strains and two mycorrhizal species on the growth of *Phaseolus vulgaris* and *Zea mays* under moderate drought conditions. Their results indicated that the combined combinations of rhizobium and mycorrhizal fungi in some cases decreased the growth of bean and corn under moderate drought conditions.

Abdel-Rahman et al. (2011) investigated the effects of single or combined inoculation with mycorrhizal fungi and *Bacillus subtilis* on the growth, oil (yield and percentage), and nutrient uptake of three different genotypes of sweet basil under the salinity levels of 0, 1000, 2000, and 4000 mg/l. The results indicated that high salinity level (4000 mg/l) significantly decreased plant growth, oil, and the nutrient uptake of N, P, and K of all the genotypes. The salinity treatment also highly increased the concentration of sodium in the plants. The effects of mycorrhizal fungi on the growth of plant under salinity stress were more than the bacteria and the combined inoculation intensified such a positive response. The response of genotypes was different under the stress. The authors accordingly indicated that it is possible to enhance the response of sweet basil to salinity stress using the single or combined use of mycorrhizal fungi and *Bacillus subtilis*.

Saia et al. (2015) investigated the single and the combined effects of mycorrhizal fungi and PGPR on the metabolic activities of durum wheat roots under N-limited and P-high conditions. The soil natural conditions were used as the control treatment. Inoculation with AM fungi highly colonized crop roots and reduced the concentrations of metabolic compounds including amino acids and saturated fatty acids in the roots. However, the combined inoculation with the fungi and PGPR increased the concentration of such compounds compared with the single inoculation with AM fungi. The authors attributed such a difference to the mineralizing role of PGPR on the organic matter and hence the release of N by PGPR for the use of the host plant compared with the single inoculation with mycorrhizal fungi.

The above details indicate how the soil microbes including mycorrhizal fungi and PGPR may interact under stress affecting plant growth and yield production. However, the other important point, which must be researched in great details, is how such microbes may interact with endophytic bacteria residing in plant roots. If such a case is indicated, it will be possible to use the combined use of soil microbes, including the endophytic microbes for inoculum production. Accordingly, the production of inoculums will be more beneficial under different conditions including stress.

2.8 Conclusion and Future Perspectives

Some important details related to the effects of soil microbes on plant growth and yield production have been indicated. The role of the most important soil microbes including mycorrhizal fungi, PGPR, and endophytic microbes on the growth of crop plants under stress has been presented. Accordingly, research work has indicated that the single use of soil microbes can positively affect plant growth. Some details are also available on the combined use of soil microbes, specifically mycorrhizal fungi, PGPR, and rhizobium affecting the growth of crop plants. However, the other important point, which must be researched in greater details, is the interactions of soil microbes with the endophytic bacteria residing in plant roots. If such details are illustrated, it will be possible to produce microbial inoculums, which are more effective on plant growth and yield production under different conditions including stress.

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