Vivek Kumar · Ram Prasad
Manoj Kumar · Devendra K. Choudhary
Editors

Microbiome in Plant Health and Disease

Challenges and Opportunities

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Editors
Vivek Kumar
Himalayan School of Biosciences
Swami Rama Himalayan University
Dehradun, Uttarakhand, India

Ram Prasad
School of Environmental Science & Engg
Sun Yat-sen University
Guangzhou, Guangdong, China

Manoj Kumar
Centre for Life Sciences
Central University of Jharkhand
Ranchi, Jharkhand, India

Devendra K. Choudhary
Amity Institute of Microbial Technology
Amity University
Noida, Uttar Pradesh, India

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Applications of Plant–Microbe Interactions in Agro-Ecosystems

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Rasheed A. Adeleke, Bhavna Nunthkumar, Ashira Roopnarain, and Linda Obi

Abstract

The natural association between plants and microorganisms has historically been linked to improved plant growth, nutrition and health. Rhizospheric and phyllospheric microorganisms have received much attention due to their applications in improved nutrient acquisition, enhanced water sequestration, induced systemic resistance, competitive exclusion of plant pathogens and remediation of environmental pollutants. Such beneficial attributes have motivated the adoption of these plant–microbe interactions in agro-ecosystems to improve productivity. The application of commercially available plant beneficial microorganisms (CAPBM) in agro-ecosystems is largely due to their compatibility and complementarity with natural processes of nutrient cycling, plant protection and other related biological processes. While numerous studies have reported the huge potential of the use of plant beneficial microorganisms in agro-ecosystems, wide-scale com-

R. A. Adeleke (✉)
Unit for Environmental Science and Management, North-West University, Potchefstroom Campus, Potchefstroom, South Africa

Microbiology and Environmental Biotechnology Research Group, Agricultural Research Council - Institute for Soil, Climate and Water, Pretoria, South Africa
e-mail: Rasheed.Adeleke@nwu.ac.za

B. Nunthkumar · A. Roopnarain
Microbiology and Environmental Biotechnology Research Group, Agricultural Research Council - Institute for Soil, Climate and Water, Pretoria, South Africa
e-mail: NunthkumarB@arc.agric.za; RoopnarainA@arc.agric.za

L. Obi
Microbiology and Environmental Biotechnology Research Group, Agricultural Research Council - Institute for Soil, Climate and Water, Pretoria, South Africa

Department of Environmental Science, College of Agriculture and Environmental Science, Pretoria, South Africa
e-mail: ObiL@arc.agric.za

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mercialization of microbial products are still lagging. Hurdles in the commercialization of CAPBM range from lack of awareness and regulatory framework to inaccurate product selection. The future prospects of the application of CAPBM will be determined by the adoption of new technologies that include multi-omics approach for improving the quality as well as applicability of these beneficial microorganisms in agro-ecosystems. Furthermore, government intervention is of utmost importance to ensure that the necessary regulatory framework is in place, thereby ensuring high quality of products. High-quality products will improve adoption rate, which would have downstream influences on job creation in the CAPBM and agricultural industries.

Keywords
Commercially available plant beneficial microorganisms · Biofertilizers · Applications · Agro-ecosystems

1.1 Introduction

As photosynthesizers, plants are primarily responsible for provision of energy for the entire ecosystem; hence, they are intimately linked to many activities in the ecosystem and do not usually exist in isolation. The type and nature of associations they form with microorganisms are crucial for their development, survival, diversity, abundance and ecology (Van Der Heijden et al. 2008). Therefore, plant–microbe associations will continue to shape and dictate the structure of the ecosystem. Over the years, scientists had capitalized on the benefits of such associations and borrowed ideas from natural ecosystems to improve practices in agro-ecosystems.

The agro-ecosystem is physiologically different from that of the immediate surrounding environments. It functions as a specialized niche due to its biological and physicochemical differences. These variations are caused by biological and chemical processes carried out by the residing macro- and microorganisms (Conway 1986). Microorganisms are ubiquitous in the environment and play key roles in agro-ecosystem functioning. The interaction of plants and microbes can be helpful or harmful to plant life, or they simply exist in mutual harmony. Pathogenic microbes can infect plants in a host–parasite relationship causing plant diseases (Gnanamanickam et al. 1999; Vurro et al. 2010). However, some commensal bacteria have been known to reside within a host plant for long periods with no damage caused to the host plant (Hardoim et al. 2008).

Although plant–microbe interactions could be positive or negative, applications in the agro-ecosystem are mainly positive with partial or full benefits to the entire ecosystem. Such relationships could be mutualistic, which involves the provision of shelter and/or nutrients by the plant for the microbes while, in turn, the microbes enhance plant growth and provide biological control against potential pathogens and predators using various strategies (Mendes et al. 2013). Important roles of microorganisms in nutrient cycling and plant protection have drawn interests of

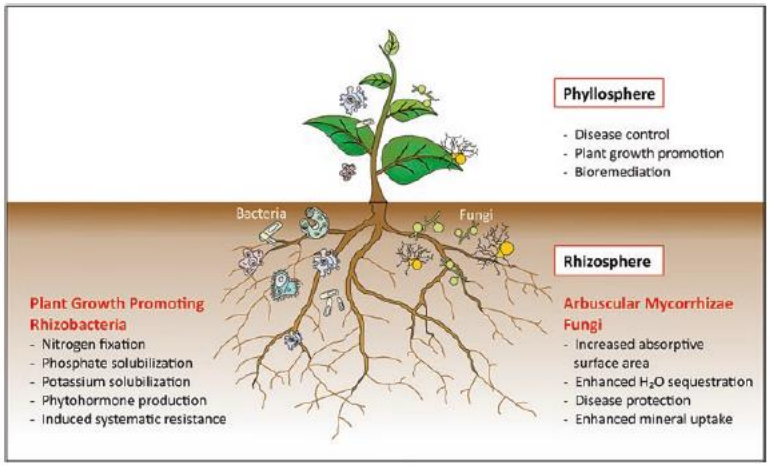

Fig. 1.1 Overview of applications of plant–microbe interactions in agro-ecosystems

researchers as they seek to replace chemical products with commercially available plant beneficial microorganisms (CAPBM) (also known as biofertilizer) for enhancing plant growth and for control of pathogens. Chemical fertilizers containing only nitrogen, phosphate and potassium, which saturate soils, can be replaced with species or a consortium of microorganisms that are able to transform unavailable substrates to an inorganic form that plants can assimilate (Sihi et al. 2017). Similarly, chemical pesticides can be replaced by CAPBM, which convey natural defences against pathogens (Mendes et al. 2013). Good crop yield and healthy soil microflora reflect the health of the agro-ecosystem. As such, this chapter focuses on plant–microbe interactions, which support agro-ecosystems, specifically, the effects of plant–microbe interactions on plant growth as well as plant and soil health in relation to the rhizosphere and phyllosphere (Fig. 1.1).

1.2 Plant–Microbe Interactions in the Rhizosphere

Although plants were the first eukaryotes to inhabit land around 450 million years ago, their survival was intrinsically linked to the symbiotic relationships they formed with microorganisms (Heckman et al. 2001). With no root structures, the earliest plants relied wholly on microorganisms for mineral nutrient acquisition. However, evolution of plants has resulted in the acquisition of vascular structures and root systems, which enables them to obtain mineral nutrients from their environment. Despite the increasing nutrient acquisition potential of plants over time, their symbiotic relationships with microorganisms are still integral to plant growth and development (Heckman et al. 2001; Kenrick and Strullu-Derrien 2014).

Plant–microbe symbiosis occurs predominantly in the rhizosphere (Lugtenberg 2015). The rhizosphere microbiome comprises a number of diverse microorganisms, which may include actinomycetes, algae, bacteria, fungi, viruses and archaea and is said to contain more than tenfold the number of microorganisms than the surrounding bulk soil (Mendes et al. 2013; Lugtenberg 2015). Actinomycetes are an important group of gram-positive bacteria that possess both fungal and bacterial characteristics (van Wezel and Vijgenboom 2004). These intermediary microorganisms as plant symbionts are capable of increasing plant growth and secrete antifungal agents such as siderophores and antifungal metabolites (Tokala et al. 2002). For example, isolates of the actinomycete *Streptomyces* spp. were proven to reduce damping-off in tomatoes caused by the fungal pathogen *Rhizoctonia solani,* and another actinomycete strain, *Streptomyces griseoviridis*, has been commercialized as a biofungicide (Minuto et al. 2006; Goudjal et al. 2014). However, it is important to note that some actinomycetes strains such as *Streptomyces scabies, Streptomyces turgidiscabies* and *Streptomyces aureofaciens* are pathogenic, causing scabbing in potatoes (Hiltunen et al. 2009).

Algae are a common occurrence in aquatic and terrestrial environments as primary producers of organic matter (Hristozkova et al. 2018). Cyanobacteria, blue-green algae and green algae are generally present in the rhizosphere. These algae play an important role in polysaccharide secretion and oxygen production, which contributes to soil aggregation and soil aeration, respectively (Hristozkova et al. 2018). In addition, algal exudates of *Ascophyllum nodosum* were used as biostimulants to improve cold tolerance in maize and drought tolerance in spinach (Xu and Leskovar 2015; Bradáčová et al. 2016).

Viruses present in the soil can cause plant diseases with deleterious effects on plant health. However, some plants exhibit increased tolerance to water and cold stress when infected with viruses such as plant mosaic and tobacco rattle viruses (Xu et al. 2008; Roossinck 2011).

Rhizospheric Fungi in Agro-Ecosystems

Fungi form one of the most diverse groups of eukaryotes and are an essential functional component of soil microbial communities. One of the most ubiquitous groups of microorganisms in the rhizosphere are the mycorrhizal fungi; they are present in harsh desert, thermal and arctic tundra soils as well as salt flats. Although there are many beneficial fungi in the rhizosphere, this chapter will focus primarily on mycorrhizal fungi. They are abundant in forest and agricultural soils (Gardes and Dahlberg 1996; Tian et al. 2006; Smith and Read 2008; Zabinski and Bunn 2014; Becerra et al. 2014). Different approaches have been advocated for the classification of this important group of fungi in the last two decades. One such approach is based on the trophic level, which consists of two major groups–ectotrophic and endotrophic mycorrhiza. Another classification approach is related to morphological and anatomical features of mycorrhizal fungi. In the latter approach, ectomycorrhiza, endomycorrhiza and ectendomycorrhiza (EM) are the recognized types. Perhaps, the

most common form of classification is the seven popular categories that have been widely mentioned in literature. These are ectomycorrhiza, arbuscular mycorrhiza, ectendomycorrhiza, arbutoid, ericoid, monotropoid and orchid mycorrhiza (Brundrett 2004; Smith and Read 2008). These groups are broadly differentiated by the nutrient exchange compartments they form within the root. For instance, mycorrhizal fungi that penetrate the root and exhibit intracellular penetration of root cells are termed endomycorrhiza, while those that colonize outside of the root cells showing only intercellular penetration are termed ectomycorrhiza (Friberg 2001; Smith and Read 2008).

Ectomycorrhizal fungi form a mycorrhizal association characterized by means of their structural mycelial formation that does not penetrate but extends between the host root cells to form a Hartig net (Smith and Read 2008). Ectomycorrhizal fungal associations are formed by higher Basidiomycotina (*Agaricus, Amanita, Lactarius, Thelephora* and *Scleroderma*) and a few Ascomycotina (*Tuber and Terfezia*) and *Zygomycota* (Endogone) (Isaac 1991; Molina et al. 1992; Lodge 2000). The resilience and perhaps survival of trees from the families of Pinaceae, Fagaceae, Betulaceae and Myrtaceae are partly due to their association with ECM fungi (Muchovej 2004), which are important, particularly in environments where growth conditions are not ideal (Isaac 1991).

Unlike the AM fungal counterparts, some ECM fungi have been successfully cultivated in vitro, but they generally grow slowly (Horton and Bruns 2001; Finlay and Söderström 1992). This has been attributed to their ability to utilize simple sugars such as glucose, mannose and fructose, independent of their host plants, and is proof of the facultative nature of some ECM fungi. It has also been shown that ECM fungi can participate in the degradation of complex carbohydrates as shown by Entry et al. (1991). It was observed that the ECM fungus *Hysterangium setchellii* was able to provide an improved microenvironment for easy decomposition of lignin and cellulose.

Generally, ECM fungi have broad host ranges within restricted plant families and their hosts may be receptive to several ECM fungi (Molina et al. 1992). This means that a plant species can act as a host to a variety of ECM fungi and an ECM fungus can also colonize different suitable host plants (Isaac 1991; Molina et al. 1992). The advantage of this is the increased survival rate of new seedling species (dispersal of the seedlings) in new environments, as they can easily associate with a variety of ECM fungi. Examples of ECM fungi with broad host compatibility include *Amanita aspera*, *Boletus calopus*, *Tuber borchii*, *Ruber brumale*, *Tuber melanosporum*, *Choiromyces venosus* and *Pisolithus tinctorius* (Molina et al. 1992). This situation boosts the plants' access to more nutrients because of the ability of the individual ECM fungus involved in the association to source nutrients in the soil on behalf of the plant (Bruns et al. 2002). In contrast, some ECM fungi are host specific. These include those that can associate with one genus of host plant such as *Amanita diemii*, *Boletus loyo*, all *Suillus* spp. and *Tricholoma robustum*. Specificity can restrict the geographic scope of the ECM fungus; those that are too specific will be restricted to areas where the host is present.

Another important group of mycorrhizal fungi are the arbuscular mycorrhizal fungi. They are named after the finely branched structures they produce intracellularly, which are referred to as 'arbuscules.' This structure is present in most members of this group (Smith and Read 2008; Muchovej 2004). They are sometimes referred to as vesicular arbuscular mycorrhiza (VAM) but only in situations where the species produce vesicles (Brundrett 2002). Arbuscular mycorrhizal fungi are believed to be much older than land plants because of their various primitive characteristics such as simple spores, absence of sexual reproduction and their relationships with a wide variety of plants (Morton 1990; Brundrett 2002). They have been found to associate with primitive plants such as mosses and ferns as well as a wide range of angiosperms and gymnosperms. Arbuscular mycorrhizal fungi are obligate symbionts having no special enzymes to degrade simple or complex carbohydrates (Finlay and Söderström 1992; Brundrett 2002).

Arbuscular mycorrhizal fungi have been classified under the phylum Glomeromycota, which consists of several genera that coevolved with plants for over 400 million years (Walker and Schüßler 2004). Arbuscular mycorrhizal fungi colonize plant roots to scavenge organic carbon from root exudates while in return providing the plant with mineral nutrients. Members of the AM fungi family have identical genetic makeup that makes it difficult to identify individual species (Hosny et al. 1999; Pringle et al. 2000). They have either aseptate or rarely septate hypha with inter- and intracellular colonization of the cortical cells of the host plants and absence of Hartig net or mantle (Smith and Read 2008).

For symbiosis to occur between plants and AM fungi, communication is essential. Such communication is mediated by signalling molecules from both the plant and the fungal symbiont. The fungal symbiont senses roots in the vicinity by the detection of plant hormones released through root exudates. Plant hormones such as strigolactone have been found to initiate hyphal branching and speed up the metabolism of AMF (Bonfante and Desirò 2015). In order to colonize the root, fungi release lipochito-oligosaccharides (Myc factors), which also promote plant growth to increase root surface area (Lugtenberg 2015). Once the fungi have adhered to the surface of the root, the hyphae intrude the plant cell and branch out within the cell to form arbuscules (Sanders and Croll 2010; Lugtenberg 2015).

In ectendomycorrhizal associations, there is a special scenario in which the fungal hyphae form a Hartig net and a primitive sheath around the roots. The hyphae penetrate the cortical root cells, and there is a formation of reduced mantle, thereby possessing the characteristics of both ectomycorrhizal and endomycorrhizal fungi (Molina et al. 1992; Smith and Read 2008). Ectendomycorrhizal fungi have been shown to colonize seedlings in early stages over ECM, possibly due to the ability of some EM to break down complex polysaccharides for use as carbon source (Egger 1986; Caldwell et al. 2000; Yu et al. 2001). Yu et al. (2001) suggest that EM fungal association is favored, as the EM could possibly provide carbon to the developing seedling prior to autotrophy development and that the EM contributes less to the carbon drain of the young seedling than ECM.

Other endomycorrhizal groups include the arbutoid mycorrhizas such as *Leccinum* sp., which form a mycorrhizal association with two genera of Ericaceae

(*Arbutus* and *Arctostaphylos*) (Molina et al. 1992). The fungi colonize the plant root both intercellularly and intracellularly, but colonization is constrained to the epidermis and cortical cells (Molina et al. 1992). Mycorrhizal fungi responsible for this association can colonize other plants (Molina and Trappe 1982). Furthermore, there is another group known as the Monotropoid. These are mycorrhizal fungi associated with the plant family Monotropoideae, and they form a thick fungal sheath (Molina et al. 1992; Smith and Read 2008).

Ericoid mycorrhizal fungi (such as *Hymenoscyphus ericae*) are associated with host plants in the family Ericales. Their hyphae are septate and grow intercellularly, and their growth is, however, restricted to the epidermal cells (Molina et al. 1992). Lastly, there is Orchid mycorrhiza, in which the mycobionts responsible for this association belong to Basidiomycotina. This group is characterized by an intracellular colonization but an absence of Hartig net, fungal sheath and vesicles. An example of the group is *Rhizoctonia repens* (Smith and Read 2008).

1.2.1 Roles and Applications of Mycorrhizal Fungi in Agro-Ecosystems

1.2.1.1 Plant Growth Promotion

Ectomycorrhizal fungi play a major role in the sequestration of mineral nutrients on behalf of their symbiont plant. The ECM can improve host mineral uptake through enzymatic mobilization of organic nitrogen, phosphorus compounds or mineral weathering by organic acids (Landeweert et al. 2001). This group of fungi secretes enzymes, which are able to break down and utilize nitrogenous compounds such as glutamine, glutamate and alanine as well as other amino acids such as peptides and nucleic acids (Bücking et al. 2012). Some of the smaller organic molecules such as simple peptides and amino acids can also be directly absorbed by ECM hyphae, and such could be utilized for plant metabolism (Chalot and Brun 1998, Landeweert et al. 2001). Furthermore, the production of organic acids such as oxalic and citric acids by ECM fungi aids in the release of mineral ions from surrounding soils and solid lattices. The released organic acids also help in the mobilization of phosphorus, potassium, calcium and magnesium ions from mineral compounds such as apatite, biotite, iron ore, micas and feldspars (Wallander and Wickman 1999; Wallander 2000a, b; Adeleke et al. 2012; Adeleke 2014).

ECM fungi aid in extending the root surface area that further enhances the ability of ectomycorrhizal plants to obtain nutrients. ECM fungi have been known to form mycorrhizal mats (networks) just beneath the surface humus in forests. These networks are able to cover areas up to several meters and facilitate communication between ECM trees involving the transfer of nutrients and even defence priming against pathogens (Landeweert et al. 2001; Song et al. 2015). For example, studies of ECM network between a donor Douglas-fir (*Pseudotsuga menziesii*) and receiver ponderosa pine indicated that if the pine plant was subjected to defoliation stress, the Douglas-fir was able to transfer labile carbon to the pine directly through the mycorrhizal network in an attempt to alleviate the stress. When the Douglas-fir was

further subjected to predation by herbivores, the defence responses of the pine were peaked at the very same time as that of the Douglas-fir, indicating the rapid transfer of defence signals to the neighbouring pine through the mycorrhizal network (Song et al. 2015).

The establishment of an ectomycorrhizal network can further increase mineral weathering and improve soil aggregation by the exudation of extracellular mucilage by fungal hyphae (Dunham et al. 2007; Smith and Read 2008). The stress ameliorating effects of the ECM fungal symbionts toward the plant hosts, including pollutant and heavy metal tolerance, increased mineral nutrient mobilization and uptake, as well as improved host plant stress responses. Hence, the ectomycorrhizal fungi can be considered for CAPBM formulation for forestry improvement. Further studies indicate capabilities of ECM in enhancing afforestation of heavy metal-polluted soils, as the fungi confer tolerance to the plants against pollutants through physical and chemical methods previously mentioned, allowing for improved plant growth in suboptimal conditions. Similar attributes of ECM fungi were reported by Bojarczuk and Kieliszewska-Rokicka (2010), where the growth of *Betula pendula* seedlings was enhanced in a 1:1 metal-contaminated soil supplemented with nonpolluted forest soil most likely due to improved mycorrhizal colonization.

Perhaps, the most important application of AM fungi is nutrient acquisition. To meet the growing phosphorus requirements, plants form symbiotic associations with AM fungi such as *Funneliformis mosseae, Rhizophagus irregularis* and *Gigaspora margarita*. Arbuscular mycorrhizal fungal hyphae branch out further from the phosphorus depletion zone, caused by direct phosphate uptake. Their smaller size allows them to explore surfaces, which plant roots cannot exploit, to obtain phosphates (Helgason and Fitter 2009) (Fig. 1.2). The fungal symbionts sequester phosphate from their surroundings using their extended hyphal network and transport it back to the plant root by translocation. The phosphate is then transported from the fungal arbuscules or coiled hyphae through an interfacial apoplast to the cortical plant cell through AM-induced phosphate transporters (Smith et al. 2011).

Phosphorus is required for many plant functions including vital nucleic acid and adenosine triphosphate (ATP) production (Shen et al. 2011). Not only does phosphorus deficiency limit plant growth but studies by Divito and Sadras (2014) have shown that a decrease in phosphorus availability to the plant causes a decrease in nodule formation and nitrogen fixation, largely due to lack of ATP metabolic actions in the associated plant cell. Hence, augmented phosphate uptake through mycorrhizal associations is a major contributor to enhanced plant growth.

An important application of AM fungi is their formulation into CAPBM, which are a sustainable alternative to chemical fertilizers (Abdullahi et al. 2015; Suhag 2016; Khan et al. 2017). For instance, inoculation of lettuce crops with the AM fungus *Rhizophagus intraradices* resulted in improvement of water use efficiency and salt tolerance – a favorable improvement under drought conditions (Aroca et al. 2008; Jahromi et al. 2008; Rouphael et al. 2015). Some mycorrhizal biofertilizers can further improve the host plant's systemic resistance against plant disease and predation by nematodes and insects (Schouteden et al. 2015; Song et al. 2015). In

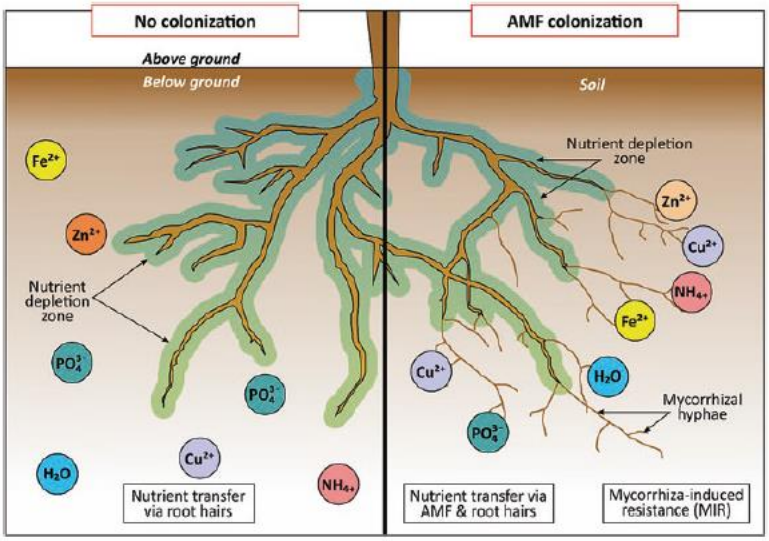

Fig. 1.2 Applications of fungi–plant interactions in agro-ecosystems

addition, AM fungi can also be used as biological control such as biofungicides and pest repellents.

Arbuscular mycorrhizal fungal inocula are usually applied on the seeds and seedlings to ensure early establishment of the mycorrhizal association (Baum et al. 2015; Malusà et al. 2016; Ercoli et al. 2017). Field trials of AMF biofertilizer have shown great potential; hence, numerous AMF biofertilizer products are commercially available (Table 1.1) (Berruti et al. 2016). Arbuscular mycorrhizal fungi biofertilizers are supplied as spores, colonized roots or AMF hyphae within a solid or liquid carrier material. The carrier material can influence the efficiency of the biofertilizer due to potential interactions between the material and different soil types (Baum et al. 2015; Rodrigues and Rodrigues 2017). Most commercially available AMF biofertilizers are 'broad spectrum' consisting of multiple species of AMF with *F. mosseae*, *R. irregularis* and *Glomus etunicatum* being the most common (Berruti et al. 2016).

1.2.1.2 Plant Protection

Drought Tolerance The AMFs extensive root structure is vital for plant protection against different environmental stresses such as drought (Fig. 1.2). The hyphal network extends further than the plant roots and is able to cover an exceptionally large surface area allowing the fungus to sequester scarce water trapped between soil particles and within bedrock micropores. Some fungal hyphae, which transport water to the plant, could measure up to 200 m per gram of soil (Van Der Heijden

Table 1.1 Biofertilizers containing plant beneficial fungi, which are commercially available on the global market

Region	Country	Company	Product	Organisms	Purpose
Europe	Sweden	**Bio-Innovation**	Myco-Rise	*Trichoderma harzianum*	Biofertilizer
			Bioderma-H	*Trichoderma harzianum*	Biofungicide
	Belgium	**Grondorts-mettingen de Cuester**	Biofungus	*Trichoderma* spp.	Biofungicide
	Germany	**Bayer-Cropscience**	Contans WG	*Coniothyrium minitans*	Biofungicide
	Hungary	**Bioved**	Trifender	*Trichoderma asperellum*	Biofertilizer/ Biostimulant
	France	**Natural Plant Protection**	Fusaclean	*Fusariuam oxysporum Fo47*	Biofungicide
	Italy	**SIAPA**	MycoApply DR	*Rhizophagus irregularis, Claroideoglomus luteum, Claroideoglomus etunicatum, Claroideoglomus claroideum* and 1% rhizosphere bacteria[a]	Biofertilizer/ Biostimulant
Asia Pacific	India	**Biotech Int. LTD**	Bioderma-H	*Trichoderma harzianum*	Biofungicide/ Biofertilizer
			Bioderma	*Trichoderma viridae*	Biofungicide
		Himalaya Pharmaceuticals Ltd.	Adhunik-VAM	AMF[a]	Biofertilizer
		PHMS Technocare Private Limited	Mycorrhizae Granular (PHMS MulShakti) GR	AMF[a]	Biofertilizer/ Biostimulant
	Thailand	**Probusiness Boonsongsuk Ltd**	Powdered organic fertilizer of Water Spraying Naga Brand	*Trichoderma* spp.[a]	Biostimulant
	Taiwan	**Yan Ten Biotech Corp**	Bio-Care Comprehensive Beneficial Effective Microorganism and PGPR	*Aspergillus* spp.[a], *Penicillium* spp.[a], other bacteria	Biofertilizer/ Biostimulant
	China	**Shandong Sukahan Bio-Technology Co., Ltd.**	BIO-GAIN ™	*Bacillus* spp., *Azotobacter* spp., *Aspergillus oryzae*, *Trichoderma* spp.[a]	Biofertilizer/ Biostimulant
			Microbial Fertilizer		

(continued)

	Australia	**Mycorrhizal Applications Int.**	MycoApply Defence	AMF[a], *Trichoderma* spp., *Bacillus* spp., other beneficial bacteria	Biofertilizer
	New Zealand	**Agrimm**	Abzorber Root Dip	*Trichoderma* spp. and AMF[a]	Biostimulant
	Australia	**Monsanto Ag**	RhizoBio	Six bacterial cultures and 18 species of endo- and ectomycorrhiza	Biostimulant
Americas	Iowa-USA	**Soil Technologies Corp.**	Plant Success – Granular Bio-Stimulant	*Rhizophagus irregularis, Funneliformis mosseae, Glomus aggregatum, Glomus etunicatum, Trichoderma koningii, Trichoderma harzianum,* other endomycorrhizae	Biofertilizer/ Biostimulant
	Columbia-USA	**Certis USA**	SoilGard	*Trichoderma virens*	Biofungicide
	California-USA	**JHBiotech Inc.**	Mycormax™	AMF[a]	Biostimulant
	Canada	**Bioworks**	RootShield Plus+ WP	*Trichoderma harzianum, Trichoderma virens*	Biofungicide
	Canada	**RiseHoP**	Myconnect Field Crops	*Rhizoglomus* sp.	Biofertilizer/ Biostimulant
		Sigma AgriScience	SigmaBio	*Rhizophagus irregularis, Funneliformis mosseae, Glomus etunicatum, Glomus aggregatum, Trichoderma harzianum, Trichoderma koningii, Bacillus* spp.	Biofertilizer/ Biostimulant
	Argentina	**Rizobacter**	Rizoderma	*Trichoderma harzanium*	Biofungicide
	Nicaragua	**Esagri**	MicoFert	*Rhizophagus irregularis*	Biostimulant
	Cuba	**National Institute of Tropical Viandas Research (INIVIT)**	EcoMic	*Glomus fasciculatum*	Biofertilizer/ Biostimulant
	Colombia		MycoBiol	*Glomus* spp., *Entrophospora colombiana, Acaulospora mellea*	Biofertilizer/ Biostimulant

(continued)

Table 1.1 (continued)

Region	Country	Company	Product	Organisms	Purpose
Africa[b]	South Africa	**Mycoroot**	Mycoroot™ SuperGro	AMF[a]	Biofertilizer
	South Africa	**Microbial Bio-fertilizers Int. (MBI)**	TRI-CURE WP	*Trichoderma harzianum*	Fungicide
	South Africa	**Zylem SA**	Nutri Life Platform	AMF[a], *Trichoderma harzianum*	Biofertilizer/ Biostimulant
	South Africa	**Biocult**	Biocult Mycorrhizae Powder	*Funneliformis mosseae, Rhizophagus intraradices, Glomus etunicatum, Scutellospora* spp., *Trichoderma harzianum*	Biofertilizer/ Biostimulant
	Kenya	**Dudutech Ltd**	Rhizatech	AMF[a]	Biofertilizer/ Biostimulant
	Kenya	**Juanco SPS LTD**	MYCORMAX WS	AMF[a]	Biostimulant

Adapted from Kaewchai et al. (2009), Uribe et al. (2010)

[a]Species not specified by producer [b]Many Northern African countries import their biofertilizers

The above table illustrates fungal biofertilizers available on the global market. Some biofertilizer producers choose not to specify the particular fungal strains. Single-species products such as Myco-Rise, Bioderma, SoilGard and Tricure WP have a specific role as biofertilizer, biofungicide or biostimulant. Products containing a 'cocktail' of fungi are more often claimed to have more than one purpose or are labelled as biostimulators. The most common mycorrhizal inoculants are *Rhizophagus irregularis, Funneliformis mosseae, Glomus aggregatum* and *Glomus etunicatum*, which feature in most mycorrhizal biofertilizers where the organisms are specified.

et al. 2008). Drought conditions are usually accompanied by low water retention in soils due to high levels of evaporation and loose soil structure. Hyphae of AMF increase soil structure by forming soil microaggregates through physical and chemical binding using AMF extracellular hyphae and exudates; often referred to as the 'sticky string bag' (Querejeta 2017). Studies by Hallett et al. (2009) have proven that AMF soils were capable of retaining more water than non-AMF soils even in the absence of plant roots, postulating that increased soil structure lead to enhanced root-soil hydraulic conduction.

The effects of drought are felt most severely by third world countries that rely on crop export and smallholder farms. For instance, in South Africa, the Western Cape has recently experienced a crop loss of up to 20% due to insufficient rains caused by the El Ninõ drought phenomenon (Chambers 2018). Planting crops with enhanced drought tolerance could reduce annual crop loss caused by drought and stabilize food production. In addition, the plant protection roles of AMF during drought condition could also be linked to the ability of the AMF to delay the onset of drought conditions through absorption of additional water absorbed by the fungus (Augé 2001, 2004; Augé et al. 2004; Querejeta 2017). Studies by Bitterlich et al. (2018) reported that transpiration rates of non-AMF plants were negatively impacted by drought conditions faster than AMF plants. This is another good evidence demonstrating the capability of drought-avoidance mechanisms associated with mycorrhizal plants.

Disease Resistance Apart from drought, plant diseases account for substantial global crop loss. Symbiont AMFs are good alternative to chemical fertilizers and biopesticides; they are able to stimulate and strengthen the host plant defence systems through the mycorrhiza-induced resistance (MIR), a form of induced systemic resistance (ISR) and disease priming (Fig. 1.2). Induced systemic resistance refers to the widespread expression of defence mechanisms in spatially separate parts of the plant, which are not under direct attack (Pieterse et al. 2014; Pieterse and Vanwees 2014). Arbuscular mycorrhizal fungi have been known to induce resistance in plants, as they have similar root invasion techniques as pathogens. Plants recognize microbial signature compounds such as bacterial flagellin or fungal hyphae, which are also referred to as pathogen- or microbial-associated molecular patterns (PAMPs). This plant recognition of PAMPs leads to PAMP-triggered immunity (PTI) (Zipfel 2008). The 'attack' on the roots of the plant by the AMF sends signal hormones to other parts of the plant to alert the plant about an invader. The defence mechanisms applied against AMF at the roots, that is, increased salicylic acid (SA) production, are then applied throughout other parts of the plant (Pieterse et al. 2014, Pieterse and Vanwees 2014).

Plant defence priming, which relies on the pre-conditioning of the host defence system by non-pathogenic AMF symbiont, potentiates the impacts of MIR. As the plant deploys some defences against the symbiont, there is an accumulation of defence signal molecules such as *MYC2* and mitogen-activated protein kinases

(MAPKs) within the plant (Pozo and Azcón-Aguilar 2007; Pieterse et al. 2014). With defence signals on "stand-by," the plant is in a primed state and able to respond to attack by pathogen or predator much faster and more efficiently than that in a non-primed state. Mycorrhiza-induced resistance relies on the jasmonic acid and ethylene signalling pathways, which respond by inducing resistance mechanisms against necrotizing pathogens and herbivorous insects (Jung et al. 2012).

Research by Song et al. (2011) has shown that priming maize plant defences with the AMF *Funneliformis mosseae* increases the plant's defences against the pathogen *Rhizoctonia solani*, the cause of sheath blight in maize plants. This resistance is conferred by enhanced production of plant antimicrobial 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4 H)-one (DIMBOA) as a result of MIR (Song et al. 2011). Mycorrhizal inoculation has also been proven to potentiate resistance against *R. solani* in potatoes, tomatoes and soybean (Wyss et al. 1991; Yao et al. 2003; Song et al. 2015).

1.2.1.3 Phytoremediation

Microorganisms are the key drivers of bioremediation processes, but their participation in remediation is usually in association with other organisms in the environment. Fungi are the primary decomposers of organic matter, and such decomposition may occur through interactions with plants (plant–microbe interactions) or in combination with other microbes (microbe–microbe interactions) (Göltenboth et al. 2006, Smith and Read 2008). Therefore, fungi such as ECM fungi have crucial roles to play in phytoremediation. ECM fungi are able to degrade low- and high-molecular-weight aromatic pollutants (Cairney and Meharg 2002; Bello-Akinosho 2018). An example of these interactions is the study conducted by Sarand et al. (1999), where a mycorrhizal fungus, *Suillus bovinus,* individually and in conjunction with *Pseudomonas fluorescens* and *Pinus sylvestris*, was involved in the biodegradation of m-toluate, a low-molecular-weight aromatic environmental pollutant. Further plant–microbe interactions with the host plant *Pinus sylvestris* showed that the ECM fungi *Paxillus involutus* and *Suillus variegatus* improve the mineralization of short-chain 2,4-dichlorophenol and *Suillus bovinus* are able to improve the uptake of 3-chlorobenzoic acid (Meharg et al. 1997; Dittmann et al. 2002). It is generally accepted that biodegradation of hydrocarbons becomes less effective as the hydrocarbons increase in molecular weight and branching (Peixoto et al. 2011; Martin et al. 2014).

In contrast to studies validating the biodegradative capabilities of ECM on organic contaminants, Genney et al. (2004) reported no effect of the ECM fungi, in association with Scots pine, on the mineralization of PAH naphthalene, while Joner et al. (2006) confirmed these results as they report ECM/Scots pines to reduce the degradation of anthracene, anthraquinone, chrysene and dibenz[a,h]anthracene. A similar observation was reported in a study in which hybrid poplar plants colonized by *Pisolithus tinctorius* were used to remediate a diesel-contaminated site. The study showed that ECM-inoculated poplar plants had reduced efficiency in the removal of diesel from the site in comparison to an uninoculated control (Gunderson et al. 2007). However, despite this outcome, the ECM-colonized plants were

reported to have greater whole-plant biomass and higher N and P concentrations in leaves than the uninoculated control. These results indicate that ECM conferred an amount of tolerance to poplar plants against the diesel contaminants. Such ability to tolerate PHC was also reported in studies relating to heavy metals. For instance, *Pisolithus tinctorium* improved growth of seedlings in a highly acidic mine soil containing heavy metals. Furthermore, in a laboratory study, the ability of *Pisolithus tinctorium* to withstand high concentrations of Al, Fe, Cu and Zn was demonstrated (Marx and Artman 1979; Tam 1995; Jentschke and Godbold 2000). With reference to these special attributes of ECM in the aforementioned examples, the stress-ameliorating effects of the ectomycorrhizal fungi on the host plant make it an ideal candidate for afforestation in polluted or disturbed soils (Bücking 2011).

1.2.2 Roles and Applications of Rhizobacteria in Agro-Ecosystems

Plants associate with a vast number of microorganisms, establishing relationships that drive many processes in the ecosystem, especially in the rhizosphere, which is a habitat for copious microorganisms including bacteria (Wu et al. 2009; Mendes et al. 2013). Rhizobacteria participate in several processes that are beneficial or detrimental to plants. Beneficial processes linked to the association between plants and rhizobacteria include improved nutrient acquisition, resistance to environmental stress and protection of plants against pathogens as well as improvement of metabolic and physiological processes in plants. Beneficial rhizobacteria involved in such processes are referred to as plant growth-promoting rhizobacteria (PGPR). On the other hand, some pathogenic bacteria are also found in the rhizosphere, which could have negative impact on plant health (Liu et al. 2010).

The PGPR are recognized non-pathogenic bacteria and have been categorized into two major types on the basis of their habitat, namely, extracellular PGPR (ePGPR) and intracellular PGPR (iPGPR). Extracellular PGPR exist in the rhizosphere or in spaces between the root cortex cells, while iPGPR are found within the root cells of plants. These PGPR are known to belong to various genera such as *Serratia, Bacillus, Allorhizobium, Paenibacillus, Actinomyces, Clostridium, Bradyrhizobium, Azoarcus, Azotobacter, Mesorhizobium, Enterobacter, Arthrobacter, Pseudomonas, Gluconacetobacter, Azospirillum, Caulobacter, Chromobacterium, Burkholderia, Micrococcus, Agrobacterium, Erwina, Flavobacterium* and *Rhizobium* (Bhattacharyya and Jha 2012; Gouda et al. 2017).

On the basis of the PGPR abilities to stimulate and improve plant growth, processes involved in such activities can be classified as direct or indirect methods. Direct plant growth-promoting methods include the ability of PGPR to enhance the availability of macronutrients such as nitrogen, phosphate and potassium in the rhizosphere to plants (Babu et al. 2015). This can be achieved through biological nitrogen-fixing abilities of PGPR, phosphate and potassium-solubilizing capabilities of the PGPR and production of phytohormones such as indole acetic acid, cytokinins, and gibberellic acid by PGPR. Indirect plant growth-promoting methods

deal with the capabilities of PGPR to inhibit lethal effects of rhizosphere-inhabiting plant pathogens on plants. These microorganisms improve plant productivity and development through the activation of useful plant enzymes to enhance physiological processes in plants and amplification of plants' ability to resist diseases and environmental stress (Wang et al. 2016). Production of siderophores, ethylene and antibiotics forms part of the indirect plant growth-promoting methods.

1.2.2.1 Plant Growth Promotion

Biological Nitrogen Fixation Nitrogen is a vital macronutrient in plant growth and development, but it is not accessible to most plants. Atmospheric nitrogen gas is transformed to ammonia by PGPR through nitrogen fixation. This form of nitrogen (ammonia) is utilizable by plants for productivity (Ahemad and Kibret 2014). Rhizobacteria that are capable of fixing atmospheric nitrogen include *Rhizobium etli, Rhizobium trifolii, Bradyrhizobium* sp., *Sinorhizobium meliloti* (Shamseldin 2013), *Azotobacter agilis, Azotobacter chroococcum, Azotobacter vinelandii* and *Klebsiella pneumoniae* (Kennedy and Bishop 2004). Biological nitrogen fixation forms a renewable source of nitrogen to crops and plant species. Complex enzymes, such as *nitrogenases,* catalyze the process of biological nitrogen fixation, and some genes responsible for the nitrogen-fixing activities include *nifH, nifD* and *nifK* (Souza et al. 2015).

Phosphate Solubilization Phosphorus is an essential macronutrient in metabolic and physiological processes in plants such as photosynthesis, biological oxidation and cell division (Gupta et al. 2012). It is also an important nutrient for plant growth and productivity. Unavailability of soluble phosphorus to plants limits their ability to perform these crucial functions, hence the need for soluble forms of phosphate (Sharma et al. 2013). Application of PGPR that are capable of solubilizing insoluble phosphate by discharging organic acids increases the availability of this element to plants thereby improving soil fertility and crop productivity (Souza et al. 2015). Some of the rhizobacteria that are capable of solubilizing insoluble P include *Serratia phosphoticum, Serratia marcescens, Thiobacillus ferrooxidans, Rhodococcus, Pseudomonas putida, Pseudomonas striata, Pseudomonas fluorescens, Pseudomonas calcis, Alcaligens* sp., *Citrobacter* sp., *Rhizobium meliloti, Gordonia* sp., *Phyllobacterium* sp., *Bacillus cereus, Bacillus subtilis, Bacillus mycoides, Bacillus pumilus, Arthrobacter* sp., *Xanthomonas* sp., *Enterobacter* sp., *Chryseobacterium* sp., *Azotobacter* sp., *Pantoea* sp., *Klebsiella* sp., *Achromobacter* sp., *Aerobacter aerogenes* and *Erwinia* sp. (Gupta et al. 2012; Sharma et al. 2013).

Potassium Solubilization Potassium is another macronutrient essential for plant growth and development. Deficiency of potassium in the rhizosphere has been associated with reduced root growth and crop productivity. Generally, there is low concentration of soluble potassium in the rhizosphere, and potassium has the capacity to form insoluble complexes when applied as an inorganic fertilizer (Gupta et al. 2015). Insoluble potassium is made available by PGPR through the production of

inorganic acids thus improving agricultural sustainability and aiding in the production of crops (Liu et al. 2012). Although many PGPRs have been linked to potassium solubilization, *Bacillus circulans, Bacillus edaphicus* and *Bacillus mucilaginosus* have been reported to be the most efficient potassium solubilizers (Meena et al. 2016). Other potassium solubilizers also comprise *Paenibacillus glucanolyticus, Burkholderia, Paenibacillus mucilaginosus* and *Enterobacter hormaechei* (Etesami et al. 2017).

Production of Phytohormones Various biochemical and physiological processes in plants are regulated by phytohormones. These hormones play a crucial role in controlling the response of plants to environmental stresses. The action of these hormones in response to environmental stimuli may be at the site of production of the hormones or in close proximity to the site (Fahad et al. 2015). In addition to the capability to stimulate plant growth and development, phytohormones may also act in defence of the plants against pathogens (da Costa et al. 2014). Such phytohormones include cytokinins, indole acetic acids (IAA) and gibberellins. Cytokinins are produced by PGPRs such as *Paenibacillus polymyxa,* and *Pseudomonas fluorescens, Enterobacter cloacae* and *Azospirillum brasilense* produce phytohormones like IAA, while gibberellins are produced by various bacteria including *Acetobacter diazotropicus, Bacillus pumilus* and *Bacillus cereus* (Kaymak 2010).

Production of Siderophores Siderophores are low-molecular-mass molecules that have strong attraction for iron – an essential nutrient for plant growth. Iron is involved in biological processes such as photosynthesis, respiration and chlorophyll production. It occurs in the form of insoluble complexes such as hydroxides and oxyhydroxides, which have low bioavailability. Siderophores solubilize iron in the rhizosphere by chelation thereby allowing its extraction from the environment. Secretion of siderophores by PGPR is their iron uptake strategy, which also benefits other organisms in the rhizosphere, especially plants (Ahemad and Kibret 2014; Ahmed and Holmström 2015). Plant growth-promoting rhizobacteria such as *Pseudomonas putida* and *Pseudomonas fluorescens* are known siderophore producers, which also protect plants against phytopathogens such as *Erwinia carotovora* and *Fusarium* sp. Other siderophore producers include *Pseudomonas cepacia, Enterobacter cloacae, Bacillus subtilis* and *Rhizobium meliloti* (Sayyed et al. 2013).

Aminocyclopropane-1-carboxylate (ACC) Deaminase Production Aminocyclopropane-1-carboxylate is a precursor of ethylene, and high concentrations of ethylene could hinder plant growth or even cause death. Production of ACC deaminase by PGPR enhances plant growth and productivity by reducing the quantity of ethylene in plants. These enzymes catalyze the metabolism of ACC to ammonia and α-ketobutyrate (Glick 2014). Absolute reduction of ACC in the environment could also protect plants against stress such as drought through the induction of water absorption from deep soil (Zhang et al. 2015).

1.2.2.2 Plant Protection

Antibiotic Production The synthesis of antibiotics to eradicate or decrease the growth of plant pathogens is a beneficial biocontrol characteristic of PGPR (Beneduzi et al. 2012; Gupta et al. 2015). For example, *Bacillus amyloliquefaciens* and *Bacillus subtilis* are known to produce an extensive range of antifungal and antibacterial antibiotics. *Pseudomonas aeruginosa* and *Pseudomonas fluorescens* are also antibiotic producers. These PGPRs repress the growth of plant pathogens by secreting an extracellular metabolite that hinders the growth of phytopathogens even at low concentration. Such metabolites include subtilin, sublancin, chlorotetain, rhizoctinins and surfactins (Goswami et al. 2016).

1.3 Plant–Microbe Interactions in the Phyllosphere

Unlike the microbiology of the rhizosphere, the phyllosphere and its associated microbiome have received less attention. However, in recent years, more investigations have been conducted on the phyllosphere microbiome (Vorholt 2012; Kirschner 2015; Remus-Emsermann and Schlechter 2018). The phyllosphere is generally considered a hostile environment for microorganisms due to fluctuating temperature and humidity, exposure to elevated levels of solar irradiation and heterogeneous availability of nutrients. Despite these challenges, the phyllosphere is colonized by numerous microbial communities comprising bacteria, archaea, fungi, protozoa and yeast (Andrews and Harris 2000; Whipps et al. 2008). The colonization of the phyllosphere is primarily through immigration of microorganisms from seeds, soil, water, air and animals (Vorholt 2012). Studies that have been conducted on phyllosphere microbiology have primarily focused on the understanding of plant–pathogen interactions due to the economic importance of such associations. Examples of these studies include analysis of pathogen colonization, spread, survival and mechanisms of pathogenicity (Wilson et al. 1999; Hirano and Upper 2000; Brandl et al. 2001). Nevertheless, of late, beneficial phyllosphere microorganisms have also been investigated with particular reference to involvement of the microbiota in plant protection and the promotion of plant growth (Rastogi et al. 2013; Senthilkumar and Krishnamoorthy 2017; Mashiane et al. 2017, 2018; Durand et al. 2018).

Leaf surfaces are a major entry point of microorganisms due to their large surface area and perhaps could be one of the largest microbial niches in the world. The cumulative, terrestrial leaf surface area is estimated to be about 6.4×10^8 km^2, and the colonization of such surfaces by bacteria contributes to a global phyllosphere bacterial population of approximately 10^{26} cells (Lindow and Brandl 2003). A majority of these bacteria are commensals and mutualists and could provide various ecosystem functions to the plant including competitive exclusion of pathogens, phytoremediation of toxic pollutants and cycling of important elements (Rastogi et al. 2013; Kembel et al. 2014; Bello-Akinosho et al. 2016, 2017) (Fig. 1.3). Some phyllosphere bacteria such as *Methylobacterium* species may be considered as plant growth-promoting bacteria (PGPB), which are sometimes referred to as 'plant probiotics' (Kwak et al. 2014). Phyllosphere bacteria may improve plant health by

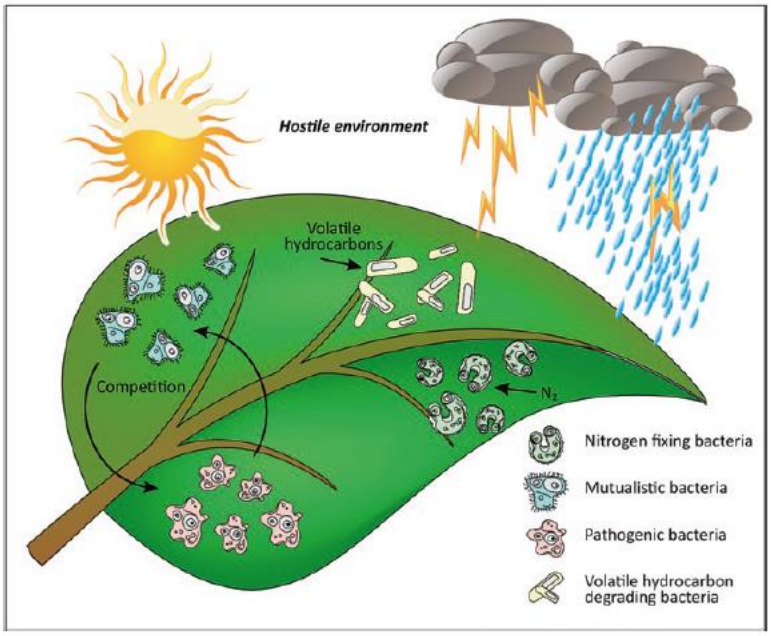

Fig. 1.3 Applications of phyllosphere–bacteria interactions in agro-ecosystems

increasing tolerance of the plant to stresses including frost-induced injury and drought stress (Lindow and Leveau 2002; Kumar et al. 2017). Furthermore, phyllosphere bacteria can influence plant growth using various mechanisms including the production of plant growth-promoting hormones, regulation of plant metabolic pathways and participation in increasing nutrient availability (Berlec 2012).

Although bacteria predominate the phyllosphere, other microorganisms such as fungi play key roles in plant eco-physiological functions. Similar to the roles played by bacteria in the phyllosphere, fungi are able to participate in competitive exclusion of pathogens as well as leaf litter degradation thereby contributing to soil organic matter with associated positive effects on plant growth (Fokkema and Van der Meulen 1976; Osono 2006; Voříšková and Baldrian 2013). Unlike phyllospheric bacteria and fungi, minimal information is available on applications of phyllospheric archaea. Studies on plant-associated archaea initially reported that these microorganisms are more widely distributed in the rhizosphere than in the phyllosphere (Knief et al. 2011). This is due to the elevated oxygen levels and environmental instability at the phyllosphere interface. However, in perennial plants, large numbers of archaea have been evidenced within phyllospheric plant tissues, referred to as the endosphere. For instance, Müller et al. (2016) attributed the archaeal population to constitute as much as 36% of the total endophytic microbial community of

Mediterranean olive tree leaves. Despite the high abundance of archaea in the plant microbiome, limited information is available on their functionality in the phyllosphere and archaea–plant interactions (Moissl-Eichinger et al. 2017).

1.3.1 Roles and Applications of Phyllospheric Microorganisms in Agro-Ecosystems

The numerous beneficial attributes associated with phyllospheric microorganisms motivate the application of these microorganisms for plant growth and environmental remediation. The recent rapid development of molecular and microscopic tools aid in unravelling the behaviour of phyllospheric microbes as well as the complexities of plant surfaces that these organisms inhabit (Singh and Kothari 2017; López-Mondéjar et al. 2017; Subudhi et al. 2018). Such information is pertinent for better understanding of plant–microbe relationships and maximizing applications of beneficial microorganisms in plant protection and bioremediation (Lindow and Leveau 2002).

1.3.1.1 Plant Growth Promotion

Phyllosphere microorganisms contribute to plant growth promotion by actively participating in nutrient cycling. Examples include volatile organic compound (VOC) production, N fixation (Freiberg 1998; Fürnkranz et al. 2008) and phosphate solubilization (Gupta and Sahoo 2010). Phyllospheric microorganisms emit VOCs, which have the potential to enhance plant growth and aid in plant stress resistance (Junker et al. 2011). Plants also emit VOCs that play a significant role in microbiome structure of the phyllosphere. This is primarily due to VOC potential as a source of carbon (Sy et al. 2005) and their antimicrobial effects (Junker et al. 2011). On the other hand, phyllosphere microorganisms inhabit the interface between the plant and the atmosphere; hence, these microorganisms are able to influence VOC production in the plant. This signifies the bidirectional relationship between plant VOC production and phyllosphere microbiota (Farré-Armengol et al. 2016).

1.3.1.2 Plant Protection

Plant pathogenic microorganisms negatively influence plant health thereby forming a major threat to global food security and ecosystem stability. Albeit agro-chemicals have been frequently utilized for plant pathogen control, this control method is gradually becoming less attractive due to their growing costs as well as a multitude of associated adverse environmental effects. Biological control of plant pathogens, a more attractive alternative to chemical control, has revolutionized the agricultural sector due to the study of the ecology of pathogens and antagonists (Compant et al. 2005). One such example is the biological control of fire blight disease of apple and pear using non-pathogenic phyllospheric bacteria. For infection to occur, the causal agent of fire blight, *Erwinia amylovora*, needs to increase its population size on the stigmatic surface of blossoms. The stigma is also colonized by other bacterial epiphytes that may have the ability to interact with and suppress the growth of *E.*

amylovora. These antagonistic bacteria such as *Pseudomonas fluorescens* A506 have been identified and are commercially available as biological control products for fire blight (Johnson and Stockwell 1998). They are sprayed onto the blossoms early in the season to enable pre-emptive competitive exclusion of the pathogen (Lindow and Leveau 2002). Recently, numerous studies have been conducted on the discovery, isolation and efficacy of antagonistic microorganisms for the control of plant diseases (Müller et al. 2016; Sartori et al. 2017).

Phyllospheric bacteria may also be used to prevent frost-induced injury. Ice nucleation-active (INA) bacteria are epiphytic bacterial species such as *Pseudomonas syringae* that contribute to frost injury of cold-sensitive plants (Lindow and Leveau 2002; Rostami et al. 2018). Frost injury is achieved by the presence of ice nucleation-active proteins (INAP) on the outer bacterial cell wall of INA bacteria, which facilitate inter- or intracellular ice formation in plant tissue. Ice formation in plant tissue is prevented in the absence of INA bacteria due to the ability of the plant to 'supercool' to temperatures below 0° to −12 °C without ice formation. This supercooling ability is reduced, in the presence of INA bacteria, where ice formation in the inter- or intracellular space of plants is evidenced at temperatures as high as 0 to −2 °C (Rostami et al. 2018). Furthermore, the temperature at which freezing occurs increases with the population size of the INA bacteria. Hence, the pre-emptive, competitive exclusion of INA bacteria with naturally occurring non-INA, phyllospheric bacteria has been proposed and tested as a method of frost control (Lindow and Leveau 2002). Initially, antagonistic bacterial products that were developed primarily targeted INA bacteria (e.g. Frostban®). However, subsequent products such as Blightban® were developed with the intention of alleviating frost injury and pathogen invasion. This was achieved by developing a dual-purpose product containing a bacterial antagonist that competitively excludes both INA bacteria and *E. amylovora*, the causative agent of fire blight of apples and pears (Skirvin et al. 2000; Lindow and Leveau 2002).

1.3.1.3 Bioremediation

Phytoremediation is a form of bioremediation in which higher plants are used in pollutant degradation or removal (Sorkhoh et al. 2010). Phytoremediation is usually achievable when pollutants are water soluble, but contributions from rhizospheric microorganisms are required when remediating soil containing water-insoluble pollutants (Ali et al. 2012). When microbes are involved, the contribution of plants is indirect, secreting root exudates that promote proliferation of pollutant-degrading, rhizospheric microbial populations (Ali et al. 2012). Although numerous studies have been conducted on the utilization of rhizospheric microorganisms for phytoremediation purposes (Radwan et al. 1995; Al-Awadhi et al. 2009; Bello-Akinosho et al. 2016), this technology is primarily targeted at decontamination of soils but not widely applicable for remediation of volatile hydrocarbons.

Phyllospheric microorganisms are well suited for the remediation of volatile/atmospheric hydrocarbon pollutants. Their abilities to remediate aliphatic and aromatic hydrocarbons (toluene, xylene and phenanthrene) have been reported in numerous studies (Sandhu et al. 2007; Scheublin et al. 2014; Sangthong et al. 2016).

Ali and colleagues (2012) showed, in their study, that the leaves of legumes harboured up to 9×10^7 cells/g of oil-utilizing bacteria. The potential of such phyllospheric microorganisms is very important for mitigation of the harmful effects of air pollution on the ecosystem. Environmentalists have now adopted an approach of utilizing these microorganisms, in association with their host plants, in bioremediation processes through their introduction (bioaugmentation) or enhancement of their growth (biostimulation) in polluted environments. One such study focused on the utilization of the toluene-degrading, phyllosphere bacterium, *Pseudomonas putida* TVA8 for the removal of airborne toluene. The bacterium was inoculated on *Azalea indica* leaves and resulted in the rapid decrease in toluene levels in the air in comparison to uninoculated plants (De Kempeneer et al. 2004).

1.4 Challenges in the Application of Plant–Microbe Interactions for the Benefit of Agro-Ecosystems

The use of plant–microbe interactions is essential for agricultural development and sustainability. However, some challenges are encountered during production, application or management of microbial formulations that contain plant growth-promoting microorganisms (PGPM). Such challenges include the following:

Climate Variation/Change About 50% of agricultural losses have been attributed to abiotic factors such as rise/fall in temperatures and reduced precipitation (Tyagi et al. 2014). These factors could also affect viability and adaptability of CAPBM. In addition, there is a possibility of compatibility challenges where products developed in a specific region may not meet the needs of plants in another region due to varying environmental conditions. This problem could be resolved by confirming compatibility of imported products before application.

Quality Control Variations in the content and efficacy of microbial formulations is a barrier to controlling the quality of CAPBMs. Inconsistency in the regulations of various countries concerning the safety of microbial strains in the environment and production of sub-standard products is another drawback for the use of CAPBMs to support agro-ecosystems. Local regulatory authorities should adopt regional, continental or other international standards and legislations to ensure consistency and proper quality management of CAPBM (Ochieng 2015).

Replication of Technology and Biofertilizer Storage One of the challenges of the application of CAPBM is difficulty in matching the results obtained in the laboratory with field results. For example, it has been reported that repeated subculture of ECM fungi on agar media, like other fungi, over a long period of time affects their natural ability to colonize host plants (Thomson et al. 1994). Fortunately, such problem could be overcome by inoculation onto and re-isolation from a compatible host (Thomson et al. 1994). Marx and Daniel (1976) showed that viability could be retained for a period of 1–3 years by storing ECM mycelia in sterile water at

5 °C. Other PGPMs exhibit similar loss of viability and biological activities during attempted replication of laboratory experiments in the field. In addition, improper storage of CAPBM or use of unsuitable carrier materials could affect the biological activities of associated microorganisms and may even result in decreased viability of PGPMs. Technological improvement of CAPBM is a potential solution to prolonging product shelf life.

Selectivity of PGPMs Commercially available plant beneficial microorganisms are generally specific in their functions. Some selective functions include nitrogen fixation, auxin and siderophore production, as well as phosphate and potassium solubilization. Application of unsuitable PGPMs could cause reductions in their efficiency when applied in the field unlike broad-spectrum chemical fertilizers, which are formulated in accordance to the basic requirements of plants to enhance productivity (Timmusk et al. 2017). Specificity is also a challenge when implementing ECM fungi as a CAPBM. Ectomycorrhizal fungal species have host-specific associations, which limit their beneficial effects to certain plant species, and as such these ECM-based products cannot be applied as biofertilizer on all ectomycorrhizal plants (Smith and Read 2008). Although, some species of ECM fungi such as *P. tinctorius* have a broad plant host range; hence, they have greater effectivity in field application (Martin et al. 2002; Brearley 2011). Further research including fungal and host plant genomic analyses could be undertaken to reveal mechanisms of fungi–host symbiosis aiding in the development of superior CAPBM products (Acioli-Santos et al. 2011).

Lack of Awareness Presently, adoption of CAPBM is not extensive due to lack of awareness and regulatory framework as well as the specificity of the available products. Awareness may be improved through government intervention, innovative policies and training programmes. This would aid farmers in the informed adoption of the CAPBM product, thereby ensuring wider usage. Subsequent increase in demand for CAPBM products would result in increased production, hence the need for proficiency of both supplier and user as well as investment into the production technology.

1.5 Conclusion

Globally, as climate change becomes inevitable, atmospheric CO_2 concentrations are expected to increase continuously during the twenty-first century. This will be accompanied by increase in temperature and alterations in precipitation patterns. Most of these climate-changing parameters will have major effects on the agro-ecosystem including plants, microorganisms and other members of this system. Proper understanding of this challenge requires more investigations about the potential applications of plant–microbe interactions, especially for adaptation and mitigation purposes. This will require more than laboratory experiments; hence, pot and field trial experiments should be prioritized. Extensive commercial adoption of

plant–microbe interactions will require special approaches to be undertaken (Timmusk et al. 2017). Perhaps, integrated -omics approaches and metabolic modelling hold the key to unravel the fundamentals of plant–microbe interactions in the future.

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