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Plant, Soil and Microbes

Volume 1: Implications in Crop Science

 Springer

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Khalid Rehman Hakeem
Mohd Sayeed Akhtar • Siti Nor Akmar Abdullah
Editors

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Foreword

The flowering plants were said to have originated approximately 125 million years ago. All through the past centuries, the number of species and diversity increased steadily. Currently they outnumber other plant groups, because more than 250,000 species of flowering plants have been described. Every year a large number of new species are added, because we are passing through an “age of angiosperms.” Their influence on the evolution of animals has been profound, and domestication is now accepted as the main factor responsible for the rise of human civilizations nearly 10,000 years ago. They are regarded as indispensable for the survival of living beings in general. All humans on our planet earth depend on crop species like wheat, rice, maize, and a few others for their survival. They also provide us with vegetables, fruits, oils, fibers, spices, drugs, and fodder, in addition to other uses, and are therefore of great importance. Their importance to humans is responsible for the great past and present interest in studying the plant world.

Keeping in view that global population has crossed the level of 6.5 billion, a major part of it being underfed or undernourished, it is of prime importance to improve the crop plants using eco-friendly and sustainable approaches. The demographic developments make it clear that improving human nutrition throughout the world must involve efficient crop production. Efforts to improve crop productivity mainly rely on the soils.

The soils are influenced by parent materials, organic matter content, pH, texture, age, drainage, vegetation, and microbial, anthropogenic, and natural processes involving the amounts of nutrients. The latter are relatively high in soils on a global basis, but their deficiencies are frequently reported in several crops all over the world due to increase in nutrient demands from intensive cropping practices and adaptation of high-yielding cultivars with high nutrient demands; production of crops on marginal soils low in nutrients; the use of high amounts of fertilizers with low nutrients; decrease in the use of animal dung, composts, and crop residues; and finally involvement of natural and anthropogenic factors limiting adequate plant availability and breaking nutrient balance. Nearly four billion ha of the earth’s ice-free land is subject to mineral stresses for plants. The increased crop yields, loss of nutrients through different ways, liming and misuse of manures, and the use of

chemical fertilizers with high purity are leading to an accelerated loss of available soil nutrients. The uptake of nutrients is a process controlled by soil, plant, microbial, and environmental factors. Plant factors such as root and root hair morphology (length, density, surface area), root-induced changes, root exudation of organic acids, sugars, nonproteinogenic amino acids, secretion of enzymes, plant demand, plant species/cultivars, and microbial associations also have an impact on plant growth and development on the soil.

In addition to the facts cited above, the microbial populations in the soil improve growth by enhancing atmospheric nitrogen fixation, producing phytohormones, enhancing root surface areas to facilitate uptake of nutrients, as well as mobilizing and solubilizing unavailable organic and inorganic nutrients. Many microorganisms produce siderophores which strongly and specifically bind nutritional elements. The microorganisms in the rhizosphere are associated with differences among cultivars in their effectiveness to grow with low mineral levels. A mycorrhizal colonization of roots increases root surface areas to enhance root exploration of large soil volumes compared to uninfected roots and increase nutrient uptake and tolerance in plants, toxics, and drought. Mycorrhizal associations particularly increase acquisition of some nutrients in the plants grown under deficiency conditions and decrease uptake of others which are in excessive amounts. They also undertake the biological control of root pathogens and in nutrient cycling. Microbial interactions may also influence nutrient mobility. Several microbes involved in redox reactions in soil have been identified. Noninfecting rhizosphere microorganisms do enhance plant nutrition by improving growth and morphology of roots, physiology and development of plants, and nutrient uptake processes by roots.

Plant, Soil and Microbes: Implications in Crop Science, with 17 contributions from Australia, Brazil, Egypt, France, India, Italy, Malaysia, Pakistan, Portugal, Bangladesh, and Saudi Arabia, contains an inclusive information and latest research results in understanding the interactions and implications between plant, soil, and microbes. This information could be useful for researchers, educators, graduate students, and industry persons for understanding and developing crop improvement strategies. In this edited volume an attempt has been made to highlight the current status of crop productivity. Emphasis has been laid on different topics related to the key principles influencing crop improvement together with an elucidation of the nature of new approaches in improvement. I am sure that a new generation of researchers will be benefitted much from this book and share the respect for the crop plants we all live by and concern for the maintenance of diversity.

Izmer, Turkey

Münir Öztürk

Preface

Soil provides an excellent and diverse ecological niche for the rhizospheric microorganisms and seems to be a hotspot for most of the microbial interactions taking place below ground level. Among the various rhizospheric microorganisms, mycorrhizal fungi, plant growth-promoting bacteria and root nodule bacteria are of prime importance, because they have the unique ability to interrelate with the soil and host plant and are also responsible for the assorted underground interactions. These microorganisms also play a vital role in nutrient uptake, water relation, ecosystem establishment, and plant diversity and also had an adverse effect on the pathogen in a diverse range of pathosystems. Besides these functions, microorganisms also influence the water use efficiency and biological function during plant–soil interactions, directly or indirectly by altering the microbial balance in the rhizosphere and suppressing the broad spectrum of plant pathogens.

Considering the importance of these ground rhizospheric microorganisms in the plant disease protection, it came into highlight from research that the combined application of these microorganisms is more beneficial than the use of a single agent and provides a better management against the soilborne plant pathogens. The interaction of these microorganisms also provides an overview about the biological functions of soil and its interaction with the plant–microbe system, nutrient management, biogeochemical cycling, various water environmental conditions in response to biotic and abiotic stresses, signaling of molecules during host–pathogen interaction, role of phytohormones against the environmental stresses, and the major challenges in the formulation of microorganisms for the biocontrol products. The molecular approach of these microorganisms is also the basis for understanding the mechanism involved in disease suppression by these hidden underground beneficial microbes.

This volume with 17 Chapters describes the basis of nutrient exchange between the microorganisms and the host plants, mechanism of disease protection, and recent molecular techniques involved in understanding these multi-tropic interactions. We hope that the book will be helpful to graduate students, teachers, researchers, and industry persons, who are interested in soil microbiology, plant pathology, ecology, environmental sciences, and agronomy.

We are highly grateful to all our contributors for readily accepting our invitation for not only sharing their knowledge and research but for venerably integrating their expertise in dispersed information from diverse fields in composing the chapters and enduring editorial suggestions to finally produce this venture. We greatly appreciate their commitment. We are also thankful to Prof. Munir Ozturk for his suggestions and writing the foreword for this volume.

We thank the Springer International team for their generous cooperation at every stage of the book production.

Selangor, Malaysia

Khalid Rehman Hakeem
Mohd Sayeed Akhtar
Siti Nor Akmar Abdullah

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About the Book

The interactions between the plant, soil, and microbes are very complex in nature and may be antagonistic, mutualistic, or synergistic, depending upon the types of microorganisms and their association with the plant and soil. The multitrophic tactics are involved in these types of interactions to nourish the plants in various habitats and conditions. Understanding the mechanisms of these interactions is highly desired to utilize the knowledge in such an eco-friendly and sustainable way, which may not only resolve the upcoming food security issues but also make the environment green by reducing the chemical inputs. *Plant, Soil and Microbes: Implications in Crop Science* provides an inclusive information on the applied, efficient, and determined efficacy of plant, soil, and microbes. The book reviews the implications of plant, soil, and microbes for the improvement in crop yield and protection against various diseases caused by phytopathogens and nutrient deficiencies.

About the Editors

Khalid Rehman Hakeem is working as a fellow researcher at the Faculty of Forestry, Universiti Putra Malaysia (UPM), Serdang, Selangor, Malaysia, and also a visiting professor at Fatih University, Istanbul, Turkey. He obtained his M.Sc. (Environmental Botany) as well as Ph.D. (Botany) from Jamia Hamdard, New Delhi, India, in 2006 and 2011, respectively. He completed his postdoctorate in the fields of forest dynamics and biotechnological studies from Universiti Putra Malaysia from 2012 to 2013. Dr. Hakeem has more than 9 years of teaching and research experience in plant ecophysiology, biotechnology and molecular biology, plant–microbe–soil interactions, as well as in environmental sciences. Recipient of several fellowships at both national and international levels, Dr. Hakeem has so far edited and authored more than sixteen books with international publishers. He has also to his credit more than 70 research publications in peer-reviewed international journals, including 25 book chapters with International publishers. He is also the editorial board member and reviewer of several high-impact international journals. Dr. Hakeem is currently engaged in studying the plant processes at ecophysiological as well as proteomic levels.

Mohd Sayeed Akhtar is working as a fellow researcher in the Institute of Tropical Agriculture, Universiti Putra Malaysia (UPM), Serdang, Selangor, Malaysia. He received his Ph.D. degree from Aligarh Muslim University (AMU), India, in 2008. He conducted his postdoctoral research at the Botanical Institute, University of Basel (BIB), Switzerland (2008–2010), and Chonbuk National University (CBNU), Republic of Korea, in 2011, respectively, and also worked as assistant professor at the Department of Biology, College of Natural Sciences, Jimma University, Jimma, Ethiopia, from 2011 to 2014. Dr. Akhtar has more than 12 years of research and teaching experience in soil microbiology, applied microbiology, environmental microbiology, molecular biology, plant pathology, and plant nanobiotechnology. Dr. Akhtar has received several prestigious fellowships at national and international levels. His promising approach and dedication stand him in the row of foremost scientist in the field of plant–microbe interaction and plant nanobiotechnology. He is an author and coauthor of about 45 research articles in peer-reviewed journals,

contributed 12 book chapters in the books published by Springer-Verlag, and also edited three books with international publishers. He is serving the scientific community as editorial board member and reviewer of several high-impact international journals. His current research is focused on the rhizospheric plant–microbe interactions and their molecular biotechnology, bioremediation, biomineralization, nanofertilizers, and nanobiotechnology.

Siti Nor Akmar Abdullah is currently the head of the Laboratory of Plantation Crops at the Institute of Tropical Agriculture and a professor in plant molecular biology at the Faculty of Agriculture, Universiti Putra Malaysia (UPM). Her Ph.D. research was mainly conducted at the John Innes Centre in UK. Her current research focuses on the transcriptional regulation of oil and vitamin E biosynthesis, fruit ripening process, host plant–pathogen interaction, and nutrient uptake mechanism in oil palm. She has led several research projects at the national level and secured research grants from oil palm industry members. She has published more than 50 papers in citation-indexed journals and also five patents granted in Malaysia and the USA particularly on oil palm tissue-specific promoters. Twenty Ph.D. students from Malaysia and other countries have graduated under her as the main or co-supervisor. She has delivered several talks as an invited speaker in various countries like China, India, and Indonesia and also served as a reviewer for many international peer-reviewed journals. She has led national and international conferences and workshops on plant biotechnology jointly organized by UPM and Wageningen University and the University of Nottingham. She has established the *Arabidopsis thaliana* laboratory in MPOB, Malaysia, and transgenic greenhouse (certified as Biosafety Level 2) in UPM.

Plant Growth-Promoting Microorganisms: Interaction with Plants and Soil

Vankayalapati Vijaya Kumar

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Abstract Soil acts as a medium for a wide variety of microorganisms such as bacteria, fungi, actinomycetes, algae, and protozoa. Soil also gives the necessary support for anchorage to plant roots. The complex interactions between soil, plants, and microorganisms lead to different associations in the rhizosphere. These interactions are useful in (a) more nutrient recycling by nitrogen fixation, phosphate and potash solubilization; (b) disease suppression in crop plants; and (c) bioremediation in contaminated soils. Plant roots secrete different inorganic and organic compounds which encourage the growth of microorganisms; in turn the chemicals secreted by

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microorganisms release the bound minerals from the organic materials in the soil, which are absorbed by plant roots. This chapter reviews bacteria, fungi and their associations and interactions with plants and soil for beneficial effects on crop plants such as mineral nutrition, disease suppression, bioremediation, etc.

Keywords Bacteria • Bioremediation • Fungi • Nutrient recycling • Disease suppression

1 Introduction

Microorganisms in the rhizosphere soil play a key role in maintaining the soil fertility (Yadav et al. 2015), which is key for successful crop production to meet the increasing global food demand. Soil is a mixture of minerals, organic matter, gases, liquids, and many other organisms that are supporting the plant life. Soil acts as a reservoir of air, water, and nutrients that is essential for plant growth. Only a few grams of soil contain hundred millions to billion microorganisms. Bacteria are the most abundant microbes in soil followed by fungi; however, the actinomycetes are ranges in between bacteria and fungi. The fungi and actinomycetes degrade various plants and animal residues that reach soil, such as complex carbohydrates, simple sugars, starch, cellulose, hemicelluloses, pectins, lignins, proteins, fats, oils, waxes, resins, and other products. Bacteria finish the degradation by eating the digestible materials. Other microbes that are found in smaller numbers are algae, cyanobacteria, protozoa, and nematodes. Soil gives the necessary support for anchorage to plant roots (Yadav et al. 2012; Bhaduri et al. 2015). The metabolism of microorganisms and root growth in the soil add to texture and fertility. The association of microorganisms with plants leads to different associations such as mutualism (both plants and microorganisms are benefited), commensalism (one partner is benefited and others remain unaffected), and parasitism (one partner benefited and the other harmed).

The microorganisms present in the rhizosphere that colonize plant roots are termed as plant growth-promoting microorganisms. The roots provide anchorage to plant, increase the uptake of water and mineral nutrients, and secrete a variety of compounds as root exudates. The secretion of the chemical compounds alters the physical and chemical properties of soil, and also regulates the microbial community in the vicinity of the rhizosphere (Yadav et al. 2012). This may help in attracting active microorganisms to metabolize the secreted compounds in the rhizosphere. Some of the root exudates attract microorganisms, while others act as repellents against a wide range of microorganisms. This chapter highlights the plant growth-promoting microorganism types, their associations and interactions with plants and soil.

2 Plant Growth-Promoting Microorganisms (PGPM)

Plant growth-promoting microorganisms are defined by three intrinsic characteristics: (1) they must be able to colonize the root/rhizosphere, (2) they must survive and multiply in micro-habitats associated with the root surface, in competition with other microbiota, at least for the time needed to express their plant promotion/protection activities, and (3) they must promote plant growth. The PGPM are either bacteria or fungi that are living in the soil. The bacteria are either free living or possess a symbiotic association with plant roots. Plant growth-promoting bacteria enhance the growth of plants by their microbial processes such as nitrogen fixation, phosphate solubilization, potash mobilization, zinc solubilization, micronutrient mobilization, and also phytohormone secretion (auxin, cytokinin, gibberellins like substances), desirable for the growth and development of crop plants (Akhtar and Siddiqui 2010; Akhtar et al. 2010). Similarly, arbuscular mycorrhizal fungi (AMF) increase P nutrition, micronutrient mobilization (Akhtar and Siddiqui 2008; Akhtar and Panwar 2011). The AM fungal hyphae extend into the soil beyond roots and transport nutrients to the plant and increase the surface area of roots (Akhtar et al. 2011). This may help mycorrhizal plants to withstand several abiotic and biotic stresses. However, the secretion of glomalin by AM fungi increases soil quality and porosity, which may assist plant roots in aeration.

2.1 Plant Growth-Promoting Rhizobacteria (PGPR)

The term PGPR was first coined by Kloepper and Schroth (1978) to describe the beneficial rhizospheric bacterial populations that may colonize plant roots and exhibit growth promotion attributes. In general, the PGPR are free-living bacteria, colonize roots, and promote plant growth directly by nitrogen fixation, phosphate solubilization, production of phytohormones and siderophores or indirectly by their biocontrol properties such as antibiotic production, production of lytic enzymes, competition with phytopathogens for nutrients and colonizing sites, and induced systemic resistance (Akhtar et al. 2011).

The application of a mixture of PGPRs (*Azospirillum lipoferum*, *Azotobacter chroococcum*, *Pseudomonas fluorescens*, and *Bacillus megaterium*) has increased germination rate, shoot and root length and dry weight, chlorophyll and nutrient (NPK) content compared to control or individual application in *Catharanthus roseus* (Lenin and Jayanthi 2012). Similarly, improvement in growth parameters (fresh and dry weight, stem diameter, seedling height, chlorophyll content, and leaf area) was reported in cabbage seedlings by the application of PGPR strains (*B. megaterium*, *B. subtilis* and *Pantoea agglomerans*) compared to control (Turan et al. 2014). Sen and Chandrasekhar (2014) reported the significant increase in plant height, and dry weight by the inoculation of *P. fluorescens* in rice seedlings under salt stress conditions. Furthermore, the application of different PGPR (*Bacillus*,

Pseudomonas, and *Serratia*) species has improved germination percentage, seedling height, root length, chlorophyll content, dry weight of maize seedlings (Almaghrabi et al. 2014). Moreover, Elekhtyar (2015) reported that *P. fluorescens* has increased plant growth attributes (seedling germination, seed vigor index, shoot and root ratio, fresh and dry weight, leaf area), chlorophyll concentration in leaves, and nutrient uptake in rice.

PGPR are also advantageous in bioremediation of contaminated sites with pollutants like hydrocarbons, chloralkali, effluents from the distillery and textiles, heavy metals, etc. Among the rhizosphere bacteria *Azospirillum*, *Azotobacter*, and *Rhizobium* are the major N₂-fixing bacteria, while the *Bacillus* spp. (*B. megaterium* and *B. subtilis*) and *Pseudomonas* spp. are P solubilizers and are used as both bio-fertilizers and PGPR. Moreover, some other bacteria (*Burkholderia*, *Enterobacter*, *Erwinia*, and *Mycobacterium*) could also be recognized as PGPR. The continuous application of NPK nutrients for crop plants leads to changes in soil pH, soil fertility, and soil microbial communities, leading to decreased yields. The PGPR enhances the growth directly by increasing the nutrient acquisition by nitrogen fixation, phosphate solubilization, potassium mobilization, and zinc solubilization. *Bacillus* isolated from different agroclimatic zones has shown good phosphate-solubilizing ability, and are positive for gelatin liquefaction, catalase test, indole production test (Patil et al. 2013). Akram et al. (2013) reported that *B. subtilis* and *B. fortis* effectively controlled *Fusarium* wilt in a split root experiment on tomato under greenhouse condition and increased the level of phenolics (55.45–67.15 %), peroxidase (56.70 %), polyphenol oxidase (41.56 %), and phenyl ammonia lyase (57.57 %). Apart from this, they also secrete vitamins, amino acids, hormones (IAA and gibberellic acid), and are now widely used in the biocontrol of a wide range of phytopathogenic fungi. Similarly, *Pseudomonas* is a good P solubilizer, and also produced significant levels of plant IAA and showed increased HCN production, siderophore production compared to control (Deshwal and Kumar 2013). The high level of chitinase activity is responsible for the degradation of the fungal cell walls of pathogenic fungi such as *Colletotrichum gloeosporioides* (58.3 %), *Alternaria brassicola* (50 %), *A. brassicae* (12.5 %), *A. alternata* (16.66 %), *Fusarium oxysporum* (14.28 %), *Rhizoctonia solani* (50 %), and *Phytophthora* (15 %) (Ramyasmruthi et al. 2012). *Burkholderia* sp. isolated from the rhizosphere of *Rhododendron arboreum* has shown good P solubilization, and IAA and siderophore production. *Burkholderia* sp. isolated from the rhizosphere of *Rhododendron arboretum* has shown good P solubilization, IAA and siderophore production. The germination percentage of treated seed was high (54.18 %) compared to control (38.12 %) (Nailwal et al. 2014).

2.1.1 Nitrogen Fixation

Azospirillum is an associative symbiotic nitrogen-fixing bacterium found in many grasses and cereals. It lives either on the root surface or inside roots. It fixes the atmospheric nitrogen by the enzyme nitrogenase in nonleguminous crops. It could

also be used as a biofertilizer because of its ability to produce plant growth-promoting substances. Inoculation of different isolates of *Azospirillum* in tomato has increased the yield from 34.9–92.4 % compared to control. Apart from yield improvement in growth parameters such as plant height, root length, and fresh weight, number of fruits/plant, fruit diameter, fruit weight, yield per plant were also recorded. Tripathi et al. (2013) reported that the leaf nitrogen content was significantly improved in *Azospirillum*-treated plots. The study conducted by Faruq et al. (2015) on maize with *Azospirillum* in the presence and absence of nitrogen has improved all test parameters such as shoot length, root length, root number, and biomass compared to control. The *Azospirillum*-treated seedlings have shown higher numbers of lateral and tertiary roots in the presence and absence of nitrogen compared to control. However, inoculation of *Azospirillum* has increased leaf area, shoot dry matter, and yield compared to control plots in maize (Marini et al. 2015).

Similarly, *Azotobacter* is an aerobic, free-living, heterotrophic nitrogen fixing soil bacterium. It fixes atmospheric nitrogen through the enzyme nitrogenase in nonleguminous crops. It secretes hormones such as IAA, gibberellins and vitamins, and also produces antifungal metabolites. *Azotobacter* evolved a special defensive mechanism for nitrogen fixation, which may reduce the concentration of oxygen in cells. It is found beneficial in a wide range of crops covering cereals, millets, vegetables, cotton, and sugarcane (Tabar 2013). Inoculation of *Azotobacter* in *Ocimum* increased plant growth, number of leaves (Shanmugapriya et al. 2013) in the potted plant in pot experiment, and grain yield of wheat (Soleimanzadeh and Gooshchi 2013) compared control treatments. *Rhizobium* is a symbiotic bacterium associated with leguminous crops and fixes atmospheric nitrogen. Trabelsi et al. (2011) reported that inoculation of *R. gallicum* and *Ensifer meliloti* increased nodule number, shoot dry weight, and grain yield in *Phaseolus vulgaris* compared to the uninoculated controls. The inoculation of *Rhizobia* in *Vigna radiata* has increased plant length and dry weight compared to control plants under pot experiments and an increase in IAA, HCN, ammonia, siderophore, and phosphate solubilization activity has also been observed (Rajpoot and Panwar 2013). In another study, Patra et al. (2012) concluded that inoculation of different strains of *Rhizobia* increased the growth and yield of soybean under field condition.

2.1.2 Phytohormones Production

Indole acetic acid (IAA) is the most common natural auxin having a positive effect on root growth. Most of the rhizobacteria colonizing the seed coat or root surface is proposed to act in conjunction with endogenous IAA in stimulating cell proliferation and uptake of minerals and nutrients from the soil (Akhtar and Siddiqui 2009). IAA affects plant cell division, extension, and differentiation; stimulates seed and tuber germination; increases the rate of xylem and root development; controls processes of vegetative growth; initiates lateral and adventitious root formation; mediates responses to light, gravity, and florescence; affects photosynthesis, pigment formation, biosynthesis of various metabolites, and resistance to stressful

conditions. Tryptophan commonly found in root exudates is identified as the precursor for the production of IAA by the rhizobacteria.

Several PGPR (*Azotobacter* sp., *B. subtilis*, *Pantoea agglomerans*, *Paenibacillus polymyxa*, *P. fluorescens*, *Rhizobium* sp., and *Rhodospirillum rubrum*) have the ability to produce cytokinins or gibberellins during growth and development events. Similarly, ethylene can also affect plant growth and development in a number of ways, including root initiation, inhibiting root elongation, fruit ripening, lowering wilt, stimulating seed germination, promoting leaf abscission, and activating the synthesis of other plant hormones.

Due to the secretion of auxins under the root exudate deficit conditions, plant roots sense the auxin molecules and lateral roots, root hairs are emitted which are the sources of root exudates to maintain the bacterial population in the root zone. Most of the *P. fluorescens* species isolated from paddy soils produced IAA (Noori and Saud 2012). However, IAA production was also reported by *Azotobacter* sp., in wheat. The IAA-producing PGPR strains lead to vigorous root growth resulting in more surface area and thus enabling access to more nutrients in the soil (Singh et al. 2013). Moreover, the production of IAA by bacteria and fungi on Pikovskaya broth under in vitro condition was reported by Priya et al. (2013). They reported that out of 28 isolates, only 18 produced IAA by using tryptophan in the growth medium. However, the IAA production was achieved in JNFb liquid medium at 100 µg/ml tryptophan concentration (Srivatsava 2013).

2.1.3 Siderophore Production

Iron is one of the most important essential nutrients for growth of microorganisms in diverse environments. It is required for various cellular, metabolic, and biosynthetic processes, including DNA synthesis, electron transport system, formation of heme, cofactor for enzymes, oxygen transport, synthesis of ATP, and nitrite reduction in the nitrogen cycle. Although it is abundant in nature, it is not easily available in the preferred state. In the presence of oxygen and neutral pH it undergoes rapid oxidation from Fe^{2+} to Fe^{3+} and finally forms insoluble ferric-oxyhydroxide, which is almost unavailable for acquisition by microbes. The siderophores are relatively low molecular weight (400–1500 Da) iron-chelating compounds produced by many bacteria and fungi under iron-starved conditions. Generally, siderophores can be classified into three categories depending upon the moiety that donates oxygen ligands for Fe^{3+} coordination: (a) catecholates (or phenolates) (b) hydroxymates (or carboxylate), and (c) mixed types. Siderophores mainly scavenge iron and also form complexes with other elements (i.e., Mo, Mn, Co, and Ni) from the surrounding environment and make them available to host microbial cells. They promote plant growth by creating an antagonistic impact on phytopathogens. In soya bean, seed germination, shoot and root length were increased by the application of siderophore-producing *Bacillus* spp. GN-01 isolated from groundnut soil (Afreen and Chavan 2014). Siderophore production was observed in iron-limited King's B medium by *P. fluorescens* isolated from the rhizosphere soil of faba bean (Alemu 2013).

Siderophore-producing *Bacillus* spp., isolated from rice, chili, ragi, and beans controlled *Fusarium oxysporum*. Maximum siderophore secretion was recorded on second and third day, and thereafter a decline was observed.

Siderophores directly stimulate the synthesis of antimicrobial compounds by increasing the availability of minerals and suppressing the growth of pathogenic organisms (Sobha and Kumudini 2012). Siderophores produced by *Arthrobacter luteolus* isolated from the rare earth environment from Kerala, India reported the accumulation of rare earth metals Samarium and Scandium (Emmanuel et al. 2012). The nodule-forming bacteria isolated from the root nodules of leguminous plants such as *Rhizobium* spp., *Bradyrhizobium* spp. and *Sinorhizobium* spp. also produced siderophores (Deshwal et al. 2013). Verma et al. (2012) reported that *R. meliloti* has the ability to produce siderophores.

2.1.4 Phosphate Solubilization

Phosphorus (P) is the most important element in the nutrition of plants, next to nitrogen (N). It plays a key role in all major metabolic process, including photosynthesis, energy transfer, signal transduction, macromolecular biosynthesis, respiration, and nitrogen fixation. Phosphorus is abundant in soils in both inorganic and organic forms. Inorganic phosphorus occurs in soil mostly in insoluble complexes, some of them appearing after frequent application of chemical fertilizers. Organic matter is also an important reservoir of immobilized P in soils. It has been suggested that the accumulated P in agricultural soils would be sufficient to sustain maximum crop yields worldwide for more than 100 years. Several bacterial and fungal species have been described for their phosphate-solubilizing abilities. *Bacillus* and *Pseudomonas* are the predominant bacteria, while *Aspergillus* and *Penicillium* are the predominant fungi. The other important P-solubilizing bacteria include *Rhodococcus*, *Arthrobacter*, *Serratia*, *Chryseobacterium*, *Gordonia*, *Phyllobacterium*, *Azotobacter*, *Xanthomonas*, *Enterobacter*, *Pantoea*, *Klebsiella*, *Vibrio*, and *Xanthobacter*. Nodule-forming *Rhizobium* has also shown P-solubilizing activity. Moreover, some species of *Trichoderma* and *Rhizoctonia* also have P-solubilizing potential. Apart from bacteria and fungi, actinomycete genera *Streptomyces* and *Micromonospora*, algae such as cyanobacteria, and arbuscular mycorrhizal fungi and *Entrophospora colombiana* have shown P-solubilizing ability. *Azotobacter* spp. isolated from slightly alkaline soils have shown a good P-solubilizing ability along with nitrogen fixation under in vitro conditions (Nosrati et al. 2014). Garg and Sharma (2013) reported that 16 rhizobial isolates from root nodules *Trigonella* and *Tephrosia* were found positive for P solubilization and 14 isolates were found positive for IAA production. *Klebsiella oxytoca* isolated from heavy metal contaminated soil has shown P solubilizing activity in the presence of various C & N sources. Highest P solubilization was recorded with glucose (460 µg/ml) followed by fructose (444 µg/ml) and galactose (435 µg/ml) in the medium. Very poor P solubilization was recorded when lactose (141 µg/ml) was used as C source. Among different N sources (NH₄)₂SO₄ (460 µg/ml) was best for growth and P solubilization of *K. oxytoca*, where as yeast resulted in

poor growth and P solubilization (215 µg/ml) (Walpolá et al. 2014). Co-inoculation of tomato plants with *P. agglomerans* and *Burkholderia anthina* has shown P solubilization under lab conditions and increase in plant growth parameters under field conditions (Walpolá and Yoon 2013).

2.2 Plant Growth-Promoting Fungi (PGPF)

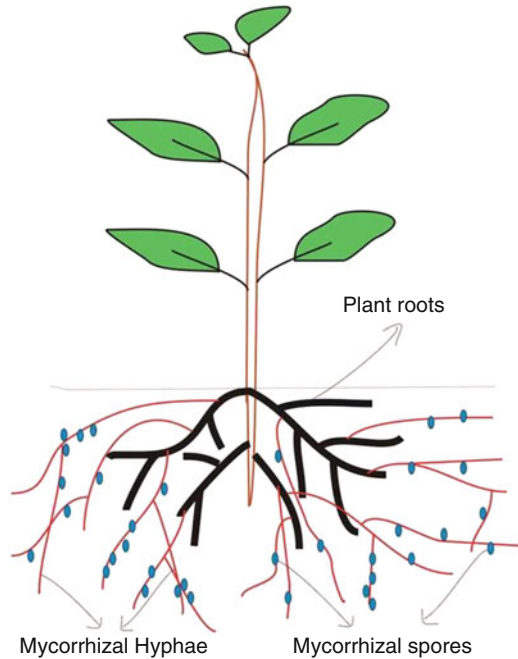
The arbuscular mycorrhizal fungi (AMF) and *Trichoderma* spp. are well recognized as plant growth-promoting fungi. AMF promote growth of crop plants by supplying various nutrients (mainly phosphorus). Through its hyphae nutrients are released into plant roots through arbuscules. The vesicles formed in the cortical region store the excess phosphorus in the form of polyphosphate, and this polyphosphate is again converted into phosphate through enzymatic action and utilized by the plant under phosphate-deficient condition, whereas *Trichoderma* promotes growth of crop plants by controlling the disease-causing fungi and also through biofertilization potential. *Trichoderma* decomposes the organic materials through the secretion of enzymes, cellulases, hemicellulases, etc., thus releasing the nutrients that are readily available to plants.

2.2.1 Arbuscular Mycorrhizal Fungi (AMF)

Arbuscular mycorrhizal fungi have unique characteristic structures known as “arbuscules” formed in the cortical region. The arbuscules are dichotomously branched structures and are the main sites for nutrient exchange between plant roots and the fungus (Akhtar et al. 2011). The host plant absorbs nutrients through the hyphae and in return the fungus obtains sugars and other essential nutrients from the plant (Akhtar and Siddiqui 2008). In the intercellular spaces the hyphae forms oval to globose structures called vesicles. These vesicles store P in the form of polyphosphate granules. Under phosphate-deficient conditions the polyphosphate from the vesicles is released by enzymatic action into the roots. Some species of AM fungi form spores within the roots known as intraradical spores (Fig. 2). The hyphae inside and outside the roots form abundant spores. AM fungi stimulate plant growth by nutrient acquisition and P uptake. AM fungi take up P from the same pool of soluble ions and act as an extension of the root system. There is also evidence that phosphatase activity is higher in mycorrhizal roots compared to non-mycorrhizal roots. AM fungi also improves the uptake of zinc, iron, calcium, copper, magnesium, and manganese and the hyphae travels beyond the nutrient depletion zone and transport nutrients to roots (Fig. 1).

AM colonization on roots increases the root surface area of the host plant. Mycorrhizal plants will withstand biotic and abiotic stresses such as heavy metal toxicity, salinity, alkalinity, pathogens and pests, etc. Mechanisms of heavy metal tolerance in fungi include reduction of metal uptake and/or increased efflux, metal

Fig. 1 Diagrammatic representation of mycorrhizal associations in plants



immobilization (e.g., cell-wall adsorption), extracellular metal sequestration, e.g., exo-polysaccharides or other extracellular metabolites, intracellular chelation, e.g., metallothioneins or phytochelatins, and metal localization/sequestration within vacuoles. Accumulation of metal ions on the cell wall has been shown to be an important mechanism leading to metal immobilization by AM fungi. AM fungi produce glomalin, a strong and irreversible sequester of Cu, Cd, and Zn. When it is applied to the plants growing in nursery in pots and polybags, the seedling survival improved on transplantation. This is due to the faster generation of new roots in nursery plants on transplantation. Mycorrhiza secrete a substance called glomalin, a glycoprotein which binds the soil particles together forming aggregates, giving way for good aeration and water-holding capacity, organic matter accumulation, and root penetration.

Significant growth enhancement was observed in bamboo seedlings inoculated with four AM fungi strains (*G. intraradices*, BEG 193 and 141; *G. mosseae*, BEG 167; and *G. etunicatum*, BEG 168). The results showed that the bamboo seedlings inoculated with all the strains of AM fungi significantly increased shoot number and diameter, leaf number, leaf area in different growth stages compared to control (Jiang et al. 2013). Similarly, Abohatem et al. (2011) reported that application of AM fungal consortium (*Acaulospora* sp., *Glomus* sp., *Sclerocystis* sp., and *Scutellospora* sp.) improved growth of seedlings in date palm and also reduced the incidence of pathogens by the stimulation of the secretion of defense-related enzymes. Najjar et al. (2012) found that use of *Glomus* sp. and *P. fluorescens* along with rock phosphate increased dry matter yield and nutrient uptake (NPK and Mg) in maize and faba bean.

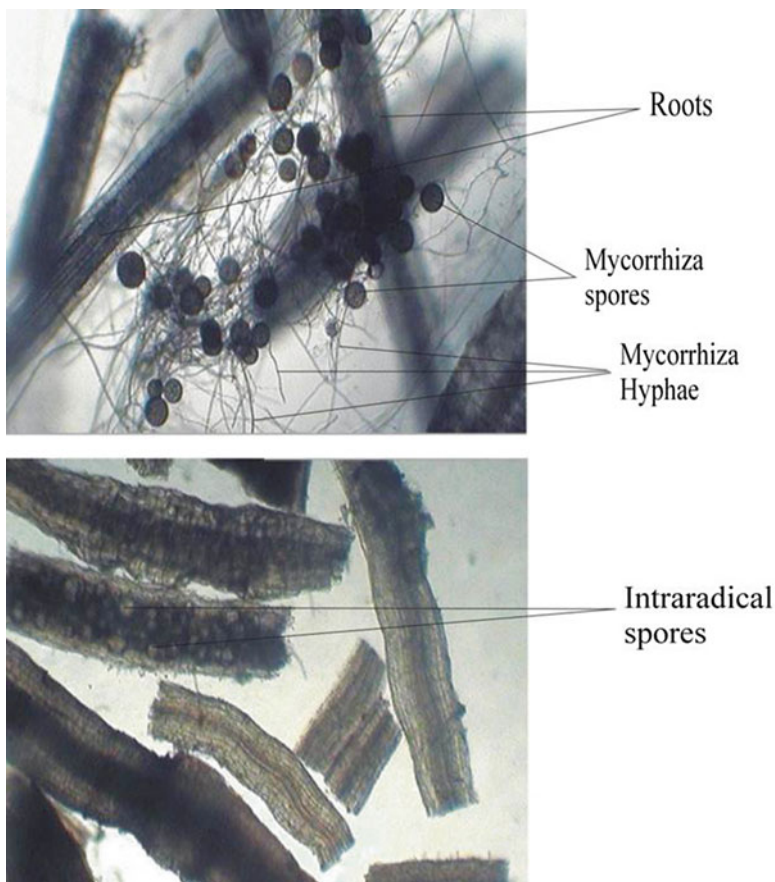


Fig. 2 Microscopic view of root showing intraradical mycorrhizal spores and hyphae

2.2.2 Trichoderma

Trichoderma is a filamentous fungus isolated from soil, dead wood, and organic materials. Currently, different species of *Trichoderma* such as *T. harzianum*, *T. viride*, and *T. virens* have proven their worth to be used as biocontrol agent against a wide range of pathogenic fungi (*Rhizoctonia* spp., *Pythium* spp., *Botrytis cinerea*, and *Fusarium* spp. *Phytophthora palmivora*). *Trichoderma* also has a unique ability to produce siderophores. The production of siderophores chelate the available iron from the environment and this iron starvation causes the death of phytopathogens. Srivastava et al. (2013) reported that all the three tested *Trichoderma* strains (MPPLUNS1, MPPLUNS2, and MPPLUNS3) had the ability to produce siderophores, but MPPLUNS1 was found best among all the tested strains. Likewise, antibiosis is another mechanism of disease protection, where the metabolites are secreted by underground parts of plants, soil microorganisms, plant residues, etc.

and resulted in the production of lytic enzymes, volatile and toxic compounds. A wide range of antibiotics such as tropolone, gliotoxin, gliovirin, viridin, viridol, trichodermin, trichozianin, pyrones, and terpenes is produced by *Trichoderma* sp. These antibiotics may play a significant role in the biocontrol of plant pathogens. Qualhato et al. (2013) concluded that the *Trichoderma* species grown in liquid cultures challenged with fungal pathogens secreted various cell wall-degrading enzymes, viz., β -1,3-glucanase, *N*-acetyl-b-D-glucosaminidase, chitinase, acid phosphatase, acid proteases, and alginate lyase.

Mycoparasitism involves sequential events such as recognition of host, attack and subsequent penetration, and subsequent killing of pathogens. The cell wall surface of the host and non-hosts contains D-galactose and *N*-acetyl D-glucosamine residues as lectin binding sites. With the help of lectins present on cell wall, *Trichoderma* recognizes the suitable sites (residues of lectins) and binds the hyphae. After attachment with pathogens, it makes a coil around the pathogens and secretes the cell wall-degrading enzymes to digest the cell wall and enters into the lumen of the host. Akrami et al. (2012) reported that use of *T. harzianum* and *T. asperellum* alone or in combination reduced Fusarium rot on *Phaseolus vulgaris* by the action of mycoparasitism. Similarly, Gajera et al. (2012) found that different species of *Trichoderma* controlled the growth of *Macrophomina phaseolina* by the action of cell wall-degrading enzymes (chitinase, β -1,3-glucanase, protease, and cellulase) under in vitro conditions. Muriungi et al. (2013) reported that the inoculation of *T. viride* and *T. koningii* effectively controlled the growth of *F. oxysporum* under in vitro conditions. Leelavathi et al. (2014) concluded that the extract of *T. harzianum* at a concentration of 100–150 μ l/ml controlled growth of *Aspergillus*, *Cladosporium*, *Rhizopus*, and *Fusarium*. Moreover, root colonization of *Trichoderma* sp. directly influenced plant growth and productivity, production of growth regulators like zeatin and gibberellin. It may also increase the uptake of nutrients and resistance against abiotic stresses.

3 Bioremediation

Bioremediation is a waste management technique that uses the organisms to remove or neutralize pollutants from contaminated sites. Bioremediation is defined as the process whereby organic wastes are biologically degraded under controlled conditions to an innocuous state, or the levels below concentration limits established by regulatory authorities. By definition, bioremediation is the use of living organisms, primarily microorganisms, to degrade the environmental contaminants into less toxic forms. It uses naturally occurring bacteria and fungi or plants to degrade or detoxify substances hazardous to human health and/or the environment. Bioremediation may occur on its own (natural attenuation or intrinsic bioremediation) or may only effectively occur through the addition of fertilizers, oxygen, etc., that help encourage the growth of the pollution-eating microbes within the medium (biostimulation). Bioremediation is classified as in situ when the pollutant is treated

at the site or ex situ when the pollutant is taken elsewhere and treated. Some examples of bioremediation are bioventing, bioleaching, landfarming, bioreactor, composting, bioaugmentation, and rhizofiltration. Bioremediation is becoming a very useful tool in many industries to prevent environmental pollution. The microorganisms applied to the contaminated sites secrete enzymes that degrade various chemical pollutants. Many microorganisms have been isolated from the polluted site, indicating that they have the ability to tolerate pollutants (Akhtar et al. 2013).

Bioremediation has been demonstrated and is being used as an effective means of mitigating hydrocarbons, halogenated organic solvents and compounds, non-chlorinated pesticides and herbicides, nitrogen compounds, metals, and radionuclides. *P. aeruginosa*, isolated from the crude oil contaminated sites in the Mangala oil field, Barmer district, Rajasthan, could be used for the bioremediation of oil spills because it has the potential to utilize crude oil as a sole carbon source (Prakash and Irfan 2011).

In an interesting experiment Ajao et al. (2011) found that the inoculation of immobilized culture of *P. aeruginosa* and *B. subtilis* into a bioreactor fitted with air sparger containing textile effluent reduced COD from 1200 to 200 mg/l, BOD from 750 to 23 mg/l in 15 days. The other parameters in textile effluent such as total solids, suspended solids, dissolved solids, heavy metals, nitrate, sulfate, phosphate also have been reduced significantly and copper disappeared within this period from the textile effluent. Similarly, use of *Trichoderma* species culture based on diffusible and volatile metabolites under in vitro conditions reduced the growth of *Pythium* in tomato Patil et al. (2012). The volatile metabolites exhibited broad-spectrum inhibition of *Pythium* compared to diffusible metabolites.

4 Interaction of PGPM with Plants and Soil

Plant roots under nutrient-deficient condition releases certain nutrients like carbohydrates, amino acids, and vitamins into the soil to attract microorganisms. The microorganisms utilize the root exudates for their growth and multiplication. The microbes produce hormones like auxins (IAA, IBA), cytokinins, GA₃, abscisic acid (ABA). The plant roots sense these auxins and start emitting lateral roots and root hairs which absorb water, minerals from the rhizosphere. The uptake of minerals is increased due to the increased surface area of the roots. Some microorganisms may colonize in the rhizosphere soil (e.g., *Azotobacter*, and phosphate-solubilizing bacteria (PSB), some (e.g., *Rhizobium*, *Azospirillum*, and AM fungi) colonize either on the surface or inside the roots.

The interaction of microorganisms with plants and soil helps in the improvement of nutrient (NPK) uptake by various mechanisms. The combined application of *Azospirillum* and *Azotobacter* in maize has resulted in the increase in plant growth, yield, and hormone (IAA, GA₃, cytokinin) production (Naseri et al. 2013). Mehran et al. (2011) reported that increase in yield was not significant between treated (bacteria inoculated) and control plots, whereas a significant increase in yield was

observed in manure applied treatment. Rafi et al. (2012) found that the co-inoculation of *Azospirillum* and PSB together resulted in increased shoot and root dry weight, panicle weight, and 1000 seed weight compared to control or individual inoculation in foxtail millet. It has been also reported that inoculation of *Azotobacter* and *Rhizobium* together resulted in increase water and nutrient uptake in faba bean (Dashadi et al. 2011). However, inoculation of *Rhizobium* with PGPR alone or in combination significantly increased the nodule number, nodule fresh and dry weights, grain yield compared to control under salt stress conditions in mung bean and also improved K/Na ratio in grains by decreasing the Na content compared to control (Aamir et al. 2013). Similarly, inoculation of *Azotobacter* and *Azospirillum* in maize significantly increased grains weight and yield when bacteria was rapped with seeds before sowing compared to control (Amiri and Rafiee 2013).

5 Conclusions and Future Prospects

The interaction of PGPM with plants and soil is very important in improving crop productivity. Soil is fortified with various root exudates of plants attracting microorganisms, which in turn help plants through nitrogen fixation, phosphate solubilization, and nutrient mobilization. Different bacteria and fungi are used as biofertilizers due to their ability in producing phytohormones, siderophores, antimicrobial compounds, developing induced systemic resistance and bioremediation. Microorganisms could be applied alone or in combination in various crops, but it is advisable to apply nitrogen-fixing bacteria along with phosphate-solubilizing bacteria because P requirement during nitrogen fixation is met by phosphate-solubilizing bacteria. The selection of microorganisms is crucial for a field application for maintaining the quality of crops. By adopting the biofertilizer strategies in sustainable agriculture practices the adverse effects of chemical fertilizers and pesticides could be easily nullified. Moreover, the isolation of microorganisms from the contaminated sites and their potential application in bioremediation is quite a permissible approach. The future research will be more focussed on the revolutionization of a consortium of microorganisms for agricultural inputs and bioremediation of contaminated sites by the efficient application of microorganisms and their interaction with the plant and soil in various ecological niches.

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