Fungal Biology

Ajar Nath Yadav · Shashank Mishra
Divjot Kour · Neelam Yadav
Anil Kumar *Editors*

Agriculturally Important Fungi for Sustainable Agriculture

Volume 1: Perspective for Diversity and Crop Productivity

Springer

Fungal Biology

Series Editors

About the Series

Fungal biology has an integral role to play in the development of the biotechnology and biomedical sectors. It has become a subject of increasing importance as new fungi and their associated biomolecules are identified. The interaction between fungi and their environment is central to many natural processes that occur in the biosphere. The hosts and habitats of these eukaryotic microorganisms are very diverse; fungi are present in every ecosystem on Earth. The fungal kingdom is equally diverse, consisting of seven different known phyla. Yet detailed knowledge is limited to relatively few species. The relationship between fungi and humans has been characterized by the juxtaposed viewpoints of fungi as infectious agents of much dread and their exploitation as highly versatile systems for a range of economically important biotechnological applications. Understanding the biology of different fungi in diverse ecosystems as well as their interactions with living and non-living is essential to underpin effective and innovative technological developments. This series will provide a detailed compendium of methods and information used to investigate different aspects of mycology, including fungal biology and biochemistry, genetics, phylogenetics, genomics, proteomics, molecular enzymology, and biotechnological applications in a manner that reflects the many recent developments of relevance to researchers and scientists investigating the Kingdom Fungi. Rapid screening techniques based on screening specific regions in the DNA of fungi have been used in species comparison and identification, and are now being extended across fungal phyla. The majorities of fungi are multicellular eukaryotic systems and therefore may be excellent model systems by which to answer fundamental biological questions. A greater understanding of the cell biology of these versatile eukaryotes will underpin efforts to engineer certain fungal species to provide novel cell factories for production of proteins for pharmaceutical applications. Renewed interest in all aspects of the biology and biotechnology of fungi may also enable the development of “one pot” microbial cell factories to meet consumer energy needs in the 21st century. To realize this potential and to truly understand the diversity and biology of these eukaryotes, continued development of scientific tools and techniques is essential. As a professional reference, this series will be very helpful to all people who work with fungi and should be useful both to academic institutions and research teams, as well as to teachers, and graduate and postgraduate students with its information on the continuous developments in fungal biology with the publication of each volume.

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Preface

Microbes are ubiquitous in nature. Among microbes, fungal communities play important roles in agriculture, environment, and medicine. These fungi are known to synthesize functional bioactive compounds, hydrolytic enzymes, and compounds for plant growth promotion and biocontrol agents for potential biotechnological applications in agriculture, medicine, industry, pharmaceuticals, and allied sectors. Vast fungal diversity has been found to be associated with plant systems. Fungi associate with plant systems in three ways: epiphytic, endophytic, and rhizospheric. The fungi associated with plant systems play an important role in plant growth, crop yield, and soil health. The fungal communities are the key components of soil–plant systems, where it is engaged in an intense network of interactions at the rhizosphere, endophytic, and phyllospheric level, areas, emerging as an important and promising tool for sustainable agriculture. The fungal communities help to promote plant growth directly or indirectly through plant growth promoting attributes. These PGP fungi could be used as biofertilizers and biocontrol agents replacing chemical fertilizers and pesticides in environmental eco-friendly manners for sustainable agriculture and environments.

The present book on "*Agriculturally Important Fungi for Sustainable Agriculture, Volume 1: Perspective for Diversity and Crop Productivity*" covers biodiversity of plant associated fungal communities and their role in plant growth promotion, mitigation of abiotic stress, and soil fertility for sustainable agriculture. This book will be immensely useful to the biological sciences, especially to microbiologists, microbial biotechnologists, biochemists, researchers, and scientists of fungal biotechnology. We are highly obliged to the leading scientists who are extensive, in-depth experience and expertise in plant–microbe interaction and fungal biotechnology took the time and efforts to make these outstanding contributions. Each chapter was written by internationally recognized researchers and scientists so that the reader are given an up-to-date and detailed account of the knowledge of the fungal biotechnology and innumerable agricultural applications of fungal communities.

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The editor Dr. Ajar Nath Yadav is grateful to his Ph.D. research scholars Tanvir Kaur, Rubee Devi, Divjot Kour, Kusam Lata Rana and colleagues for their support, love, and motivation in all his efforts during this project.

We are very sure that this book will be of great interest to scientists, graduates, undergraduates, and postdocs interested in fungal biology and biotechnology.

Contents

Editors

About the Editors

Ajar Nath Yadav is an Assistant Professor (Sr. Scale) in the Department of Biotechnology, Dr. Khem Singh Gill Akal College of Agriculture, Eternal University, Baru Sahib, Himachal Pradesh, India. He has 5 years of teaching and 11 years of research experience in the field of Microbial Biotechnology, Microbial Diversity, and Plant–Microbe Interactions. Dr. Yadav obtained doctorate degree in Microbial Biotechnology, jointly from IARI, New Delhi and BIT, Mesra, Ranchi, India; M.Sc. (Biotechnology) from Bundelkhand University and B.Sc. (CBZ) from the University of Allahabad, India. Dr. Yadav has 176 publications with h-index of 37, i10-index of 76, and 3145 citations (Google Scholar). Dr. Yadav has published 115 research communications in different international and national conferences. Dr. Yadav has got 12 Best Paper Presentation Awards, and 01 Young Scientist Award (NASI-Swarna Jayanti Purskar). Dr. Yadav received the "Outstanding Teacher Award" in 6th Annual Convocation 2018 by Eternal University, Baru Sahib, Himachal Pradesh. Dr. Yadav has a long-standing interest in teaching at the UG, PG, and PhD level and is involved in taking courses in microbiology and microbial biotechnology. Dr. Yadav is currently handling two projects. Presently, he is guiding 05 scholars for Ph.D. degree and 01 for M.Sc. dissertations. He has been serving as an editor/editorial board member and reviewer for different national and international peer-reviewed journals. He has lifetime membership of Association of Microbiologists in India and Indian Science Congress Council, India. Please visit https://sites.google.com/site/ajarbiotech/ for more details.

Shashank Mishra is presently working as Scientist "C", Biotech Park, Lucknow, Uttar Pradesh, India. He obtained his doctorate degree in Science "Industrial Biotechnology" in 2015, from Birla Institute of Technology, Mesra, Ranchi, India; M.Phil. (Biotechnology) in 2008 from Alagappa University, Tamil Nadu; M.Sc. (Botany) in 2005 from Dr. R.M.L. University, Ayodhya; M.Sc. (Biotechnology) in 2004 from Barkatullah University, Bhopal, and B.Sc. (Botany and Chemistry) in 2001 from Dr. R.M.L. University, Ayodhya, India. He has made pioneering contributions in the area of Microbial Biotechnology; Natural product synthesis and Environmental Microbiology for food, pharmaceutical, and Human Health. In his credit 21 publications [06 research papers, 02 review articles, 03 books, and 10 book chapters] in different reputed international and national journals and publishers with 82 citation, h-index-05, and i10-index 04 (Google Scholar). He has reported first time with high concentration of phenolic compounds by optimizing various parameters and published in peer-reviewed and refereed international journals. He has published 16 abstracts in different conferences/symposiums/workshops. He has presented 16 papers presentation [12 poster + 04 oral] in conferences/symposiums and got 01 best poster presentations Award, Dr. Mishra has contributed in organizing 07 conference/workshops. He has deposited 03 nucleotide sequences to NCBI GenBank databases: in public domain. Dr. Mishra and group have isolated and characterized 03 microbes (bacteria and microalgae) from Tulsi and paddy plantation site and transformed ferulic acid into value-added phenolic compounds, viz., vanillin, vanillic acid, and 4-vinyl-guaiacol. He has a long-standing interest in teaching at the UG, PG, and Ph.D. level and is involved in taking courses in industrial biotechnology, bioprocess engineering and technology, environmental biotechnology, environmental microbiology, industrial microbiology, microbial biotechnology and techniques in microbiology and biotechnology. He is reviewer in 06 international journals including BMC Microbiology, Indian Phytopathology, PLOS One, Scientific Reports and Archive of Phytopathology and Plant Protection, and 3 Biotech. He has lifetime membership of Association of Microbiologists of India (AMI) and Vigyan Bharti (VIBHA).

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Neelam Yadav is currently working on microbial diversity from diverse sources and their biotechnological applications in agriculture and allied sectors. She obtained her post graduation degree from Veer Bahadur Singh Purvanchal University, Uttar Pradesh, India. She has research interest in the area of beneficial microbiomes and their biotechnological application in agriculture, medicine, environment, and allied sectors. In her credit 35 research/review/book chapters publication in different reputed international, national journals and publishers. She is editor of 02 books in Elsevier, 03 in CRC press, Taylor & Francis, and 03 in Springer. She is the Editor/associate editor/reviewer of different international and national journals including Plos One, Extremophiles, Annals of Microbiology, Journal of Basic Microbiology, Advance in Microbiology and Biotechnology. She has lifetime membership of Association of Microbiologists in India, Indian Science Congress Council, India, and National Academy of Sciences, India.

Anil Kumar is Director, Education, Rani Lakshmi Bai Central Agricultural University, Near Pahuj dam Gwalior Road, Jhansi (UP). He has 30 years of research, teaching, and administrative experience in various capacities. He had worked as Professor & Head (2006–till date), Associate Professor (2003–2006), and Assistant Professor (1993–1999), Dept. of Molecular Biology & Genetic Engineering, G. B. Pant University of Agriculture & Technology, Pantnagar. He has to his credit more than 200 publications including research papers, reviews, and chapters contributed to books, popular articles, books/bulletins/manuals. His research interests focus on diverse but specific areas of agricultural importance at national and international level employing the tools and techniques of molecular biology and immunology. Dr. Kumar has strengthened the area of molecular plant pathology, for combating the Karnal bunt which is an economically important disease of wheat, he followed three approaches, viz., Plant disease surveillance through molecular/immunological diagnostics; Pathogen Indexing Programme through Molecular Pathotyping, and Characterization of disease resistance and Pathogenesis through Molecular signaling investigating the role of MAP kinases and Cystatin gene families as candidate genes. It was postulated that stoichiometric balance of cystatin and cysteine protease might be contributing to disease resistance and susceptibility. Dr. Kumar has filed several patents on synthesis of nano delivery vesicles for facilitation of uptake of fat soluble vitamins, nano-curcuminoids for better bio-availability, and nano-iron pro-booster technology for agronomic bio-fortification. His pioneer research work has been highlighted by several magazines like NATURE and published in several international journals of repute with citation index: >2398, h-index 27, and i10 index 82. He has been an outstanding teacher and researcher who is credited with many awards and recognitions, viz., Dr. Radhakrishnan Best Teacher Award, INSA Best Teacher Award, Dr. C. Subramaniam Outstanding Teacher Award, Outstanding Faculty Recognition, Dr. B.B. Singh Outstanding Researcher Award, and also conferred three times "Governor's Award" for best research in the year 2015, 2017, and 2019 from different organizations including university ICAR, INSA, and DBT.

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Chapter 1
Agriculturally Important Fungi: Plant–Microbe Association for Mutual Benefits

Fatma Ahmed Abo Nouh, Hebatallah H. Abo Nahas, and Ahmed M. Abdel-Azeem

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1.1 Introduction

Plants represent a very dynamic system, reflecting a great capacity for adaptation in constantly fluctuating surroundings. This ability is particularly advantageous in the areas that are prone to intensive agriculture or biotic or abiotic vagaries (Bhandari and Garg 2017). Plants are exposed to huge numbers of microorganisms that are present in the top soil and are found on leaves and stems (Sivakumar and

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Thamizhiniyan 2012). Plant–microbe interactions are an extensively studied area and date back to the nineteenth century. The spectrum of plant–microbe interactions is highly complex, comprising of phylogenetically diverse microbial species (Hirsch 2004) as plants are constantly interacting with a range of microbes both in the rhizosphere and within the plant itself (Badri et al. 2009; Evangelisti et al. 2014). Plant–microbe interactions play a vital role to ensure sustainability in agriculture and ecosystem restoration (Badri et al. 2009). Plant–microbe interaction is a mode of communication between plants and microbes which is initiated by the secretion of different signaling molecules (Rastegari et al. 2020a, b; Verma et al. 2017). One of the important questions of communication pathways is how the plant distinguishes a microbial mutualist from pathogen. It has been reported that during the course of evolution, plants have evolved unique and sophisticated defense mechanism that involves innate immune system consisting of two classes of immune receptors that recognize the presence of nonself molecules both inside and outside of host cells (Jones and Dangl 2006). Encounter with nonself molecule evokes powerful immune responses which in turn prevents the multiplication of microbial pathogens. An increasing number of pattern recognition receptors have been identified on the plant cell surface during the past few decades (Boller and Felix 2009).

Microbial communities affect the plant physiology directly or indirectly, in a positive or negative manner, by various interactions like mutualism, commensalism, amensalism, and pathogenic consequences (Yadav et al. 2017, 2020). In plants, commensalism or mutualism is one of the most common interactions found (Campbell 1995). The interactions may be categorized as positive, negative, or neutral which largely depends on the nature of microorganisms associating the host (Abhilash et al. 2012). Positive interactions stimulate plant growth by conferring abiotic and/or biotic stress tolerance and help the plants for the revitalization of nutrient-deficient and contaminated soils. Negative interactions involve host–pathogen interactions resulting in many plant diseases and adverse effects and host life (Akram et al. 2017). Moreover, some microbes reside in the soil surrounding the plant roots just to obtain their nutrition from root exudates. They do not influence the plant growth or physiology in a positive or negative way, thus forming neutral interactions (Akram et al. 2017).

Mutualism is an obligatory or highly specific interaction between two populations in which both of them benefit from each other. It usually required close physical connection in which both partners may act as if they are one. When they exist separately, the physical tolerance and metabolic activities will be different for each single symbiont (Leung and Poulin 2008). Boucher et al. (1982) identified four key types of mutualism: dispersal, pollination, nutrition, and protection. Community-level effects of nutritional mutualisms, such as mycorrhizal fungi N-fixing bacteria (Hartnett and Wilson 1999) may depend on the degree to which benefits are private and whether the mutualism enhances the dominance of a single (or few) species to the detriment of others. Finally, protection mutualisms may be more likely to have strong community-level effects than other types of mutualism because they are inherently indirect interactions that require the involvement of at least three species, rather than a simple pair such as endophytes (Rudgers and Clay 2008).

Mutualism could be classified into different types according to partner's selection and function or purposes of the relationship. Mutualism according to the partner's selection: (1) obligate mutualism occurs when both microorganisms live together in close proximity, and both species cannot survive without its mutualistic partner. (2) Facultative mutualism: it occurs when one of the two partners can survive without its mutualistic partner by itself in some conditions. Mutualism according to interaction purposes: (1) Trophic mutualism: it is also called resource–resource interactions. It is a type of mutualistic association, which comprises the exchange of nutrients between two species. (2) Defensive mutualism: it is also called service–resource relationships. It appears when one organism provides shelter or protection from predators or pathogens, while the other provides food. (3) Service–service mutualism: it appears when one species receives service from its partner in return for transporting another service to the other organism (Selim and Zayed 2017).

Mutualistic relationship such as those formed with nitrogen-fixing bacteria (van Rhijn and Vanderleyden 1995; Richardson et al. 2000; O'Hara 2001; Zhang et al. 2012; Selim and Zayed 2017; Suman et al. 2016), mycorrhizal fungi (Wu et al. 2013; Zayed et al. 2013; Manaf and Zayed 2015; Sengupta et al. 2017), endophytes (Hilszczańska 2016; Arora and Ramawat 2017; Jain and Pundir 2017; Lata et al. 2018; Khare et al. 2018; Rana et al. 2019c). Most of the plant–microbe interaction research in the past has focused on the ancient symbiosis between plants and arbuscular mycorrhizae (Parniske 2008), nitrogen fixation by rhizobia within the nodules of legume roots (Oldroyd et al. 2011) and pathogenesis, and management of plant diseases by natural antagonistic microorganisms (Heydari et al. 2004; Sang et al. 2013). However, the role of endophytes that reside in plants is yet to be explored to its fullest potential. Endophytic microorganisms and their role in crop health are now attracting great interest from researchers (Jain and Pundir 2017; Kour et al. 2019c; Rana et al. 2019a; Suman et al. 2016; Yadav 2019b).

1.2 Plant-Symbiotic Nitrogen Fixation Association

There are two main symbiotic nitrogen-fixation systems: those involving symbioses between legumes and Proteobacteria (e.g., *Bradyrhizobium* spp. and *Rhizobium* spp.), and those between actinorhizal plants and actinomycetes (e.g., *Frankia* spp.). Both systems can convert gaseous nitrogen to ammonia in a process known as nitrogen fixation. The reaction is catalyzed by the nitrogenize enzyme complex which comprises two enzymes, a dinitrogen reductase and a dinitrogenase (Richardson et al. 2000). The bacteria *Rhizobium* and *Bradyrhizobium* (collectively known as rhizobia) and the actinomycetes (filamentous bacteria) *Frankia* form nodules on plant roots and are major contributors to symbiotic nitrogen fixation. The nitrogen-fixing bacteria provide the plants with nitrogenous compounds, while in return the plants provide the nitrogen-fixing bacteria with carbohydrates. This mutualistic association improves plant growth and health (Selim and Zayed 2017; Kour et al. 2020; Rana et al. 2020).

1.2.1 Nitrogen Fixing in Legumes

Rhizobia are motile, rod-shaped, Gram-negative bacteria with polar or subpolar flagella. They live in the soil and, almost exclusively, form nodules on roots of members of one of the three families of legumes. Nodule-forming bacteria (rhizobia) require inorganic nutrients for metabolic processes to enable their survival and growth as free-living soil saprophytes and for their role as the nitrogen (N)-fixing partners in legume symbioses (Rana et al. 2019c; Yadav 2018). Nitrogen-fixing pasture and pulse legumes are important for maintaining productivity in many agricultural systems (Graham and Vance 2000). A key benefit from using symbiotic legumes in agriculture is the fixation of atmospheric N by the rhizobia located in nodules formed on legume roots. Nitrogen fixation is strongly inhibited in the presence of oxygen so part of the function of the nodule is to provide an anaerobic environment in which nitrogen fixation can take place. Anaerobic conditions are achieved by excluding oxygen from the central tissue of the nodule (O'Hara 1998).

Nodules are globose to elongate outgrowths of plant tissue which vary in length from a few millimeters to a few centimeters. They do not develop near the root tips, but are abundant on older parts of the root system. The morphology of nodules is determined by the host, not the symbiont, which occurs within host cells in the central tissue of the nodule. The symbionts occur singly or in small groups within membrane-bound vacuoles. They are called bacteroids to distinguish them from bacteria outside the host cell because they are often much larger and may develop branches so they are Y' or 'X shaped (O'Hara 2001). Rhizobia are classically defined as symbiotic bacteria that invade the roots and stems of leguminous plants to fix nitrogen (van Rhijn and Vanderleyden 1995). It is a synthesis of NH_4^+ (a plant usable form of N) using atmospheric N_2 (plant non-usable form of N) by rhizobia in nodules of leguminous plants. The important nitrogen-fixing rhizobia genera in legumes are about 30 named species of nodule bacteria among the 6 accepted genera of *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium,* and *Sinorhizobium* of the family Rhizobiaceae (Young 1996). The majority of symbiotic legumes used for agriculture and forestry are nodulated by species of the genera *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium,* and *Sinorhizobium* (O'Hara 2001). In agricultural settings, perhaps 80% of the biologically fixed N comes from family Rhizobiaceae in association with the leguminous plants. *Rhizobium* and *Bradyrhizobium* establish symbiotic associations with roots in leguminous plants such as soybean, pea, peanut, and alfalfa, convert N_2 into ammonia, and make it available to the plants as a source of N (Badawi et al. 2011). Among the legumes (Fabaceae), of which approximately 18,000 species have been described, the occurrence of nodulation varies considerably among subfamilies. There are successful nodulation by the *Rhizobium* strain TAL 1145 on *Acacia farnesiana, Calliandra calothyrsus, Gliricidia sepium,* several species of *Leucaena, Mimosa invisa, M. pudica,* and *Sesbania grandiflora* (Richardson et al. 2000).

1.2.2 Nitrogen Fixing in Actinorhizal Plants

Besides rhizobia, many *Frankia* species have also been reported to form nodules in non-leguminous actinorhizal plants for N_2 fixation (Zhang et al. 2012). At least 194 plant species in 24 genera are nodulated by actinomycetes in the genus *Frankia* (Frankiaceae). These "actinorhizal" plants are woody, dicotyledonous angiosperms in the Betulaceae, Casuarinaceae, Coriariaceae, Datiscaceae, Elaeagnaceae, Myricaceae, Rhamnaceae, and Rosaceae (Benson and Silvester 1993). They are typically early successional plants on nutrient-poor sites. Many species are widely used in afforestation (including agroforestry) and agriculture (Richardson et al. 2000). At least the following actinorhizal species are important invaders of natural systems: *Casuarina equisetifolia, Elaeagnus angustifolia, E. umbellata, E. pungens,* and *Myrica faya* (Richardson et al. 2000). *Frankia* strains exhibit various degrees of host specificity. Actinorhizal are much larger than legume nodules, often measuring several centimeters across. They are essentially infected lateral roots which branch profusely and have very restricted apical growth, resulting in long-lived, coral-like structures (Benson and Silvester 1993). It is clear that, as with legumes, there are differences between actinorhizal taxa in their ability to form associations with local microsymbiont. Alders are nodulated wherever they are transplanted throughout the world, including places where they have no natural presence (Clawson et al. 1997; Yadav et al. 2018a, b).

1.3 Plant–Mycorrhizas Association

Mycorrhizae are highly evolved soil fungi involved in tripartite interaction mutualistic associations amid soil and plant. The associations formed by Glomeromycota fungi in plants usually colonize in arbuscules and often vesicles, thus known as arbuscular mycorrhiza (AM) and vesicular-arbuscular mycorrhizas (VAM). These are members of Zygomycetes, Ascomycetes, and Basidiomycetes classes of fungi kingdom (Morton 1988; Morton and Bebtivenga 1994). The common mycorrhizal associations are vesicular-arbuscular mycorrhizas (VAM): zygomycetous fungi produce arbuscules, hyphae, and vesicles within root cortex cells, ectomycorrhizal (ECM): basidiomycetes and other fungi form a mantle around roots and a Hartig net between root cells, orchid mycorrhizas: fungi produce coils of hyphae within roots (or stems) of orchidaceous plants, and ericoid mycorrhizas: fungi have hyphal coils in outer cells of the narrow "hair roots" of plants in the Ericales (Prasad 2017).

AM fungi found in rhizosphere and associated with several vascular plants have tremendous contribution in sustainable agriculture as well as agricultural ecosystems management (Kour et al. 2019a, b). The beneficial effects of indigenous AM fungi on the nutrition replenishment for plants depend on both the abundance and type of fungi present in the soil (Prasad and Gautam 2005; Prasad 2005). AM fungi are the obligate biotrophs that have been documented to form symbioses with the roots of more than 80% of terrestrial plant species (except in the plants belonging to families Amaranthaceae, Brassicaceae, Proteaceae, Commelinaceae, Polygonaceae, Cyperaceae, Juncaceae, and Chenopodiaceae). They are ubiquitous soilborne fungi, whose origin and divergence dates back to over 450 million years (Redecker et al. 2000). AM fungi belong to the phylum Glomeromycota (Bhandari and Garg 2017). In general, it has been estimated that approximately 20% C of net primary productivity is allocated to AM fungus (Fellbaum et al. 2014; Bücking and Kafle 2015) which is used to maintain and extend its hyphal network in the soil and in turn provide a majority of the plant nutrients (Leake et al. 2004). There are mutualistic association among mycorrhizal fungi and plant roots, in which plants provide fungus with carbohydrates and offer it protection (Yadav et al. 2019a, b, c). In turn, the fungus increases the surface area of plant roots for absorbing water, nitrogenous compounds, phosphorus, and other inorganic nutrients (e.g., phosphate) from the surrounding soil and delivers them to the plant which improves plant growth and health (Zayed et al. 2013).

1.3.1 Examples of Specific Activities of AMF

AMF increase seed yield than the controlled groups of flax seeds, and it depends on status of nutrient, management, and type of soil. The other beneficial role of AMF is to control root pathogens and their hormonal production that has higher potential to withstand synergistic interaction and water stress (Thompson 1994). Also, mycorrhizal fungi shelter plant roots from invasion by soilborne root-infecting pathogens. Endomycorrhizal symbiosis increases plant performance through improving their tolerance to different environmental stresses, which may be biotic, e.g., pathogen attack, or abiotic (e.g., drought, salinity, and heavy metal toxicity) (Garg and Chandel 2010; Garg and Pandey 2015), or presence of organic pollutants and also enhancing soil structure through formation of hydro-stable aggregates essential for good soil structure (Manaf and Zayed 2015). In addition, growing evidence indicates that association with AM fungi can improve overall plant growth and reproducibility by improving root length, leaf area, plant biomass, plant tissue hydration, and nutrient uptake under water-deficit condition (Bhandari and Garg 2017).

Ruth et al. (2011) estimated that about 20% of root water uptake taken by roots of mycorrhizal barley plants is caused by the presence of fungal mycelium. Gholamhoseini et al. (2013) stated that inoculation sunflower plant with *G. mosseae* improved availability of P, thus minimizing the impact of stress on seed oil percentage and oil yield. Studies have further depicted that AM-mediated alleviation of drought stress could also be allied with enhancement observed in the activities of antioxidants such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) in plants (Wu and Zou 2010; Baslam and Goicoechea 2012). AM inoculation can also modulate plant water status by accumulating osmolytes such as free amino acids (FAA), Pro, GB, SS, and organic acids (Garg and Baher 2013; Evelin and Kapoor 2014) which not only lower down osmotic potential but also permit cells to maintain turgor-related processes (Ruiz-Lozano et al. 2012). Mycorrhizal inoculations enhance root hydraulic conductivity (Smith et al. 2010) by altering the morphology of root in a structural, spatial, quantitative, and temporal manner which not only results in production of greater root system and better root system architecture (RSA) in mycorrhizal plants (Bhandari and Garg 2017). In addition to K+, Ca2+, ERM of AM fungi, displays the ability to proliferate and exploit the rhizospheric area, thus stimulating the uptake of other mineral components including N, P, Mg, Cu, Fe, and Zn, thereby alleviating salt-induced mineral deficiency (Hajiboland 2013; Garg and Pandey 2015). Several studies have validated that AM fungi play a vital role in improving growth and productivity of host plants in metal-contaminated soils (Garg and Bhandari 2014; Nadeem et al. 2014). In addition, more than 30 species of AM fungi have been identified in contaminated soils worldwide and some at high frequencies, such as *Paraglomus occultum, G. clarum, G. intraradices*, and *Scutellospora pellucida* (Bhandari and Garg 2017).

1.4 Plant–Endophyte Association

The interrelationship that exists between host plant and its endophyte is considered as “balanced antagonism”—a cohabitation in which host plant gains resistance against pathogenic organisms and phytophagous insects and its overall growth or biomass quality improves (Rana et al. 2019a). In most cases, various bioactive metabolites have been involved (Chowdhary et al. 2012; Kumar and Kaushik 2013). Numerous fitness benefitting factors conferred by microbes inhabiting inside host plants. These benefitting attributes hold a huge promise in sustainable agriculture and disease management of plants (Kaul et al. 2012; Kumar and Kaushik 2013).

1.4.1 Fungal Endophyte

Research on fungal endophytes in various plants has progressed significantly. Fungal species that were majorly reported as endophytes in agricultural crops include *Piriformospora indica* (Varma et al. 1999), *Trichoderma* spp. (Romao-Dumaresq et al. 2012; Sharma et al. 2019), *Epicoccum nigrum* (Fávaro et al. 2012), *Penicillium* spp.*, Alternaria, Cladosporium, Fusarium* spp. (Paul et al. 2012), *Fusarium oxysporum* (Kim et al. 2007), *Chaetomium globosum, Cladosporium cladosporioides* (Naik et al. 2009), *Aspergillus, Curvularia, Gilmaniella, Arthrobotrys foliicola* (Zakaria et al. 2010), *Acremonium zeae, Aspergillus flavus, A. niger, Alternaria alternata, Colletotrichum graminicola, Fusarium verticillioides, Saccharomyces cerevisiae, Trichoderma koningii* (Oldroyd et al. 2011), and others. Entomopathogens such as *Beauveria bassiana* and *Paecilomyces spp.* were also reported as endophytes in cotton and tobacco (Ek-Ramos et al. 2013).

Endophytic fungi living asymptomatically in plant tissues may present in almost all plants (Saikkonen et al. 1998). One species of an endophyte may be associated with many plant species, and many species of endophytes may be present in the same species (Rana et al. 2019a). Some endophytes remain as latent in the host plant, while others may interact with other endophytes, pathogenic or non-pathogenic (Zabalgogeazcoa 2008). Endophytes are known to provide various types of protections to their host plant, viz. endurance to grow in hot springs, deter herbivores by producing toxic alkaloids in grasses, and provide protection from pests in dicots (Zhang et al. 2006). Colonization by endophytic fungi promotes plant growth by protecting against several fungal and bacterial borne diseases, improving the ecological adaptation abilities of the host by providing tolerance to counteract against biotic and abiotic stresses (Schulz and Boyle 2005; Rana et al. 2019a, b; Yadav 2019a), production of phytohormone is also considered as a significant contribution to enhancement of plant growth (Zhou et al. 2014) and nutrients uptake (Zhang et al. 2013; Jain and Pundir 2017).

1.4.2 Bacterial Endophyte

Bacterial endophytes are widely present in agricultural crops and include *Serratia* spp., *Bacillus* spp.*, Enterobacter* spp.*, Agrobacterium radiobacter, Burkholderia gladioli, B. solanacearum* (McInroy and Kloepper 1995), *Pseudomonas putida* (Aravind et al. 2009), *P. fluorescens* (Ramesh et al. 2009), *Achromobacter xylosoxidans* (Forchetti et al. 2010), *P. aeruginosa* (Paul et al. 2013), *Micrococcus spp., and Flavobacterium* spp. (UmaMaheswari et al. 2013), *Acetobacter diazotrophicus, Herbaspirillum seropedicae, H. rubrisubalbicans* (Varma et al. 2017). Utmost bacterial endophytes interact with plants in a biotrophic and mutualistic association (Hallmann et al. 1997; Kobayashi and Palumbo 2000). They are also associated with the exchange of nutrients, enzymes, functional agents, and signals (Hardoim et al. 2015). Bacterial endophytes colonize above (vegetation) and beneath soil (root) host tissues establishing long-haul natural associations, without doing substantive harm to the host (Hallmann et al. 1997; Hardoim et al. 2015).

Endophytic bacteria provide a large array of beneficial effects to their host plant. It promotes plant growth by producing plant growth-enhancing substances such as indole acetic acid IAA (Naveed et al. 2015), cytokinins CK (Garcia de Salamone et al. 2001), gibberellic acid GA (UmaMaheswari et al. 2013), and improving nutrient absorption, including nitrogen fixation (Mirza et al. 2001). Besides growth enhancement, endophytic bacteria also benefit the host plant by enhancing adaptation for abiotic or biotic stress via phytohormone signaling. The endophytic bacteria get advantage of being close to the host and protected from the harsh external environment (Sturz et al. 2000). Besides PGP activities, the anti-plant pathogenic activities of these bacterial endophytes are also well documented (Varma et al. 2017). It produces a wide spectrum of compounds such as antibiotic, exoenzymes, siderophores, and other antimicrobial compounds which can suppress the growth of pathogens and act as a biocontrol agent (Brader et al. 2014; Wang et al. 2014). It has found to be stimulating an underlying pathogen defense mechanism, called as induced systemic resistance (ISR) that provides an increased level of protection to a wide variety of pathogens (Pieterse et al. 2014).

1.4.3 Examples of Specific Activities of Endophytes

Herbivory is a well-manifested mechanism exhibited by endophytes that protect plant species from herbivores. Several direct and indirect effects of alkaloids produced by endophytes are witnessed. For example, the endophyte, *Neotyphodium occultans* when present in neighboring *Lolium multiflorum* has reduced the aphid infestation in *Trifolium repens* plants. This phenomenon can be described as association protection of non-host plants due to changes in host-volatile compounds which is an indirect effect (Parisi et al. 2014). Direct effects of alkaloids by endophytes in host plants are a common phenomenon as in *Fescue* grass (by the endophytes *Neotyphodium* spp. and *Epichloe* spp.), wherein the host plant leaves are protected from herbivores by the production of alkaloid, loline, produced by mutualistic fungal endophytes (Roberts and Lindow 2014). Secondary metabolite like colletotric acid, isolated from the endophytic fungus *Colletotrichum gloeosporioides*, dwelling in *Artemisia annua* (Zou et al. 2000), a Chinese traditional herb, was shown to have activity against pathogenic plant fungi and human pathogenic bacteria (Lu et al. 2000).

This Chinese traditional herb has already been reported to produce artemisinin (an antimalarial drug). *Pestalotiopsis sp.* an endophyte of *Rhizophora mucronata*, a mangrove, produced pestalotiopen A, exhibiting activity against *Enterococcus faecalis* (Hemberger et al. 2013). *Phomopsis spp.* occurring as endophytes on different host plants produces several chemically diverse bioactive compounds. *Phomopsis longicolla*, associated with mint plant *Dicerandra frutescens*, was found to produce dicerandrol A, B, and C with antimicrobial activity exhibiting zones of inhibition of 11, 9.5, and 8.0 mm against *B. subtilis* and 10.8, 9.5, and 7.0 mm against *S. aureus*. Similarly, *Phomopsis longicolla* strain C81, associated with seaweed *Bostrychia radicans*, produced dicerandrol C active against *S. aureus* and *S. saprophyticus* (Wagenaar and Clardy 2001).

Endophyte-mediated induction of resistance to plant diseases is also reported. In sunflower, resistance to stem rot caused *by Sclerotium rolfsii* is reported with the endophytes *Penicillium citrinum* LWL4 and *Aspergillus terreus* LWL5 (Waqas et al. 2015). The fungal pathogens of corn such as *Fusarium verticillioides, Colletotrichum graminicola, Bipolaris maydis,* and *Cercospora zeae-maydis* are antagonized by the endophyte *Bacillus spp.* (Varma et al. 2017). Similarly, the endophyte harboring wild and ancient maize is antagonistic to its fungal pathogen, *Sclerotinia homoeocarpa* (Shehata et al. 2016). Other important examples of endophytes having antagonistic activity are *Bacillus* spp., *Pseudomonas putida,* and *Clavibacter* *michiganensis* against *Fusarium solani* and *Alternaria alternata* in *Curcuma longa* (Kumar et al. 2016). In banana, the endophytic species of *Bacillus* such as *B. amyloliquefaciens, B. subtilis subsp. subtilis,* and *B. thuringiensis* are antagonistic to fungal pathogens such as *Fusarium oxysporum* and *Colletotrichum graminicola* (Souja et al. 2014). Colonization of *P. indica* controlled various plant diseases such as powdery mildew, eyespot, Rhizoctonia root rot, Fusarium wilt, black root rot, yellow leaf mosaic, Verticillium wilt, cyst nematode, and leaf blight in barley, wheat, maize, tomato, and Arabidopsis plants. Reduced severity of Verticillium wilt by 30% in tomato caused by *Verticillium dahlia*, and increased leaf biomass by 20% (Chhipa and Deshmukh 2019) The inoculation of an endophytic E. nigrum strain from an apple tree in the model plant *Catharanthus roseus* triggered defense responses against "Candidatus Phytoplasma mali" and reduced symptom severity (Fávaro et al. 2012). *E. nigrum* has shown biocontrol activity against bacterial pathogen pseudomonas savastanoi pv. Savastanoi (Psv) causing olive knot and reduced Psv growth/biomass up to 96% (Berardo et al. 2018). Endophytes *Epichloe* in temperate grass produce bioactive compounds in host plant which works as a deterrent to herbivores and pests (Chhipa and Deshmukh 2019).

Antibiotic-mediated resistance is also commonly noticed in certain cases. The antibiotics like Taxol by *Pestalotiopsis microspora* in *Taxus wallichiana* (Strobel et al. 1996), ecomycins B and C in *Lactuca sativa* by *Pseudomonas viridiflava* EB 273 (Miller et al. 1998), and trichodermin in garlic by *Trichoderma brevicompactum* (Shentu et al. 2014) are effective against specific plant pathogens. Besides production of antibiotics, HCN is another antimicrobial compound that is produced by certain endophytes in crops. For example, *Bacillus* produces HCN in avocado and black grapes (Prasad and Dagar 2014). Similarly, *Pseudomonas putida* produces HCN that has antibacterial activity against *Escherichia coli* and *Klebsiella pneumoniae*, and antifungal activity against *Pythium ultimum* (Kumar et al. 2015). Sobolev et al. (2013) reported antibiosis by the endophytic bacterium, *Bacillus amyloliquefaciens*, in peanut. The isolate of sugarcane has shown biocontrol activity against fungal pathogen Sclerotinia sclerotiorum in sunflower and Pythium in the cotton crop, and has antibacterial activity against Phytoplasma in apple and Monilinia sp. in peach fruit and nectarines (Chhipa and Deshmukh 2019).

Pathogen-related enzymes such as lipase, cellulose, protease, amylase, chitinases, and pectinases are also produced by these endophytes (Varma et al. 2017). *Trichoderma* and *Phanerochaete* are the most comprehensively studied fungi responsible for lignocellulolytic degradation (Tiquia et al. 2002). Other fungi involved in cellulolytic degradation of composting materials are *Penicillium, Fusarium, Aspergillus, Rhizopus, Chaetomium, Alternaria,* and *Cladosporium* (Yadav et al. 2019a). In addition, bacteria are involved in cellulose degradation, and many species including those belonging to *Cytophaga, Bacillus, Cellulomonas, Pseudomonas, Klebsiella,* and *Azomonas* are commonly involved in aerobic decomposition of substrates (Mishra and Sarma 2018). Fouda et al. (2015) isolated Alternaria alternata, and sterile hyphae from *Asclepias sinaica*. It was observed that these endophytes had the ability to produce several extracellular enzymes including amylase, pectinase, cellulase, gelatinase, xylanase, and tyrosinase.

Plant growth-promoting activities by endophytes are well established as is evident in Echinacea by *Pseudomonas stutzeri* (Lata et al. 2006), in rice by *Pseudomonas, Bacillus, Enterobacter, and Micrococcus* spp. (Mbai et al. 2013). PGP activities of endophytes are attributed to the production of iron-chelating agents, siderophores as in rice by *Enterobacter spp.* and *Burkholderia spp.* (Souza et al. 2013), indoleacetic acid (IAA), and other growth hormones as in cashew by *Staphylococcus saprophyticus* and *Escherichia coli* (Lins et al. 2014). Endophytic *Azospirillum* spp. are reported to accumulate the abscisic acid (ABA) in mitigating water stress tolerance in maize. Plant growth-promoting hormones IAA and gibberellins further enhance the effect (Cohen et al. 2009). Few of the soilborne pathogens like *Fusarium oxysporum, Pythium* spp.*, Phytophthora* spp.*, Aphanomyces* spp., *Sclerotium rolfsii, Gaeumannomyces graminis, Rhizoctonia solani, Verticillium* spp., and *Thielaviopsis basicola* are found to be negatively affected by PGPR (Sahu et al. 2017).

Water stress alleviation was reported in maize by abscisic acid (ABA) accumulating endophytic *Azospirillum spp.* Furthermore, the effect was also seen in IAA and gibberellin accumulation. Under stress condition, ABA level increases and regulates plant growth (Sahu et al. 2017) and *Bacillus pumilus* are reported to promote growth under water stress (Varma et al. 2017). *P. indica*-infected barley plants showed higher biomass when compared with non-infected plants at salt stress condition (Waller et al. 2005). Similarly, the plant growth-promoting rhizobacterial (PGPR), *P. fluorescens*, an endophyte in eggplant, is antagonistic to *Ralstonia solanacearum* by production of siderophores (Ramesh et al. 2009). *Neotyphodium* and *Epichloë* of *Festuca rubra* are a plant growth promoting endophyte which increase the plant growth with high uptake of nutrients (Jain and Pundir 2017; Chhipa and Deshmukh 2019). *Penicillium sp.* from cucumber roots has been found to synthesize Gibberellic acid and IAA. Inoculating these strains in cucumber plants under drought stress has shown a significant increase in plant biomass, growth parameters, and assimilation of essential nutrients and reduced sodium toxicity (Waqas et al. 2012).

Major activities of endophytes include their role as biofertilizer as evident in banana by *Rahnella* spp. and *Pseudomonas* spp. (Ngamau et al. 2012) and corn by *Azotobacter vinelandii, B. subtilis,* and *Enterobacter cloacae* (Varma et al. 2017). A number of endophytic diazotrophic bacteria have already been reported to colonize the interior roots of maize, rice, and grasses (Barraquio et al. 1997) and are believed to be capable of contributing nitrogen nutrition in sugarcane (Boddey et al. 1995), rice (Yanni et al. 1997), and wheat (Webster et al. 1998). *P. indica*, a root endophyte, has been promoted as plant protector, plant growth regulator, and fertilizer in both agricultural and nonagricultural crops (Schafer et al. 2007). Anuar et al. (2015) isolated *Hendersonia Amphinema* and *Phlebia* fungi from trunk and root tissues of oil palms and observed that Phlebia could serve as a biofertilizer promoting the oil palm seedlings eventually. These are used as empty fruit bunches (EFB) powder and real strong bioorganic fertilizer (RSBF) with Phlebia as formulation. The simulations of plant growth executed by plant growth promoters could be attributed in terms of tolerance to biotic and abiotic stresses and improved plant nutrition (Machungo et al. 2009).

1.5 Conclusion and Future Prospects

Soil harbors great diversity of microorganisms; this diversity is responsible for biological equilibrium created by the associations and interactions of all individuals found in the community. Plants are the main responsible for most of these interactions due to their root exudates. These interactions perform significant roles on plant growth and health and the ecological fitness and resistance of plants to different biotic and abiotic stresses in soils. Plant–microbe interaction in positive relationship is very beneficial to each other. Mutual relationship in plant microbe associations are mycorrhizas, symbiotic nitrogen-fixing bacteria, and more recently and most interesting microorganisms endophytes.

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Chapter 2
Endophytic Fungi: Diversity, Abundance, and Plant Growth-Promoting Attributes

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2.1 Introduction

Evidence of plant-associated microorganisms found in the fossilized tissues of stems and leaves has revealed that endophytic-plant associations may have evolved >400 million years ago (Kusari and Spiteller 2012). Studies of endophytic fungi were initiated nearly 200 years ago, when in 1772 the species *Sphaeria typhena* described, now known as *Epichloe typhina* (Khiralla et al. 2016). Since the first description of symbiosis (De Bary 1879) several symbiotic lifestyles have been defined based on fitness benefits to or impacts on host and symbiont (Lewis 1985). After >100 years of research it is reasonable to conclude that most, if not all, multicellular life on earth is symbiotic with microorganisms. Endophytes are ubiquitous in the plant world; no report of a plant species not associated with them is known; in a given plant species, individuals without endophytes are rare (Zabalgogeazcoa 2008). Unlike mycorrhizal fungi, fungal endophytes are microfungi that internally infect living plant tissues without causing disease or any harm to plant, and live in mutualistic association with plants for at least a part of their life cycle (Kusari and Spiteller 2012; Anitha et al. 2013; Lugtenberg et al. 2016; Arora and Ramawat 2017; Jain and Pundir 2017; Lata et al. 2018; Khare et al. 2018; Chhipa and Deshmukh 2019; Abo Nouh 2019). Fungi, bacteria, or even viruses can be classified as endophytes (Hilszczańska 2016; Rana et al. 2019c). Among them, the most abundant are fungi endophytes which can be found on every plant irrespective of size, shape, or taxonomy (Strobel and Daisy 2003; Kusari and Spiteller 2012; Khare et al. 2018).

These fungi comprise phylogenetically diverse groups that are members of the dikarya (Carroll 1988; Girlanda et al. 2006; Arnold and Lutzoni 2007). Endophytic fungi have been classified into *Clavicipitales*, with few hosts within the monocots, and nonclavicipitaceous species inhabiting both monocots and eudicots (Carroll 1988) which probably represent the majority of microbial symbionts which interact with plants, with a great diversity occurring both at taxonomical and at functional levels (Jain and Pundir 2017). While most fungal endophytes belong to the Ascomycota clade, some belong to the Basidiomycota. Although these fungi are often grouped together, they can be discriminated into different functional groups (Rodriguez and Redman 2008). Currently, endophytes can be subdivided into four classes based on host range, colonization pattern, transmission, and ecological function (Rodriguez and Redman 2008). The diversity of endophytic fungi is greater in tropical regions (Rana et al. 2019a, b; Suman et al. 2016). Plants in these regions are considered to be true reservoirs of fungal diversity (Fávaro et al. 2012). Endophytes gain importance in recent past for their commercial and industrial exploitation. It was after the landmark discovery of toxicosis caused by *Neotyphodium coenophialum* (Family Clavicipitaceae) in cattle eating the grass (*Festuca arundinacea*).

It was recorded that the grass infected by the fungus without apparent symptoms, and produces several toxic alkaloids which were the actual cause of toxicosis in cattle (Arora and Ramawat 2017). Recent studies indicate that fitness benefits conferred by mutualistic fungi contribute to or are responsible for plant adaptation to stress (Read 1999; Stone et al. 2000; Rodriguez et al. 2004). Collectively, endophytes have been shown to confer fitness benefits to host plants including tolerance to herbivory, heat, salt, disease, and drought, promote nutrient acquisition, and increased below- and above-ground biomass (Bacon and Hill 1996; Sahay and Varma 1999; Redman et al. 2001; Arnold et al. 2003; Waller et al. 2005; Márquez et al. 2007; Suman et al. 2016). It has become clear that at least some plants are unable to endure habitat-imposed abiotic and biotic stresses in the absence of fungal endophytes (Rodriguez and Redman 2008). The symbiotic association of endophytic fungi with crops may be responsible for an increase in crop growth and yield without supplementing extensive fertilizers (Rana et al. 2019a). On the other hand, subsequent to this the symbiont improves the plant abilities to resist against biotic and abiotic stresses. Thus, endophytic fungi provide solutions of modern agricultural constraints and increase food production thereby (Jain and Pundir 2017).

2.2 Endophytic Fungi Diversity

Traditionally the ecologists have emphasized climate, resource levels, disturbance frequency, and plant–plant and plant–herbivore interactions as major determinants of plant biodiversity (Harper 1990). The potential role of microorganisms—for example, mutualistic symbionts—has been largely ignored despite their ubiquity. Recent research suggests that microbial interactions may play a major role in structuring plant communities by affecting colonization, competition, coexistence, and soil nutrient dynamics (Vitousek and Walker 1989; Rana et al. 2019c, 2020; Verma et al. 2017; Yadav 2018, 2019). However, this conclusion is based primarily on observations of unmanipulated communities, extrapolations from artificial environments, and extrapolations from field applications of biocides that may have confounding effects on non-target species.

The cultivation-dependent studies for unraveling diversity of endophytes is due to the bias towards fast-growing, ubiquitous species, whereas rare species with minor competitive strength and more specialized requirements may remain undiscovered (Unterseher and Schnittler 2009; Sun et al. 2011). Even, highly discriminant DNA-based techniques are advancing our knowledge of taxonomic units, leading to a more accurate identification and phylogenetically congruent accommodation of sterile morphotypes and of unculturable fungi, and expand our appreciation of the breadth and depth of fungal endophytic diversity (Arnold and Lutzoni 2007; Arnold et al. 2007; Tejesvi et al. 2011; Yadav et al. 2019b, c, d).

Through a study examining the diversity and host specificity of endophytes associated with ecologically important hosts in the biotically diverse woodlands of the Madrean Archipelago, endophytes were isolated from apparently healthy, mature leaves of *Quercus* sp. (Fagaceae), *Pinus ponderosa* (Pinaceae), *Cupressus arizonica* (Cupressaceae), and *Platycladus orientalis* (Cupressaceae) in and near Tucson, Arizona, USA. Those fungi were genotyped using the nuclear ribosomal internal transcribed spacer region, which is frequently sequenced in fungal systematics at the species level due to its higher degree of variation compared to other regions of rDNA. Sequence deviations for four common genera of endophytes (*Botryosphaeria*, *Colletotrichum*, *Mycosphaerella*, and *Xylaria*) with an average of ca. 1–2% difference in sequence composition among conspecifics were observed. Thus, the method provided resolution of lineages of the detected endophyte taxa below the species level (Arnold et al. 2007).

Many endophytes (biotypes) of the same species are isolated from the same plant and only one of the endophytes will produce a highly biologically active compound in culture (Li et al. 1996). Many factors changing in the host as related to the season and age, environment, and location may influence the biology of the endophyte. Indeed, further research at the molecular level must be conducted in the field to study endophyte interactions and ecology. These interactions are probably all chemically mediated for some purpose in nature. An ecological awareness of the role these organisms play in nature will provide the best clues for targeting particular types of endophytic bioactivity with the greatest potential for bioprospecting (Yadav et al. 2020).

Two endophytic groups have been discriminated based on phylogeny and life history traits, Clavicipitaceous (C) and Nonclavicipitaceous (NC). NC-endophytes represent three distinct functional groups based on host colonization and transmission, in planta biodiversity and fitness benefits conferred to hosts. Using this framework, we contrast the life histories, interactions with hosts, and potential roles in plant ecophysiology of C- and NC-endophytes, and highlight several key questions for future work in endophyte biology (Rodriguez et al. 2008).

Since the first description of symbiosis as “the living together of dissimilar organisms” (De Bary 1879), an array of symbiotic lifestyles have been defined based on fitness benefits or impacts to macroscopic hosts and microscopic symbionts (Lewis 1985). Collectively, more than 100 years of research suggests that most, if not all, plants in natural ecosystems are symbiotic with mycorrhizal fungi and/or fungal endophytes (Petrini 1986).

Clavicipitaceous endophytes (C-endophytes) are those taxa infect some grasses; while the nonclavicipitaceous endophytes (NC-endophytes) that can be recovered from asymptomatic tissues of nonvascular plants, ferns and allies, conifers and angiosperms. Most reviews have focused only on C-endophytes (e.g. Clay and Schardl 2002), or have examined C- and NC-endophytes together (but see Arnold et al. 2007), often treating NC-endophytes with distinctive life histories as a single group. This bias is partially a result of the significant agricultural impacts of C-endophytes and a dearth of knowledge about the ecological significance of NC-endophytes. However, NC-endophytes are highly diverse fungi that represent at least three distinct functional groups based on an array of life history characteristics and their ecological significance. The goal of this review is to describe an operational framework for clarifying the taxonomy and ecological roles of endophytes, and for addressing key research questions, in each functional group. C-endophytes (hereafter, Class 1 endophytes) represent a small number of phylogenetically related clavicipitaceous species that are fastidious in culture and limited to some cool- and warm-season grasses (Bischoff and White 2005). Typically these endophytes occur within plant shoots, where they form systemic intercellular infections. Clay and Schardl (2002) recognized three types of clavicipitaceous endophytes, ranging from symptomatic and pathogenic species (Type I) to mixed interaction and asymptomatic endophytes (Types II and III, respectively). In this review we discuss all three types of C-endophyte with a focus on Type III C-endophytes, because they—like the NC-endophytes treated here—grow within plant tissues without manifesting symptoms of disease.

Nonclavicipitaceous endophytes are highly diverse, representing a polyphyletic assemblage of primarily ascomycetous fungi with diverse and often poorly defined or unknown ecological roles. NC-endophytes have been recovered from every major lineage of land plants, and from all terrestrial ecosystems, including both agroecosystems and biomes ranging from the tropics to the tundra. The scale of their diversity, their ecological roles, the insights they provide into the evolution of various ecological modes in fungi, their potential applications, and the ability of many fungi to switch between endophytic and free-living lifestyles (Vasiliauskas et al. 2007; Macia'-Vicente et al. 2008; Selosse et al. 2008) are becoming more apparent, engendering growing enthusiasm from mycologists, ecologists, physiologists, and applied scientists.

They can be differentiated into three functional classes based on host colonization patterns, mechanism of transmission between host generations, in planta biodiversity levels, and ecological function. Although all three classes have broad host ranges, Class 2 endophytes may grow in both above- and below-ground tissues. By contrast, Class 3 and 4 endophytes are restricted to above-ground tissues and roots, respectively. Colonization of host tissues also differs: Class 3 endophytes form highly localized infections, while Class 2 and 4 endophytes are capable of extensive tissue colonization. In general, the diversity of Class 2 (Rodriguez et al. 2008) endophytes in individual host plants is quite limited, whereas the diversity of Class 3 endophytes within a host plant or tissue can be extremely high. The diversity of Class 4 endophytes within individual plants has not been sufficiently evaluated. Differences in planta biodiversity of Class 2 and 3 endophytes may reflect differences in host colonization and transmission patterns: although members of both classes are transmitted horizontally, Class 2 endophytes also are transmitted vertically via seed coats, seeds, or rhizomes.

Rodriguez et al. (2008) mentioned in their study that Class 2 endophytes have the ability to confer habitat-specific stress tolerance to their host plants. Endophyte-conferred fitness benefits are defined here as habitat-adapted if the benefits are a result of habitat-specific selective pressures such as pH, temperature, and salinity; or as no habitat-adapted if the benefits are common among endophytes regardless of habitat. Only Class 2 endophytes have been shown to confer habitat-adapted stress tolerance (Rodriguez et al. 2008). Because most Class 3 and 4 endophytes have not been assessed for the conferring of fitness benefits to hosts, mode of transmission, or rhizosphere competence, the composition of these Classes may be more complex than presented here and may be revised in years to come. In this discussion, we define these endophytic groups and describe their life histories, symbiotic dynamics, and ecological functions.

2.2.1 C-Endophytes (Class 1)

C-Endophytes (Class 1) of grasses were first noted by European investigators in the late nineteenth century in seeds of *Lolium temulentum*, *Lolium arvense*, *Lolium linicolum*, and *Lolium remotum* (Guerin 1898; Hanausek 1898; Vogl 1898). From their earliest discovery, investigators hypothesized a link to toxic syndromes experienced by animals that consume infected tissues. However, these hypotheses were largely untested until Bacon et al. (1977) linked the endophyte *Neotyphodium coenophialum* to the widespread occurrence of "summer syndrome" toxicosis in cattle grazing tall fescue pastures (*Festuca arundinacea*). In 1988, Keith Clay proposed that clavicipitaceous endophytes are defensive mutualists of host grasses (Clay 1988). As a result of the beneficial effects of C-endophytes, turf grass breeders now offer a variety of cultivars identified as "endophyte enhanced" (Funk and White 1997).

2.2.1.1 The Evolutionary Origins

Clavicipitaceae (Hypocreales; Ascomycota) include free-living and symbiotic species associated with insects and fungi (e.g. *Cordyceps* spp.) or grasses, rushes, and sedges (e.g. *Balansia* spp., *Epichloë* spp., and *Claviceps* spp.) (Bacon and White 2000). The family is relatively derived within the Hypocreales (Spatafora and Blackwell 1993; Rehner and Samuels 1995; Spatafora et al. 2007), a lineage well known for plant pathogens, saprotrophs, and endophytes, many of which produce bioactive compounds. Soil-inhabiting species, which include some of the most geographically widespread taxa in the group, are placed particularly deeply in phylogenetic trees based on molecular sequence data (Spatafora et al. 2007), suggesting that saprobism was common among the earliest members of the family.

Ancestral state reconstructions in a multilocus phylogenetic framework suggest that clavicipitaceous endophytes arose from insect-parasitic ancestors and diversified through a series of inter-kingdom host jumps (Koroch et al. 2004; Spatafora et al. 2007; Torres et al. 2007). The evolution of endophytic *Epichloë*/*Neotyphodium* and *Balansia* is thought to have begun with free-living insect parasites, and then progressed to epibiotic plant biotrophic forms (e.g. similar to *Hypocrella* spp.) that gained access to plant nutrients by (1) first infecting and necrophytizing scale insects and whiteflies and (2) then developing on the stream of nutrients emerging to the surface of the plant through the insect's stylet or stylet wound. Finally, the capacity to infect grass hosts directly arose, with forms that are epibiotic (e.g. *Myriogenospora* spp.) and others that are endophytic.

This scenario highlights a shortcut to biotrophy that did not involve the often-expected transition from virulent plant pathogens to endophytism. Endophytes descended from insect pathogens likely did not possess enzymes or toxins for killing or degrading plant tissues, such that plant defensive mechanisms would not limit their colonization. Nutrient-use studies suggest that evolution of biotrophy and endophytism in this group involved (1) reduction of enzymatic capabilities, (2) increasing dependence on the host plant to provide nutrients for growth, and (3) an apparent increase in the production of particular secondary metabolites beneficial in the symbiosis (e.g. ergot alkaloids) (Torres et al. 2007; Yadav et al. 2019a).

2.2.1.2 The Life History

Epichloë is an ascomycetes genus (anamorphs: *Neotyphodium*), hosted as symbionts, cool-season grasses and occurs in intercellular spaces of leaf sheaths, culms, and rhizomes, and may also be present, if sparsely, on the surface of leaf blades (White et al. 1996; Moy et al. 2000; Tadych et al. 2007). When the grass flowers, the fungus grows over the developing inflorescence to form a stroma. The inflorescence primordium remains at an arrested stage of development within the fungal mycelium, and development of the seed head is prevented (i.e. choke disease). Some species *Epichloë* of recommended to be Type II endophytes (Clay and Schardl 2002) exhibit stromata only in a proportion of the tillers, allowing partial seed production and thus vertical transmission within seeds; while others (Type I endophytes) produce stromata on all or most of the tillers and any tillers that escape the fungus are free of endophyte infection. *Epichloë* also can produce auxins that alter development of plant tissues (De Battista et al. 1990). *Epichloë* stromata bear spermatia and fungal populations contain two mating types that must be transferred between stromata before perithecia and ascospores develop (White and Bultman 1987). Symbiotic flies of the genus *Botanophila* (Diptera: Anthomyiidae) act as "pollinators" of stromata, vectoring spermatia (Bultman and White 1988; Steinebrunner et al. 2008).

Fertilized stromata produce infective ascospores; however, precisely how initial infections occur is only partially understood (Chung and Schardl 1997; Steinebrunner et al. 2008). Notably, stromata production and the sexual cycle of *Epichloë* occur only on grasses in the northern hemisphere: C-endophytes in the Southern Hemisphere are unable to form stromata and do not reproduce sexually. This suggests that endophyte spread in Southern Hemisphere grasses has occurred through epiphyllous conidial production or by a means other than stromata production, or that Southern Hemisphere endophytes once possessed the capacity to produce stromata but that capacity was lost. Some species of *Epichloë* have lost the capacity for development of the sexual stage.

These have been referred to as asexual or Type III endophytes (Clay and Schardl 2002) and are classified as species of *Neotyphodium* (White 1988). No obvious symptoms of Type III endophyte infection are observable at any stage of plant development. These fungi are endophytes of leaves, culms, and rhizomes, and they frequently colonize inflorescence primordia. As inflorescences develop the mycelium grows into ovules, and within seeds it colonizes the scutellum and embryo axis (Philipson and Christey 1986) before germination. Considerable evidence suggests that Type III C-endophytes have evolved numerous times and are distributed in both the Northern and Southern Hemispheres (White 1988; Moon et al. 2002; Schardl and Moon 2003). Type III C-endophytes are transmitted vertically through seeds but many retain an epiphyllous mycelium where conidia form, suggesting the potential for horizontal transmission.

Tadych et al. (2007) demonstrated that epiphyllous conidia are released from conidiophores only in water, suggesting that they may spread among plants via rain or dew. The likely, but as yet unconfirmed, sites of infection are tillers, where the fungi colonize meristems epiphyllously in plant crowns. Most Type III endophytes produce conidia in culture and perhaps epiphyllously, suggesting that these propagules retain some function. Tiller colonization may result in infection of some ovules and seeds of neighboring plants, but the original mature neighboring plant tissues would not bear endophytic mycelium: C-endophytes grow rapidly in nutrient-rich meristematic tissues but show limited capacity to grow through mature plant tissue (Western and Cavett 1959; White et al. 1991).

2.2.2 NC-Endophytes

More than 1000 papers have been published on NC-endophytes since 1970. The majority present data concerning the distribution and abundance of endophytes in asymptomatic leaf tissue; the isolation and analysis of bioactive compounds; their potential use as biocontrol agents; and phylogeny-based identification and systematics (Selosse et al. 2004; Schulz 2006; Arnold et al. 2007; Higgins et al. 2007; Kithsiri Wijeratne et al. 2008). While these studies are critically important for understanding the parameters of NC-endophyte—plant associations, very few papers focus on the ecological and evolutionary significance of NC-endophytes, and even fewer demonstrate symbiotic functions in planta. Despite a paucity of functional studies, several NC-endophytes have been shown to establish mutualisms with plants, conferring fitness benefits such as biotic and abiotic stress tolerance, nutrient acquisition, and increased growth and yields (Redman et al. 2002; Arnold et al. 2003; Mucciarelli et al. 2003; Waller et al. 2005; Schulz 2006; Rodriguez et al. 2008).

Class 2 endophytes comprise a diversity of species, all of which are members of the Dikarya (Ascomycota or Basidiomycota). Most of them belong to the Ascomycota, with a minority of Basidiomycota. Members of the former are restricted to the Pezizomycotina, wherein they represent several classes. Class 2 endophytes within the Basidiomycota include a few members of the Agaricomycotina and Pucciniomycotina. Class 2 endophytes are distinct from the other NC-endophytes because in general they colonize roots, stems, and leaves; are capable of forming extensive infections within plants; are transmitted via seed coats and/or rhizomes; have low abundance in the rhizosphere; confer habitat-adapted fitness benefits in addition to nonhabitat-adapted benefits; and typically have high infection frequencies (90–100%) in plants growing in high-stress habitats.

2.2.2.1 The Historical Perspective

Phoma sp. in *Calluna vulgaris* was the first detailed description of a Class 2 endophyte (Rayner 1915). A recent analysis of Mediterranean plants revealed that *Phoma* spp. is common root endophytes that confer fitness benefits to plants (Macia'-Vicente et al. 2008). During the remainder of the twentieth century, a limited number of reports appeared describing fitness benefits conferred to plants by Class 2 endophytes. One common example is the brown alga *Ascophyllum nodosum* that needs the fungus *Mycophycia ascophylli* for normal growth and development (Garbary and Macdonald 1995). In addition to being required for the normal development of some plants, some of Class 2 endophytes increase plant root and shoot biomass (Newsham 1994; Gasoni and deGurfinkel 1997; Ernst et al. 2003; Mucciarelli et al. 2003) and confer tolerance to a variety of biotic and abiotic stresses such as disease (Danielsen and Jensen 1999; Narisawa et al. 2002; Campanile et al. 2007; Redman et al. 2001, 2002; Márquez et al. 2007; Rodriguez et al. 2008).

2.2.2.2 The Life History

These fungi, like all endophytes, colonize plants via infection structures such as appressoria or by direct penetration of plant tissues via hyphae (Ernst et al. 2003). The growth is dominantly intercellular with little to no impact on host cells (Rodriguez-Galvez and Mendgen 1995; Ernst et al. 2003; Gao and Mendgen 2006). While there may be a low level of sporulation or appressorial formation in healthy plants, these fungi rapidly emerge and sporulate during host senescence (Weber et al. 2004). There have not been sufficient ecological studies to permit full understanding of the distribution and abundance of Class 2 endophytes in the rhizosphere; however, some species (*Phoma* sp. and *Arthrobotrys* spp.; Newsham 1994; Lopez-Llorca et al. 2006) are known to occur in soils at high abundance while others (*Fusarium culmorum*, *Colletotrichum magna*, and *Curvularia protuberata*; Rodriguez et al. 2008) are present at very low abundance. Analysis of soil fungi typically involves making soil suspensions, dilution plating, and enumerating colony-forming units; therefore, it is difficult to discern the ability of endophytes to propagate in soil versus the deposition of spores derived from senescing plants that are colonized by the fungi (Yadav et al. 2019d). Nematophagous fungi such as *Arthrobotrys* spp. can express endophytic or free-living lifestyles (Lopez-Llorca et al. 2006); therefore, it is not surprising that *Arthrobotrys* spp. achieve high abundances in rhizosphere soils as nematodes are so plentiful and provide a source of nutrition. However, the high abundance of *Phoma* sp. in soil may be attributable to its emergence and sporulation in senescing plants and subsequent dissemination of spores into the surrounding soils.

2.2.3 Class 3 Endophytes

Class 3 endophytes are distinguished on the basis of their occurrence primarily or exclusively in above-ground tissues; horizontal transmission; the formation of highly localized infections; the potential to confer benefits or costs on hosts that are not necessarily habitat-specific; and extremely high in planta biodiversity. Class 3 endophytes include the hyperdiverse endophytic fungi associated with leaves of tropical trees (Lodge et al. 1996; Fröhlich and Hyde 1999; Arnold et al. 2000; Gamboa and Bayman 2001), as well as the highly diverse associates of above-ground tissues of nonvascular plants, seedless vascular plants, conifers, and woody and herbaceous angiosperms in biomes ranging from tropical forests to boreal and Arctic/Antarctic. In addition to occurring within photosynthetic and herbaceous tissues, Class 3 endophytes are found in flowers and fruits, as well as in asymptomatic.

Many fungi with similar life histories to Class 3 endophytes also occur within asymptomatic lichens, and in that case are known as "endolichenic" fungi (Arnold et al. 2009). Class 3 endophytes are especially notable for their high diversity within individual host tissues, plants, and populations. For example, apparently healthy leaves in lowland moist tropical forests contain numerous, independent infections, rather than systemic or otherwise extensive growth of hyphae (Lodge et al. 1996; Arnold and Herre 2003; Arnold et al. 2003). Different leaves on the same tree may have quite distinctive assemblages of endophytic fungi (Arnold et al. 2003). Individual plants may harbor hundreds of species, and plant species across their native ranges may be inhabited by thousands of species, so this tremendous diversity, showcased in some tropical plants and localities, is not exclusively a tropical phenomenon: plants in temperate and boreal communities also harbor an astonishing richness of Class 3 endophytes. For example, Higgins et al. (2007) found that species-accumulation curves for boreal and Arctic endophytes were nonasymptotic, with >50 species recovered among only 280 isolates examined. Similarly, Petrini and Müller (1979) recovered >80 endophyte species from *Juniperus communis* in Switzerland, and Halmschlager et al. (1993) isolated 78 species from leaves and twigs of *Quercus petraea* in Austria. Although horizontally transmitted, Class 3 endophytes are typically distinct from pathogens associated with the same host species (Ganley et al. 2004) and from epiphyllous fungi even on the same leaves (Santamaría and Bayman 2005). Their distinctiveness relative to saprotrophic communities is a matter of some debate (Selosse et al. 2008), but increasingly it appears that Class 3 endophytes comprise species not known among the saprophytic decay fungi (U'Ren et al. 2008, but see Promputtha et al. 2007).

Diversity of Class 3 endophytes raises several questions regarding their ecological roles. Indeed, most recent studies of Class 3 endophytes have focused on characterizing bioactive strains (e.g. Jiménez-Romero et al. 2008) or enumeration of species, leaving aside the potential ecological roles of these fungi in planta (but see Arnold et al. 2003) or their evolutionary implications for plants. It is challenging to imagine general rules given the occurrence of tens to hundreds of phylogenetically diverse endophytic fungi within the foliage of a single host.

The experiments that take into account the natural complexity of these endophyte communities, and consider multitrophic interactions, are especially needed in years to come. Similar to the explosive growth of studies examining the diversity and ecological roles of mycorrhizal symbioses over recent decades, the study of hyperdiverse Class 3 endophytes is in an exceptionally wide-open and exciting phase.

2.2.3.1 The Life History

As Class 2 endophytes, the majority of Class 3 endophytes are members of the Dikaryomycota (Ascomycota or Basidiomycota), with a special concentration in the Ascomycota. The Pezizomycotina are especially well represented, although some endophytic Saccharomycotina are known (Higgins et al. 2007). Within the Pezizomycotina, Class 3 endophytes occur among all of the major nonlichenized clades. They are common among the Pezizomycetes, Leotiomycetes, and Eurotiomycetes, and especially among the very endophyte-rich Sordariomycetes and Dothideomycetes (Arnold et al. 2007; Higgins et al. 2007). Numerous ascomycetous plant pathogens and saprotrophs are derived from these same lineages (Lutzoni et al. 2004; James et al. 2006). The relative prevalence of members of each class in endophyte communities differs markedly among biomes and among host lineages (Arnold and Lutzoni 2007): for example, endophytic Leotiomycetes are especially common in conifers, and endophytic Sordariomycetes are particularly common in tropical plants. Members of the Basidiomycota belonging to the Agaricomycotina, Pucciniomycotina, and Ustilaginomycotina also are known as Class 3 endophytes, although they are reported much less frequently than ascomycetous endophytes. In general, basidiomycetous endophytes are found more often in woody tissues than in foliage (Arnold et al. 2007).

Endophytic Basidiomycota may be more common in foliage than culture-based studies have indicated to date. Arnold et al. (2007) reported a fourfold increase in the number of basidiomycetous species recovered from leaves of *Pinus taeda* when endophyte communities were assessed using culture-free methods (environmental PCR of surface-sterilized foliage) instead of culturing. Moreover, Pan et al. (2008) reported that *Ustilago maydis* is well represented among the endophyte community in maize (*Zea mays*). Class 3 endophytes reproduce by hyphal fragmentation and/or by the production of sexual or asexual spores on dead or senescent tissue (Herre et al. 2005). Spores and hyphal fragments may be released passively, by herbivores (through frass; Monk and Samuels 1990), or by physical disturbances such as wind or rain. Some, produce slimy spores that rely at least in part on rain for dispersal (Kirk et al. 2001) and the Ingoldian fungi produce spores that depend on water for dispersal and infection (Selosse et al. 2008). Although heavy wind and rain are especially effective in moving spores, even light precipitation can disperse conidia of Colletotrichum (Guyot et al. 2005). Similarly, light wind and the currents produced by diurnal cycles of heating and cooling are significant for dispersal of dry propagules (Arnold 2008). Some Class 3 endophytes also may travel about as spores adhering to the bodies of insects such as moths (Feldman et al. 2008).

Generally, seedlings raised under sterile conditions do not contain culturable Class 3 endophytes, highlighting a key difference relative to Class 2 endophytes (which may be transmitted vertically). Colonization by Class 3 endophytes proceeds rapidly given the presence of airborne inoculum and high relative humidity or wetting of leaf surfaces by dew, rain, or fog (Arnold and Herre 2003).

Diversity of Class 3 endophytes generally follow a strong latitudinal gradient, with higher values of all of these measures in the tropics relative to Arctic tundra or boreal forest (Arnold and Lutzoni 2007). However, local abiotic and land-use conditions can lead to unexpected abundances and diversities of endophytic fungi in certain regions (e.g. wet microclimates in the temperate zone), and some hosts—especially those with long-lived foliage, such as evergreens—often harbor more, and more diverse, endophytes than their latitudinal position would suggest (Arnold and Lutzoni 2007).

2.2.4 Class 4 Endophytes

Merlin (1922) observed a brown to blackish, pigmented fungus associated with terrestrial plant roots while studying and isolating ectomycorrhizal fungi. He called these sterile, root-associated fungi “mycelium radicus astrovirens” (MRA). MRA were often found to co-exist with mycorrhizal fungi, and were referred to as “pseudomycorrhizal” fungi (Merlin 1922). Shortly thereafter, Peyronel reported >135 species of angiosperms associated with dark pigmented fungi in root tissues (Peyronel 1924). Presently, these fungi are referred to as “dark septate endophytes” (DSE) and are grouped together as Class 4 endophytes. Also Class 4 endophytes (DSE) are distinguished as a functional group based on the presence of darkly melanized septa, and their restriction to plant roots. In general, Class 4 endophytes are primarily ascomycetous fungi that are conidial or sterile and that form melanized structures such as inter- and intracellular hyphae and microsclerotia in the roots. They have little host or habitat specificity; and they have been reported in association with c. 600 plants including plants that are nonmycorrhizal, from Antarctic, Arctic, alpine, sub-alpine, and temperate zones, as well as from African coastal plains and lowlands, and some tropical ecosystems (Jumpponen and Trappe 1998; Jumpponen 2001). DSE are often found in boreal and temperate forests associated with the fine roots of trees and shrubs, especially of conifers (Richard and Fortin 1974). These fungi are not thought to be pathogenic, as they are observed on healthy fine roots, and in this context, will be referred to as endophytes in a broad sense in that DSE “colonize living plant organs without any apparent, overt negative effects” (Hirsch and Braun 1992; Jumpponen and Trappe 1998). These observations suggest that DSE may play an important role in the ecophysiology of plants. However, almost a century after their discovery little is still known about the role of these mysterious and rather elusive fungal symbionts.

2.2.4.1 The Phylogenetic Diversity, Classification, Life History

Two latitudinal studies encompassed a large number of plant species from the North to the South Pole to address this issue (Jumpponen and Trappe 1998; Mandyam and Jumpponen 2005). Dark septate endophytes (DSE) were reorded associated with 587 plants species representing 320 genera and 114 families. Colonization studies were then conducted using five described anamorphic taxa of DSE (*Chloridium paucisporum*, *Leptodontidium orchidicola*, *Phialocephala dimorphospora*, *Phialocephala fortinii*, and *Phialophora finlandia*) under natural and experimental conditions (inoculation of root systems in pots). These DSE species had a large host range and/or lacked host specificity: collectively, they were able to colonize 66 different plant species, with *P. fortinii* alone able to colonize >20 species.

DSE appear to represent a large and interesting class of endophytes that have as yet not been well defined taxonomically and/or ecologically. Therefore, classification of fungi as DSE should be approached with some caution as identification is based on rather broad and ambiguous criteria. Presently, the presence of asexual, darkly pigmented, septate endophytes in plant roots is the primary criterion for DSE designation. However, dark pigmented endophytes belonging to other classes have been mistaken as DSE. The Class 2 endophyte *Curvularia protuberata* which symbiotically confers temperature tolerance to the geothermal plant *Dichanthelium lanuginosum* is a darkly pigmented, asexual septate fungus that colonizes plant roots (see “Endophyte-conferred fitness benefits and ecological adaptations of plants” in Sect. 2.4). However, *C. protuberata* is not a true DSE: it colonizes virtually all parts of the plant (roots, crown, stem, leaves, and seed coat). Researchers must analyze portions of plants representing all developmental tissues (roots, crown, stem, leaves, and seed coat) to avoid erroneous classification, for fungal colonization before DSE classification.

Lately, the asexual designation of DSE may need to be addressed as “an unknown number of taxa (anamorphic and/or teleomorphic) are involved, and that a considerable functional and ecological overlap might exist between soil fungi, saprophytic rhizoplane-inhabiting fungi, strictly pathogenic fungi, mycorrhizal fungi and fungal endophytes” (Jumpponen and Trappe 1998). Due to the presence of DSE in soils and plant roots, transmission is most likely horizontal. Mycelial fragmentation and dispersal of conidia appear to be the means of transmission as demonstrated under laboratory conditions (Jumpponen and Trappe 1998). Although anamorph–teleomorph connections have not yet been identified for most DSE, the possibility of sexual reproduction should not be discounted. Root colonization by *P. fortinii* is described by several authors as a classic representative of DSE (Currah and Van Dyk 1986).

The Colonization begins with superficial and/or runner hyphae that form a loose network of hyphae on the root surface. Individual hyphae then grow along the main axis of the root and can grow between cortical cells and also within the depressions between epidermal cells (O’Dell et al. 1993). It may also be intracellular without causing any distortion to host roots but the endophyte may form clusters of closely packed thick-walled cells within the cortical cells collectively referred to as “thick pseudoparenchymatic mass, sclerotia, microsclerotia, or sclerotial bodies" (Wang and Wilcox 1985; Jumpponen and Trappe 1998). Little is known about the large group of fungi that constitute the Class 4 endophytes. DSE colonization may play a role in deterring pathogens by minimizing available carbon in the rhizosphere, and that high melanin levels may potentially be involved in the production of secondary metabolites toxic to herbivores, both factors giving Class 4 symbiotic plants a competitive edge.

2.3 Endophytic Fungi Abundance

By definition, fungal endophytes live internally and asymptomatically within organs of their host plant (Wilson 1995). These asymptomatic fungal infections are ubiquitous, abundant, and taxonomically diverse residents in all terrestrial plants (Rodriguez et al. 2009). Almost all the plant species (~400,000) harbor one or more endophytic organisms (Anitha et al. 2013). It is estimated that there are approximately more than one million endophytic fungal species worldwide which represent a significant genetic resource for biotechnology (Kumar et al. 2019). Most studies have indicated that the abundance, diversity, and species composition of endophyte assemblages and infection frequencies vary according to (1) host species, (2) tissue type and tissue age, (3) site characteristics, (4) local microclimate conditions, and (5) anthropogenic factors (Torres et al. 2011). Usually one to a few species dominates the community, while the majority of the species are rare (Torres et al. 2011). Endophyte communities from higher latitudes are characterized by relatively few fungal species, whereas tropical endophyte are dominated by a small number of classes but a very large number of different endophytic species (Lugtenberg et al. 2016). Endophytic fungi are predominantly ascomycetes that appear to be ubiquitous among all plant lineages and have been recovered from asymptomatic tissues of land plants, including algae, mosses and other nonvascular plants, ferns and fern allies, conifers and angiosperms (Carroll 1988; Stone et al. 2000; Schulz and Boyle 2005; Arnold et al. 2007; Arnold and Lutzoni 2007). Some endophytic fungi, known as "endolichenic" fungi also occur within asymptomatic lichens (Li et al. 2007; Arnold et al. 2009).

Fungal endophytes recovered from plant hosts growing in terrestrial ecosystems, including both agroecosystems and natural ecosystems (Arnold and Lutzoni 2007), ranking from tropical and subtropical (Arnold et al. 2000; Holmes et al. 2004), mangroves, grasslands and savannahs, croplands (Arnold and Lutzoni 2007), hot desert (Hoffman and Arnold 2008; Abdel-Azeem et al. 2016, 2018, 2019; Abdel-Azeem 2020; Abo Nahas 2019), temperate (Stone et al. 2000), boreal, tundra, Arctic/Antarctic biomes (Torres et al. 2011), alpine, xeric environments (Ali et al. 2018). Tropical and temperate rainforests are the most biologically diverse terrestrial ecosystems on earth represented 60% of the world's terrestrial biodiversity. The competition is great, resources are limited, and selection pressure is at its peak. This gives rise to a high probability that rainforests are a source of biologically active compounds (Strobel and Daisy 2003). Endophyte communities from higher latitudes are characterized by relatively few fungal species, whereas tropical endophyte assemblages are dominated by a small number of classes but a very large number of different endophytic species (Arnold et al. 2000; Arnold and Lutzoni 2007). Xylariaceous Ascomycetes are the most dominant endophytes in tropical region. They found high endophytic diversity in the tropical plants in comparison to the temperate ones. Temperate region endophytes showed host specificity, while tropical region endophytes are less host specific (Chhipa and Deshmukh 2019).

Fungal endophytes hosted many different plant tissues e.g. roots, stems, leaves; branches, twigs, petioles, flowers, bark, fruit, and seeds scales, resin canals and even from meristems (Clay 1990; Guo et al. 2000; Evans et al. 2003; Holmes et al. 2004; Stone et al. 2004; Rubini et al. 2005; Torres et al. 2011; Khan et al. 2012; Arora and Ramawat 2017; Kumar et al. 2019; Abdel-Azeem et al. 2019; Abo Nahas 2019). The spectrum of fungi within a plant varies in space, time, and function. For example, leaves, stems, and roots of alfalfa plants are colonized by distinct fungi that produce different ranges of secondary metabolites (Lugtenberg et al. 2016). The main tissues types that have been analyzed for the presence of endophytes in woody perennials have been leaves, twigs, branches, and roots (Petrini and Fisher 1990), and few studies have looked for endophytes in the trunks or fruits of woody perennials (Evans et al. 2003). In an individual organ or a tissue, the endophyte assemblages profile can be completely different from that in other organs or tissues of the same plant (Evans et al. 2003; Holmes et al. 2004; Rubini et al. 2005). As a consequence of horizontal transmission, older organs or tissues are likely to accumulate greater species diversity than younger tissues. Thus, perennial species can be expected to harbor greater diversity than annuals. Similarly, evergreen foliage and woody stems are likely to harbor more diverse fungal endophyte assemblages than deciduous leaves or annual plants (Stone et al. 2004). Endophyte communities are influenced more by site than by plant host species. Also showed significant differences in endophyte assemblages from different sites but those differences were less pronounced than those observed for host species (Torres et al. 2011).

Host specificity is the relationship in which a fungus is restricted to a single host or a group of related species, but does not occur in other unrelated plants in the same habitat (Holliday 1998). There are two different terms, establishment specificity and expression specificity, to identify the relationship. Establishment specificity was defined when an endophyte colonizes only selected plant species, while expression specificity is colonization of several hosts by a given fungus, but forming specific structures (usually fruiting bodies) on a limited number of plant taxa.

Some researchers found very little evidence of host specificity in endophytes (Khiralla et al. 2016). Plants colonized by clavicipitaceous endophytic fungi usually harbor one dominant fungal isolate/genotype (Wille et al. 1999), while plants colonized by horizontally transmitted endophytes harbor high diversity, polyphyletic assemblage of fungi, especially plants with endophytes occurring in aerial tissues as a result of numerous, independent infections (Arnold and Herre 2003; Arnold et al. 2003).

A variety of relationships exist between fungal endophytes and their host plants, ranging from mutualistic or symbiotic to antagonistic or slightly pathogenic (Arnold et al. 2007). The range of symbiotic lifestyle expression from mutualism to parasitism has been described as the symbiotic continuum (Rodriguez and Redman 2008). Studies on host genotype versus symbiotic lifestyle expression revealed that individual isolates of some fungal species could span the symbiotic continuum by expressing either mutualistic or pathogenic lifestyles in different host plants (Redman et al. 2001). For example, *Colletotrichum* species are classified as virulent pathogens, yet several species can express mutualistic lifestyles in non-disease hosts (Rodriguez and Redman 2008).

2.4 Endophytic Fungi Plant Growth-Promoting Attributes

Colonization by endophytic fungi promotes plant growth by protecting against several fungal and bacterial borne diseases, improving the ecological adaptation abilities of the host by providing tolerance to counteract against biotic and abiotic stresses (Schulz and Boyle 2005); production of phytohormone is also considered as a significant contribution to enhancement of plant growth, Producing enzymes (Zhou et al. 2014) and nutrients uptake (Zhang et al. 2013; Jain and Pundir 2017).

2.4.1 Piriformospora indica

The endophytic fungus *P. indica* promotes nutrient uptake, allows plants to survive under water, temperature, and salt stress; confers (systemic) resistance to toxins, heavy metal ions, and pathogenic organisms; and stimulates growth and seed production (Verma et al. 1998; Varma et al. 1999; Sahay and Varma 1999; Oelmüller et al. 2004, 2005; Peškan-Berghöfer et al. 2004; Sherameti et al. 2005; Waller et al. 2005, 2008). *Piriformospora* has been shown to serve as a model to describe the mechanisms of host growth promotion. *P. indica* is one of the most studied fungi for its plant growth promotion activity and stress resistance as do the AM fungi, but has the added trait of being able to be grown in axenic cultures (Varma et al. 1999; Franken 2012; Kumar et al. 2012). *P. indica*, which can regulate development, is also able to act as a biofertilizer and also is a good candidate to improve commercial plant production and might be especially useful in agroforestry and flori-horticulture applications (Varma et al. 1999). *P. indica*, a wide host root-colonizing, has been used as a model to study the mechanisms and evolution of mutualistic symbiosis (Dong et al. 2013).

Plant growth promotion by endophytes is another confirmed beneficial for the root-colonizing endophyte *P. indica*. This is likely achieved through enhanced nutrient uptake and translocation, and by the modulation of phytohormones involved in growth and development (Johnson et al. 2014; Lugtenberg et al. 2016). Malla et al. (2004) have shown that *P. indica* contains substantial amounts of an acid phosphatase which has the potential to solubilize phosphate in the soil and delivers it to the host plant. A lot of studies have shown *P. indicia* as phosphorus mobilizer (Singh et al. 2000). Furthermore, Sherameti et al. (2005) observed nitrogen accumulation in the shoots of *N. tobaccum* and *A. thaliana*. In a study, Barazani et al. (2005) confirmed the growth increase in *Nicotiana tobaccum* due to *P. indica* and showed that the growth promotion was related to better aptness, as enhanced seed production was observed in treated plants. Rai et al. (2004) also presented similar results of *Spilanthes calva* and *Withania somnifera*, whereas Waller et al. (2005) of *Hordeum vulgare*. Sirrenberg et al. (2007) reported the production of indole acetic acid in submerged culture of *P. indica* when colonized with *Arabidopsis thaliana*. *P. indica* can synthesize a hormone and release it into the root tissue, influence a phytohormone level by interfering with its synthesis, degradation, or modification, or interfere with a phytohormone signaling pathways, or any combination of these possibilities (Oelmüller et al. 2009).

In axenic culture, *P. indica* does not exhibit antifungal activity to *Fusarium culmorum* or *Cochliobolus sativus*, indicating that the protective potential of the endophytic fungus does not rely on antibiosis. These results show that *P. indica* exerts beneficial activity against two major cereal pathogens that cause enormous worldwide economic losses (Waller et al. 2005). The endophyte significantly elevated the amount of ascorbic acid and increased the activities of antioxidant enzymes in barley roots under salt stress conditions (Oelmüller et al. 2009). In barley, the root endophyte *P. indica* confers disease resistance by a different mechanism. Symbiotic plants are thought to resist necrotrophic root pathogens due to increased activity of glutathione–ascorbate antioxidant systems (Waller et al. 2005). It is not clear if *P. indica* increases antioxidation systems in the absence of pathogens or if other aspects of host physiology are involved in resistance (Rodriguez et al. 2008). *P. indica* showed as a biocontrol agent against plant pathogen in maize, tomato, wheat, and barley (Kumar et al. 2009). *P. indica* showed the reduced severity of *Verticillium* wilt by 30% in tomato, caused by *Verticillium dahlia*, and increased leaf biomass by 20% (Fakhro et al. 2010). It also reduced density of Pepino mosaic virus of tomato which has been reported in the greenhouse of South and North America, China, and many European countries (Chhipa and Deshmukh 2019).

P. indica enhanced barley grain yield, tolerance to mild salt stress, and resistance against root and leaf pathogens, including the necrotrophic fungus *F. culmorum* (root rot) and the biotrophic fungus *Blumeria graminis*. Beneficial effects are also observed for the crop for wheat, maize, and rice (Oelmüller et al. 2009). Colonization of *P. indica* controlled various plant diseases such as powdery mildew, eyespot, *Rhizoctonia* root rot, Fusarium wilt, black root rot, yellow leaf mosaic, *Verticillium* wilt, cyst nematode, and leaf blight in barley, wheat, maize, tomato, and *Arabidopsis* plants (Chhipa and Deshmukh 2019). *P. indica* readily colonizes the *Arabidopsis thaliana* and increases the yield and salt tolerance in *Hordeum vulgare* (Waller et al. 2005), and barley plant (Oelmüller et al. 2009; Chadha et al. 2014). *P. indica* showed drought and salt tolerance in cacao, barley, and Chinese cabbage plants (Abo Nouh 2019). Tolerance to abiotic stress was induced in *Arabidopsis thaliana*; overall growth and biomass production were achieved in herbaceous mono- and dicots, medicinal plants, and other important crops (Chadha et al. 2014).

2.4.2 Epichloë *spp.*

Epichloë species often provide numerous benefits to their hosts, such as increased tolerance to drought (Gundel et al. 2013a), disease resistance (Vignale et al. 2013), resistance to herbivory and parasitism (Gundel et al. 2013b), and enhanced above-ground and below-ground vegetative and reproductive growth (Tadych et al. 2014; Song et al. 2016). *Epichloë* endophytes have importance in pasture systems in delivering both economic and sustainable agricultural solutions (Lugtenberg et al. 2016). Endophytes *Epichloë* sp. and *Neotyphodium* sp. (teleomorph of *Epichloë*) of *Festuca rubra* is a good example of plant growth-promoting endophyte which increase the plant growth with high uptake of nutrients (Jain and Pundir 2017; Chhipa and Deshmukh 2019). It has also been reported that plant–fungal interaction enhances the temperature tolerance to host plant by inducing heat shock protein expression (Chhipa and Deshmukh 2019). *Epichloë* species may enhance the ecophysiology of host plants and enable plants to counter abiotic stresses such as drought and metal contamination. *Neotyphodium coenophialum* infection leads to the development of extensive root systems that enable plants to better acquire soil moisture and absorb nutrients, resulting in drought avoidance and faster recovery from water stress (Rodriguez et al. 2009). *Neotyphodium* sp. increased drought tolerance in grass plant by osmo- and stomatal regulations and protected plants in water stress and nitrogen starvation (Abo Nouh 2019).

Epichloë infection also increased the germination of *Elymus dahuricus* under different osmotic potential pressures, but germination success was variable among populations (Zhang and Nan 2010). Several studies have shown that *Epichloë* infection can improve the relative fitness of grasses under drought stress (Iannone et al. 2012). Under drought stress, *Epichloë* infected (EI) of *Leymus chinensis* had significantly more total biomass than *Epichloë*-free (EF) *L. chinensis*, regardless of fertilizer levels (Ren et al. 2014). EI *Hordeum brevisubulatum* grass exhibited significantly increased N, P, and K+ concentrations, which led to an increase in total biomass. The *Epichloë* infection also reduced Na+ accumulation in the EI plants compared to EF plants (Song et al. 2015a). It has been reported that *Festuca rubra* when inoculated with the fungal endophyte *E. festucae* resulted in the increase in the uptake and concentration of phosphorus (Zabalgogeazcoa et al. 2006; Pineda et al. 2010). Zhang and Nan (2007) showed that EI *E. Dahuricus* produced more biomass, more tillers, and taller plants under low water treatment, but EI had no influence on plant biomass in the high water treatment. However, in a study of EI *A. sibiricum*, the addition of fertilizer resulted in greater plant growth, but this advantage decreased under reduced water and/or nutrient availability (Ren et al. 2011). Moreover, Song et al. (2015b) demonstrated that asexual *Epichloë* endophyte infection can increase resistance to water logging stress in *H. brevisubulatum.*

Epichloë endophytes confer stress tolerance to native grasses in China and play a significant role in the survival of some plants in high-stress environments, such as cadmium (Cd)-contaminated soils and nutrient-depleted soils (Song et al. 2016). *Epichloë*-infected *A. inebrians* (Zhang et al. 2010a, b) and *E. dahuricus* (Zhang et al. 2012a) had higher germination rates, more tillers, longer shoots and roots, and more biomass compared to EF plants in high Cd2+ concentrations. There was no significant difference between EI and EF plants under low Cd2+ concentrations, indicating that *Epichloë* infection was only beneficial to the growth and development of *A. inebrians* and *E. dahuricus* exposed to high Cd2+ concentrations (Song et al. 2016). Studies of nutrient acquisition in EI grasses have focused on the influence of nitrogen (N), since this element is a constituent of alkaloids in infected plants and is also one of the most important limiting resources for plant growth in general (Li et al. 2012).

It has been documented that increased N availability may change the relative availability of other nutrients, such as phosphorus (P) (Van Der Wouder et al. 1994). Only a few studies have confirmed that *Epichloë* endophytes can increase salt tolerance in a grass host (Reza Sabzalian and Mirlohi 2010). Li et al. (2012) found that EI *A. sibiricum* are conditional on both N and P availability, but are more conditional on N than P. Changes in N allocation increase the photosynthetic ability of EI plants and also significantly increase their biomass. Thus, EI plants have higher photosynthetic N use efficiency and shoot biomass than that of EF plants when fertilizer is limited (Ren et al. 2014). Zhang et al. (2012b) found that *A. inebrians* infected with *E. gansuensis* reduced the survival of the aphids *Rhopalosiphum padi, Tetranychus cinnabarinus, Oedaleus decorus,* and *Messor aciculatus* under laboratory and field conditions. Additionally, EI had an anti-herbivore effect on a wide range of arthropod groups (Song et al. 2016).

2.4.3 **Trichoderma** ***sp.***

Trichoderma sp. plays a major role in controlling the plant diseases. *Trichoderma* sp. is a free-living fungus that is highly interactive in root, soil, and foliar environments (Sharma et al. 2019). *Trichoderma* spp. is present in nearly all agricultural soils and in other environments such as decaying wood (Saba et al. 2012). *Trichoderma* sp. is a fungal genus found in many ecosystems and the most successful biofungicides used in today's agriculture with more than 60% of the registered biofungicides worldwide (Mukherjee et al. 2012). Also are commercially marketed as biopesticides, biofertilizers, and soil amendments (Saba et al. 2012). Some strains have the ability to reduce the severity of plant diseases by inhibiting plant pathogens, mainly in the soil or on plant roots, through their high antagonistic and mycoparasitic potential (Hermosa et al. 2012). *Trichoderma* is widely used as biocontrol agent against phytopathogenic fungi, and as a biofertilizer (Saba et al. 2012).

Trichoderma sp. uses several mechanisms such as antibiosis, mycoparasitism, and competition for nutrients and space, and is also able to promote growth and development of plant and induce the defense response of plants (Talapatra et al. 2017). *Trichoderma* sp. has used as biocontrol agent (BCA) against plant-pathogenic fungi such as *Botrytis cinerea*, *Fusarium* spp., *Pythium* spp., and *Rhizoctonia* spp. (Park et al. 2018). Fungal endophytes identified as *Trichoderma* from an essential medicinal plant of Assam, *Rauwolfia serpentina*, showed antagonistic activity against *Fusarium oxysporum* and *Phytophthora* spp. (Li et al. 2000; Doley and Jha 2010). El-Kafrawy (2002) reported that *T. harzianum*, *T. hamatum*, *T. pseudokoningii*, and *T. polysporum* inhibited the radial mycelial growth of *R. solani* in vitro test from 59.6 to 78.4%. The endophytic fungi *T. viride* showed antagonistic activity against all the fungi except *Aspergillus* but hyphae of *T. viride* overgrew on pathogen mycelium (Talapatra et al. 2017).

The endophyte *T. atroviride* D16 from the root of *Salvia miltiorrhiza* promoted the growth of hairy roots of *S. miltiorrhiza* (Jain and Pundir 2017). *T. citrinoviride* isolated from mountain-cultivated ginseng (*Panax ginseng*) has fungal activity against *Botrytis cinerea*, *Pythium* spp., *Rhizoctonia solani*, and *Cylindrocarpon destructans* (Park et al. 2018). *Trichoderma* sp. produced different secondary metabolites; these compounds are reported as a plant defense activator in canola, pea, and tomato (Chhipa and Deshmukh 2019). *Trichoderma* spp. produces extracellular β-(1, 3) glucanases, chitinases, lipases, and proteases when they are grown on cell walls of pathogenic fungi (Haran et al. 1996). Treatment of seed with *T. harzianum* ameliorates a wide variety of biotic, abiotic, and physiological stresses to seed and seedlings. Mycoparasitic *Trichoderma* species are used commercially as biological control agents against plant-pathogenic fungi such as *Rhizoctonia solani, Botrytis cinerea, Sclerotium rolfsii, Sclerotinia sclerotiorum, Pythium* spp., and *Fusarium* spp. *T. harzianum* protected bean seedlings against pre-emergence damping off infection, reduced the disease severity, and increased the plant growth in the presence of *R. solani* pathogen (de Paula et al. 2001). *T. pseudokoningii* isolated from tomato roots from central Himalaya exhibited plant growth-promoting activities of phosphate solubilization and synthesis of auxins, siderophores, HCN, and ammonia (Chadha et al. 2015). The use of *Trichoderma* fungi in agriculture can provide numerous advantages: (1) colonization of the root and rhizosphere of plant, (2) control of plant pathogens by different mechanisms such as parasitism, antibiosis production and induce systemic resistance, (3) improvement of the plant health by promoting plant growth, and (4) stimulation of root growth (Abd-El-Khair et al. 2010). *Trichoderma* sp. showed drought and salt tolerance in cacao, barley, and Chinese cabbage plant (Abo Nouh 2019).

2.4.4 **Penicillium** ***spp.***

Khan et al. (2008) isolated *P. citrinum* and showed the growth promotion activity on dune plants due to the presence of bioactive gibberellins in the filtrate of fungi. You et al. (2012) demonstrated the plant growth-promoting activity of endophytic fungus *Penicillium* sp. isolated from the roots of halophytes using Waito-C rice seedlings. *Penicillium* sp. from cucumber roots has been found to synthesize Gibberellic acid and IAA (Yadav et al. 2018b). Inoculating these strains in cucumber plants under drought stress has shown a significant increase in plant biomass, growth parameters, and assimilation of essential nutrients and reduced sodium toxicity

(Waqas et al. 2012). Gibberellic acid and indole-3-acetic acid are synthesized by endophytic fungi *Penicillium* sp. These fungi play a vital role in both mutant- and wild type rice by promoting shoot length, chlorophyll contents, biomass, and growth attributes of rice during stresses like salinity and drought (Waqas et al. 2012). Nath et al. (2012a) studied *Penicillium species* isolated from tea leaves as phosphate solubilizer. It was revealed from the study that there was remarkable phosphorous solubilizing activity by *Penicillium* up to 8 days with an increase in acidity of the medium. *P. citrinum* also produce siderophores which chelate the iron and activate the plant defense mechanism (Chhipa and Deshmukh 2019).

P. indica increased the resistance in barley against root rot causing agents *Fusarium culmorum* and *Blumeria graminis* (Waller et al. 2005). *P. citrinum* enhanced the sunflower growth (*Helianthus annuus L.*) and disease resistivity against the stem rot caused by *Sclerotium rolfsii* and leaf spot and blight caused by *Alternaria alternata* (Waqas et al. 2015). *P. brevicompactum* has been reported to suppress various seed-borne pathogens including *Rhynchosporium, Pyrenophora, Fusarium,* and *Cochliobolus* and soil-borne pathogen *Gaeumannomyces graminis var. tritici* (Murphy et al. 2015). Fouda et al. (2015) isolated *P. chrysogenum* from *Asclepias sinaica*. It was observed that this endophyte had the ability to produce several extracellular enzymes including amylase, pectinase, cellulase, gelatinase, xylanase, and tyrosinase. In addition, these isolates were found to improve root growth (Jain and Pundir 2017).

Penicillium sp. significantly increased plant biomass, related growth parameters, assimilation of essential nutrients such as potassium, calcium, magnesium and reduced the sodium toxicity in cucumber plants under salinity and drought stress, when compared with control plants (Lata et al. 2018). *P. brevicompactum* isolated from wild barley species was helpful in drought tolerance improvement of barley plant in drought condition (Abo Nouh 2019). *P. brevicompactum* also increased the germination index of the barley seed and also increased the yield by suppressing the seed-borne infectious organism (Chhipa and Deshmukh 2019). The different species of *Penicillium* genera were also identified as gibberellin producers, such as *P. corylophilum, P. cyclopium, P. funiculosum, Penicillium* sp., and *P. citrinum* (Hasan 2002; Khan et al. 2011), which also induce the production of defense hormone salicylic and jasmonic acid. Production of auxin hormone indole acetic acid (IAA) has been reported by endophytes P. *verruculosum*, *P. funiculosum*, and *Penicillium* sp. (Khan et al. 2012; Khan and Lee 2013). Endophytic fungi like *P. sclerotiorum* and *P. chrysogenum*, isolated from *Camellia sinensis* growing in Assam, India, showed auxin production, phosphate solubilization, potassium solubilization, and zinc solubilization (Nath et al. 2012a, b).

2.4.5 Fusarium *spp.*

Leymus mollis is colonized by one dominant fungal endophyte *Fusarium culmorum* that can be isolated from above- and below-ground tissues and seed coats. *F. culmorum* confers salt tolerance to the host plant which cannot survive in coastal habitats without the habitat-adapted endophyte. A comparison of *F. culmorum* isolates from *L. mollis* and a non-coastal plant revealed that the ability to confer salt tolerance was specific to isolates from the coastal plants, indicating that the ability to confer salt tolerance is a habitat-adapted phenomenon (Rodriguez et al. 2008). The *F. culmorum* isolate FcRed1 from dunegrass is a mutualist in dunegrass and tomato conferring salt tolerance, and isolates from non-coastal plants do not confer salt tolerance (Rodriguez and Redman 2008).

F. pallidoroseum has a significant positive role in plant growth and development. Inoculation of tomato seeds with *F. pallidoroseum* enhanced proline content; acid and alkaline phosphomonoesterase activity; and peroxidase activity. The fungus enhanced shoot dry weight and shoot length of wheat, maize, marigold, okra, moongbean, and brinjal over control (Srivastava et al. 2011). *F. proliferatum* from *Physalis alkekengi* have shown strong plant growth-promoting activity due to its ability to produce gibberellins (Rim et al. 2005). *F. tricinctum* isolated from leaves of potato *Solanum nigrum* produced IAA and also enhanced the growth of rice plants (Khan et al. 2015a, b). *F. culmorum* (Fc18) and *F. culmorum* (FcRed1) confer drought and salt resistance to *Leymus mollis*, *Oryza sativa*, *Lycopersicumesculentum*, respectively (Rodriguez et al. 2008). *Fusarium* spp. confer heat resistance to *L. esculentum* (Rodriguez and Redman 2008).

2.4.6 **Colletotrichum *spp*.**

Mutualistic benefits conferred by *Colletotrichum* spp. include disease resistance, growth enhancement, and/or drought tolerance (Redman et al. 2001). *Colletotrichum*-conferred disease resistance is localized to tissues that the fungus has colonized, and is not systemic. The results suggest that the endophyte may be acting as a type of biological trigger that activates host defense systems (Rodriguez et al. 2008). Many *Colletotrichum* species have been shown to exist as endophytes for part or most of their life cycle in many groups of plants; the majority of *Colletotrichum* isolates fall within the gloeosporioides, graminicola, and boninense species complexes. Many endophytes isolated from grasses poaceae belong to the gloeosporioides and boninense species complexes (Silva et al. 2017). *Colletotrichum* spp. cause drought resistance in *Lycopersicum esculentum* (Rodriguez et al. 2004) *C. gloeosporioides* increased plant biomass and conferred drought tolerance to tomato plants (Redman et al. 2002). *C. gloeosporioides* isolated from *Theobroma cacao* tissues showed antagonistic activity against black pod rot pathogen *Phytophthora palmivora*, frosty pod rot pathogen *Moniliophthora roreri*, and witches broom pathogen *M. perniciosa* in in vitro and field studies (Chhipa and Deshmukh 2019). *C. gloeosporioides* isolated from healthy and mature leaves of tea plants show significant antagonistic activity against both the test pathogenic *Pestalotiopsis theae* and *Colletotrichum camelliae*. The degree of growth inhibition ranged from 51.77 to 63.73% for *P. theae* and 18.33–36.73% for *C. camelliae*, respectively (Rabha et al. 2014).

2.4.7 Curvularia *spp.*

One plant species (*Dichanthelium lanuginosum*) has been studied and found to be colonized by one dominant endophyte (*Curvularia protuberata*). *C. protuberata* confers heat and drought tolerance to the host plant, and neither the fungus nor the plant can survive separately from one another when exposed to heat stress ranging between 38 °C and 65 °C (Redman et al. 2002) and *C. magna* confers disease but not heat or salt tolerance (Rodriguez et al. 2008). *Curvularia* spp. also confer heat and drought stress to *Lycopersicum esculentum* (Rodriguez and Redman 2008). The ability of the grass *D. lanuginosum* to survive soil temperatures ranging between 38 °C and 65 °C in Yellowstone National Park was directly linked to an association with the fungus *C. protuberata* and its mycovirus, *Curvularia* thermal tolerance virus (CThTV) (Lata et al. 2018; Kumar et al. 2019). *Curvularia* sp. confer thermo-tolerance to grasses, and also provided thermo-tolerance ability to other plants tomato, watermelon, and wheat (Abo Nouh 2019). While *Curvularia* species are not known to have broad disease-host ranges, *C. protuberata* from the monocot *D. lanuginosum* is a mutualist (confers heat tolerance) in the eudicot tomato, and isolates from non-geothermal plants do not confer heat tolerance (Márquez et al. 2007; Rodriguez et al. 2008). Fungal endophytes identified as *Curvularia* from an essential medicinal plant of Assam, *Rauwolfia serpentina*, showed antagonistic activity against *Fusarium oxysporum* and *Phytophthora* spp. (Li et al. 2000; Doley and Jha 2010).

2.4.8 Epicoccum nigrum

Notably, the ascomycete *E. nigrum* has been frequently isolated as an endophyte of sugarcane plants (Stuart et al. 2010). Similar to other ubiquitous fungi, *E. nigrum* can display an endophytic lifestyle (Schulz and Boyle 2005) in a variety of plants that are not taxonomically related (Fisher and Petrini 1992) which suggests the development of adaptations to overcome the different types of plant defenses (Fávaro et al. 2012). *E. nigrum* is especially known for its biocontrol activity against pathogens, such as *Sclerotinia sclerotiorum* in sunflower, *Pythium* in cotton (Hashem and Ali 2004), *phytoplasma* in apple trees (Musetti et al. 2011), and *Monilinia* spp. in peaches and nectarines (De Cal et al. 2009). In another study, the inoculation of an endophytic *E. nigrum* strain from an apple tree in the model plant *Catharanthus roseus* triggered defense responses against "*Candidatus Phytoplasma*" and reduced symptom severity (Musetti et al. 2011). Physiological and structural alterations, such as callose accumulation, have been observed in *C. roseus* plants inoculated with an endophytic apple tree *E. nigrum* strain to control *C. phytoplasma* symptoms (Musetti et al. 2011). *E. nigrum* is also known for its biocontrol potential against bacterial and fungal plant pathogens (Lugtenberg et al. 2016). *E. nigrum* has shown biocontrol activity against bacterial pathogen *Pseudomonas savastanoi pv. savastanoi* (Psv) causing olive knot and reduced psv growth/biomass up to 96% (Berardo et al. 2018).

2.4.9 Beauveria bassiana

B. bassiana is an entomopathogenic fungus with worldwide distribution, which can live as a plant endophyte; colonization of plant tissues by *B. bassiana* has proved to provide protection against insect damage and inhibition of insect establishment and development (Vega et al. 2008; Allegrucci et al. 2017). Fungal endophytes *B. bassiana* collected of coffee plants from Hawaii, Colombia, Mexico, and Puerto Rico appeared to be pathogenic to the coffee berry borer (*Hypothenemus hampei*) that is the most devastating pest of coffee throughout the world (Vega et al. 2010). The endophytic growth of *B. bassiana* in maize (*Zea mays*) plant tissues causes higher mortality of larvae of the European maize borer *Ostrinia nubilalis* (Vidal 2015). *B. bassiana* was able to infect *T. absoluta* (leaf miner pest of tomato leaves) either by direct contact with conidia or indirectly by ingestion of tomato leaves colonized endophytically resulting in mortality up to 50% or higher (Allegrucci et al. 2017).

2.4.10 Other Endophytic Fungi

Dai et al. (2008) reported production of abscisic acid by *Phomopsis* sp. isolated from *B. polycarpam* plant. The different species of *Aspergillus genera* were also identified as gibberellin producers, such as *Aspergillus flavus, A. niger* (Hasan 2002; Khan et al. 2011), which also induce the production of defense hormone salicylic and jasmonic acid. Production of auxin hormone indole acetic acid (IAA) has been reported by endophytes *Chaetomium globosum, Fusarium* sp*., Fusarium oxysporum, Phomopsis* sp*., Phoma glomerata,* and *Paecilomyces formosus* (Khan et al. 2012; Khan and Lee 2013). Waqas et al. (2012) reported that *Phoma glomerata* could secrete gibberellins (GAs) and indole acetic acid to significantly promote the growth of GAs-deficient rice. *Galactomyces geotrichum* isolated from *Trapa japonica* has been reported for IAA, jasmonic acid, and gibberellin production (Waqas et al. 2014b). Khan et al. (2012) *Phialemonium dimorphosporum* was reported to produce phytohormone (Indole Acetic Acid) that can promote plants growth. Indole acetic acid (IAA) is a group of auxin which involved as promoter of plants growth (Kandar et al. 2018).

Gibberellic acid and indole-3-acetic acid are synthesized by endophytic fungi *Aspergillus fumigatus, Paecilomyces* sp*., Phoma glomerata, Chrysosporium pseudomerdarium,* and *P. formosus* (Kour et al. 2019; Verma et al. 2017; Yadav et al. 2018a). These fungi play a vital role in both mutant- and wild type rice by promoting shoot length, chlorophyll contents, and biomass (Waqas et al. 2014a, b). Also *Alternaria alternate* isolated from leaves of potato (*Solanum nigrum*) produced IAA and also enhanced the growth of rice plants (Khan et al. 2015a, b). *Phoma glomerata* from cucumber roots have been found to synthesize gibberellic acid and IAA. Inoculating these strains in cucumber plants under drought stress has shown a significant increase in plant biomass, growth parameters, and assimilation of essential nutrients and reduced sodium toxicity (Waqas et al. 2012). Similar effects were observed by the same research group working on cucumber endophyte *Paecilomyces formosus* (Khan et al. 2012). Mahmoud and Narisawa (2013) studied fungal endophyte, *Scolecobasidium humicola*, which is able to enhance growth and biomass of tomato plant.

Many fungal endophytes such as *Scolecobasidium tshawytschae* (Hamayun et al. 2009a), *Arthrinium phaeospermum* (Khan et al. 2009b), *Chrysosporium pseudomerdarium* (Hamayun et al. 2009b), *Cladosporium sphaerospermum* (Khan et al. 2008; Hamayun et al. 2009c), *Cladosporium* sp. (Hamayun et al. 2009c), *Gliomastix murorum* (Khan et al. 2009c), *Fusarium fujikuroi, Sphaceloma manihoticola* (Shweta et al. 2010), *Phaeosphaeria* sp. (Kawaide 2006), *Phaeosphaeria* sp. (Hamayun et al. 2010), *Aspergillus fumigatus* (Khan et al. 2011a), *Exophiala* sp. (Khan et al. 2011b), *Chrysosporium pseudomerdarium, Exophiala* sp.*, Fusarium oxysporum, Chaetomium globosum, Phoma herbarum, Phoma glomerata, Paecilomyces formosus, Scolecobasidium tshawytschae,* and *Rhizopus stolonifer* (Nadeem et al. 2010; Khan et al. 2011, 2012; Khan and Lee 2013; Waqas et al. 2012; You et al. 2012) have been reported as gibberellin producers.

Griffith and Hedger (1994) isolated endophytic fungi from *Theobroma cacao* and evaluated their ability to inhibit *Moniliophthora perniciosa*, which was reported to be a major pathogen of cacao plant. Hasan (2002) revealed the growth promotion activity of endophytic *Phoma herbarum* and *Chrysosporium pseudomerdarium* on Soybean and proved that some endophytes are host specific. It was also revealed that *M. perniciosa* could also act as an endophyte (Lana et al. 2011). The root endophyte *Heteroconium chaetospira* has been shown to significantly increase the biomass production of Chinese cabbage due to nitrogen transfer (Usuki and Narisawa 2007). Vega et al. (2010) isolated many coffee endophytes including *Acremonium*, *Cladosporium*, *Clonostachys rosea*, and *Paecilomyces* from Mexico, Puerto Rico, Hawaii, and Colombia. *C. rosea* were found pathogenic to coffee berry borer *Hypothenemus hampei* and worked as entomopathogenic endophytic fungi.

Similarly, *Aspergillus niger* and *A. flavus* isolated as endophytes from *Cannabis sativa* have been shown to inhibit *Colletotrichum gloeosporioides* and *Curvularia lunata*, two common plant pathogens (Gautam et al. 2013). Anuar et al. (2015) isolated *Hendersonia, Amphinema* and *Phlebia* fungi from trunk and root tissues of oil palms and observed that *Phlebia* could serve as a biofertilizer promoting the oil palm seedlings eventually. These are used as empty fruit bunches (EFB) powder and real strong bioorganic fertilizer (RSBF) with *Phlebia* as formulation. The simulations of plant growth executed by plant growth promoters could be attributed in terms of tolerance to biotic and abiotic stresses and improved plant nutrition (Machungo et al. 2009; Yadav 2017; Yadav 2019; Yadav et al. 2017). *A. terreus* enhanced the sunflower growth (*Helianthus annuus L.*) and disease resistivity against the stem rot caused by *Sclerotium rolfsii* (Waqas et al. 2015). The findings showed that there were three isolates which were identified as *Phialemonium dimorphosporum, Gaeumannomyces graminis,* and *Gaeumannomyces amomi* which gave significant stimulation on growth of rice seedlings (Kandar et al. 2018). *Phialocephala scopiformis*, endophytes from *Picea glauca* (white spruce), produce anti-insecticide compound rugulosin which controls the budworm *Choristoneura fumiferana* which is a severe pathogen of the white spruce tree in Canada (Chhipa and Deshmukh 2019). Fouda et al. (2015) isolated *Alternaria alternata*, and sterile hyphae from *Asclepias sinaica*. It was observed that these endophytes had the ability to produce several extracellular enzymes including amylase, pectinase, cellulase, gelatinase, xylanase, and tyrosinase. In addition, these isolates were found to improve root growth (Jain and Pundir 2017).

Endophytic fungi like *Aspergillus niger*, and *Fusarium oxysporum* isolated from *Camellia sinensis* growing in Assam, India, showed auxin production, phosphate solubilization, potassium solubilization, and zinc solubilization (Nath et al. 2012a, b). Waqas et al. (2015) demonstrated that fungi *Aspergillus terreus* showed control of harmful effects of *Alternaria alternata* in leaf spot and blight disease of sunflower. *Phomaglomerata* significantly increased plant biomass, related growth parameters, assimilation of essential nutrients such as potassium, calcium, magnesium and reduced the sodium toxicity in cucumber plants under salinity and drought stress, when compared with control plants (Lata et al. 2018; Abo Nouh 2019). *Aspergillus terreus* also produce siderophores which chelate the iron and activate the plant defense mechanism (Chhipa and Deshmukh 2019).

2.5 Conclusion and Future Prospects

Endophytes comprise a diverse group of species that vary in symbiotic and ecological functions. We used host range, colonization and transmission patterns, tissue specificity, and symbiotically conferred fitness benefits to differentiate endophytes into four functional classes, while the impact of each class on plants may differ significantly, the vast majority of endophytes have yet to be adequately characterized. It is clear that these fungi can have profound impacts on the survival and fitness of plants in all terrestrial ecosystems, and therefore likely play a significant role in plant biogeography, evolution, and community structure. As more researchers perform Koch’s postulates to assess host range, colonization and transmission patterns, and symbiotic/ecological function, our perspective on endophytes will change. In addition, several new and emerging molecular (e.g. denaturing gradient gel electrophoresis (DGGE) and terminal-restriction fragment length polymorphism (T-RFLP)) and biochemical (e.g. stable isotope profiling (SIP) and metabolic incorporation of nucleotide analogs such as bromodeoxyuridine (BrdU)) technologies are now being applied to better characterize endophytes and their roles in plant ecophysiology (see review by Johansson et al. 2004; Vandenkoornhuyse et al. 2007). For example, molecular techniques can be used to assess community structure of endophytes across landscapes (e.g. Arnold and Lutzoni 2007; Macia’-Vicente et al. 2008), and biochemical techniques can indicate which members of the community are metabolically active. These data can be used directly into several studies on the systematics and taxonomy of these overlooked ecological group of fungi. In addition, as we learn more about the contribution of endophytes to plant gene expression, it will be possible to profile gene expression patterns to assess the symbiotic status of plant communities. Ultimately it should be possible to determine the community structure and metabolic activity of all fungal symbionts associated with plants across landscapes. Surely, this may allow the development of new tools to assess changes in ecosystems resulting from natural fluctuations, climate change, and other anthropogenic features of environmental modification.

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Chapter 3
The Role of Arbuscular Mycorrhizal Fungal Community in Paddy Soil

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3.1 Introduction

Paddy soil is a type of anthropogenic wetlands on earth. Arbuscular mycorrhizal fungi (AMF) are usually found in paddy soil, their efficient role in such environments has usually been probed or overlook. They may originate from any type of soil in pedological terms but are highly modified by anthropogenic activities. Anaerobic condition alternations due to paddy organization regulator microbial community structure and role and thus short-range biogeochemical processes (Kögel-Knabner et al. 2010; Suzuki et al. 2015). It is presented that short- and long-term effects of waterlogging (Fig. 3.1). All of these factors influenced nutrient bioavailability and microbial activity.

Rice (*Oryza sativa* L.) is one of the important crops grown expansively in numerous countries. Paddy used to cultivate rice is the most prevalent method of farming

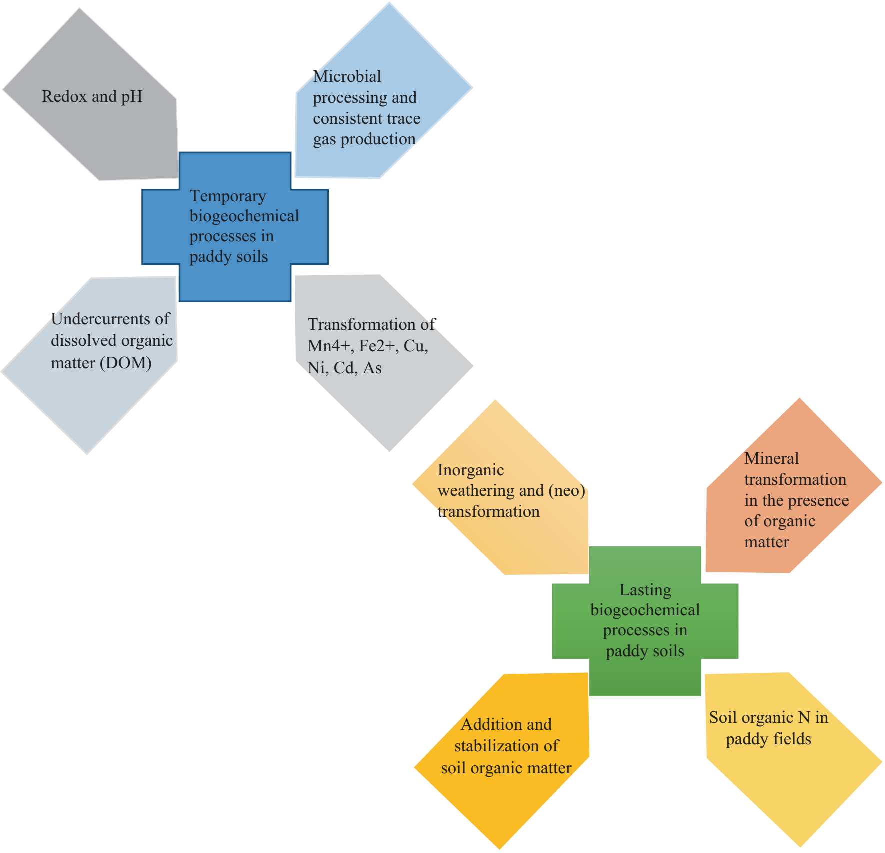

Fig. 3.1 Specific characteristics of biogeochemical processes in paddy soils (in according to Trolldenier 1988; Greipsson 1995; Liu et al. 2005; Lui et al. 2008; Bravin et al. 2008; Kögel-Knabner et al. 2010)

in some sites, where it utilizes a small fraction of the total land yet feeds the common of the country population (Anonymous 2019).

The most usual symbiotic association of plants with microbes is Arbuscular mycorrhiza (AM). Arbuscular mycorrhizal fungi (AMF) are typically found in wetlands, their efficient role in such surroundings has been probed (Khan 2004; Bao et al. 2019). Some studies showed a number benefits of AMF application. In the following diagram, we summarized these (Fig. 3.2).

In addition to these benefits to plants, AMF may progress soil structure, decrease drought and salinity stress, and affect the variety of plant communities (Van der Heijden et al. 1998; Rillig and Mummey 2006; Smith et al. 2010). The benefits of AMF are serious in increasing agricultural production and efficiency in a low-input method.

The most important fungi are AMF because they organized impel symbioses that supply phosphorus and nitrogen to 70–90% of the plant, as well as almost all crops including cereals, vegetables, and fruit trees; therefore, they had efficient application in sustainable agriculture. It helps plants to uptake nutrients such as phosphorus, sulfur, nitrogen, and micronutrients from the soil (Yadav et al. 2019). Some researchers regarded that the expansion of the AMF symbiosis had a vital role in the primary colonization of land by plants. Formation of unique structures, arbuscules, and vesicles by fungi of the phylum Glomeromycota are characteristics symbiotic relationship. Also, AMF were existed in the rhizosphere of the first land plants and more than 80% of vascular plants, as well as most crops (Barbour et al. 1980; Brundrett 2002, 2009; Smith and Read 2010; Taylor et al. 2017; Brundrett and Tedersoo 2018; Bao et al. 2019).

However, the occurrence of AMF in aquatic ecosystem has been known for lasting, and evidence present that AMF is widespread these places (Sondergaard and Laegaard 1977; Nielsen et al. 2004; Wilde et al. 2009; Wang et al. 2010; Wang et al. 2011; Wang et al. 2014; Dolinar and Gaberščik 2010). Recently, the existence and

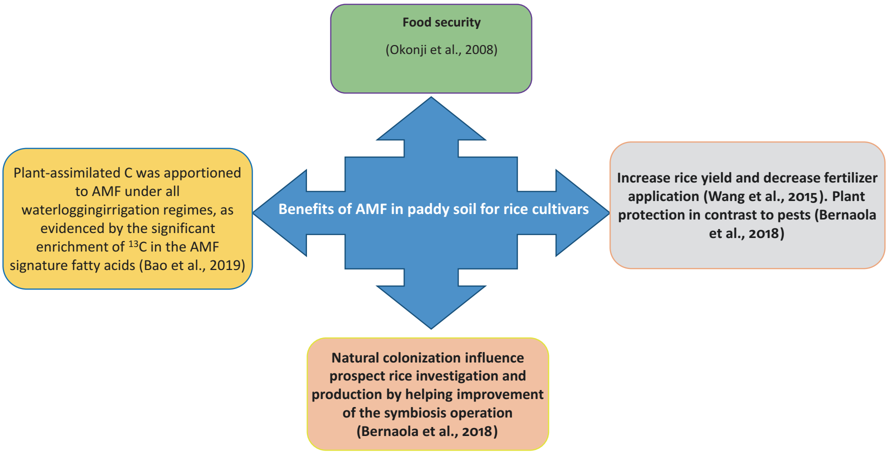

Fig. 3.2 Some benefits of AMF in paddy soil for rice cultivars

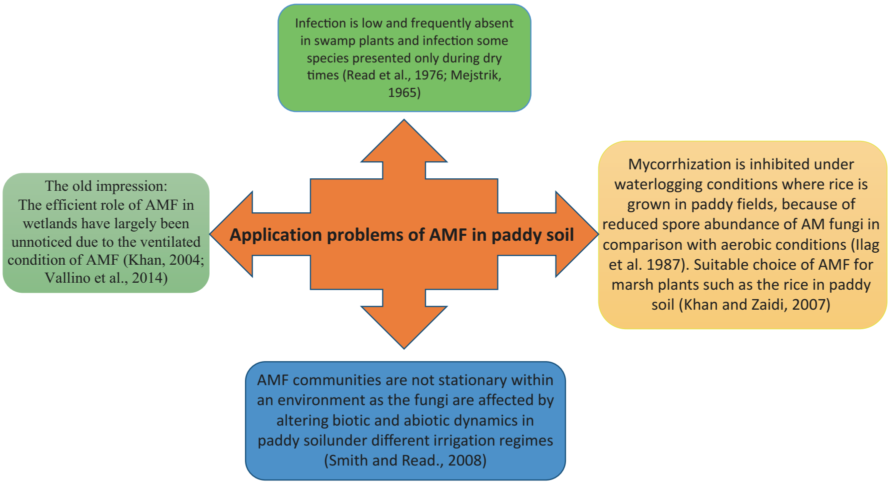

Fig. 3.3 Application problems of AMF in paddy soil

accumulation of AMF has been specially attended in wetland environments (Wilde et al. 2009; Wang et al. 2010, 2011, 2014; Lumini et al. 2011).

AMF-facilitated improvement in inorganic uptake may lead to increased growth and development of plants and may consult survived to abiotic and biotic stress (Liu et al. 2007; Smith and Read 2008; Gianinazzi et al. 2010). Along with all of their benefits, there are some problems with their application, conceptually (Fig. 3.3).

Arbuscular mycorrhizal fungi (AMF) are necessary for proper control of advantageous symbiosis in an agricultural production ecosystem. The present chapter describes the biodiversity and functional role of Arbuscular Mycorrhizal Fungal from various sources and its applications in paddy fields as a maker of bio-active compounds in agriculture as plant growth prompter and harmless and bio-control factors. In the end, it will be discussed that the current study methods, concerns and appropriate future for its application in agricultural paddy soils.

3.2 Biodiversity of AM Fungi and Plant in Paddy Soils

Some of the researches have been accompanied by plant and AMF biodiversity in paddy soils (Kosaka et al. 2006, 2006; Lakshmipathy et al. 2012). The following are some studies being detailed in the following:

Kosaka et al. (2006) reported a paddy plant was arranged in order of irrigation regimes from a shorter to longer hydroperiod by DCA. A total of 184 wild herbaceous species and 17 cultivated species were recorded by Kosaka et al. (2006) in the wetland of their case study. The factors associated with high species diversity were: (1) the species unique to various paddy types; (2) the remnant species from original vegetation; and (3) the effect of agricultural practices. DWARF 14 LIKE is gene among the 26 genes deleted in Habiba the one responsible for the loss of symbiosis. Some consequences discovered an unanticipated plant recognition strategy for AMF and a previously unknown signaling association among symbiosis and plant improvement (Gutjahr et al. 2015b). Rice seedlings grown under natural sunlight exhibited various MGR to F. mosseae, from −4.4% to 118.9%, depending on cultivar. ARC5955, an indica rice, showed the highest MGR, whereas Nipponbare, popular japonica rice, showed an MGR of only 18.7%. Suzuki et al. (2015) focused on these two cultivars. However, un-inoculated roots observed no fungal structure because MGR and root length colonization were not powerfully associated in their research and individual differences in root colonization were large Smith and Read (2008) did not further examine the colonization. Other studies showed different results. In contrast to *F. mosseae*, ARC5955 and *Nipponbare* showed little reaction to *Rhizophagus irregularis* (formerly Glomus intraradices). Plant growth responses to AM fungi be contingent on the combination of plant and fungus (Smith and Read 2008).

All of the AM fungal species are positioned in four orders, i.e. *Archaeosporales*, *Diversisporales*, *Glomerales, and Paraglomerales* which comprise 13 families and 19 genera that belong to class *Glomeromycetes* of the phylum *Glomeromycota* (Sieverding and Oehl 2006; Oehl et al. 2008; Palenzuela et al. 2008). The plant species is in the specified ecosystem determined its inhabitants and diversity, so these fungi are obligate symbionts (Harinikumar and Bagyaraj 1988). According to Wang et al. (2015), the 639 AMF sequences from roots and soils were clustered into 101 OTUs based on 97–100% sequence resemblance by the mothur program and finally based on phylogenetic analysis, it assigned to 16 phylotypes. Wang et al. (2015) showed that AMF collected at the seedling, tillering, heading, and ripening stages in the roots of wetland rice (*Oryza sativa* L.) in four paddy wetlands that had been under a high-input and severely irrigated rice cultivation for more than 15 years. It was found that AMF colonization was mainly formed in the heading and ripening stages. The AMF community was observed in the root and rhizosphere area of paddy soils (LT and HN) (Fig. 3.4).

Two AMF phylotypes (Rhi1 and Par6) were found to be the dominant AMF groups in roots throughout the tillering, heading, and ripening stages in the LT paddy wetland (Fig. 3.4), it representing that rice development caused well adapted in the environment of rice roots. Watanarojanaporn et al. (2013) showed that it is also obligatory to study whether any variations in species composition may be expressively affected by nutrient availability and plant growth since the AMF community changed by cultivation system and the application of compost types. Two major AMF in the genera *Glomus* and *Acaulospora* were distinguished from rice roots with or without compost application in this study.

Lakshmipathy et al. (2012) investigated that the effect of land-use intensity on the community (abundance and diversity) of arbuscular mycorrhizal fungi (AMF) was explored at various land-use types. In pre-monsoon season, the spore density and number of infective propagules were higher compared to the post-monsoon season in other land-use types, this is on condition that the land flora is different

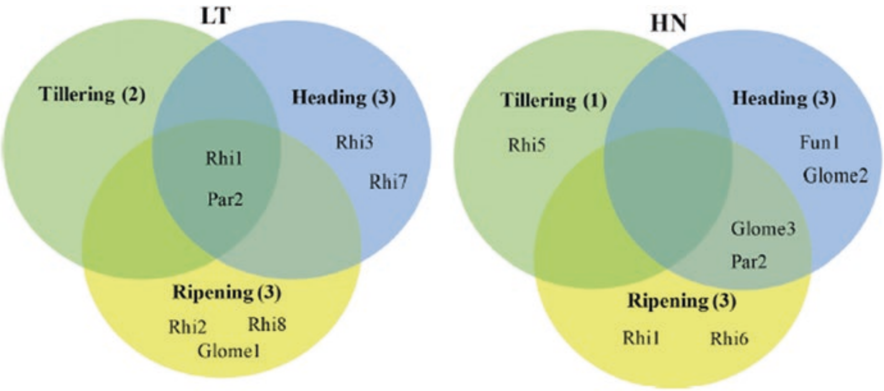

Fig. 3.4 Distribution pattern of AMF phylotypes in the roots collected at the tillering, heading, and ripening stages of rice in two paddy soils. The numbers in the parentheses indicate the number of constructed SSU-ITS-LSU libraries at the corresponding growth stage (Wang et al. 2015)

with the season and many species of herbs are documented. The dominant herbaceous weeds are in that area including *Panicum repens*, *Grangea maderaspatana*, *Centella asiatica*, *Blumea barbata*. The AMF community composition and diversity may be influenced by plant growth and community composition (Lin et al. 2015). In general, the AMF community is directly related to the cultivated plant species and this relationship is a two-way interaction (AMF-plant species) in paddy soil. Also, it changes according to the AMF community, the cultivation conditions such as organic matter application, the variability of soil moisture content and land-use history, and so on.

3.3 Colonization of Rice by Arbuscular Mycorrhizal Fungi

Inside the root and in the soil is the AMF community. The AMF community exists inside root and soil. The hyphae and other fungal structures, such as arbuscules and vesicles are present intraradical mycelium; the extraradical mycelium forms spores in soil for nutrient element uptake (Tommerup and Sivasithamparam 1990). The relationship between arbuscular mycorrhizal fungi (AMF) and bacteria within the rhizosphere section can motivate plant growth by a symbiotic. These communications are vital for increasing soil fertility, productivity, and sustainability, in addition to food security (Okonji et al. 2008). Legumes have benefited from biologically fixed nitrogen that association or symbiosis with root-nodulating bacteria, however, most non-leguminous plants, being the Gramineae (cereals), do not have a natural association (Hurek and Reinhold-Hurek 2003). So, the combination of these plants with AMF application can be important in terms of field product quality.

Vascular plants, including most crops, are widely established that the symbiotic arbuscular mycorrhizal fungi (AMF; phylum Glomeromycota) play an important function in suitable production systems and that rice freely organizes a symbiotic association (Lumini et al. 2011).

The arbuscules separated in the peri-arbuscular membrane significantly improved contact surface. In order to energizing of nutrient transport and the peri-arbuscular membrane, the symbiotic interface is acidified (Fig. 3.5) (Alexander et al. 1989; Guttenberger 2000; Krajinski et al. 2014; Wang et al. 2014) in paddy soil.

A vastly branched hyphal an arbuscule grows in the cortical cells and helps for nutrient exchange between the host plant (which make available photosynthates) and the AMF (which provides mainly phosphate along with other nutrients). To survive in phosphorus-deficient soil, external hyphae growing from the mycorrhizal roots permit host plants to assimilate phosphate from outside the root region (Nakagawa and Imaizumi-Anraku 2015) (Fig. 3.6).

Bernaola et al. (2018) indicated that root colonization proportion alternating from around 2% to 62% in all the rice samples given from various locations over many years were colonized by AMF. These organs tend to decomposition rapidly, a few arbuscules were observed in some studies. Hyphae were the most common

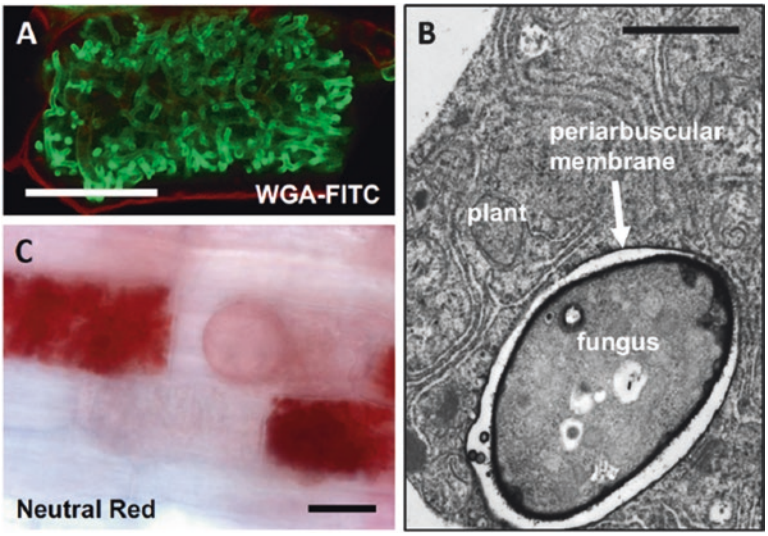

Fig. 3.5 Distinguishing of AM fungal arbuscules. (**a**) Arbuscules are highly branched hyphal structures that nearly fill the cortex cells of the host. Green staining of fungal structures with wheat germ agglutinin (WGA) coupled to *fluorescein isothiocyanate* (FITC), red staining of the cell wall with propidium iodide (from Kretzschmar et al. 2012). (**b**) Transmission electron micrograph of a colonized host cell with an arbuscular branch (fungus), surrounded by the peri-arbuscular membrane. (**c**) A colonized root stained with Neutral Red which accumulates in acidic compartments, in this case, the space between the peri-arbuscular membrane and the fungal cell wall [compare with (**b**)]. Size bars, 20 µm in (**a**, **c**); 1 µm in (**b**) (Chen et al. 2018)

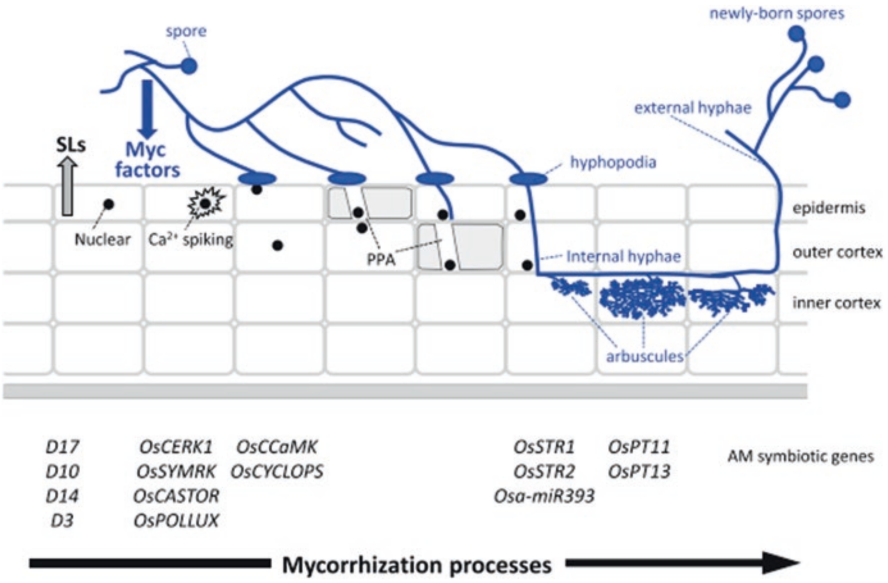

Fig. 3.6 Schematic view of mycorrhization and rice genes directly involved at each stage. SLs derived from host roots induce hyphal branching of AM fungi. Myc factors secreted from AM fungi induce symbiotic Ca^{2+} spiking. Hyphopodia are organized on the epidermis of host roots at the tips of branched hyphae. Immediately beneath the hyphopodia, the pre-penetration apparatus (PPA) develops to guide hyphal penetration. In the inner cortex, arbuscules develop and act as a nutrient exchanger between the host plants and AM fungi (Nakagawa and Imaizumi-Anraku 2015)

structures for delivery of mineral nutrients in the symbiosis interaction (Parniske 2008); vesicles were set up in more quantity. N1, N2, and N3 represent for N chemical fertilization at 100%, 75%, and 50% of the optimum rate, respectively; P1, P2, and P3 represent for P chemical fertilization at 100%, 75%, and 50% of the optimum rate, respectively; M, mycorrhizal fungi. Accordingly to Hoseinzade et al. (2016), the least rate of colonization (%) was observed by N1P1M (N1, N2, and N3 represent for N chemical fertilization at 100, 75, and 50% of the ideal rate, respectively); the highest rate of colonization was resulted by N2P3M (47), N3P2M (46), and N3P3M (48). Some results indicating the significant effects of bio-active fertilizers including H. *seropedicae* and G. *mosseae*, on the rice yield, the time of appropriate application is presented in the following table during the rice plant growth stages (Hoseinzadeh et al. 2016)

Hattori et al. (2013) showed that in the flooding treatment, most root nodules were organized on the adventitious roots, especially. Among two treatments including flooding and non-flooding, there was no significant difference in the number of nodules on the adventitious roots and the total number of nodules, because the values had a significant difference between plants, completely in the flooding. AM colonization and nodule formation on the two different types of roots were detected in the flooding treatment, that is, the root system was divided into (primary and lateral roots as) basal roots, and adventitious roots appeared below the lower place of the hypocotyl. The hypocotyls were dispersed on the soil surface in the shallow soil layer, in the flooding treatment. Hence, the roots are not damaged by poorer oxygen situations in anaerobic conditions. In fact, the roots had a higher AM colonization ratio and many root nodules were formed in wetland soil. Enlarged diameter and partial cracking of the surface tissues were found in the flooding treatment, they were characteristic morphological modifications in water logging hypocotyls on the soil surface (Fig. 3.7).

According to Lynch (2007), adventitious roots have more plenty of aerenchyma than other root types. The ratio of the aerenchyma/stele area in the roots was more than 80% in the flooding treatment. The adventitious roots have high rates of AM infection and nodule in persuaded in the flooding treatment because the microorganisms are aerobic (Ray and Inouye 2006; Maekawa et al. 2011). As follows, two approaches were founded for AMF application in paddy soil. Suzuki et al. (2015) show that rice under well-drained conditions (aerobic) is positively quick to respond to AM fungi and that colonization and growth response were different widely.

Gutjahr et al. (2015a) showed that the jasmonate-deficient rice (*Oryza sativa*) mutant hebiba cannot establish symbiosis with either of two AMF rhizophagus irregularis and Gigaspora rosea—as reflected by the absence of hyphopodia, intraradical colonization and induction of colonization marker genes (Fig. 3.8a–c). Growing hebiba alongside colonized wild-type plants caused the lack of fungal interaction persisted upon increased inoculum strength imposed (Fig. 3.8d). This suggested that during pre-symbiotic signaling, the mutant is compromised at a very early stage of the interaction.

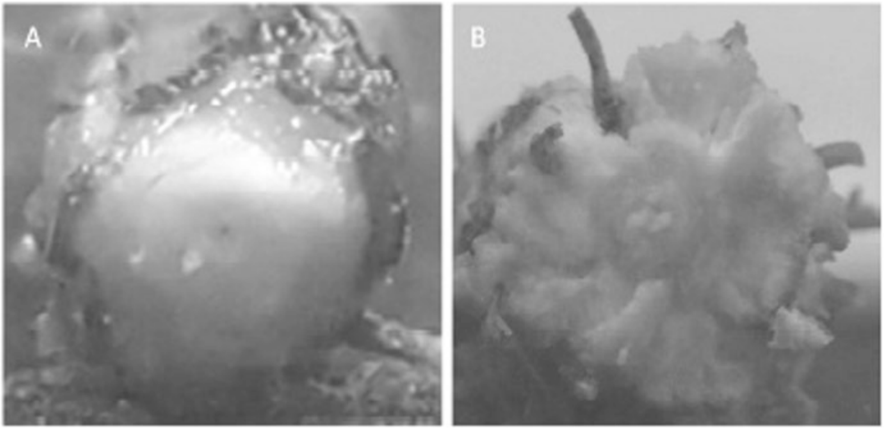

Fig. 3.7 Aerenchymatous tissues in soybean seedlings after flooding. (**a**) Irrigation, (**b**) flooding (Hattori et al. 2013)

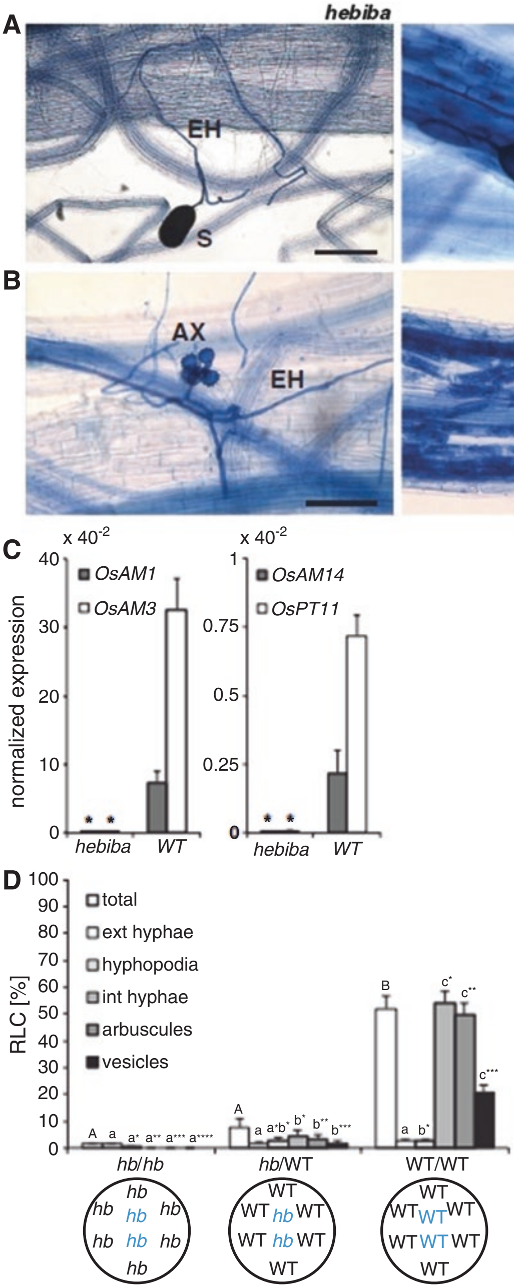

Fig. 3.8 AM phenotype of hebiba. (**a** and **b**) Roots of hebiba and wild type (WT) stained with trypan blue to visualize AM fungal structures 6 weeks post-inoculation (wpi) with R. irregularis (**a**) and G. rosea (**b**). Labels refer to A, arbuscule; AC, arbuscular coil; AX, auxiliary cell; EH, extraradical hypha; HP, hyphopodium; V, vesicle; scale bar, 100 mm. (**c**) Expression of early (AM1 and AM3, left) and late (AM14 and PT11, right) AM marker genes in hebiba and WT 6 wpi

3.4 Arbuscular Mycorrhiza Community Under Different Irrigation Regimes in Paddy Soils

Irrigation regimes are determined by the rate, number, and time of water applications to agricultural products. It depends on the biologic characteristics of plants, climatic, soil, and hydrologic conditions. Water is a vital section of soil fertility. Other views, some crops are planted in upland fields that have been converted from rice paddies in the several countries of Asia. In such fields, waterlogging conditions extensively damage this crop during the rainy season. The lack of oxygen in the root system caused these damages including prevented the growth and nutrient uptake and often reduced seed yields (Hattori et al. 2013; Linkemer et al. 1998; Miao et al. 2012).

Wetlands are productive bio-systems that collect large amounts of organic matter in the soil, so functioning as significant C sinks (Mitra et al. 2005). In these places, waterlogging leads to soils dominated by anaerobic processes. The presence and practical role of AMF in wetlands have largely been overlooked due to the aerobic nature of AMF (Khan and Zaidi 2007; Vallino et al. 2014). Also, most studies being about Arbuscular mycorrhiza have been carried out on upland rice (not flooding irrigation) and the number of studies is relatively little in lowland (Yimyam et al. 2008; Rajeshkannan et al. 2009) but anthro-saturation occurs as soil is deliberately flooded and ponded for agronomic aims. Most of this occurs are in the crop growing of rice (paddy soils). Paddy soils are consequent from different kinds of parent materials under waterlogging cultivation over various parts. They are exposed through alternate processes of oxidation and reduction. They are usually anaerobic and possess a low redox potential during the growing period of rice. Vesicles, hyphae, and arbuscules (Characteristic AMF structures) were observed in all roots inoculated with R. irregularis, and there were no AMF colonization in the non-mycorrhizal (NM) controls (Bao et al. 2019).

The explored paddy fields were under waterlogged conditions most of the time, and as AMF is aerobic, the occurrence of AMF in paddy wetlands could be correlated to the expansion of aerenchyma in the rice plant. At the heading and ripening stages, the aerenchyma provides oxygen in rice roots; but the aerenchyma tissue has

◄

Fig. 3.8 (continued) with R. irregularis as assessed by quantitative PCR. Expression values were normalized to those of the housekeeping gen Cyclophilin2 (LOC_Os02g02890). Means and SEs of four biological replicates are shown. Expression was significantly less in hebiba than WT ($P = 0.02$ for each gene; Kruskal–Wallis test with Benjamini–Hochberg adjustment for multiple testing). (**d**) Percentage of root length colonization (RLC) by R. irregularis of two central "tester" surrounded by six "donor" plants at 7 wpi. Means and standard errors of five biological replicates are shown. ext hyphae, extraradical hyphae; int hyphae, intraradical hyphae. For each of the six fungal structures in the figure, separate Kruskal–Wallis tests were performed, using the Benjamini–Hochberg adjustment for the post hoc tests. The P values were as follows: P (total) ≤ 0.01, P (ext. hyphae) $= 0.43$, P (hyphopodia) ≤ 0.05, P (int. hyphae, arbuscules, vesicles) ≤ 0.001.The letters above each bar show growth conditions that were not significantly different in the post hoc pairwise comparisons (Gutjahr et al. 2015b) not been well developed at the early developmental stages (Wang et al. 2013) and the AMF may be oxygen incomplete. Although results of some research showing that AMF are usually present in about types of wetlands, such as mangrove (Wang et al. 2011, 2013, 2014), salt marsh (Wilde et al. 2009), the AMF community in wetland habitats poorly known. The relatively high number of AMF phylotypes in the surveyed conventional paddy wetlands from this study indicates that the AMF diversity in an aquatic ecosystem is not unavoidably low (Wang et al. 2011). This can be explored by aerenchyma in rice roots (Fig. 3.9) and the high ecological adaptability of some AMF species. Up to now, the role of AMF in wetland ecosystems was poorly understood (Wang et al. 2011; Zhang et al. 2014), but several researches have been found that the AMF colonization of aquatic plants produces a wide range of advantages to AMF-plant partners (Wang et al. 2011; Zhang et al. 2014; Stevens et al. 2011). It offered that AMF is an important component in the traditional rice cultivation systems in paddy soil. Considering the high fertilizer inputs and the frequent disruption that happens in the paddy fields, the observed high AMF diversity indicated that some AMF groups can be adaptive to a high-input and severely managed ecological unit.

The AM colonization ratio in flooding was lower than in the irrigation regime. Some results showing different rates of AM colonization and root nodule formation between the two different types of roots increase the appreciative of responses of

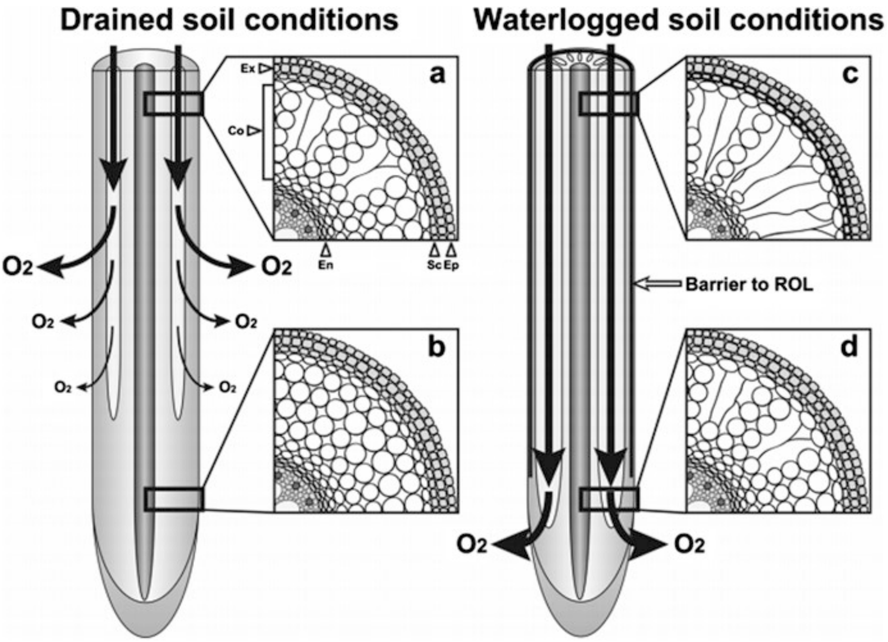

Fig. 3.9 Differences in lysigenous aerenchyma formation and patterns of radial O2 loss (ROL) in rice roots under drained soil conditions and waterlogged soil conditions (Nishiuchi et al. 2012)

soybeans grown in drying-rewetting (lowland and upland) fields (Hattori et al. 2013). Generally, rice is grown under thin flooded or wet paddy conditions, but it is also cultured where floodwater with meters deep; therefore, rice appears to have a high water requirement. The system of rice intensification (SRI) is another system for rice cultivation, made in Madagascar in the early 1980s to cultivate rice, and these managements have now been approved in over 20 countries. Five main differences in SRI compared to conventional practices (constant waterlogging) including (1) transplanting younger seedlings, (2) transplanting seedlings singly, (3) widespread spacing application, (4) interchanging soil flooding with draining during the vegetative growth phase, and (5) applying organic amendment (as compost) rather than mineral fertilizer (Watanarojanaporn et al. 2013).

Other studies showed that AMF is usually present in high-input and intensification irrigated rice cultivation management and that AMF colonization and community are dependent on the growing stage of the rice plant (Wang et al. 2015), proposing that development stage plays an important role in their relations. Solaiman and Hirata (1995) showed that the role of AMF varies in nutrient uptake ratio in plant organs, plant growth stages, and application intensity. AMF considerably reduced shoot N concentration and did not affect shoot P concentration at the development stage. N and P concentrations in unhulled grain were significantly increased due to AMF inoculation only under flooded conditions. These results recommend that AMF may accelerate N and P transmission from shoots and soils to rice grains even under flooded conditions and along with the trend to rise the harvest index under the flooded conditions, AMF increased the harvest index due to a decrease in shoot dry matter production while under non-flooded conditions, AMF decreased it due to a decrease in the dry matter of unhulled grains itself. There was a significant relation between AMF inoculation and irrigation regimes on AMF colonization (Solaiman and Hirata 1995).

Previous studies have reported a significant effect of hydrology management on the AMF community structure in waterlogging conditions (Wang et al. 2015, 2016). In the all typical AMF structures, the root colonization was generally lesser following increased flooding intensities at the rice and showed an increasing tendency at the second growth stage compared to the first (Bao et al. 2019). The percentage of AMF colonization by the three types [*Glomus versiforme* (GV), *Glomus mosseae* (GM), and *Glomus diaphanum* (GD)] on the rice cultivars ranged from 30% to 70%. Mycorrhizal colonization of upland rice cultivars had a large effect on plant development by increasing the shoot and root biomass (Zhang et al. 2005).

AMF community structure was affected by different irrigation systems, alternating flooding, and draining of water management in paddy fields. Rice plants grown under SRI (the system of rice intensification) had a more various AMF community than those grown under conventional rice cultivation systems (Watanarojanaporn et al. 2013). The AMF colonization ratio was 12.5% in the primary and lateral roots and 14.5% in the adventitious roots in the irrigation treatment. The ratios in the irrigation treatment were significantly more than those in flooding treatment. The AM colonization ratio in the adventitious roots (7.5%) was significantly high in the primary and lateral roots, while it was not necessarily low in the flooding treatment

(0.8%). Under upland conditions, rice plants readily form mycorrhizal associations, but under water logging conditions, infection is rare due to anaerobic conditions (Ilag et al. 1987). Nevertheless, AMF has necessitated aerobes in nature but can stay alive under submerged conditions, and this is sustained by the fact that AMF as *Glomus etunicatum* showed properly high colonization in rice roots and best survival under water logging conditions (Vallino et al. 2009).

3.5 Arbuscular Mycorrhiza Under Water: Carbon–Phosphorus Exchange Between Rice and Arbuscular Mycorrhizal Fungi

It has before been recommended that mycorrhiza should be combined into global models of C and mineral cycling for the plan of ecosystem reactions and responses to climate change. Global carbon and phosphorus cycling are significantly contributed by AM symbiosis (Averill et al. 2014; Terrer et al. 2016; Treseder 2016). AMF organizes mutualistic associations with the roots of most plants, including many crops. These mutualistic associations have shown the potential to increase crop efficiency, thereby playing a key role in the functioning and sustainability of agricultural systems (Gianinazzi et al. 2010). The most important role of these symbiotic associations consist of the transfer of nutrients such as organic carbon in the form of sugars and lipids (Jiang et al. 2017; Luginbuehl et al. 2017), to the fungi by the plants, and the transfer of phosphorus (P) and nitrogen (N) to the plants by the fungi (Smith and Read 2008).

Bao et al. (2019) observed that alternative water logging led to no obvious decline in AMF colonization intensity and, although sharp decreases in C–P exchange under flooding treatments at growth stages. These consequences describe the significant dynamic force of flooding in AM symbiosis in wetlands (Vallino et al. 2014), and showed that it can be observed nutrient influence from both AMF and plants change in response to flooding before a significant decrease in mycorrhizal colonization. The flooding-induced reduction in oxygen availability could describe the reduced role of the AM symbiosis, particularly in the extra-radical mycelium, which had lesser availability to the transported oxygen through root aerenchyma, despite established aerenchyma in rice.

It was observed that the improved P uptake due to AMF colonization under non-flooding conditions by Vallino et al. (2014) and Bao et al. (2019) but not during flooding and, the intraradical: extraradical ratio of 13C allocation increased with increased flooding intensity. Flooding conditions caused a decrease in C-P exchange may also be related to the change in morphology of the rice root (Vallino et al. 2014). Hydrologic cycle is being intensified the global climate change, and the occurrence of crop flooding can be probable to increase in the future (Milly et al. 2002). The response of AM symbiotic functionality to flooding observed by Bao et al. (2019) study. The plant C distribution to AMF declined at increased flooding intensity and was significantly greater at the growth stage when the rice plants had a higher nutrient necessity.

The relationship between the arbuscular and the root cell of the plant is demonstrated as a model in Fig. 3.13. The sucrose is released root cortical cells into the interfacial apoplast, acid invertase hydrolyzed it into hexoses that can be taken up by the fungus (Fig. 3.13, [1]). Once taken up by the fungus, the C is integrated into lipids and transported throughout the fungal mycelium. The glyoxylate cycle metabolized the lipids and characterize the major C source for supportive the spread of the extra-radical mycelium in the soil. The hyphal tips catch P via high-affinity mineral P (Pi) transporters (Fig. 3.13). Mainly in the form of polyphosphate, P is collected and transported along the hyphae to the roots of the host plant (polyP), phosphoanhydride-bound Pi polymer residues. Alkaline phosphatases depolymerized PolyP in the intraradical mycelium, and Pi is abandoned into the between apoplast (Fig. 3.13, [3]). Plants catch the Pi by mycorrhiza-specific Pi transporters in the periarbuscular membrane (Fig. 3.13, [4]); (Smith et al. 1994; Harrison and van Buuren 1995; Bago et al. 2000; Douds et al. 2000; Ezawa et al. 2002; Bucking and Shachar-Hill 2005; Schaarschmidt et al. 2006; Schüβler et al. 2001; Rausch et al. 2001; Javot et al. 2007; Xu et al. 2007; Hijikata et al. 2010). This process is illustrated in Fig. 3.10, completely.

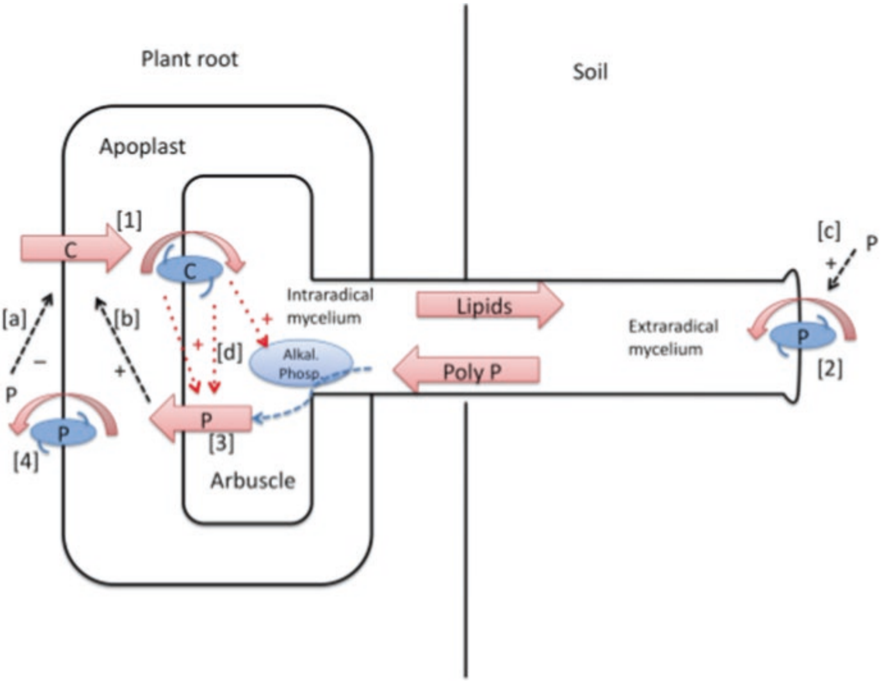

Fig. 3.10 The nutrient exchange between plants and AMF is a theoretical model. The flows are identified by numerals and adjustment mechanisms as letters in square brackets. Mycorrhiza-specific Pi transporters give Pi to plants in the peri-arbuscular membrane (**a**) Under high plant P levels C release to the fungus declines, and plant peri-arbuscular P transporters are down-regulated premature arbuscule senescence is induced under low P delivery (**b**) Fungal nutrients can motivate plant C statement (**c**) Hyphal P adsorb is P induced, as the P transporter gene is regulated by the environmental P concentration but C flow to the fungus does not influence P uptake from the medium place (**d**) researchers hypothesized that P transfer to plants can be controlled by the fungus that provides low-C benefit (Hammer et al. 2011)

Hammer et al. (2011) showed that G. *intraradices* gathered more than six times more nutrients in its spores, and up to more eight times more in its hyphae, when the C sink available decreased by 50%. Potassium and chorine were also collected, while no accumulation of iron or manganese was established. They recommended a useful relation between C and P exchange. The highest effect they establish for phosphorus (P) considered to be the most vital nutrient in the AM symbiosis.

3.6 The Role of Arbuscular Mycorrhizal Fungi in Improving Yield, Nutrient Uptake Management and Stress Tolerance in Paddy Soils

AM fungi are present in the majority of natural ecosystems and they provide a range of important environmental services, in particular by improving plant nutrition, tension resistance and tolerance, physic and chemical soil characteristics (Kour et al. 2019). Basic research of the past decade has exposed the existence of a devoted recognition and signaling pathway that is required for AM. Additionally, recent evidence delivered a new vision into the exchange of nutritional benefits between the symbiotic partners. The great potential for the application of AM has given an increase to a prosperous industry for AM-associated products for agriculture, horticulture, and landscaping work. Here, we debate new developments in these fields, and we highlight prospect potential and limits toward the use of AM fungi for plant production (Chen et al. 2018).

The basis for AM symbiosis is this exchange of resources, and it is responsible for considerable nutrient transfer globally and is critical for carbon sequestration in earthly ecosystems. Plants transfer averaged (~5 billion tonnes of C per year: 20% of their photosynthetic products) to fungal symbionts (Bago et al. 2000) and receive up more than 80% of the mineral nutrients from AMF (Smith and Smith 2011). The improvement of the plant's ability in tolerating toxic elements, the AMF has been shown to increment the nutrient station of their host plant (Aggangan et al. 1998). Low-C availability to the plant did not cause to reduce the hyphal length colonization, but the number of arbuscules was lower, indicating that P transfer was reduced, which established by isotope probing that mycorrhizal 33P transfer was intensely reduced to root that was C-ravenous in a communal mycorrhizal network (Lekberg et al. 2010; Hammer et al. 2011).

Although phosphorus (P) shortage strongly restricts rice production in some soils (Nishigaki et al., 2019), P uptake and plant growth are increased by colonization of plant roots with AMF (Bernaola et al., 2018; Hajiboland et al., 2009). Although AMF colonization did not increase rice growth, a significant amount of P was transported to plants through the mycorrhizal way under wetland conditions. This is understood by the gene expression profiles and rice P levels (Bao et al. 2019). Two pathways are present for nutrient absorption in AM (arbuscular mycorrhizal) roots, which include: the root epidermis and root hairs (the direct pathway (DP)); and root cortical cells are the mycorrhizal pathway (MP) via AM fungal hyphae (Smith and Smith 2011). Optimistic effects escalate principally from the increasing P uptake via the MP, improving P efficiency (Smith and Read 2008; Smith and Smith 2011).

Mycorrhiza had supporting effects against the toxicity of Cu, Zn, Pb, and Cd in the contaminated soil conditions. In the two cultivars, colonization by AMF reduced the translocation of heavy metals from root to shoot. The mixture of Cu, Zn, Pb, and Cd and immobilization of the heavy metals in roots decrease the potential toxicity to shoots. When un-inoculated condition, the two rice cultivars presented significant differences in uptake of Cu, Zn, Pb, and Cd. AMF inoculation had the most protective effects under the combined soil contamination (Zhang et al. 2005). Mycorrhiza had supporting effects against the toxicity of Cu, Zn, Pb, and Cd in the contaminated soil conditions. In the two cultivars, colonization by AMF reduced the translocation of heavy metals from root to shoot. The mixture of Cu, Zn, Pb, and Cd and immobilization of the heavy metals in roots decrease the potential toxicity to shoots. When un-inoculated condition, the two rice cultivars presented significant differences in uptake of Cu, Zn, Pb, and Cd. AMF inoculation had the most protective effects under the combined soil contamination (Zhang et al. 2005).

Significant effects of biological fertilizers including H. *seropedicae* and G. *mosseae,* on the rice production as well as on soil factors, were gained. However, biological fertilizers almost related to the soil and plants were importantly affected by the bacteria and the fungi (Hoseinzade et al. 2016). The K and Mn concentration appeared somewhat higher with colonization. On the other, the levels of Fe, Cu, Zn, B, and Al reduced with colonization in some India rice cultivars. Co contents in AM roots increased significantly in both cultivars of rice (Nipponbare and ARC5955). Colonization of F. mosseae imitated the above growth motivation, and also improved the P concentration. Response of rice to *F. mosseae* was stated by the increase of P concentration in colonization of *F. mosseae* and increase beneficial elements concentration and decrease deleterious element concentration (Suzuki et al. 2015). P accumulated in definite regions within the spores, together with K the elemental maps obtained with PIXE (Fig. 3.11). In vacuole-like structure, P accumulation was seemed spot-wise. It revealed that the concentrations of K and Ca were the highest near the spore wall in the full-C treatment, analysis was done on a cross-section of two separate spores from mycelium (Hammer et al. 2011). Organic amendments including paddy straw, maize straw, and *Pongamia* leaf improved the mycorrhizal activity in the paddy soils. Addition of *Pongamia* leaf enhanced AM fungal infection to the maximum, and then followed by maize straw in three amendments addition (Harinikumar and Bagyaraj 1988).

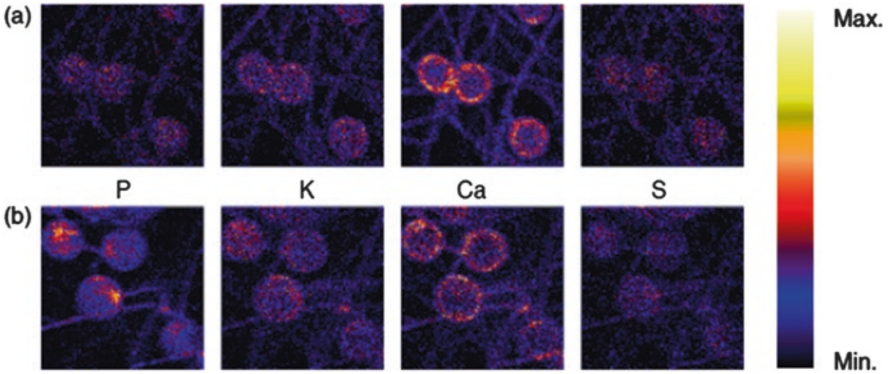

Fig. 3.11 PIXE elemental distributions of Ca, K, P, and S in hyphae and spores from two areas of the mycelium [(**a**) full-C; (**b**) half-C] of *Glomus* intraradices. The color scale shows the gradient from low to high elemental concentrations (Hammer et al. 2011)

3.7 Effect of Arbuscular Mycorrhiza Community on Rice Cultivation Systems (Growing Steps)

Rice (*Oryza sativa* L.) is the main food crop cultivated in wetland environments and one of the financially most important plant production worldwide (Wang et al. 2014). It is a semi-aquatic plant species that are adapted and staple food to a partially flooded environment. It is for more than half of the world's population (FAO 2004). In non-legume plants, rice displays one of the perfect model plants used for understanding the molecular, biochemical, and physiological origin of AM symbiosis (Paszkowski et al. 2002; Yang et al. 2012; Fiorilli et al. 2015). Rice production be accomplished in wetlands characterized by noticeable differences in soil flooding more than 85% of global (FAO 2004). AMF colonization of rice roots under wetland conditions has even been the subject of debate because little is known about the nutrient transfer between AMF and rice roots in flooded fields, and the (Vallino et al. 2009, 2014; Lumini et al. 2011; Watanarojanaporn et al. 2013). In recent last 50 years, some areas of Asia, rice production has more than tripled, mostly due to increased grain yield. The today concern is that serious challenges regarding water and soil pollution has been induced the overuse of nitrogen and phosphorus fertilizers as well as pesticides in rice production. "Green" rice production system is calling for a serious need to develop without a yield decrease that can replace the traditional intensive cultivation (Wang and Bjorn 2014; Wang et al. 2014).

Rice rhizosphere had a key role in the uptake of water and nutrients from paddy soil. Some researchers showed that there was a positive relationship between the presence of arbuscular mycorrhizal fungi (AMF), the number of spores in separate root systems, and the development of rice (Sanni 1976). Mycorrhizal inoculums application could be one approach to increase rice production and decrease fertilizer use (Wang et al. 2015). All arbuscular mycorrhizal fungi (AMF or AM fungi) are obligate symbionts and are clustered in the phylum Glomeromycota (Schüßler et al. 2001). Wang et al. (2015) showed that a total of 639 AMF sequences were obtained, and these were finally apportioned to 16 phylotypes founded on a phylogenetic analysis, including 12 phylotypes from *Glomeraceae*, one phylotype from *Claroideoglomeraceae*, two phylotypes from *Paraglomeraceae*. There was an obvious difference between the communities gained from root and soil, but the AMF phylotype compositions in the soils were alike between the two measured places. The comparatively high number of AMF phylotypes at the surveyed sites suggests that the conditions are suitable for some species of AMF and that they may have an important role in traditional rice cultivation systems. The species enriched of root-colonizing AMF improved along with the rice growth, and next researches should study the developmental stages of this crop in the survey of AMF role in paddy soils (Wang et al. 2015).

According to Fig. 3.12, regarding management patterns of P distribution, +m rice displayed higher panicle P: shoot P proportions, but lower leaf P: shoot P ratios than

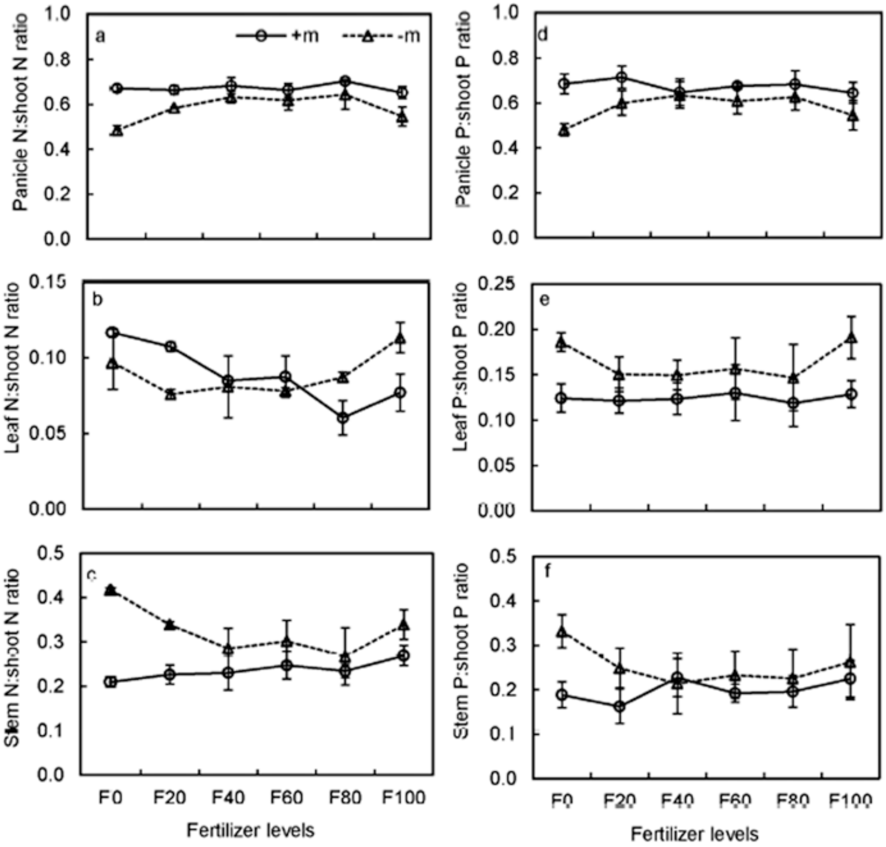

Fig. 3.12 Effect of fertilization and inoculation on plant biomass making and portion to shoots and roots. F0, F20, F40, F60, F80, and F100, delivered with 0, 20, 40, 60, 80, and 100% of the local norm of nutrient input (Zhang et al. 2014)

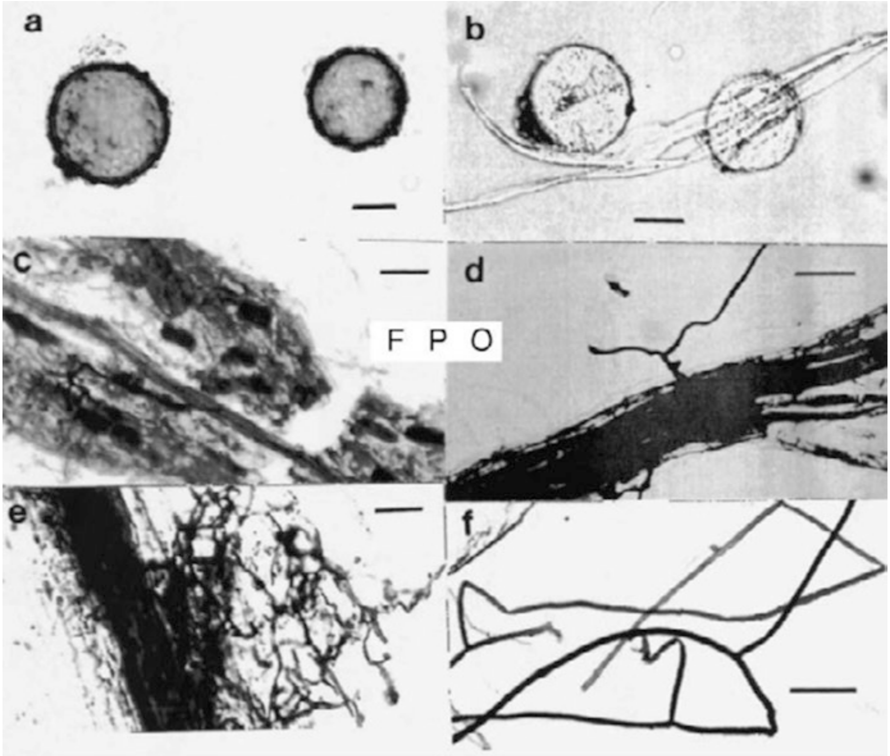

Fig. 3.13 AMF sporulation (**a**, **b**) and colonization (**c**) at the nursery stage and colonized roots at 30 days (**d**); 52 days (**e**); external hyphae at 130 days (**f**) after transplanting under field conditions; Bars = 50 µm (Solaiman and Hirata 1995)

−m treated rice across all fertilizer concentrations (Fig. 3.12). Stem P: shoot P ratios of −m rice at low fertilizer levels were significantly higher than those of +m rice. These correlations display the role that treatment-mediated alterations in biomass portion play in responsible patterns of nutrient element portion within rice shoots (Zhang et al. 2014).

Two kinds of spores were identified as Glomussppat (Fig. 3.13a, b) the nursery during inoculation: Internal hyphae (Fig. 3.13c–e) and external hyphae (Fig. 3.13f). They showed widespread colonization at the different time.

Arbuscular mycorrhizal fungi (AMF) form symbiotic associations with the roots they live in, and potentially change resistance against pests. Rice-AMF associations were the greatest in Arkansas followed by Mississippi and Texas (Fig. 3.14) (Bernaola et al. 2018).

AMF colonization intensity is various at the different growth stages of rice. AMF constructions were lacking or very infrequent at the seedling and tillering periods. On the other hand, typical vesicular and arbuscular structures of AMF were gener-

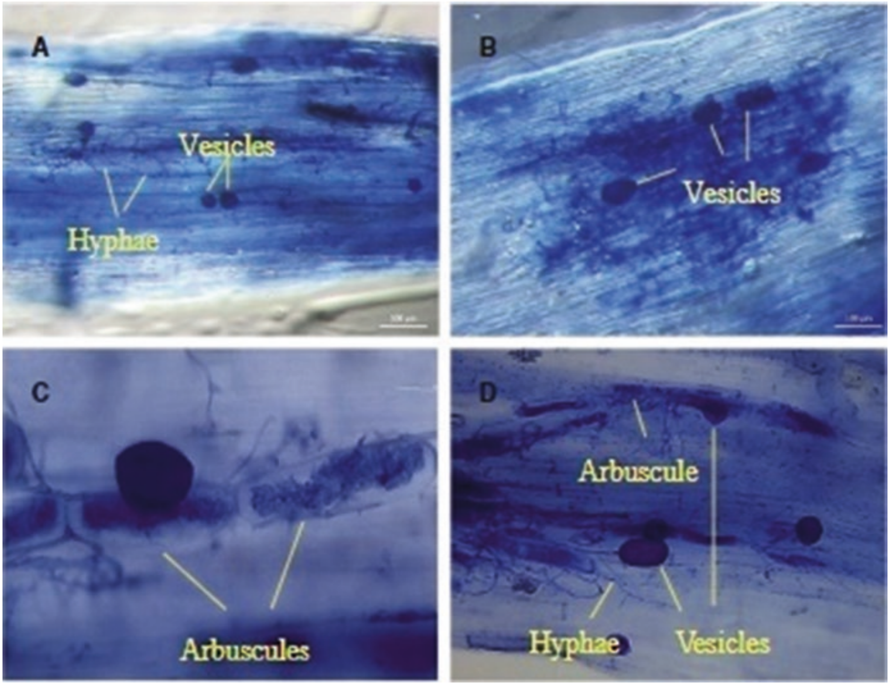

Fig. 3.14 Examples of arbuscular mycorrhizal fungal structures used as indicators of rice root colonization collected from Mississippi (**a**), Arkansas (**b**), Texas (**c**), and Louisiana (**d**, Crowley) rice fields (Bernaola et al. 2018)

ally observed at the heading and ripening stages. AMF colonization intensities (including hyphal, vesicular, and arbuscular colonization rates) at the heading stage were significantly lower than at the ripening stage. AMF colonization intensities (including hyphal, vesicular, and arbuscular colonization rates) at the heading stage were significantly lower than at the ripening stage. AMF colonization intensities at HN, BY, and LT were lower than at TX those, while at both heading and ripening stages, the colonization intensities among the last three sites were similar (Wang et al. 2015).

Another possible explanation for the higher P levels in the more slowly growing low-C mycelium might be that younger hyphae could contain higher element concentrations than older Hyphae (Hammer et al. 2011). In general, soil moisture, the inorganic nutrient available in the soil, pH, species of AMF, the host plant species, and several agricultural management practices have effects on the AMF community (abundance and activity). A long with these, soil biological communities could influence the establishment of the AMF symbiosis and its impact on plant agricultural production (Fig. 3.15) (Lekberg and Koide 2005; Bernaola et al. 2018).

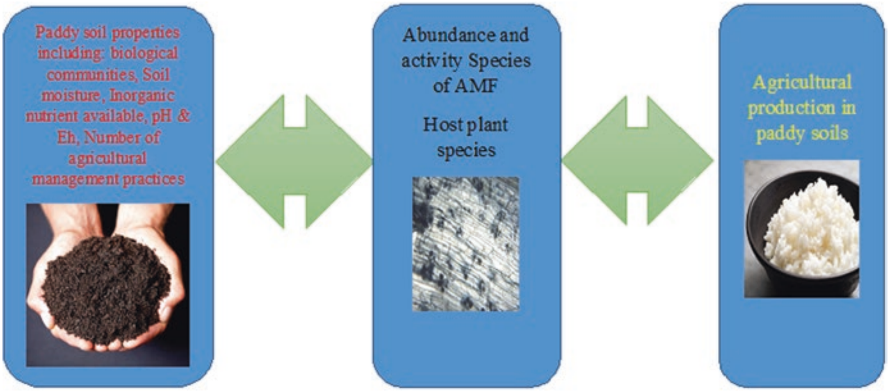

Fig. 3.15 The role of arbuscular mycorrhizal fungal community in paddy soil and agricultural productions

3.8 AMF Research

Laboratory or greenhouse experiments were involved in the majority of research on AMF associations, in which plants are cultivated in sterilized soil, with specific AMF species. They disregard native AMF species that could change plant responses or compete with the AMF inoculant (Munkvold et al. 2004). Some of the measurement methods are taken the following;

3.8.1 Quantification of AMF Colonization

Mycorrhizal colonization by AMF structures was determined by considering five slides with ten segments per slide from each sample and calculating the amount of colonization using the extended connections method of McGonigle et al. (1990) with negligible changes.

The seven to ten samples root colonization percentage averaged at each site and calculated by the following formula: Root colonization percentage (%) = No. of segments colonized with AMF/No. of segments observed × 100 (Bernola et al. 2018)

3.8.2 PIXE Analysis

A multi-elemental analytical technique is particle-induced X-ray emission founded on the detection of characteristic X-rays produced by MeV ions (protons or heavier ions). When protons pass through the sample, STIM is based on the detection of energy loss. Several spores, hyphae from a particular sample and detailed elemental maps of at least P, S, K, Ca, and Fe were analyzed (Hammer et al. 2011).

3.9 Conclusion and Future of AMF in Paddy Soils

Rice is one of the economically most important plants worldwide cultivated in wetland environments, so finding several AMF species that are capable of surviving in the flooding conditions makes a great help in symbiotic relationships. Our review showed that natural AMF communities that are more appropriate than others. Improving the activity of native arbuscular mycorrhizal fungi (AMF) has benefits in wetland agriculture.

It is a shortage severely limits in rice production worldwide, while colonization of plant roots with AMF often enhances nutrient element uptake and water logging plant growth. Little is known about the nutrient exchange between AMF and rice roots in flooded fields, under wetland conditions has even been the subject of debate. Colonization intensity between AMF and rice at different growth stages. The role of AMF is more noticeable in the early stages of growth terms of increased yield, nutrient concentration, and reduced heavy metals in plant tissue of cultivation in paddy fields. The AM colonization ratio in flooding was lower than in irrigation. Therefore, by adjusting the irrigation regimes and the application of organic matter amendments along with AMF application, it can be achieved maximum crop yields in paddy soils. This review will help appeal research to colonization of AMF in paddy soils of the worldwide that can impact future rice production by facilitating agricultural application of the AMF symbiosis.

By comparing the results and discussion of Van der Heijden et al. (2015), a better future can be considered for AMF application and increased production in paddy soil by following:

The various biochemical and genetic endeavors describe supporting by enormous efforts to structure the genomes of various fungal symbionts in paddy soils. Determination of the role of mycorrhizal fungi in waterlogging plant rhizosphere, paddy soil structure, and responses to environmental changes, and global C and nutrient cycles. Investigation of symbiotic gene networks in the molecular dialogue between wetland plants and fungus is a key challenge to understand plant-fungal cohabitation and the elements responsible for the organization of AMF symbiosis. The main challenge is to make known the fluxes of energy, metabolites, signaling molecules, and nutrients through mycorrhizal networks in paddy fields. Understand coevolutionary processes between wetland plants and mycorrhizal fungi. Now, we need to improve biogeochemical models that help us to forecast when, and under what conditions, application of mycorrhizal technology is profitable.

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Chapter 4
Natural Arbuscular Mycorrhizal Colonization of Wheat and Maize Crops Under Different Agricultural Practices

Luciana P. Di Salvo, María D. Groppa, and Inés E. García de Salamone

Contents

4.1 Introduction

Wheat (*Triticum aestivum* L.) and maize (*Zea mays* L.) are cereal crops usually included in the crop rotations systems. Their grain yield increases are traditionally based on genetic improvement and high inputs of chemical fertilization, an expensive practice which could produce negative impacts on ecosystem (Tilman et al. 2002; Rana et al. 2020). Thus, it is necessary to improve crop yields through the implementation of more sustainable agricultural practices (Altieri and Nicholls 2000; Tilman et al. 2002; Kour et al. 2020b). Among these sustainable agricultural practices, the mycorrhiza-forming fungi are a group of soil beneficial microorganisms for crop production (Barea 2004; Johansson et al. 2004). The symbiotic association between these fungi hyphae and plant roots is called mycorrhiza and the arbuscular type is a mycorrhiza established between arbuscular mycorrhiza fungi (AMF) and

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the most of wild and crop plants (Koide and Mosse 2004). During their life cycle they produce typical structures denominated arbuscules, spores and, in some cases, vesicles (Peterson and Massicotte 2004). Mycorrhizal symbiosis increases root exploration area and nutrient uptake (Richardson et al. 2009), and enhances soil aggregation (Rillig et al. 2002). Due to these effects, this symbiosis is important to ecosystems sustainability (Barea et al. 2002), being natural mycorrhization a bioindicator of soil quality (Jeffries et al. 2003; García de Salamone et al. 2006). However, some agricultural practices, such as monoculture, chemical fertilization or an indiscriminate use of agrochemicals, could reduce or eliminate the ecosystem mycorrhizal potential (Oehl et al. 2003; Treseder 2004; Schalamuk et al. 2006; Willis et al. 2013).

Plant growth-promoting rhizobacteria (PGPR) are another group of soil microorganisms that increase crop production through direct and indirect effects on plant growth and grain yields (Verma et al. 2010; Kour et al. 2019). In this sense, PGPR inoculation is an economic and ecological alternative to increase field productivity (Cassán and García de Salamone 2008). Within PGPR, the genus *Azospirillum* promotes plant growth through the so-called additive effect in which various mechanisms are involved (Cassán and Díaz-Zorita 2016). Several authors have shown increases in plant growth and grain yield of wheat and maize inoculated with this bacterium, and their results have been reviewed (Cassán and García de Salamone 2008; Cassán and Díaz-Zorita 2016). The inoculation response depends on interactions between native and inoculated microorganisms (Bashan 1999) as well as between them and the crop plants (García de Salamone 2012). Besides, these interactions are modified by the physicochemical conditions of the environment, such as the nutrient availability (Dobbelaere et al. 2001).

It has been reported that PGPR can interact with other soil microorganisms such as AMF and stimulate their growth (Johansson et al. 2004; Antoun and Prévost 2006). Thus, this microbial interaction promotes plant growth and grain yield of several plant species (Azcón-Aguilar and Barea 1997; Muthukumar et al. 2001; Vessey 2003; Bellone and Carrizo de Bellone 2008; Marulanda et al. 2009; Arthurson et al. 2011; Wang et al. 2011; Cosme and Wurst 2013; Verma et al. 2017). Because of that, some PGPR including *Azospirillum brasilense* and *Pseudomonas fluorescens* (Vázquez et al. 2000; Antoun and Prévost 2006; Ruíz-Sánchez et al. 2011), have been classified as mycorrhiza-helper bacteria (MHB) (Frey-Klett et al. 2007). MHB show several mechanisms for mycorrhization enhancement (Miransari 2011), including an improvement of the fertilizer-use efficiency (Adesemoye et al. 2008).

The knowledge of the above-belowground ecology is important for the understanding of how plant interactions with beneficial microorganisms affect crop production, biodiversity, and response to global changes (Ramirez et al. 2018). Due to the complexity of interactions in the microbial ecology of rhizosphere, it is necessary to improve the knowledge about those interactions in order to increase grain production to feed the increasing population of our planet. In this chapter, results of different field experiments performed in different locations of the Buenos Aires province, Argentina are shown. In those field experiments, natural AMF establishment and performance were evaluated under different crop managements. Table 4.1 summarizes edaphoclimatic description of the sites, crop managements, experimental designs, treatments, and sampling dates of each field experiment. Differences in AMF colonization (Sect. 4.2), AMF spores density, and diversity of AMF spores morphotypes (Sect. 4.3) in response to PGPR inoculation and chemical fertilization of wheat and maize crops were evaluated. Besides, changes in the AMF colonization of crop roots during crop development were discussed (Sect. 4.4). Results were compared to information previously described by the literature in order to advance in the knowledge about microbial ecology of crop rhizosphere. We finalized this chapter with some conclusions and future prospects about this topic (Sect. 4.5).

4.2 AMF Colonization of Wheat and Maize Crops

Plants can improve their nutrient uptake from soils through increases in root development in order to maximize the volume of total explored soil (Yadav et al. 2018, 2020). Since the symbiosis with AMF increase soil exploration and nutrient acquisition, it is important to evaluate if different agricultural practices modify root development and, in consequence, affect this symbiosis association. In this regard, at field conditions, the most frequently measurement used is root biomass determination. However, this parameter tends to underestimate root development because it does not consider the finest roots, unlike total length of root density that considers different root thicknesses. Total length of root density is the ratio between the total root length, determined by the line intersection method (Newman 1966), and the volume of soil sampled. This methodology was applied for field-growing root samples as described recently (Di Salvo et al. 2018a).

In the field experiments, some agricultural practices modified total length of root density of wheat and maize plants. A complete discussion about the effect of agricultural practices on total length of root density was published previously (Di Salvo et al. 2018a). In average, wheat fertilization with 60 or 120 kg triple superphosphate (TSP) ha^{-1}increased by 45% the total length of root density compared with control plants without fertilization, only at tillering stage of wheat crop in Experiment 1. In addition, in Experiment 2, maize inoculation with *A. brasilense* 40M strain increased by 57% the total length of root density compared with control plant without inoculation, only at R3 stage of maize crop. Regarding these results, other authors have showed that high phosphorous availability modifies the number of lateral roots of wheat plants (Mollier and Pellerin 1999) and *A. brasilense* inoculation increases the number or length of root hairs and adventitious roots (Okon and Vanderleyden 1997).

During mycorrhizal symbiosis, AMF form typical structures with different functions for the fungus. The arbuscules are ramifications of AMF hypha inside the cells of the radical cortex and constitute structures for substance exchange among both symbionts. The vesicles are intercellular thickening of the hypha usually used for nutrient storage, and the spores are fungal reproductive structures (Willis et al. 2013). The mycorrhizal symbiosis performance is frequently evaluated by the anal-

Table 4.1 Features and experimental design of the three field experiments

Features	Experiment 1	Experiment 2	Experiment 3
Cereal crop	Wheat Baguette 19 (Nidera™)	Maize AX886 MG (Nidera™)	Wheat Klein Castor (Klein™)
Location	30 de Agosto, Buenos Aires	Pehuajó, Buenos Aires	Villa Moll, Buenos Aires
Soil texture	Sandy loam	Silty loam	Sandy loam
pH[1] (1:2.5 soil:water)	6.6	5.8	6.1
Electrical conductivity[a] (dS m^{-1})	0.19	0.92	0.45
Organic matter[a] (%)	2.9	3.2	3.9
Nitrogen (N)[a]	52.3 ppm ($N\text{-}NO_3$)	0.19% (organic N)	59.7 ppm ($N\text{-}NO_3$)
Available phosphorous (P)[a] (ppm)	8.35	8.54	5.37
Preceding crop	Soybean	Soybean	Soybean
Sowing date	May 31st, 2011	September 30th, 2010	June 18th, 2009
Fertilization	None	20 kg P ha^{-1} as monoammonium phosphate	20 kg P ha^{-1} as TSP
Experiment design	Split-plot design with factorial arrangement	Completely randomized block design with a factorial arrangement	Completely randomized block with factorial arrangement

Treatments	• 2 levels of inoculation[b]: – control (no inoculation) – Inoculated with both strains (40M + 42M) • 3 levels of N fertilization: 0, 75 and 150 kg urea ha^{-1} • 3 levels of P fertilization: 0, 60, and 120 kg TSP ha^{-1}	• 5 levels of inoculation[d]: – control (no inoculation) – Inoculated with commercial inoculant[e] – Inoculated with 40M strain (40M) – Inoculated with 42M strain (42M) – Inoculated with 40M + 42M (40M+42M) • 3 levels of N fertilization[f]: 0, 90, and 180 kg urea ha^{-1}	• 4 levels of inoculation[h]: – control (no inoculation) – Inoculated with 40M (40M) – Inoculated with 42M (42M) – Inoculated with 40M + 42M (40M+42M) • 2 levels of N fertilization[i]: 0 and 46 kg N ha^{-1}
Sampling dates	Tillering (118 DDS)[c] Grain-filling (182 DDS)	V5 (62 DDS) R3 (132 DDS)[g]	Jointing (88 DDS) Grain-filling (133 DDS)

[a] Upper soil layer (0–20 cm)

[b] The dose per each kg of seed was 12 ml of inoculant containing 4.3×10^9 CFU ml^{-1}. Both strains were previously isolated from maize rhizosphere (García de Salamone and Döbereiner 1996), identified (García de Salamone et al. 2010), and vastly characterized (Di Salvo et al. 2014)

[c] Tillering, jointing, and grain-filling are three phenological stages as described by Zadoks et al. (1974)

[d] The dose per each kg of seed was 10 ml of the 40M, 42M, and 40M+42M inoculants containing 3.8×10^{10}, $2.9 \times 10^{10,}$ and 4.5×10^{10} CFU ml^{-1}, respectively

[e] Commercial formulation of *Azospirillum brasilense* and *Pseudomonas fluorescens* (Rhizoflo Premium Maíz®, Laboratorios CKC®, Argentina). The dose per each kg of seed was 5 ml of commercial inoculant

[f] N fertilization was performed at V4 stage (Ritchie et al. 1982)

[g] V5 and R3 are two phenological stages as described by Ritchie et al. (1982)

[h] The dose per each kg of seed was 15 ml of the 40M, 42M and 40M + 42M inoculants containing 6.6×10^8, 2.0×10^8 and 3.7×10^8 CFU ml^{-1}, respectively

[i] N fertilizer was Solmix™ (PASA Fertilizantes Petrobras; 28% N and 2.6% S)

ysis of these typical structures because changes in the percentages of them can show alterations in the plant–fungus interaction. This analysis is based on root depigmentation and staining. It was necessary to adapt the classical Phillips and Hayman (1970) method because roots of wheat and maize have low content of lignin. Washed roots were submerged in 10% KOH solution and incubated at 60°C for 20 min. The KOH was discarded, and the depigmentation was repeated with a new KOH solution (10%) during 10 min at 60°C. After KOH discarding, roots were submerged in HCl 1N solution during 10 min at room temperature. Roots were washed with distilled water and stained with a Trypan blue solution (0.05% in lactic acid). Stained roots were examined using a light microscope under 100X and 400X magnifications in order to quantify AMF root colonization and typical structures.

Differences in root development due to chemical fertilization or bacteria inoculation could modify the symbiosis with AMF. Thus, these agricultural practices could change AMF root colonization of wheat and maize crops. However, only in one of the three field experiments, the chemical fertilization modified the percentage of root colonization by AMF at both phenological stages (Tables 4.2, 4.3 and 4.4).

Although no differences in the percentage of typical structures of AMF were observed in the maize experiment (Table 4.3), chemical fertilization modified the percentage of arbuscules and spores at different phenological stages of wheat crops (Tables 4.2 and 4.4). Phosphorous fertilization decreased the percentages of arbuscules and increased the percentage of spores at tillering stage of wheat crop (Table 4.2). The decline observed in the percentage of arbuscules due to P fertilization emphasizes the role of mycorrhiza in the uptake of nutrients such as phosphorous (Collins-Johnson et al. 2003). Nitrogen fertilization increased the percentage of arbuscules at tillering stage of Experiment 1 (Table 4.2) but decreased it at grain-filling stage of Experiment 3 (Table 4.4). Besides, nitrogen fertilization decreased the percentage of spores at this phenological stage (Table 4.3). Interestingly, PGPR inoculation did not change the percentages of typical AMF structures (Tables 4.2, 4.3 and 4.4). Nutritional improvement of the symbionts could probably be the main reason to explain why the association between plants and AMF is the oldest of the symbioses (Lambers et al. 2009). It has been established that plant species determine the mycorrhizal dependence and the radical colonization response to both phosphorous and nitrogen availability for plant growth (Siqueira and Saggin-Júnior 2001; Corkidi et al. 2002; Klironomos 2003). Some authors have established that phosphorous fertilization negatively affects internal fungal structures, such as arbuscules and vesicles (Collins-Johnson et al. 2003; Blanke et al. 2005). In our field experiments we observed negative effects on arbuscules due to both phosphorous and nitrogen fertilizers (Tables 4.2 and 4.4). Besides, it was reported that nitrogen fertilization affects extraradical fungal structures, such as hypha and spores (Collins-Johnson et al. 2003; Blanke et al. 2005). Regarding to this, we observed positive and negatively effects due to phosphorous (Table 4.2) or nitrogen fertilization (Table 4.4) on the percentage of spores in wheat roots, respectively.

An increased percentage of spores can be produced by AMF in symbiosis with plants both under stress conditions (Bothe et al. 2010) or high nutrients availability, due to a high photosynthates production (Douds Jr. and Schenck 1990a). However,

Table 4.2 Effect of chemical fertilization and *A. brasilense* inoculation on mycorrhizal colonization and typical structures of arbuscular mycorrhiza at two different phenological stages of wheat, at field conditions (Experiment 1)

	Tillering stage				Grain-filling stage			
	Root colonization (%)	Arbuscules (%)	Vesicle (%)	Spores (%)	Root colonization (%)	Arbuscules (%)	Vesicles (%)	Spores (%)
A. brasilense inoculation								
Control	63.5^{a}	31.9^{a}	17.6^{a}	1.5^{a}	55.5^{a}	9.0^{a}	35.5^{a}	3.4^{a}
Inoculated (40M + 42M)	68.7^{a}	34.1^{a}	14.9^{a}	1.1^{a}	63.7^{a}	7.3^{a}	33.3^{a}	5.4^{a}
Phosphorous fertilization[a]								
0	73.0^{b}	43.0^{b}	21.6^{a}	1.4^{a,b}	75.3^{b}	11.4^{a}	41.0^{a}	5.3^{a}
60	65.3^{a,b}	26.0^{a}	15.1^{a}	0.5^{a}	54.7^{a}	9.0^{a}	35.5^{a}	2.7^{a}
120	60.1^{a}	29.9^{a}	12.1^{a}	2.0^{b}	48.8^{a}	4.1^{a}	25.7^{a}	5.2^{a}
Nitrogen fertilization[b]								
0	55.8^{a}	24.1^{a}	12.7^{a}	1.1^{a}	53.0^{a}	7.5^{a}	34.1^{a}	4.4^{a}
75	71.1^{a}	33.3^{a,b}	16.8^{a}	1.4^{a}	57.4^{a,b}	7.3^{a}	32.4^{a}	3.2^{a}
150	71.5^{a}	41.5^{b}	19.3^{a}	1.4^{a}	68.4^{b}	9.6^{a}	36.8^{a}	5.6^{a}

Different letters indicate significant differences between treatments with Tukey's test ($P < 0.05$)

[a] Phosphorous fertilization in kg triple superphosphate ha^{-1}

[b] Nitrogen fertilization in kg urea ha^{-1}

Table 4.3 Effect of chemical fertilization and PGPR inoculation on mycorrhizal colonization and typical structures of arbuscular mycorrhiza at two different phenological stages of maize, at field conditions (Experiment 2)

	Vegetative stage (R3)				Reproductive stage (V5)			
	Root colonization (%)	Arbuscules (%)	Vesicles (%)	Spores (%)	Root colonization (%)	Arbuscules (%)	Vesicles (%)	Spores (%)
A. brasilense inoculation								
Control	67.1^{a}	60.7^{a}	11.1^{a}	0.5^{a}	32.3^{a}	31.6^{a}	5.6^{a}	0.9^{a}
Commercial	57.5^{a}	53.1^{a}	9.9^{a}	0.0^{a}	32.6^{a}	30.7^{a}	16.7^{a}	2.7^{a}
40M	54.7^{a}	48.1^{a}	3.0^{a}	1.1^{a}	33.9^{a}	30.9^{a}	8.8^{a}	0.9^{a}
42M	61.3^{a}	56.8^{a}	7.2^{a}	0.0^{a}	34.8^{a}	34.1^{a}	8.8^{a}	3.6^{a}
40M+42M	62.1^{a}	55.1^{a}	18.6^{a}	0.5^{a}	21.7^{a}	21.4^{a}	9.8^{a}	3.5^{a}
Nitrogen fertilization^{a}								
0	51.0^{a}	46.5^{a}	7.2^{a}	0.4^{a}	33.1^{a}	32.5^{a}	8.3^{a}	2.6^{a}
90	64.3^{a}	57.1^{a}	10.1^{a}	0.6^{a}	31.7^{a}	29.9^{a}	11.9^{a}	1.8^{a}
180	66.3^{a}	60.7^{a}	12.7^{a}	0.2^{a}	28.4^{a}	26.7^{a}	9.6^{a}	2.5^{a}

Different letters indicate significant differences between treatments with Tukey's test ($P < 0.05$)

[a] Nitrogen fertilization in kg urea ha^{-1}

Table 4.4 Effect of chemical fertilization and *A. brasilense* inoculation on mycorrhizal colonization and typical structures of arbuscular mycorrhiza at two different phenological stages of wheat, at field conditions (Experiment 3)

	Jointing stage				Grain-filling stage			
	Root colonization (%)	Arbuscules (%)	Vesicles (%)	Spores (%)	Root colonization (%)	Arbuscules (%)	Vesicles (%)	Spores (%)
A. brasilense inoculation								
Control	67.5^{a}	37.9^{a}	14.8^{a}	2.1^{a}	73.0^{a}	53.7^{a}	7.5^{a}	6.1^{a}
40M	66.1^{a}	42.7^{a}	21.5^{a}	4.4^{a}	72.3^{a}	51.5^{a}	7.1^{a}	6.5^{a}
42M	57.5^{a}	38.8^{a}	20.6^{a}	1.1^{a}	75.2^{a}	52.7^{a}	5.0^{a}	8.5^{a}
40M+42M	65.2^{a}	42.9^{a}	21.9^{a}	4.2^{a}	72.9^{a}	46.5^{a}	7.9^{a}	8.3^{a}
Nitrogen fertilization[a]								
0	61.4^{a}	41.5^{a}	16.6^{a}	1.9^{a}	75.0^{a}	55.6^{b}	7.1^{a}	10.1^{b}
46	66.8^{a}	39.7^{a}	22.8^{a}	4.0^{a}	72.0^{a}	46.6^{a}	6.7^{a}	4.6^{a}

Different letters indicate significant differences between treatments with Tukey's test ($P < 0.05$)

[a] Nitrogen fertilization in kg N ha^{-1}

this response is variable according to plant (Saito et al. 2011) and AMF species (Douds Jr. and Schenck 1990b). This response could explain the differences in the percentage of spores present in the roots of wheat crop. In this regard, wheat plants with high nitrogen availability showed higher percentage of spores than plants without nitrogen fertilization (Table 4.4), according to the data reported by other authors under controlled (Douds Jr. and Schenck 1990a) and field (Douds Jr. et al. 1997) conditions. These wheat plants, which were growing under both phosphorous and nitrogen non-limited conditions, showed a very active mycorrhizal symbiosis with an elevated percentage of arbuscules. Thus, the AMF could be stressed by a carbon-limited condition, what could explain the differences in the percentage of spores between control and fertilized plants in the Experiment 3.

All the results indicate that it is not possible to predict the effects of chemical fertilization on AMF symbiosis because it is depending on plant genotype, type and dose of chemical fertilization, and environmental conditions during the crop season. These differences on chemical fertilization response were previously reported (Liu et al. 2000; Covacevich et al. 2007). Likewise, some authors have shown increases in maize roots colonization (García de Salamone et al. 2006) and wheat mycorrhization (Rubio et al. 2003) due to phosphorous fertilization, whereas others have reported negative responses (Ellis et al. 1992; Treseder 2004; Blanke et al. 2005).

Regarding the effects of phosphorous or nitrogen fertilizers individually, it is interesting to analyze the simultaneous effect of both nutrients on AMF symbiosis. Some authors reported increases in root colonization and the percentage of arbuscules due to nitrogen fertilization under phosphorous-limited conditions but decreases under non-limiting phosphorous conditions (Sylvia and Neal 1990; Treseder and Allen 2002; Collins-Johnson et al. 2003; Blanke et al. 2005). Under stress conditions, plants provide carbon compounds to their roots in order to maintain the symbiosis, due to the benefits in the absorption of the limiting nutrient (Douds Jr. and Schenck 1990a). If phosphorous is the limiting nutrient, the response is more significant than if the nitrogen is the limiting nutrient (Treseder and Allen 2002; Blanke et al. 2005; Kour et al. 2020a), possibly because AMF provides inorganic phosphorous to plants more efficiently than inorganic nitrogen (Treseder 2004). In our field experiments, we observed two different results which should be discussed because they seem to be contradictory. On the one hand, nitrogen fertilization increased wheat mycorrhization, whereas phosphorous fertilization decreased it (Table 4.2), in relation with nutrients availability and the benefits of this symbiosis previously discussed. On the other hand, nitrogen fertilization decreased wheat mycorrhization (Table 4.4). These results seem to be opposite to those of the other wheat experiment. However, nitrogen fertilization did not increase wheat biomass production and grain yield of the wheat crop in Experiment 3 (Di Salvo et al. 2018b), which had been also fertilized with phosphorous (Table 4.1). Due to this, we concluded that nitrogen and phosphorous, the main macronutrients for plant production were not limiting nutrients. Without phosphorous and nitrogen limitation, plant growth and mycorrhizal symbiosis could be more limited by carbon than of nitrogen (Douds Jr. and Schenck 1990a, b; Muthukumar and Udaiyan 2000;

Treseder and Allen 2002). Therefore, these results are in accordance with the carbon-limited conditions, as is discussed below.

Although inoculation of maize and wheat plants with *A. brasilenseand P. fluorescence* would enhance the mycorrhizal symbiosis, no differences in root colonization were observed due to PGPR inoculation in the three field experiments (Tables 4.2, 4.3 and 4.4). These results are not related with crop responses to inoculation treatments since PGPR inoculation increased biomass production and grain yield of maize (Di Salvo et al. 2018a; Di Salvo and García de Salamone 2019) but did not modify the agronomic response of wheat crops (Di Salvo et al. 2018b; Di Salvo and García de Salamone 2019). The high complexity of the plant–microbe and microbe–microbe interactions in the rhizosphere not only determines crops responses to PGPR inoculation and chemical fertilization but also the effects of these agricultural practices on the ecology of this particular environment.

4.3 Density of AMF Spores and Diversity of AMF Spores Morphotypes

The density of AMF spores and the diversity of AMF spores morphotypes can be evaluated with the use of a light microscope after AMF spores isolation from soil samples. For this regard, soils samples from wheat (Experiment 1) and maize (Experiment 2) field experiments were suspended in water and successively passed through three different sieves sizes. The most important is the 53 μm sieve size because it holds the AMF spores. Spores were separated from soil particles with one step of centrifugation with a sucrose solution (45% p/v). After the centrifugation, the spores were washed with distilled water in order to avoid spore's destruction and placed in a plate with a grid in order to examine them using a light microscope under 40X and 100X magnifications. After examination of the samples, AMF spore density (spores/g of dry soil) in each one was calculated. Besides, spores morphotypes were classified according to their color, size, and shape (Lebrón et al. 2012).

In the maize field experiment, no differences between agricultural practices or phenological stages were observed in the AMF spore's density, with an average of 27 spores per gram of dried soil. By the contrary, phosphorous fertilization increased the density of AMF spores at both phenological stages (Fig. 4.1). For the two phenological stages, no differences in the AMF spore's density were observed.

Regarding AMF spore morphotypes, eight and nine different morphotypes were found in the rhizosphere of wheat and maize crops, respectively (Fig. 4.2). Agricultural practices and phenological stages did not affect the diversity of AMF spores in the maize rhizosphere, with an average Shannon's diversity index of 1.34. The diversity of AMF spores in the wheat rhizosphere was also not affected by nitrogen fertilization or *A. brasilense* inoculation. However, phosphorous fertilization modified the diversity of AMF spores morphotypes at both phenological stages (Fig. 4.3). Some authors have reported that fertilization, as well as other agricultural

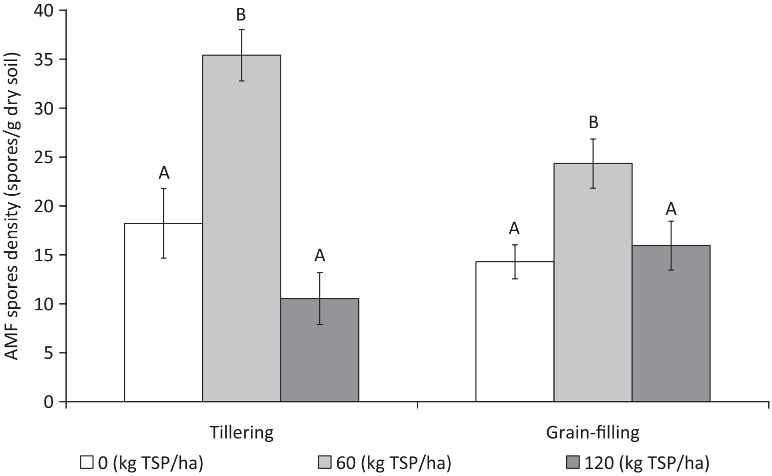

Fig. 4.1 Density of AMF spores in the rhizosphere of wheat crop (Experiment 1) at two phenological stages. Error bars correspond to standard error values. Different letters indicate significant differences between phosphorous fertilization doses at each phenological stage with Tukey's test ($p \leq 0.05$)

practices, can positively or negatively affect the diversity of AMF species present in the ecosystems (Collins-Johnson 1993; Oehl et al. 2003; Johansson et al. 2004; Schalamuk and Cabello 2010). In this work, only phosphorous fertilization of wheat crop modified spores diversity, whereas nitrogen fertilization and PGPR inoculation did not affect them. In addition, although it has been previously observed that crop development modified root colonization and the percentage of spores in the roots, crop phenology did not modify spore's diversity of AMF in the rhizosphere of these crops. It is important to note that the dose of 60 kg of TSP increased both AMF spore density (Fig. 4.1) and diversity of AMF spore morphotypes (Fig. 4.3) compared with both control plants without fertilization and plants with the highest phosphorous fertilization dose.

4.4 AMF Colonization of Wheat and Maize During Crop Development

Total length of root density was expected to increase along crop development. In this sense, total length of root density in both wheat field experiments showed differences between phenological stages, but this was not the case for the maize field experiment (Table 4.5). As plant radical systems experience changes along time, it is interesting to evaluate how AMF colonization varies during crop cycle.

The AMF are obligate microbial symbionts (Barea et al. 2005). Thus, mycorrhiza colonization is expected to be related to the annual life cycle of the crops,

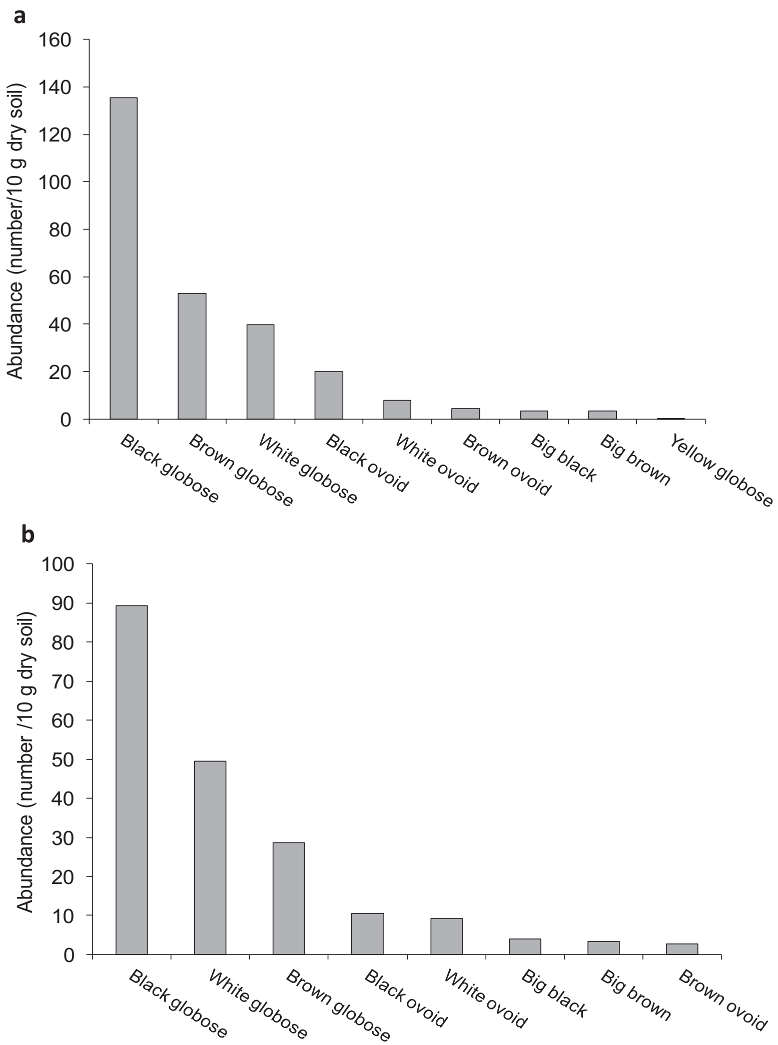

Fig. 4.2 Abundance of AMF spores morphotypes in the rhizosphere of wheat (**a**) and maize (**b**) crops

according to the results of Pongrac et al. (2007). In this regard, it was observed that maize root colonization decreased as the crop cycle progressed; whereas wheat root colonization increased or did not show differences between phenological stages (Table 4.5). Other authors reported similar results for wheat and other winter cereals (Covacevich et al. 2007; Dodd and Jeffries 1986), associated with crop phenology and environmental conditions (Abbott and Robson 1991; Mohammad et al. 1998). It is important to note that wheat root colonization was in the range of 60–66% dur-

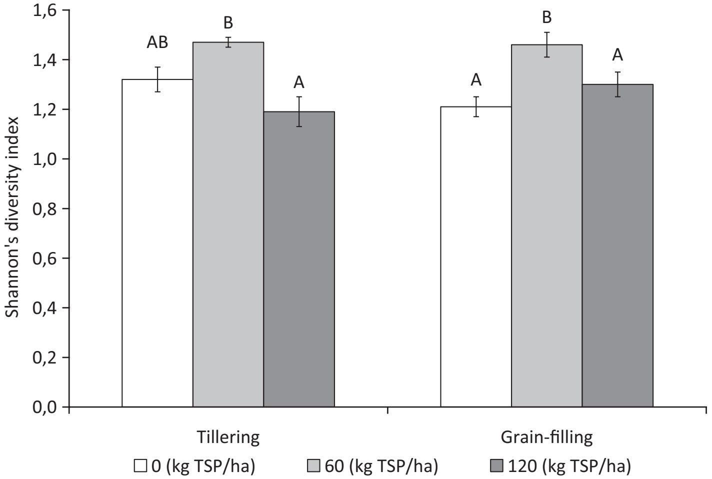

Fig. 4.3 Shannon's diversity index of AMF spores morphotypes from wheat rhizosphere (Experiment 1). Error bars correspond to standard error values. Different letters indicate significant differences between phosphorous fertilization doses at each phenological stage with Tukey's test ($p \leq 0.05$)

Table 4.5 Total length of root density, mycorrhizal colonization and typical structures of arbuscular mycorrhiza at two different phenological stages of wheat and maize experiments, at field conditions

	Total length of root density (cm cm^{-3})	Root colonization (%)	Arbuscules (%)	Vesicles (%)	Spores (%)
Wheat (Experiment 1)					
Tillering stage	0.52 a	66.1 a	33.0 b	16.3 a	1.3 a
Grain-filling stage	1.73 b	59.6 a	8.2 a	34.4 b	4.4 b
Maize (Experiment 2)					
Vegetative stage (V5)	0.76 a	60.5 b	54.8 b	9.97 a	0.4 a
Reproductive stage (R3)	0.84 a	31.1 a	29.8 a	9.91 a	2.3 b
Wheat (Experiment 3)					
Jointing stage	0.32 a	64.1 a	40.6 a	40.0 b	2.9 a
Grain-filling stage	0.38 b	73.5 b	51.1 b	25.0 a	7.4 b

Different letters indicate significant differences between treatments at each field experiment with Tukey's test ($P < 0.05$)

ing the crop cycle, whereas maize root colonization decreased from 60% to 30% from vegetative to reproductive stages. Similar results were previously reported, where low levels of maize root colonization and high levels of wheat root colonization were shown in relation to the total length of root density (García de Salamone et al. 2006).

Phenological stages modified the percentage of arbuscules, vesicles, and spores in crop field experiments (Table 4.5), in addition to the changes in root colonization by AMF. It is noteworthy that in the three field experiments, the percentage of spores was greater towards the end of the crop cycle than in the vegetative stages of the crops. The percentages of arbuscules and vesicles, mycorrhiza development were shown differences between wheat and maize crops. At vegetative stages of wheat (Experiment 1) and maize (Experiment 2), the percentage of arbuscules was high, which indicates that the symbiosis was being strongly active. As crop cycle progressed, the percentage of vesicles in wheat roots increased but no differences were observed in maize roots. Different results were observed in the other wheat field experiment (Experiment 3) probably because in this assay the sampling at vegetative stage was performed at jointing stage, a phenological stage more advanced than tillering, the vegetative stage of sampling in Experiment 1 (Table 4.1). In summary, the symbiosis between AMF and these plants developed differently according to the plant species and, most likely, to AMF species combinations. In view of this, other authors reported similar results to those presented here for different plant species (Abbott and Robson 1991; Siqueira and Saggin-Júnior 2001; Trindade et al. 2001; Escobar Ortega and García de Salamone 2017).

4.5 Conclusion and Future Prospects

Wheat and maize crops showed differences in the dynamics of natural mycorrhization. However, inoculation with 40M and 42M strains of *A. brasilense* did not affect wheat and maize mycorrhization at field conditions. In addition, the inoculation of maize crop with commercial formulation which combines two different PGPR—*A. brasilense* and *P. fluorescens*—did not affect natural mycorrhization of the crop. In relation to the response of natural mycorrhiza to chemical fertilization, we observed that the availability of both nitrogen and phosphorous is more important than the dose of a particular type of fertilizer. Besides, we observed that wheat inoculation with 40M + 42M partially reduced negative effects of phosphorous fertilization on the development of the arbuscular mycorrhiza. This is an interesting topic to consider in upcoming research projects. Finally, chemical fertilization of wheat crops modified the percentage of AMF spores, which constitute one of the mechanisms of perpetuation of AMF in soils. However, PGPR inoculation and nitrogen fertilization did not modify the diversity of AMF spores, whereas phosphorous fertilization of wheat increased the diversity of spore morphotypes. The results of this work represent a contribution to the knowledge about the establishment of natural mycorrhiza in extensive agroecosystems. These results acquire great relevance for the management of cereal crops in order to increase the efficiency of available resources under a more sustainable agricultural production.

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Chapter 5
Arbuscular Mycorrhizal Fungi and Their Potential Applications for Sustainable Agriculture

Muriel da Silva Folli-Pereira, Juliana Garlet, and Amanda Azevedo Bertolazi

Contents

5.1 Introduction

The global problems of environmental degradation and the need for sustainable and ecologically sound agricultural production emphasize the need for studies on soil microbiological processes, as these are an essential functioning part of all terrestrial ecosystems. Soil microorganisms play an essential role in the productivity of agricultural ecosystems and the functioning of natural ecosystems (Yadav et al. 2017), and they may be beneficial or harmful (Antoun 2012; Zachow et al. 2016).

Among beneficial soil microorganisms are arbuscular mycorrhizal fungi (AMF), which enhance plant establishment and nutrition in most terrestrial ecosystems (Wei 2016). These fungi form the most common symbiosis in nature, arbuscular mycorrhizae, formed between the latter and the roots of approximately 80% of vascular plants (Invan 2019). By establishing the interaction between AMF with plant roots,

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they increase plant nutrient uptake, notably phosphorus, since fungal hyphae considerably increase the soil area explored by the roots. At the same time, plants provide fungi with the carbohydrates produced in photosynthesis for their use as an energy source. Thus, this biological interaction can change the development of plants, making them more tolerant to the most diverse environmental conditions, such as damage caused by pest insects, mainly through the improvement of induced defences.

AMF are considered a very diverse group of microorganisms, both taxonomically and functionally (Fitter 2005). Although still evolving and with many points to be clarified, studies involving mycorrhizae have advanced in recent years, providing a broader view of their role in plant development (Borowicz 2013; Fitter 2005). The role played by AMF in the absorption of nutrients by plants to which they associate remains the main objects of these studies and for this reason it corresponds to the most elucidated point regarding this association so far. Furthermore, studies on the carbon cost to the host plant (about 20%) resulting from this association point to a series of effects that portray what may actually occur under uncontrolled environmental conditions, which is: under certain conditions of environmental stress AMF may range from mutualists to parasites (Basu et al. 2018; Vannette and Hunter 2009a).

In addition to improvements in plant nutritional status (especially phosphorus uptake), AMF can influence the interaction of these plants with other organisms, including pathogens and pest insects, which translates into a potential of these fungi for integrated management, and consequently for the establishment of more environmentally and economically sustainable agricultural production systems (Borowicz 2013). Therefore, the use of mycorrhizae to control pest insects requires a better understanding of the processes and compounds that influence the AMF-Plant–Insect interaction for the maintenance of sustainable agriculture (Yadav et al. 2019a, b, 2020).

The effects of AMF on plant tolerance against pest insects have been studied over the past decade, but general patterns regarding molecules involved in AMF, plant and insect interaction have not yet been identified (Borowicz 2013). According to Borowicz (2013) the identification of clear patterns on the effects of AMF on the plant–insect pest interaction could guide the studies in relation to the processes underlying their effects on plant-herbivorous relationships. Some questions surrounding the use of AMF for pest management still need to be clarified: if AMF promote the growth of host plants, could they also promote resistance against attack by pests? Are the effects of AMF on plant–insect pest interaction due to the combination of host plant, AMF, insect pest and environment?

5.2 Arbuscular Mycorrhizae in Plant–Insect Interaction

The arbuscular mycorrhizal association is a symbiosis formed by arbuscular mycorrhizal fungi (AMF), that occurs in almost all vascular plant species and families of interest (Invan 2019), which makes mycorrhizae to be considered a rule rather than an exception in nature. Therefore, the understanding of the mechanisms for the establishment of this association, as well as the benefits that it can bring to sustainable agricultural crops, has become the object of study among several research groups around the world.

The effects of AMF on plants are usually evaluated by comparing the growth of inoculated and uninoculated plants, and the benefits of this better plant growth and development rate against the environmental conditions under which these plants are subjected (Smith and Read 2008). Most studies have focused on evaluating the benefits of AMF on plants which they interact through isolated direct effects analysis. However, studies of mycorrhizae effects on plants should not neglect the interactions that plants establish with other groups of organisms, such as pollinators and herbivores, given that the direct effects of AMF on plants can rearrange the characteristics that regulate these interactions, with important consequences for plant fitness.

In addition to agricultural crops, it has been observed that several tree species have also shown different responses regarding the colonization of their roots by different AMF species. These fungi can provide different benefits to host plants, acting, for example, as potential resistance agents, mitigating the effects or damages caused by phytopathogens and insects, probably by indirect pathways, by better plant nutrition, or increased root system resistance (Singh and Yadav 2020; Santos 2008).

Considering the benefits that this association brings to colonized plants, several studies have been conducted in recent years and indicate a greater nutrient absorption (Folli-Pereira et al. 2012), increased tolerance to abiotic stresses, especially water stress (Zhao 2015) and protection against phytopathogens and pest insects (Dell Fabbro and Prati 2014). With respect to the increased tolerance of plants to pest attack, several studies have demonstrated that soil symbionts can alter interactions between plants and other above-ground organisms, for example, by attracting or repelling pollinators and herbivores (Ballhorn et al. 2013; Barber and Soper Gorden 2015) and changing the suitability of these organisms (Bezemer et al. 2005; Pineda et al. 2013; Gols 2014).

Studies on pollinator interactions with mycorrhizal plants have focused only on the direct effects of AMF on the morphological characteristics of flowering plants, indicating changes in flower number (Gange et al. 2005a) and size (Varga and Kytöviita 2010), nectar compositions (increased sugar concentration in nectar) and the diversity and intensity of fragrance emission from flowers (Becklin et al. 2011). This last study found that changes in floral nectar compositions and volatile compound diversity provided by AMF decreased floral damage caused by ants. Davis et al. (2019) found, for example, that AMF influenced the flowering phenology and floral chemistry of *Nicotiana tabacum* L. plants, decreasing nicotine concentrations in plant pollen when mycorrhizal plants were subjected to high soil fertility levels, whereas the anabasine concentration in plant pollen was strongly influenced by arbuscular mycorrhizae, regardless of soil fertility.

There is little information on pollinator preference and attractiveness for flowers of mycorrhizal plants in the field, and existing research is limited to analysing the effects of AMF on pollinator visits to mycorrhizal plants. What these few studies have shown is a change in pollinator behaviour with an increased visitation in mycorrhizal plants compared to non-mycorrhizal plants, and this behaviour is consistent even when different pollinators were evaluated (Hymenoptera and Diptera) (Gange and Smith 2005). Varga and Kytöviita (2010) verified that the preference of Hymenoptera and Diptera may vary depending on the AMF species used as inoculants, indicating that the effects of these fungi on the interaction of plants and pollinators may depend on both the AMF species used as inoculants and the pollinators.

The plant tolerance and chemical defence mechanisms in mycorrhizal plants and the possible contribution of AMF in altering these mechanisms have been increasingly studied. However, the effects of AMF on plant–insect interaction vary widely: from negative, neutral and positive effects, to both tolerance and plant chemical defence (Davis et al. 2019; Anandakumar et al. 2019; Tao et al. 2016; Andrade et al. 2013; Barber et al. 2013; Reidinger et al. 2012; Currie et al. 2011; Vannette and Hunter 2009b). Thus, the benefits of arbuscular mycorrhizae seem to depend on the inoculums potential and the colonization capacity of plant roots by AMF.

Several studies, conducted by different research groups, for the same plant species have found quite contrasting effects with the different AMF species used, with respect to compounds involved in plant chemical defence (Schoenherr et al. 2019; Jung et al. 2009; O'Herlihy et al. 2003), which suggests some functional specificity of AMF in relation to the increased production of these compounds for plants.

According to Azcón-Aguilar and Barea (1996), some of the plant resistance mechanisms promoted by AMF are: improvement of host plant nutritional status, compensation of damage caused by the pathogen, competition for the infection and colonization site, anatomical and morphological changes in the host root system, changes in the rhizosphere microbiological population and activation of defence mechanisms that may be localized or systemic (Pozo et al. 2002). Due to the low natural fertility of soils and high prices of industrialized fertilizers, the associations of plants with microorganisms that favour nutrient utilization in low availability media have been widely studied.

AMF can affect plant tolerance and chemical defence against herbivores through different mechanisms. Plants, in turn, present two distinct defence strategies, and several evidences indicate that AMF can influence each one separately (Tao et al. 2016). Studies involving simultaneous analysis of mycorrhizae effects on chemical defence and tolerance of plants against herbivory are still scarce. However, Tao et al. (2016) showed an increased tolerance against herbivory in six plant species of Milkweeds (*Asclepias curassavica*, *Asclepias latifolia*, *Asclepias syriaca*, *Asclepias purpurascens*, *Asclepias verticillata* and *Asclepias incarnata*) with increasing leaf P concentration. Also, both cardenolide leaf concentration and latex exudation increased with leaf N concentration but decreased with plant growth rate. Based on these results, these authors state that due to the effects of mycorrhizae on N and P concentrations in plants, as well as their growth rates, AMF can then alter plant tolerance and chemical defence against herbivory simultaneously, suggesting the existence of general mechanisms by which AMF mediate plant–herbivorous interactions.

Once arbuscular mycorrhizal association has been established, one of the first responses of plants to AMF colonization is decreased root exudation (Marschner et al. 1997). Since both herbivores and AMF use plant-produced organic carbon compounds, which are exuded by roots as an energy source, they compete for these plant-produced compounds and can modulate carbon allocation for other rhizosphere microorganisms that also use this carbohydrate as a source of energy.

Although studies involving plant–herbivore interactions and their influence on the activities of soil symbiotic microorganisms are quite scarce (Wamberg et al. 2003), they have shown very conclusive results, showing, for example, that the damage resulting defoliation of plants lead to increased sugar exudation by the roots (Holland et al. 1996), thereby stimulating microbial activity and increasing the density of microorganisms in the rhizosphere (Wamberg et al. 2003). The establishment of arbuscular mycorrhizae, however, seems to be inhibited by leaf herbivory, but once arbuscular mycorrhizae is established before the insects reach the leaves, it can inhibit leaf chewing by insects (Gange et al. 1999). Thus, the AMF-Soil Microbial Biomass-Plants ratio can be identified as an important prerequisite for agricultural sustainability (Fortin et al. 2002).

Santos (2012) and Peres Filho et al. (2002) observed that leaf-cutting ants are attracted to certain plants and not attracted to others. This fact may be associated with plant resistance control of ants, in which some hormonal, genetic, nutritional or chemical factor causes some plant resistance to the attack of leafcutter ants.

Although the establishment of arbuscular mycorrhizae may alter defence strategies in plant leaf tissues (both constitutive and induced) (Bennett et al. 2009), few studies have shown whether this same pattern of plant response can be observed in the root tissues. When colonizing plant roots, AMF cause changes in the concentrations and types of secondary root metabolites (Schliemann et al. 2008), and it is likely that root herbivory is more influenced by the presence of AMF in the roots of these plants than the species of insects that feed on the leaves. Similarly, to what occurs in leaves, it is also likely that plant–root herbivore interaction occurs due to changes related to plant chemical defence (Bowers and Puttick 1988).

Recent studies have shown that the benefits of mycorrhizae formed in one plant can extend to other plants in a given community, thus contributing to the transport of signalling compounds involved in plant defence. In addition, water, carbon and nutrients can be translocated between plants due to the mycelial network formed by AMF below the ground surface, giving AMF an important role in communication between plants, even between those of different species. In this context, a mycorrhizal plant that suffers some damage from pest insects in both shoot and root may be able to induce other plants growing in its surroundings to increase its tolerance for such damage.

Although many studies have shown a great contribution of AMF in plant resistance to pest attack, most of them contain insufficient and inconclusive information about the protection mechanisms of these plants. Still, we cannot disregard the use of AMF as an important tool for biological control of pests and diseases and their contribution to the establishment of sustainable agriculture, since several evidences have shown that arbuscular mycorrhizae increase the tolerance of plants against pests and diseases, either by improving plant nutrition or by inducing the activity of plant defence metabolism.

5.3 Arbuscular Mycorrhizal Fungi as a Sustainable Alternative for Integrated Pest Insect Management

One of the main challenges for the establishment of agricultural and forestry crops is the damage caused by pest insects. Thus, the development of sustainable production systems with alternative ways of controlling these agents is one of the main challenges of the agroforestry sector. Alternative pest controls such as biological control have gained prominence in recent years, but the use of plants resistant to pest attack has proved to be an even more promising alternative. Since Integrated Pest Management (IPM) currently guides crop protection against insect attack, the development of alternative and sustainable ways to regulate the population of agents that could cause economic damage to crops becomes essential, especially in cultivated areas in the tropical region, where the number of registered species causing some kind of economic damage is significantly higher, and growing annually.

In this context, different strategies have been used to induce or improve the resistance in cultivated plants, such as the development of bt plants, which are genetically modified with the addition of *Bacillus thuringiensis* bacteria, making them less susceptible to pest attacks. Or even the addition of micronutrients, such as boron and silicon, which have been shown to be effective in reducing sucking insect attacks (Rastegari et al. 2020a, b; Yadav et al. 2018).

Plant resistance may be an alternative to pest insect regulation, utilizing and/or enhancing its own natural defence system. The plant defence system is constituted by constitutive (continuously expressed and independent of the action of aggressors) and induced (expressed only after injury events) defences. And they can also have direct or indirect action, being morphological (rigid tissues, trichomes and disposition of structures in the plant) or chemical (secondary metabolites, volatile and non-volatile substances) (Carrano-Moreira 2014). Plants use their defence system mainly associated with secondary metabolites as a strategy to reduce pest insect attacks, and it is noted that this defence system can be affected by different factors such as soil and climate. Some studies have shown that soil microbiota, which is composed by bacteria, actinomycetes, fungi, algae and protozoa, can exert significant influence on plant resistance to herbivorous attack. Andreola and Fernandes (2007) highlight that although soil microbiota constitutes only 1–4% of total soil carbon and occupies less than 5% of soil porous space; the amount of these microorganisms is significantly diverse. These living soil microbial components are also called biomass, and bacteria and fungi account for about 90% of soil microbial activity. It is in this soil microbiota that AMF are found, making associations with roots of several plant species, and playing important roles in plant nutrition, growth and resistance.

According to Vannette and Hunter (2009a) mycorrhizal fungi act as mediators in the defence against pest insects in cultivated systems. The authors demonstrate that plants with mycorrhizal associations may be more tolerant to insect damage and may have available nutritional resources to compensate for the enzymatic costs of defence production. In addition, the positive effect of AMF on plant defence systems may be related to their nutritional balance, in which plants in good physiological condition have a better defence system with increased production of secondary metabolites, and some phytohormones involved in their defence system like jasmonic acid (JA). Jung et al. (2012) describe that JA induces the synthesis of toxins and proteins that interfere with physiological processes in the insect, thus reducing its growth and survival, and can act by triggering indirect plant defences against herbivore, regulating the emission of volatile mixtures, which attract predators or parasitoids that attack pest insects.

Beneficial effects of mycorrhizal association on cultivated plants, decreasing the incidence of insect pest attack have been reported for tomato (*Solanum lycopersicum*), in which mycorrhizal colonization altered plant defence through action of JA (Jung et al. 2012). In strawberry (*Fragaria x ananassa*) attacked by larvae of the weevil *Otiorhynchus sulcatus* (Fabricius 1775) (Coleoptera), mycorrhizal plants showed reduced larval survival compared to non-mycorrhizal (Cange 2001). Soybean (*Glycine max* (L.) Merr.) inoculated with *Glomus mosseae* had a negative effect on *Heliothis zea* (Boddie 1850) (Lepidoptera) and *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera) (Rabin and Pacovsky 1985). *Eucalyptus urophylla* S.T. Blake inoculated with *Laccaria laccata* also had a negative effect on the development of *Anomala cupripes* (Hope 1839) (Coleoptera) (Gange et al. 2005b).

In a general context, it is noted that the negative effect of mycorrhizae on pest insects seems to be more evident in generalist chewing species than in sucking pests. However, according to Gehring and Bennett (2009) inoculation with AMF does not always lead to changes in the plant defence system. Although differences in feeding strategy probably explain some of the variations in herbivore response to inoculated hosts, other mechanisms have yet to be explored.

Roger et al. (2013) demonstrated that the beneficial effects of AMF on plant resistance to pest insect attacks vary according to fungus, plant, soil type, or herbivore. Barber et al. (2013) found that the effects of AMF on plant nutrition depend on soil type and, therefore, soil characteristics may influence colonization by AMF and their effects on herbivores. Roger et al. (2013) found that different *Rhizophagus irregularis* isolates associated with *Fragaria vesca* L. (strawberry) had different effects on the development of *Spodoptera littoralis* Boisduval (Lepidoptera).

Analysing the available literature, there is a lack of studies on the benefits of mycorrhizal associations and the plant defence system, mainly related to productive systems in the tropics. Roger et al. (2013) consider that the mechanisms by which mycorrhizal colonization alters plant resistance and the effects of agricultural practices on the presence and efficacy of AMF symbiosis in plants are not yet fully understood.

Vannette and Hunter (2009a) also highlight that the positive effects of AMF on plant defence, as a result of increased nutritional quality, will be more evident in organic production systems than in conventional systems, which use large amounts of agrochemicals. Mycorrhizal symbioses in agro ecosystems are affected by agricultural practices such as fertilization and plant protection measures such as pesticide application. Also, the reported effects of pesticides on arbuscular mycorrhizal symbiosis are very diverse and depend on many parameters such as the active ingredient, mode of action, mode of application and dosage, soil type, and amount of substances to which AMF have been exposed (Ahmed et al. 2019).

Thus, the importance of research based on these symbiotic associations is emphasized, in order to improve the productivity of sustainable agro forestry systems, providing greater supply of organic products in the market, thus enabling society to have access to products with less amount of agrochemicals and produced in a balanced way, also contributing to the improvement of environmental quality.

5.4 Conclusion and Future Prospects

Twentyfirst century agriculture has been based on expanding agricultural frontiers, with production systems that are economically viable and have the least possible impact on environment and human health. All of this necessarily passes through the biological component of the soil, and in this case, mycorrhizae play an important role, as they influence not only crop productivity, but also the sustainability of agricultural systems, especially by altering the interaction of plants with other organisms like pest insects. However, in the literature there are few studies about the effects of AMF on plant–insect interaction and their potential use in the biological control of agricultural pests. This lack of research together with the difficulties in producing viable inoculants on a commercial scale have been one of the major challenges for advances in the application of mycorrhizae in large areas of agricultural cultivation.

Studies involving the effects of AMF on plant–insect pest interaction have progressed in recent years and data meta-analysis have brought great advances, being widely used to analyse the role of AMF in plant resistance against pest insects, to evaluate plant growth responses to mycorrhizal colonization as a function of plant and environment characteristics, and to assess whether insect leaf attack can suppress mycorrhizal colonization. Future studies should continue to examine how the environment may be able to determine plant responses to arbuscular mycorrhizae.

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Chapter 6
Phosphate-Solubilizing Fungi: Current Perspective, Mechanisms and Potential Agricultural Applications

Ashok Kumar, Eamani Sivasurya Teja, Vandana Mathur, and Renu Kumari

Contents

6.1 Introduction

Phosphorus (P) is regarded as the most important macronutrient after nitrogen and plays a vital role in plant development (Mahdi et al. 2011; Kour et al. 2020a) and also involved in various metabolic processes such as photosynthesis, nutrient transfer, carbohydrate metabolism energy production and storage, membrane formation, as well as nitrogen fixation in legumes (Saber et al. 2005). Phosphorus is an important structural component of biomolecules such as coenzymes, phospholipid, cell membranes, phosphoproteins, and nucleic acids. Phosphorus deficiency leads to numerous physiological disorders in plants such as leaf darkening, thin stem, and

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stunted growth and also effects root architecture and seed development ultimately reducing the crop yield (Khan et al. 2013). In plants, phosphorus is translocated readily from older to younger tissues. A significant amount of phosphorus absorbed by the plant in ionic form is stored as “phytase” within the grains, and its deficiency leads to an adverse effect on grain yield. Hence, phosphorus deficiency in plants may have a drastic impact on the food security, for future generations (Kour et al. 2019b).

The concentration of organic P in organic matter rich soils may be as high as 40–80% of total soil P with phytate P as the most predominant and recalcitrant form of organic P. Despite the huge amount and abundant distribution of phosphorus in the soil in both inorganic and organic forms, globally many plants are suffering from phosphorus deficiency owing to the reality that plant growth and metal immobilization are not apparent (Park et al. 2011). Even though the elemental phosphorus has an integral role in plant life, due to some reasons it is not readily available to the plants. At first, the soil microbes convert the insoluble form of phosphorous into soluble form in the soil, i.e., organic form. Next, the soil particles are adsorbed with the accessible phosphorus. The soil pH should be maintained in between 4 and 8; otherwise, phosphorus may start forming bonds with other compounds (Khan et al. 2018). Their structural and chemical properties reduce its ready availability and make it a limiting nutrient for plant growth (Mehta et al. 2013).

In soil, phosphatase enzymes, organic acids as well as some complex intermediaries released by the plants and microorganisms can solubilize the insoluble phosphorus compounds. Various management approaches are being devised to solubilize these specified insoluble forms, in an attempt to improve plant growth and development (Satyaprakash et al. 2017). One of the approaches to tackle this challenge is the use of phosphorus containing fertilizers. As, only a limited quantity of fertilizer applied is accessible to the crops; frequent application of the fertilizer results in precipitation, by reacting with Al^{3+} and Fe^{2+} in acidic and Ca^{2+} in calcareous (or) ordinary soils, and its residues have a negative impact on environment by contaminating the water bodies, and eutrophication.

The use of soil-microflora is often one of the better sustainable approaches which may alter the current situation. This proves to be a robust, eco-friendly and economically viable approach that can substitute the use of excess chemical fertilizer and generate a highly efficient strategy for residual phosphorus solubilization and increase its availability to plant resulting in a good growth and development of the plants without effecting the environment (Kour et al. 2020b; Yadav et al. 2020c). These groups of microorganism are altogether known as phosphate-solubilizing microorganisms (PSMs). They can eliminate the phosphorus deficiency in soil and ensure the ample supply of phosphate to the plants. Archaea (Yadav et al. 2015c), Bacteria (Verma et al. 2016; Yadav et al. 2015a, b, 2016), Fungi, Arbuscular Mycorrhizal (AM) fungi, and Actinomycetes are the predominant microbial population of the soil, which can solubilize the soil phosphate and make it available to plants (Verma et al. 2019; Yadav et al. 2017b, 2019a; Thakur et al. 2014). While host–microbe interactions are mainly responsible in maintaining the soil fertility and plant growth, the effective use of such microbes requires a complete knowledge

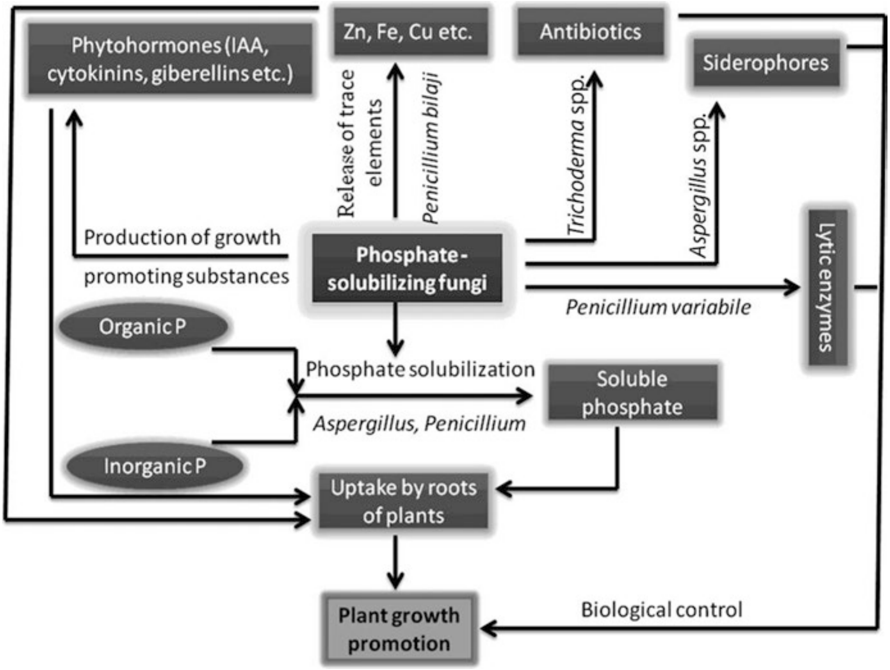

Fig. 6.1 Phosphorus translocation in ecosystem "SPAC"

of the complicated relationships between host–soil-microbes interactions (Satyaprakash et al. 2017). This chapter deals with the isolation of phosphate-solubilizing fungi, their screening and also studies their mechanism of phosphate solubilization, as well the biosynthesis of phytohormones by different approaches and applications (Fig. 6.1).

6.2 Phosphate-Solubilizing Microorganisms (PSMs)

Since, the manufacturing of phosphorus fertilizer is extremely costly nearly accounting for more than US$3–4 billion per annum with a huge consumption of electricity—to satisfy the worldwide demand for phosphorus required for plant development (Goldstein et al. 1993), it is necessary to glance critically at the ways to formulate a viable approach. Thus, the concern of excessive dependency on fossil fuel as an energy source for fertilizer manufacturing, which may lead to the prospects of decreasing availability of expensive fertilizer input in the future, clearly pushed the topic of phosphorus solubilization to the center of studies. The microorganism with the phosphorus solubilizing capacity have demonstrated to be an economically feasible solution to the use of more costly superphosphates, and prove better under various soil and agro-climatic circumstances and also have a greater agronomic value (Rastegari et al. 2020a, b; Singh and Yadav 2020). Microorganisms with the phosphate solubilizing ability enhance the availability of readily accessible phosphorus that can be easily absorbed by plant root and can also promote biological nitrogen fixation and consequently enhance the crop production (Ponmurugan and Gopi 2006).

Microbial communities by their metabolic activities directly or indirectly affect the physico-chemical properties of soils. Microorganisms of the rhizosphere, including fungi, can improve the plant growth through various processes such as decomposition of organic matter, mineralization and mobilization of nutrients, storage of water and nutrients, denitrification and fixation of nitrogen (Kour et al. 2019c, d; Verma et al. 2017; Yadav et al. 2018a). Most crop plants were noticed to be stably established in phosphorus-deficient soils via association with rhizospheric microorganisms. This association could either lead to improved phosphate uptake or make unavailable sources of phosphorus accessible to the plant. The P-solubilizing microorganisms are omnipresent whose populations differ from soil to soil and are significantly affected by soil nutritional condition and environmental variables. In soil, phosphate-solubilizing bacteria make up 1–50% and fungi 0.5–0.1% of the entire population. The level of iron ore, temperature, carbon and nitrogen components significantly affects the P-solubilizing potential. In contrast, in the rhizoplane, salt, pH and temperature tolerant phosphate solubilizing bacteria were noted to be maximum followed by rhizosphere and root-free soil in alkaline soils (Johri et al. 1999).

Most of the effect is geared towards knowing biological nitrogen fixation with the use of microorganisms as biofertilizers (Kour et al. 2020b). On the other hand, the basic research on phosphate solubilization by nodule forming bacteria was significantly less; although phosphorus is recognized to be the most limiting factor for nitrogen fixation by the symbiosis of rhizobium-legume. Among the microbes of the rhizosphere, *Bacillus* and *Pseudomonas* (Illmer and Schinner 1992; Wani et al. 2007; Kour et al. 2019a) are the major genera of P-solubilizing bacteria, whereas *Aspergillus* and *Penicillium* are the major genera of fungi (Wakelin et al. 2004; Souchie et al. 2006; Yadav et al. 2018b). Many fungal species can solubilize tricalcium phosphate, aluminum phosphate and rock phosphate such as *Aspergillus tubingensis*, *Rhizoctonia* sp., *Penicillium rugulosum*, *Pythium* sp., *Penicillium italicum*, *Fusarium oxysporum*, *Aspergillus niger Humicola* sp., *Aspergillus fumigatus*, *Penicillium radicum*, *Curvularia lunata*, *Aerothecium* sp., *Aspergillus terreus Phoma* sp., *Aspergillus awamor*, *Pseudogymnoascus* sp., *Cladosporium* sp., *Rhizoctonia solani*, *Cunninghamella* sp., *Sclerotium rolfsii*, *Rhodotorula* sp., *Candida* sp., *Schwanniomyces occidentalis*, and *Oideodendron* sp. (Kour et al. 2019c; Rana et al. 2019a, b; Sharma et al. 2019; Whitelaw et al. 1999; Isbelia et al. 1999; Sparks, 1999; Helen et al. 2002).

6.3 Isolation and Screening of PSMs

Phosphate-solubilizing microorganisms (PSMs) can be isolated by Pikovaskaya's medium (Pikovaskaya 1948) from rhizospheric and non-rhizospheric soil as well as from other areas through serial dilution or culture techniques (Gaur 1990). PSM is identified by the development of clear halo zone around the colonies when the microorganisms are incubated on solid plates comprising insoluble phosphates. Recently, a few other techniques have been proposed to isolate and select PSMs. Since certain strains of PSMs show many changes in phosphate-solubilizing capacity (Illmer and Schinner 1992), they are sub-cultured continuously to evaluate the presence of phosphate-solubilizing capacity. Once the effective phosphate-solubilizing microorganisms are chosen, they are screened for their potential under the liquid culture medium to solubilize insoluble phosphates. Furthermore, the selected phosphate solubilizing cultures are used to make the inoculants and their performance is assessed under pot/field conditions and is tested on various field crops for their efficacy. Detection of halo zone on the solid medium is not a proper P-solubilization test; quantitative assays are needed in the liquid medium. The feasible P-solubilizing microbial cells are usually referred to as microphos (Zaidi et al. 2009). Before their mass production as bioinoculants, microbes exhibiting considerable capacity for P-solubilization under in vitro conditions are further examined on plants.

6.4 Phosphate-Solubilizing Fungi

Over the past few years, a wide range of phosphate-solubilizing fungi has been recognized including the genera *Penicillium*, *Aspergillus*, *Piriformospora*, *Curvularia*, and other endophytic symbionts such as arbuscular mycorrhizal (AM) fungi (Khan and Khan 2002). The facilitating access to soil mineral nutrients in exchange for photosynthetic carbon (Smith and Read 2008) and symbiotic root colonizers, AM fungi sustain plant mineral nutrition (Yadav et al. 2019b). Root endophytic fungi have been well-characterized for associating and facilitating the growth of diverse plant varieties (Verma et al. 1998; Varma et al. 2001; Deshmukh et al. 2006; Rana et al. 2019a). Promoting plant growth by AM fungi is aligned primarily with their potential to solubilize and mobilize soil phosphorus. In addition to AM fungi, many other endophytic fungi can colonize and enter the plant roots and enhance the performance of the plant (Harman et al. 2004). Depending on the fungal partner and host interaction and physico-chemical properties of the soil, their effect on plants may be positive or negative (Mayerhofer et al. 2012). Promotion of growth in certain plants colonized by endophytic fungi was mainly related to their contribution to plant phosphorus nutrition (Neubert et al. 2006; Franken 2012; Vitorino et al. 2016). Hence fungal inoculants can be regarded as a reliable biofertilizer and are an eco-friendly sustainable approach to further uses as phosphatic fertilizers with phosphate-solubilizing behavior in plant growth. Phosphate-solubilizing fungi can be isolated from different regions and can contribute to the plant growth promotion through phosphate solubilization. According to the region, the phosphate-solubilizing fungi are categorized as rhizospheric fungi, endophytic fungi, and mycorrhizal fungi.

Rhizosphere is a region where microbes are under plant roots influence. Roots are the main sites for nutrient uptake and organic compound exudation, which serve as carbon source and energy supplies for indigenous microorganisms. In the rhizosphere, there are a huge number of microbes than in bulk soil resulting in "rhizosphere effect" (Hinsinger et al. 2009; Kour et al. 2019c). In the rhizosphere, plant–microbe interactions are critical for controlling biogeochemical mineral element recycling and preserving the structure and function of rhizosphere's microbial community (Singh et al. 2007). In several instances, plant-microbe associations are developed in such a manner that some fungi form symbiotic relationship with roots called mycorrhizae while some fungi emerged as "endophytes" as they reside non-pathologically within plant roots (Gehring et al. 2006). Endophytes were known to originate in the rhizosphere and then penetrate inside the roots through natural gaps, injuries, and at the development site of seedling (Gaiero et al. 2013) (Table 6.1).

6.4.1 Rhizospheric Fungi as a Phosphate-Solubilizer

Rhizospheric fungi lead to chemical and physical changes that influence plant health constantly. In the latest findings, rhizospheric thermo-tolerant fungi *Aspergillus terreu*s isolated from the rhizospheric region of the *Suaeda monoica*, a wild halophilic plant in Jizan, Saudi Arabia, were tested for their phosphate-solubilizing and zinc-phosphate-solubilizing potential (Abdel-Ghany and Alawlaqi 2018). Khan et al. (2018) screened nineteen P-solubilizing fungi from wheat rhizospheric soil and 12 out of 19 isolates reported as beneficial in P-solubilization. *Aspergillus* spp. was proven to be the best isolate which had an enormous potential to solubilize the phosphate. Approximately eight *Trichoderma* spp. were tested for their potential of phosphate solubilization (Resende et al. 2014) from the rhizospheric region of *Calophyllum brasiliense*.

Mahadevamurthy et al. (2016) have isolated 22 rhizospheric fungi from distinct rhizosphere soil of healthy plants of Mysore, Karnataka, India and evaluated for phosphate solubilization potential on Pikovskaya medium. Only *Penicillium* sp. RFUOM 14 was found to be effective among the 22 fungal isolates by generating clear halo zone around the colony by solubilizing phosphate. In addition, *Penicillium* sp. RFUOM 14 inducers were tested for various crop plants and noted that seed germination and seedling vigor were improved by the treatment of this fungus. Among the treatments, conidial suspension in pearl millet, brinjal and tomato showed a maximum of 85.75%, 80% and 83% of plant germination and seedling strength of 985.25, 523 and 673.5, respectively. Yin et al. (2017) performed a study evaluating P-solubilizing potential of *Aspergillus aculeatus* isolated from the wheat

Table 6.1 Phosphate-solubilizing fungi in different habitats

S. No.	Habitat	Fungi	References
1	Rhizosphere	*Aspergillus terreus*	Abdel-Ghany and Alawlaqi (2018)
		Aspergillus spp.	Khan et al. (2018)
		Aspergillus ustus and *Aspergillus tamari*	Pany et al. (2018)
		Aspergillus aculeatus	Yin et al. (2017)
		Aspergillus awamori	Jain et al. (2012)
		Aspergillus niger and *Penicillium notatum*	Malviya et al. (2011)
		Aspergillus niger	Tallapragada and Seshachala (2012)
		Penicillium oxalicum	Singh and Reddy (2011)
		Penicillium spp. *and Talaromyces* spp.	Scervino et al. (2010)
		Absidia spp.	Nenwani et al. (2010)
2	Endophytic	*Piriformospora indica*	Wu et al. (2018)
		Aspergillus oryzae	Devi and Packialakshmi (2018)
		Aspergillus spp.	Sarbadhikary and Mandal (2018)
		Aspergillus fumigatus and *Fusarium proliferatum*	Bilal et al. (2018)
		Aspergillus flavus	Asaf et al. (2018)
		Byssochlamys nivea	Dolatabad et al. (2017)
		Xylaria regalis	Adnan et al. (2018)
		Piriformospora indica	Ngwene et al. (2016)
		Aspergillus versicolor, Aspergillus niger, Fusarium fusarioides and *Chaetomium globosum*	Chadha et al. (2015)
		Penicillium sclerotiorum	Nath et al. (2015)
		Trichoderma gamsii	Rinu et al. (2014)
3	Mycorrhizal	*Rhizophagus irregularis*	Zhang et al. (2018)
		Rhizophagus irregularis and *Penicillium aculeatum*	Efthymiou et al. (2018)
		Glomus fistulosum	Osorio and Habte (2013)
		Glomus aggregatum and *Glomus mosseae*	Zhang et al. (2011)
		Glomus intraradices and *Glomus mosseae*	Suri et al. (2011)

plant rhizosphere. Pany et al. (2018) isolated two fungi, *Aspergillus ustus* and *Aspergillus tamarii*, from their rhizosphere and have been researched for great P solubilization ability for the growth of a medicinal plant (*Pongamia pinnata*).

6.4.2 Endophytic Fungi as a Phosphate-Solubilizer

Endophytes are the microorganisms that live within the plant, and strive to enhance the plant growth by using different mechanisms (Rana et al. 2019a; Yadav et al. 2017c). The uptake of phosphorus from the soil is one such process. Several endophytes that have phosphate-solubilizing potential have been discovered. In the findings of Devi and Packialakshmi (2018), fungal isolates from the roots of *Cardiospermum halicacabum* have been isolated and *Aspergillus oryzae* has been reported to have potential P-solubilizing capability. Sarbadhikary and Mandal (2018) revealed that strains of *Aspergillus*, an endophytic fungus isolated from the leaves of *Schima wallichii* had powerful plant growth ability for supporting multiple plant growth functions including P-solubilization. *Xylaria regalis*, an endophytic fungus isolated from *Thuja plicata's* cones, has been evaluated by the P-solubilization ability for its multiple plant growth promotion activities, including improved performance of plant (Adnan et al. 2018). Likewise, there was a significant phosphate-solubilizing potential to *Trichoderma gamsii*, isolated from the lateral roots of *Lens esculenta* (Rinu et al. 2014). Khan et al. (2011) explored the potential of *Penicillium funiculosum* for P-solubilization as well as its function in physiology of *Glycine max*—soybean (host plant) growing under salt stress. The growth promoting characteristics of some epiphytic and endophytic yeast isolates extracted from rice and sugar cane leaves were assessed in which selected yeast showed calcium phosphate-solubilizing potential (Nutaratat et al. 2014).

Nath et al. (2015) conducted a research on an endophytic fungus, *Penicillium sclerotiorum* isolated from *Camellia sinensis* (tea plant) of Assam land and suggested it to be the most potent P-solubilizer. Chadha et al. (2015) isolated endophytic fungi from tomato roots and showed significant P-solubilizing potential in isolates such as *Aspergillus versicolor, Aspergillus niger, Fusarium fusarioides* and *Chaetomium globosum. Byssochlamys nivea* is an endophytic fungus isolated from *Pistacia vera* plant has been suggested as a P-solubilizing fungus (Dolatabad et al. 2017). *Piriformospora indica,* a soil endophytic fungus, was evaluated for its P-solubilizing ability (Ngwene et al. 2016; Bilal et al. 2018) and had isolated two fungi, *Aspergillus fumigatus* and *Fusarium proliferatum* from *Oxalis corniculata* roots and then positively screened for the P-solubilization capabilities. Table 6.2 represents various phosphate solubilizing fungal sp., secreting a different range of organic acids.

Table 6.2 Organic acids released by P-solubilizing fungi

Organisms	Predominant organic acids	References
Aspergillus flavus, A. candidus, A. niger, A. terreus, A. wentii, Fusarium oxysporum, Penicillium sp., *Trichoderma isridae, Trichoderma* sp.	Lactic, maleic, malic, acetic, tartaric, citric, fumaric, gluconic	Akintokun et al. (2007)
A. flavus, A. candidus	Glutaric	
Penicillium oxalicum	Malic, gluconic, oxalic	Shin et al. (2006)
Aspergillus flavus, A. niger, P. canescens	Oxalic, citric, gluconic, succinic	Maliha et al. (2004)
Penicillium rugulosum	Citric, gluconic	Reyes et al. (2001)
A. niger	Succinic	Vazquez et al. (2000)
Penicillium variabile	Gluconic	Fenice et al. (2000)
Penicillium rugulosum	Gluconic	Reyes et al. (1999)
Penicillium radicum	Gluconic	Whitelaw et al. (1999)
Penicillium variabile	Gluconic	Vassilev et al. (1996)
A. awamori, A. foetidus, A. terricola, A. amstelodami, A. tamari	Oxalic, citric	
A. japonicus, A. foetidus	Oxalic, citric, gluconic, succinic, tartaric	
Penicillium bilaji	Citric, oxalic	
A. niger, P. simplicissimum	Citric	
A. awamori, P. digitatum	Succinic, citric, tartaric	Gaur (1990)
Penicillium sp.	Oxalic, itaconic	
Aspergillus niger	Succinic	Venkateswarlu et al. (1984)
Aspergillus sp., *Penicillium* sp., *Chaetomium nigricolor*	Oxalic, succinic, citric, 2-ketogluconic	Banik and Dey (1983)
A. fumigatus, A. candidus	Oxalic, tartaric	Banik and Dey (1982)

6.4.3 Mycorrhizal Fungi as a Phosphate-Solubilizer

Mycorrhizae are the symbiotic association between fungus and the roots of vascular plants and are much more peculiar in structure. When they colonize root tissues intracellularly and extracellularly, they are called as arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi, respectively. Among the wide range of benefits given by AMF fungi, the most prominent one is improved phosphorus nutrition of the host plant with low phosphate levels which is achieved by the large surface area of their hyphae and their high-affinity for P-mobilization mechanisms. They were well studied for their participation in enhanced uptake of phosphate and other nutrients in plants. The inoculation of these fungi in the plant has also been shown to assist the plant to use more soluble phosphate from the fertilizer (Kour et al. 2020a; Rana et al. 2019c, 2020). This is because, due to the existence of extraradical mycelium, mycorrhizae have expanded root phosphate absorbing sites (Khan et al. 2007). It has been well known that mycorrhiza also involves other microorganisms on their surface as they are recognized to develop substantial soil hyphae biomass and also assist them to discharge inorganic P in the plant (Scheublin et al. 2010; Agnolucci et al. 2015; Zhang et al. 2018).

Zhang et al. (2018) researched that AMF exuded fructose, *Rhizophagus irregularis*, assisted the bacterium, *Rahnella aquatilis* (phosphate-solubilizing bacteria) to increase phosphate gene expression and phosphatase release rate in the growth medium. Moreover, a study carried out by Yousefi et al. (2011) suggested the relationship of PSB and AMF in increasing inorganic P uptake by the wheat plant. Enhanced P-solubilizing activity was explored with two other mycorrhizal fungi, *Glomus aggregatum* and *Glomus mosseae* (Zhang et al. 2011).

6.5 Mechanism of Phosphate Solubilization by Soil Fungi

The solubilization of P compounds by naturally abundant P-solubilizing microbes is common under in vitro conditions (Souchie et al. 2006). Indeed, soil microorganisms are effective in releasing P from inorganic P through solubilization and from organic pools of total soil P by mineralization (Yadav et al. 2018a). The microbial biomass in soil also contains a significant quantity of immobilized P that is potentially available to plants. However, several theories have been proposed to explain the mechanisms of microbial solubilization of P. Broadly, these theories have been categorized into three groups: (a) the organic acid theory (Cunningham and Kuiack 1992), (b) the sink theory and (c) the acidification by Hþ excretion theory (Illmer and Schinner 1992). Of these, the organic acid theory is well recognized and accepted by majority of the workers across the globe. In this theory, the insoluble sources of P are solubilized by P-solubilizing fungus either by (a) lowering the pH or (b) by enhancing chelation of the cations bound to P.

The lowering in pH of the medium suggests the release of organic acids by the fungal or any other P-solubilizing microorganisms (Whitelaw 2000; Maliha et al. 2004). Such organic acids can either directly dissolve the mineral P as a result of anion exchange of PO_4^{2-} by acid anion or can chelate both Fe and Al ions associated with P. Thus, the synthesis and discharge of organic acid by the fungal strains into the surrounding environment acidify the fungal cells and their surrounding environment that ultimately lead to the release of P ions from the P mineral by Hþ substitution for Ca2þ Of the different organic acids involved in the solubilization of insoluble P, succinic, citric, gluconic, a-ketogluconic and oxalic acids are the most prominent acids released by fungal strains (Table 6.1). For example, the main mechanism for P solubilization in *Penicillium radicum* was acid production leading to a decrease in pH. Evidence from an abiotic study using HCl and gluconic acid to solubilize P also indicated that chelation of Al3þ by gluconic acid may have been a factor in the solubilization of colloidal Al phosphate (Whitelaw et al. 1999). Organic acids produced by P-solubilizing microorganisms can be detected by high performance liquid chromatography and enzymatic methods (Whitelaw 2000). However, acidification does not seem to be the only mechanism. Solubilization of insoluble P by fungal strains on Pikovskaya (Plate A) and modified Pikovskaya plate (Plate B) amended with bromophenol blue. Solubilization as the ability to reduce the pH in some cases did not correlate with the ability to solubilize mineral P.

The chelating ability of the organic acids is also important, as it has been shown that the addition of 0.05 M EDTA to the medium has the same solubilizing effect as inoculation with *Penicillium bilaii*. In another study, the capability of the plant growth promoting and biocontrol fungus *T. harzianum* T-22 to solubilize in vitro insoluble minerals including RP. Organic acids were not detected in the culture filtrates and hence the authors concluded that acidification was probably not the major mechanism of solubilization as the pH never fell below 5. The fungal solubilizing activity was attributed both to chelation and to reduction processes, which could also play a role in the biocontrol of plant pathogens. Further, the involvement of the Hþ pump mechanism in the solubilization of small amounts of P in *Penicillium* rugulosum is reported (Reyes et al. 1999). Although organic acid has been suggested as the principal mechanism of P solubilization, the solubilization of insoluble P by inorganic acid (e.g. HCl).

In the sink theory, P-solubilizing organisms remove and assimilate P from the liquid and hence activate the indirect dissolution of calcium phosphate compounds by consistent removal of P from liquid culture medium. For instance, the P content in the biomass of *Pseudomonas* sp. and *P. aurantiogriseum* was similar to those observed in non-P-solubilizing microorganisms. The sink theory generally explains the mineralization of organic P compounds in which the P content in biomass of organisms is consistently correlated with the decomposition of P containing organic substrates. Different mechanisms involved in the solubilization of insoluble P by naturally occurring microbial communities of soils are briefly illustrated in Fig. 6.2.

Phosphorus is one of the most important essential macronutrients required for the plant growth and metabolism. For making the insoluble phosphate available to the plants, phosphate-solubilizing fungi could play an important role in making P available for plants and it can be better future perspective for assisting in the supply of required phosphorus to the plants in both organic as well inorganic forms by solubilizing the insoluble phosphorus. Such conversion is most common under in vitro condition by various fungi. Phosphate-solubilizing fungi haveing various traits such as production of secondary metabolites, mineral solubilization, etc. The present scenario focuses on the mechanism of plant growth promotion by phosphate-solubilizing fungi.

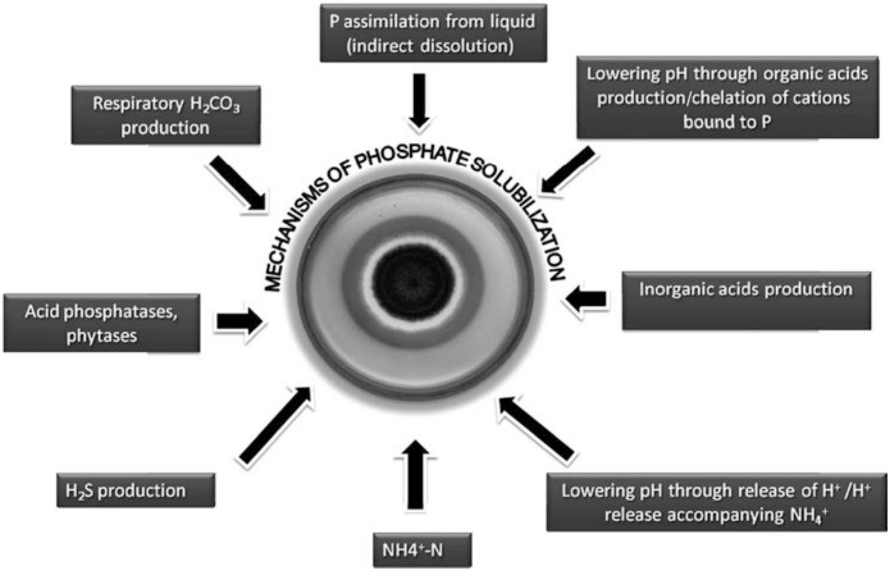

Fig. 6.2 Mechanisms involved in phosphate solubilization by plant growth promotion phosphate-solubilizing fungi—Image courtesy: Khan et al. (2007)

6.6 Plant Growth Promoting Characteristics of Phosphate-Solubilizing Fungi

Plant growth promoters play an important role in plant growth, metabolism and their further development. The plant needs different phytohormones as well micro- and macronutrient for its different metabolic processes. Hence, for balancing the soil fertility there is need of macronutrient (N&P) for plant growth promotion and phytohormones such as auxins, cytokinin, etc. For plant growth promotion phosphate solubilization must occur adjacent to the plant root. Therefore, it should be kept in mind to choose such phosphate-solubilizing fungi that can act closely to the root system (Kour et al. 2019d). Few species of *Penicillium* was found to increase plant growth applied in inoculant form. Researchers found that the phosphate-solubilizing fungi results in plant growth promotion by providing enough availability of P to the soil and many species of *Penicillium* was found to increase the yield and growth of plant in wheat crop plant (Kucey et al. 1987; Kour et al. 2019b, d).

6.6.1 Auxin Production

Plants as well as different microorganisms produce phytohormones like Indole 3-acetic acid (IAA). The IAA plays pivotal role in plant growth and development and both the pathways (Trp-dependent and independent) co-exist in plants and microorganism. IAA is responsible for cell division, apical dominance and also relates to tissue differentiation. The interaction between the fungi and plant is quite not known but few researchers concluded that phosphate-solubilizing fungi releases phytohormones which may act directly and, in some cases, indirectly also to enhance the plant growth and the nutrient availability to the host plant (Yadav et al. 2017a; Contreras-Cornejo et al. 2009). The production of IAA by fungi can enhance the lateral root growth and also increase the fruit and shoot biomass. Therefore, the fungal produced IAA increases the plant growth and defense mechanism at the basal point of the plant against different pathogen (Jogaiah et al. 2013).

6.6.2 Siderophore Production

Siderophore production helps the host plant to protect itself from the abiotic and biotic stress and results in the survival of plant in the harsh condition. *Trichoderma*sp. was found to have the characteristics feature to produce siderophore and prevent plant from abiotic stress as reported in cucumber plant and olive trees under salinity stress (Porras-Soriano et al. 2009; Sharma et al. 2019). The phosphate-solubilizing fungi having the ability to counteract and protect the plant from environmental stress and it was carried out by reduction in reactive oxygen species (ROS) level and protecting the photosynthetic machinery, respectively. Thus, it was reported that AM fungi can cope up with the salinity stress by compensating the salt level in the plant and *Trichoderma* sp. could be the upcoming warrior for protecting the plant under salinity stress.

6.7 Applications

6.7.1 Biofertilizers

Phosphate-solubilizing fungi have characteristic activity which solubilize insoluble phosphorus in both ways that is quantitatively and qualitatively under lab conditions which attracts the microbiologists to make it possible to be used in the form of biofertilizers (Khan et al. 2007; Yadav et al. 2020a, b). Plant requires macronutrient such as nitrogen and phosphorus in more amounts as compared to other beneficial nutrient and in this context when the seed of chickpea was inoculated with the phosphate-solubilizing fungi, it shows yield more than expected. P-solubilizing fungi such as *Aspergillus niger, Aspergillus fumigatus, P. pinophilum* and *R. leguminosarum* biovar viciae showed a significant increase in the plant height and nutrient uptake in *vicia faba* plant, respectively (Mehana and Wahid 2002). The P-solubilizing fungi secrete organic acids which enhance phosphate availability while it decreases the chemical abundance of phosphorus in the soil (Venkateshwarlu et al. 1984). Therefore, the use of phosphate-solubilizing fungi makes a new way to replenish the phosphorus availability in the soil and also for better yield of leguminous crop plant as biofertilizers.

6.7.2 Bioremediation

Bioremediation is one of the important processes which clean up the inorganic and organic pollution from the environment. Few fungi of genus *Aspergillus, Penicillium* and *Fusarium* can be used for the reclamation of land or detoxification of metallic and radionuclide pollutants. The plant requires phosphorus for growth and development; hence, the phosphate-solubilizing fungi solubilize the insoluble phosphorus and make it abundant in the soil as well in the form of biofertilizers and can be helpful for bioremediation practices. Few fungi such as *Aspergillus* is used for biodegradation of organic pollutants such as phenolic, aromatic and other many other compounds which are discharged from the industries (Yadav et al. 2019c). There are few investigations which have been carried out to find the characteristics feature of phosphate-solubilizing fungi in bioremediation as it degrades chlorsulfuron and metsulfuron methyl and *Penicillium* sp. and its other species can degrade the different xenobiotic compounds at a very low-level substrate concentration (Zanardini et al. 2002). Furthermore, it potentially makes it feasible to use it for degradation of organic and inorganic pollutants, respectively (Leitao 2009). Table 6.3 represents the application of various fungi in bioremediation.

Table 6.3 Various fungal sp. helping in bioremediation

Fungal species	Functions	References
P. simplicissimum	Adsorption of Zn (II) and to produce citric acid	Franz et al. (1991)
P. Janthinellum F-13	Reduce aluminum toxicity and to produce citric acid	Zhang et al. (2002)
Aspergillus flavus	Degrade the violet-2RL dye	Agnes et al. (2012)
A. Fumigatus		
Aspergillus sp.	Biodegradation of polycyclic aromatic hydrocarbons	Ali et al. (2012)
	Biodegradation of bisphenol	Kamaraj et al. (2012)

6.8 Conclusion and Future Prospects

Future research work should also investigate or improve the performance and stability of the phosphate solubilization trait once the fungi have been inoculated in soil as in by both genetically modified and natural strains. It is a great challenge to scientist for development of efficient and synergistic consortia of phosphate-solubilizing fungi and bacteria for decrease the load of chemical fertilizers application in the world. Nowadays, bioremediation is pre-requisite because of the industrial phase and it can be an eco-friendly approach to recompense availability of nutrients such as nitrogen, phosphorus, potassium and other beneficial nutrients in the soil at optimum level rather than the chemical dyes, organic compounds, etc. This can be used for various future prospectuses such as biofertilizers and in the bioremediation approaches.

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Chapter 7
Fungal Phytohormones: Plant Growth-Regulating Substances and Their Applications in Crop Productivity

Anna Goyal and Anu Kalia

Contents

7.1 Introduction

Excessive use of fertilizer and pesticides in the agricultural practices has resulted in the degradation of the environment that includes air, soil, water, and microbial populations. Resource degradation and environmental stresses tend to cause substantial yield losses (Kour et al. 2020). Further, continuous use of pesticides over the years has led to development of resistance in pests and pathogens (Aktar et al. 2009). These issues necessitate figuring out alternate avenues for improvement and stabilization of the production systems for sustainable agriculture practices. Possible options may include genetically enhanced productivity, reduction in chemical inputs, improved nutrient use efficiency, biotic and abiotic stress tolerance that

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includes disease and pest resistance. A novel alternative is to improve input use efficiency through integration of beneficial plant microbiomes with the cultivation process where the microbes metabolize the carbon present in the rhizosphere as a primary source for their survival (Denef et al. 2007; Yadav et al. 2020). Incorporating the plant growth-promoting fungi can prove to be a promising tool which is environmental friendly and can enhance the crop yield also (Kour et al. 2019b; Yadav et al. 2017a). Consequently, it may be very important to investigate root microbial activity in context of plant genotype, which may have an indirect influence on rhizosphere microbial function in regard to nutrient (especially N and P) acquisition. Also the plants have the innate mechanism by virtue of which it selects the rhizospheric microbiome and promotes the growth of specific microorganism that benefits the plant growth and development to give better yield (Mendes et al. 2013). Plant productivity is governed by the mutual interactions between the rhizospheric microorganisms and plant roots (Lakshmanan et al. 2014). This necessitates studies to be conducted aiming for identification of model host–microbiome systems for which associated microbial cultures in form of biofertilizers are available. Such studies may also help to define plant genotype by its environment, microbiome, and its mutual interactions.

Rhizosphere is a dynamic and complex interface between the nutrient-rich bulk soil and the plant root surface and rhizosphere microorganisms (fungi, archaea, bacteria) which are involved in processes that may directly or indirectly affect plant health (Kour et al. 2019a). Abiotic factors like temperature, light, nutrient, and water and biotic factors including competition, predation, parasitism, mutualism shape the microbiome turnout (Yadav et al. 2017a). It has been well established that plant roots secrete primary metabolites that include organic acids, amino acids, and carbohydrates along with the secondary metabolites including alkaloids, terpenoids, and phenolic compounds that modifies the rhizospheric microflora. Further, root exudates can enhance the occurrence of specific microbes and their metabolic functions as and when required while switching off the core microbiome expression, for example, during N-fixation, phosphorus uptake, and defense against pathogens. The rhizosphere is also important for microorganism-driven carbon sequestration, ecosystem functioning, and nutrient cycling in agricultural systems. There are reports which suggest that plants and the rhizomicrobiome communicate with each other by means of the exchange of signals in the form of chemicals (Chaparro et al. 2014; Rastegari et al. 2020a, b; Yadav et al. 2017b, 2020).

Recent work addressing the association between crop genotype and microbial diversity using 16S rRNA gene microarrays in a greenhouse setting or fingerprinting under field conditions supports the notion that microbial diversity is related to plant genotype (Peiffer et al. 2013). With the escalating importance of microbial diversity and its functioning, recent advancement in omics techniques including genomics, gene expression studies or the transcriptomics, cellular protein profiling, 'the proteomics' and high through-put bioinformatic and data analytics technologies will aid in improving our know-how on microbiome structure and functioning.

7.2 Plant Growth-Promoting Fungi

Plant growth-promoting fungi (PGPF) belong to a broad and heterogeneous group of non-pathogenic fungi inhabiting different habitats. PGPF supports the growth and improves the resistance to the biotic and abiotic factors. Fungi belonging to genera *Penicillium*, *Aspergillus*, *Fusarium,* and *Trichoderma* are reported to be PGPF as these enhance growth and development of the plants (Hossain et al. 2017). PGPFs can also improve the water and nutrient uptake and assimilation and improve resistance against the pathogens through acquired systemic immunity. PGPF acts in the similar way as the plant growth-promoting rhizobacteria (PGPR) interact with the host plants (Yadav et al. 2019c). Planting seeds along with PGPF inoculum aids in breaking seed dormancy, improves germination, root and shoot development, and resistance to pathogens thereby improving crop yield.

PGPF differ according to scientific classification, habitats, physiology, plant interaction, and mode of action. Their impact may fluctuate under various ecological conditions. PGPFs are pervasive saprobes and they exist in the rhizosphere of the plant. Normally 44% of the rhizosphere fungal species can be cosidered as PGPF (Hyakumachi 1994). Most PGPFs belong to phylum *Ascomycota* which includes species like *Aspergillus*, *Cladosporium*, *Colletotrichum*, *Fusarium*, *Gliocladium, Penicillium*, *Trichoderma,* and *Talaromyce*s, besides genera belonging to *Basidiomycota* (*Rhodotorula*, *Rhizoctonia*) and *Zygomycota* (*Mucor* and *Rhizopus*) (Yadav et al. 2019a, b, c). Symbiotic mycorrhizal fungi act as the beneficial biotrophs and involved in mutualist partnerships with the plants (Mehrotra 2005). Free living fungi, on the other hand, establish a non-symbiotic relationship to benefit the plants (Bent 2006). Endophytic fungi improve the plant growth (Waqas et al. 2015) with species like *Fusarium*, *Penicillium,* and *Alternaria* (Khalmuratova et al. 2015).

PGPFs also promote the flowering phenology in plants as these microbes may trigger the flower initiation, budding, and can alter the number, and size of the flower in the interacting plant. This may be attributed to enhanced plant nutrient uptake (especially K^+) (Perner et al. 2007), which regulates bud formation through better transmission of gibberellins (Das et al. 2012). Cytokinins regulate the initiation of flowering and ovule differentiation (Zhang et al. 2014). *Trichoderma* spp. enhanced flowering in chrysanths and Petunia (Ousley et al. 1994). Likewise, it also resulted in early flowering in alyssum and marigold (Chang et al. 1986). Early flowering was also observed due to positive effects of *P. indica* in *C. forskohlii* (Das et al. 2012), *T. harzianum,* and *P. chrysogenum* in *Solanum lycopersicum* (Jogaiah et al. 2013).

PGPFs can help in suppression of plant diseases directly by producing antibiotics, and indirectly by outraging the pathogens through induction of systemic resistance (Pieterse et al. 2014). PGPF decreases the effect of different pathogenic fungi (Nassimi and Taheri 2017), bacteria (Yoshioka et al. 2012), viruses (Elsharkawy et al. 2012), and nematodes (Vu et al. 2006) by activating the plant defenses i.e. through induction of systemic resistance. Moreover, transcript-profiling studies have demonstrated that plant response to PGPF relies on the intervening number of genes or proteins in plants. Current information additionally recommends that hereditary inconstancy in plant genotypes decides the result of phyto-incitement and ISR communications with PGPF (Hossain et al. 2017).

PGPF treated plants also showed significant imrovement in yield possibly due to better absorption of the nutrients as PGPFs solubilize inorganic compounds present in the soil to soluble forms for the ready uptake by the plants (Wakelin et al. 2007). Yedidia et al. (2001) recommended that occurrence of PGPF in the rhizosphere expands effective root surface area for absorption enabling the roots to investigate bigger volumes of soil. *T. harzianum* seed treatment led to yield increments in many maize genotypes (Harman et al. 2004). PGPF likewise adjusts the nitrogen-use proficiency and nitrogen take-up limit in yields (Alberton et al. 2013), helps to withstand biotic and abiotic stresses (Shoresh et al. 2010), improves photosynthetic proficiency (Babu et al. 2015), and therefore adds to improvement in harvest yield. Srivastava et al. (2006) have revealed the impact of *T. harzianum* and *T. viride* on the yield of sugarcane. Comparable impacts utilizing *Trichoderma*-advanced biofertilizers have improved yield in mustard and tomato (Haque et al. 2012), chickpea and pea (Akhter et al. 2015). Immunizing the banana plants with *F. oxysporum* strains increased the yields up to ~20 to ~36% (Waweru et al. 2014). Root inhabitation by *P. indica* brings about a general increment in grain yields (Waller et al. 2005). It has now turned out to be evident that plant flagging pathways prompting improved development by PGPF depend on endogenous controllers or the phytohormones, for example, auxin, ET, CKs, GAs, and ABA. Phytohormone flagging systems produce perfect communications between the organism and host advancing the development of the plants to give better yields (Fig. 7.1).

7.3 Phytohormones

Phytohormones are naturally occurring organic substances that at minimal dosage level controls several stages or phases of plant development and advancement (Costacurta and Vanderleyden 1995). Plant growth regulatory substances are produced by pathogenic and harmonious microflora including fungi over different growth stages of plant. Numerous investigations have helped to identify various key roles played by phytohormones produced by plant associated fungi. Fungal-derived molecules may affect plant processes, either decidedly or contrarily so as to support their attack, supplement take-up, and development. These substances additionally go about as a sign for the organisms themselves to take part in appropriate formative stage and physiological procedures according to the natural conditions.

Fungi are known to deliver a wide range of metabolites, for example, protein effectors, to set up conditions suitable for invading plant tissues, and furthermore to upgrade the plant's immunity or fungal virulence (Kamoun 2007). PGPF additionally produces compounds which are comparable to phytohormones in structure and function, for example, auxins, cytokinins (CKs), gibberellic acids (GAs), ethylene (ET), abscisic corrosive (ABA), jasmonic corrosive (JA), and salicylic corrosive

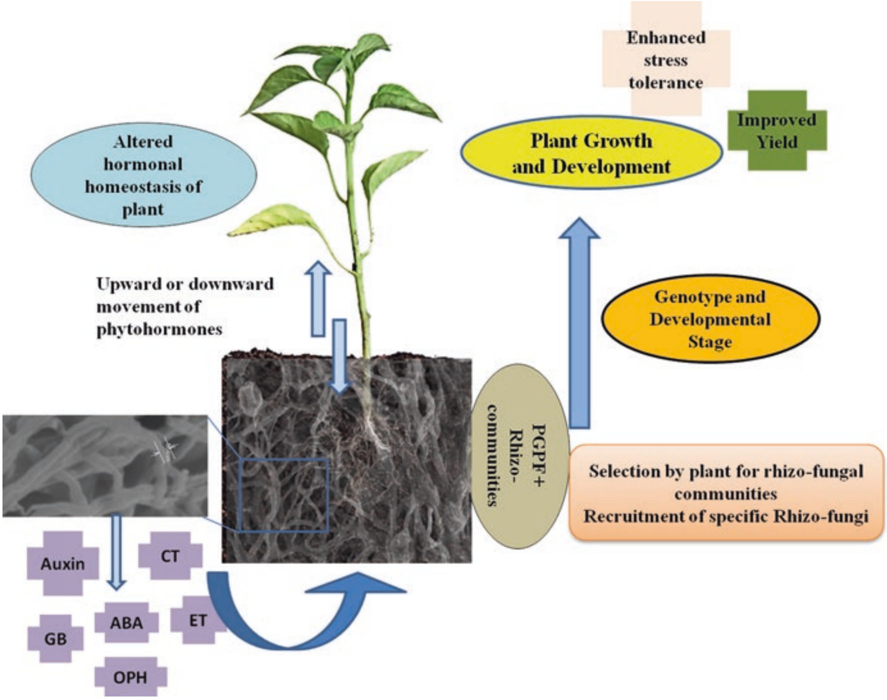

Fig. 7.1 Overview of fungal phytohormones and its impact on plant growth

(SA) (Singh and Yadav 2020; Verma et al. 2017; Yadav 2019; Yadav et al. 2018). These hormones are very much depicted to control plant growth and development and to trigger significant plant signaling during unfavorable environmental conditions including biotic and abiotic stresses (assessed in Spence and Bais 2015). Fungal-derived hormones were first assessed to be engaged with virulence of gall forming pathogens (Denancé et al. 2013). For symbiotic fungi, generation of such hormones is predictable with root changes regularly required in these cooperations (Hirsch et al. 1997). It can be proposed that abscisic acid, gibberellic acid, and ethylene produced by fungi regulate pathogenicity inferring the role of auxin and cytokinins as controllers of virulence (Chanclud and Morel 2016).

Fungi belonging to the genera, *Cercospora* and *Botrytis,* are known to produce ABA in large amounts (Assante et al. 1977). The arrangement of phytohormones additionally is by all accounts a significant factor in the advancement of exceptionally particular mutualistic associations, for example, mycorrhizae. *Dactylorhiza incarnata* (L.) and *Rhizoctonia sp* produce auxin and different phytohormones during symbiotic association and increment in nitrogen fixation can prompt a move from mutualism to pathogenesis (Beyrle et al. 1991). Under non-symbiotic conditions, low levels of IAA and cytokinins have been recorded. Fungal associations can prompt a sharp increase in phytohormone levels; however, high auxin concentrations bring about pathogenicity that can be watched even after cell lysis. Fungal phytohormones are being depicted in the surrounding areas.

7.3.1 Auxins

Auxins are development controllers which exihibit different stimulatory impacts. These compounds are involved with symbiotic associations among plants and fungi. Auxins are indole-derived hormones required during plant organogenesis, for example, cell division, separation, and organ arrangement other than senescence (Asgher et al. 2015; Yadav et al. 2018). Auxins additionally regulate the biotic and abiotic stress reactions in plants (Kazan 2013). Indole acetic acid (IAA), the major endogenous plant auxin, follows tryptophan- (TRP) dependent and TRP-independent pathways that may act through the indole-3-acetamide (IAM) pathway; indole-3-pyruvic acid (IPA) pathway; the tryptamine (TAM) pathway; and the indole-3-acetaldoxime (IAOX) pathway. Auxins synthesis by fungi was first detected in *Rhizopus suinus*. Similar to plants, fungal IAA synthesis occurs via TRP-dependent and TRP-independent pathway involving the IPA or the IAM intermediates. It has been reported that it is synthesized from indole-3-acetamide, in fungal species like *Fusarium* and *C. gloeosporioides* (Tsavkelova et al. 2012). However, in *Ustilago* and *Rhizoctonia,* the precursor is indole-3-pyruvate (Reineke et al. 2008).

Auxins have a pivotal role in regulation of growth and development of the plant. However, this class of phytohormones interacts with other phytohormones in a coordinated or consorted manner in response to many stress conditions. Auxins control shoot and root development in plants. *T. virens* treatment in *Arabidopsis* enhanced plant biomass due to the expression of AUX1, BIG, EIR1, and AXR1 genes which are regulated by IAA (Contreras-Cornejo et al. 2009). *P. indica* induces expression of auxin-related genes in barley (Schäfer et al. 2009) and Chinese cabbage (Lee et al. 2011). A significant decline in IAA during salinity stress induced growth modulations which triggered other phytohormones like ABA (Iqbal and Ashraf 2013) through the membrane bound transcription factor NTM2 (Jung and Park 2011).

According to the reports by Iqbal and Ashraf (2007), a critical moderation of salt stress induced antagonistic impacts in wheat coated with IAA through ionic homeostasis and triggering of synthesis of SA. Salinity restricts the synthesis of IAA; however, the exogenous use of SA demonstrated the effective antagonistic impacts by alleviating the inhibition induced by salinity (Fahad and Bano 2012). These investigations show the presence of conceivable crosstalk among auxin and SA that intercede the resilience reactions in plants.

Auxins are additionally known to promote substantial metal resistance. The harmful effect of lead (Pb) on sunflower plant growth was relieved by adding IAA at lower concentrations, which strengthened the augmentation in root volume, surface zone, and distance crosswise over (Fässler et al. 2010). IAA also promoted the shoot biomass and enhanced lead and zinc resistance in plants, demonstrating the ability of auxins to overhaul the metal phytoextraction. Deviation in shoot to root transport and synthesis of IAA was seen to be fundamental components for limited root development of *Medicago sativa*. This was affirmed in the wake of investigations aiming for the gene expression analysis. However, use of IAA relieved the aluminum stress to some extent by keeping up more prominent articulation of the AUX1 and PIN2 genes as reported by Wang et al. (2016). A beneficial outcome was recorded subsequent to utilizing auxins as preparing sources.

Auxin induces several developmental responses in fungi, such as cellular elongation, hyphal growth, and spore germination. Auxins play a prime role during the plant and fungal symbiotic interactions. Auxins are required for the invasion of mycorrhizal fungi to triggering of nodule formation (Etemadi et al. 2014). IAA stimulates spore germination in *Neurospora crassa* (Nakamura et al. 1978, 1982). In contrast, *in Fusarium oxysporum lycopersici*, a tomato pathogen, auxins reduced the spore germination (Sharaf and Farrag 2004). Auxins are required for the initiation of invasion of mycorrhizal fungi (Etemadi et al. 2014). Invading fungi contains higher content of auxins (Meixner et al. 2005). *Hebeloma cylindrosporum* could invade root tissues of *Pinus pinaster* due to its ability to produce auxins (Laurans et al. 2001). Maor et al. (2004) proposed that *C. gloeosporioides* f. sp. *aeschynomene* produces auxins during the early phases of colonization in the plants.

Fungi also produce auxins to modify the hormonal homeostasis in the plants. As per the reports by Cohen et al. (2002), in pathogenic biotrophs, for example, *F. oxysporum*, an upgraded articulation of biosynthetic genes of auxin, tryptophan-2-monooxygenase and indole-3-acetamide hydrolase activated hyper-assimilation of auxins in *Orobanche*. In lieu of these perceptions, the transient silencing in *Puccinia graminis* f. sp. *tritici* of a gene for auxin biosynthesis was observed in wheat contaminated leaves. The twofold abatement of the transcript prompted a reduction in pustule arrangement. Despite the fact that auxins were not estimated subsequent to silencing, these outcomes propose that auxins resulted in full parasitic pathogenicity. Consequently, auxins appear to assume a job in pathogenicity, and further functional studies with fungal mutants will help to better understand how they participate in virulence (Yin et al. 2014). In addition, infections caused by *P. brassicae* and *Taphrina* species promoted severe organ deformation disrupting the host auxin biosynthesis. Nevertheless, the role of fungal auxins in promoting virulence and tumor formation during similar organ deformation caused by *U. maydis* in corn is still unclear.

Auxins exhibit cross-talks with other phytohormones. The susceptibility of host plant to fungal attack gets enhanced due to auxin-enabled variations in SA levels and signaling. Rice blast fungus, *Magnaporthe oryzae* can regulate plant auxin-dependent transcriptional activation, suggesting control over the plant development or host hormonal balance by the fungal phytohormone. Moreover, *A. brassicicola* infection increased plant IAA levels and led to induction of the JA pathway, suggesting a synergetic interaction between IAA and JA to increase defense responses against necrotrophic pathogens.

Auxins can affect plant defense mechanisms. Obligate symbionts such as mycorrhiza elicit increased auxin levels in plants during association to induce formation of lateral roots that provide more number of fungal penetration sites or receptors (Ludwig-Müller and Güther 2007). However, the enhanced auxin levels do not always guarantee a benefit to host plant. For instance, the overproduction of auxin by mutants of ectomycorrhizal *Hebeloma cylindrosporum* enhances *Pinus pinaster* root tissue invasion but it did not enhance the plant growth. However, in the plant mycoparasitism of *Trichoderma* spp. several auxinic metabolites produced by the fungi induced lateral root development and plant growth (Estrada-Rivera et al. 2019).

7.3.2 Gibberellins

Gibberellins (GA) are terpenoid derived secondary metabolites synthesized from geranyl diphosphate and were first identified from the phytopathogenic fungus *Gibberella fujikuroi (*or *Fusarium fujikuroi*). The *G. fujikuroi* infection causes aberrant elongation in rice plants ("bakanae" or "foolish seedling" disease). Gibberellins exist as acid moieties, gibberellic acids (GAs) which control various physiological processes; germination, cell division, internode elongation (Lange and Lange 2006), and other reproductive events such as flowering, and inhibition of the leaf and fruit senescence (Wang and Irving 2011; Claeys et al. 2014). Therefore, this class of phytohormones play a vital role in seed dormancy, formation of floral organs, and lateral shoot growth (Olszewski et al. 2002) besides stimulation of plant growth and development under various abiotic stress conditions (Ahmad 2010). GA prompts better uptake and parceling of ions inside the plant framework, prompting improved development and support of the plant metabolism in normal and abnormal conditions, by bringing down the degrees of receptive reactive oxygen species (ROS) which adds to better development (Iqbal and Ashraf 2013; Manjili et al. 2012). It is notable that gibberellins enhance leaf zone and incite the development of lateral roots. Metabolically, Gibberellic acid influences protein and RNA synthesis in germinating embryo tissues.

GA biosynthesis pathway in fungi is similar to that of plants (Tudzynski 2005). Endophytes and arbuscular mycorrhizal (AM) fungi can also produce several GAs. Fungal species like *Aspergillus fumigates, Aspergillus flavus*, *A. niger*, *Gibberella fujikuroi*, *Phaeosphaeria sp*., *Neurospora crassa*, *Phaeosphaeria*, *Penicillium corylophilum*, *P. cyclopium*, *Penicillium citrinum*, *Penicillium funiculosum*, *Chrysosporium pseudomerdarium,* and *Scolecobasidium tshawytschae* (Hasan 2002) have been reported to produce GAs. It was reported that *Paecilomyces formosus* LHL10 produced many physiologically active and inactive GAs and IAA that helped to survive the negative impacts of salinity stress on cucumber plants (Khan et al. 2012). GAs have a crucial role in germination of conidia and growth of young hyphae in *N. crassa* (Tomita et al. 1984). During mycorrhizal associations, the GA content is increased in host plant (Barker and Tagu 2000). Super-elongation disease of cassava plants has been reported which is caused by attack of fungal pathogen *Sphaceloma manihoticola* due to overproduction of GA (Lozano 1972). The head smut fungus *S. reilianum,* in sorghum (Matheussen et al. 1991) can cause reduction of plant height because of fungal interference with the synthesis of GA in host plant. *Ustilago maydis* which causes maize smut exhibits enhanced levels of IAA, cytokinins, and gibberellin production in the host plants (Saville and Leong 1992).

Endophytes *Phoma glomerata* and *Penicillium sp.* produce biologically active GAs that can improve the growth and stress responses of host such as cucumber (Rana et al. 2019a, b). The root endophyte *Piriformospora indica* has been reported to enhance the tolerance of rice to abiotic stresses through manipulation of the GA and JA pathway balance by the fungus. In symbiotic arbuscular mycorrhizal fungi, GA signaling is involved in the development of the fungal symbiosis through DELLA proteins (key repressors of GA pathway in host), that act as positive regulators for arbuscule formation (Fonseca et al. 2017). Under saline conditions, improved water uptake by plants and diminished stomata opening were observed after treating the tomato plants by GA (Maggio et al. 2010). Khan et al. (2004) have detailed that increased yield, leaf area, and uptake of major elements like NPK in tomato occurred because of exogenous supply of GAs. Further, the water potential in plants get expanded in presence of salt stress (Alonso-Ramírez et al. 2009) and GA also seem to help in upkeep of tissue water content (Ahmad 2010). Such impacts have additionally been seen in wheat (Manjili et al. 2012) and maize (Tuna et al. 2008).

7.3.3 Cytokinins

Cytokinins (CKs) are the important phytohormones involved in several plant developmental processes, such as maintenance of accumulation and differentiation of cells, inhibition of premature leaf senescence besides having role in source to sink distribution of nutrients (Peleg et al. 2011). CKs are derived from adenosine phosphates (ATP/ADP/AMP) or from the degradation of t-RNA pathway that exist in two forms, *viz.* free active forms and the inactive conjugated forms that are present as translocation or storage forms in the xylem sap. The key enzyme isopentenyl transferase (IPT) acts on ATP/ADP/AMP to form CK. Otherwise, aromatic CKs are synthesized by modification and catabolism of specific t-RNA molecules by t-RNA isopentenyl transferases (t-RNA-IPT). Sakakibara (2006) has assessed that exchange of the isopentenyl chain from the methylerythritol phosphate (MEP) takes place on the adenosine phosphate, prompting the arrangement of the ribosylated phosphorylated CK structures. The end product from the both pathways is then activated by the LONELY GUY (LOG) which is the cytokinin activating enzyme that coverts CK to free active forms, *trans*-zeatin, and isopentenyladenine (Peleg and Blumwald 2011).

Decreased cytokinin levels bring about ABA-initiated stomatal closure and carbon uptake and assimilation. Mohapatra et al. (2011) exhibited that cytokinins improve grain filling and grant resistance to plant developed under stressed conditions. The application of kinetin to chickpea invigorated plant development and advancement under salt stress (Bozcuk 1981), and in another report, kinetin mitigated cadmium stress in eggplant by improving its cell antioxidant potential (Singh and Prasad 2014). Same has been exhibited in transgenic cassava developed under dry spell conditions (Zhang et al. 2010).

Fungi can likewise deliver isoprenoid and aromatic cytokinins indistinguishable from the plant hormones. A huge assorted variety of fungal species, regardless of being symbiotic, pathogenic, or saprophytic been represented to synthesize the CKs (Cooper and Ashby 1998). Representative *IPT* and *LOG* genes are accessible in various fungal genomes (Chanclud et al. 2016). A biotrophic pathogen *Claviceps purpurea* has advanced a solitary enzyme with both the IPT and LOG capacities required for *de novo* CK biosynthesis.

CK assumes to play role in fungal physiological processes like hyphal advancement and uptake of nutrients (LeJohn and Stevenson 1973), in vitro spreading of ectomycorrhizal mycelia (Barker and Tagu 2000), hyphal layer consistency, and ion and water transport (Gogala 1991). In *Suillus variegatus,* CKs can alter the concentration of Na, P, K, and Ca in the mycelia (Gogala 1991). Restraint of the mycelial development of *Amanita muscaria* brought about by aluminum toxicity has been seen as fundamentally correlated with a diminishing in the CK level (Kovac and Zel 1995). Lee (1961) reported that CKs likewise influence sexual proliferation in the ascomycete *N. crassa*, recommending a job in correspondence inside fungal growths.

Mycorrhizal-plant interactions are associated with the CK acquisition in root and shoot of the host (Allen et al. 1980). Further, it contributes towards nutrients absorption and increased photosynthesis in the host leaves (Drüge and Schonbeck 1993). CK-mediated pathogenesis induces the photosynthetically active zone, tumor gall, or “green island” formation in the host (Choi et al. 2011) and modifies host growth dynamics by creating a new source-sink for the nutrients. *U. maydis* and *Claviceps purpurea* produce CKs in infected host areas and CK accumulation correlates with *U. maydis* virulence. An increase in CK concentration in wheat and maize leaves was observed due to infection of *Pyrenophora teres* and *Dreschslera maydis*, respectively (Debi et al. 2005). The metabolites also get accumulated near infective areas (Angra-Sharma and Sharma 1999). CKs play role in oxidative stress tolerance in rice blast fungus *Magnaporthe oryzae* (Chanclud et al. 2016). It is possible because of the presence of the conserved gene, t-RNA-IPT gene in *M. oryzae.* The same results were also demonstrated in gall forming bacteria, *Agrobacterium tumefaciens* which transfers an *IPT* gene into the host genome and modulates the plant CK synthesis. The plant CK levels can also be regulated by production of fungal β-glucosidase cleaving zeatin-O-glucoside [(OG)Z], which is present in many biotrophic and hemibiotrophic fungi that accumulates and releases the stored conjugated CKs at the infection site.

7.3.4 Abscisic Acid

Abscisic acid (ABA) has been considered as the key hormone for plant abiotic stress responses and its synthesis and accumulation increase in response to stress conditions in plant (Peleg and Blumwald 2011). It acts as an inhibitor of growth and RNA synthesis, induces dormancy in plants by acting combative to the GA pathway (Debeaujon and Koornneef 2000), improves the adaptation in stress and stomata closure contributing to plant tolerance to the drought conditions (Beardsell and Cohen 1975), and promotes aging and senescence (Norman et al. 1983). It acts as an anti-transpirant by inducing stomatal closure and reducing the expansion of canopy (Wilkinson and Davies 2002). In response to water deficit, ABA inhibits the K^+ ions uptake and prevents the increase of turgor pressure in guard cells; therefore, the stomata are maintained in closed state to prevent water loss (Pegg 1981). ABA also alters the defense responses of the plants like SAR (systemic acquired resistance) and ISR (induced systemic resistance) through antagonistic action to defense signaling molecules such as SA and ET. Under abiotic stress, the expression of stress responsive genes directed by ABA are instigated that prompts better evocation of resilience reactions (Sah et al. 2016). Moreover, ABA likewise controls root development in the soil to intercede optimal water and nutrient uptake during dry season conditions by regulation of the reinforcement of the cellular framework and aggregation of the good osmolytes to sustain the relative water level (Cutler et al. 2010). Notwithstanding, a sudden increment in ABA fixations brings about hindered development (Asgher et al. 2015).

It belongs to a group of naturally occurring sesquiterpenoid, the key phytohormones which are involved in growth regulation (Wilkinson et al. 2012). ABA is an isoprenoid and in plants, is synthesized from isopentenyl phosphate (IPP) either by direct or indirect pathways, where mevalonate (MVA) or methylerythritol phosphate (MEP) is the corresponding source of IPP, respectively (Nambara and Marion-Poll 2005). Other precursors of ABA include geranyl pyrophosphate and farnesyl pyrophosphate. Its chemical structure is similar to gibberellic acid, but both induce opposite effects on plants. Indirect pathway for biosynthesis is plastid specific and is predominant, whereas the cytosolic MVA pathway is the direct one which is auxiliary. *Physcomitrella paten* is the most ancient land plant with the complete genome sequenced that retains this indirect plastid specific ABA synthesis pathway.

All types (saprophytic, symbiotic, and pathogenic) of fungi are capable of synthesizing ABA through the mevalonate pathway and involve production of different precursors (Morrison et al. 2015). ABA producing fungi have a role in phytopathogenesis. Norman et al. (1983) reported the first fungal synthesis of ABA in *Cercospora rosicola*. Other fungal species include *Alternaria brassicae*, *Botrytis cinerea*, C. *cruenta*, *Fusarium culmorum,* and other pathogens. In the case of *B. cinerea*, the *BcABA14* genes are responsible for ABA biosynthesis. Knocking out of *ABA4 gene*, homologous of the *B. cinerea*, resulted in reduced biosynthesis, by twofold, in *M. oryzae* (Spence et al. 2015). The pathogenicity of the fungal ABA involves stimulation of fungal ABA biosynthesis by the host; release of ABA or its precursor by the fungus; stimulation of biosynthesis of plant ABA by the fungus; and inhibition of its metabolism by the fungus (Kettner and Dorffling 1995). Ward et al. (1989) proposed that ABA may influence the interpretation of plant defense genes. *Glomus* sp., a arbuscular mycorrhizal (AM) fungus likewise delivers ABA, and its concentration in xylem sap is distinctive among mycorrhizal and non-mycorrhizal plants (Esch et al. 1994). Fungal ABA unequivocally restrains collection of the protective phytoalexins, lubimin, and rishitin, in potato tubers upon fungal infection (Li and Heath 1990), for example, on infection by the *Phytophthora infestans* and *Cladosporium cucumerinum* in tubers.

In several plant pathogen associations, ABA influences resistance to plant disease either positively or negatively (Xu et al. 2013). ABA concentration in infected plant is triggered by the pathogenic fungal growth. Kettner and Dorffling (1995) demonstrated that high ABA producing strain produces more ABA than the counter strain in tomato plants. Correspondingly, ABA was amassed at the initial stages of *U. maydis* infection and can be correlated to the pathogenicity of the fungus (Morrison et al. 2015). In *B. cinerea* and *U. maydis*, the level of ABA present in the fungus correlates with infection levels. In addition, ABA contributes to susceptibility to *B. cinerea* and *Plectosphaerella cucumerina* by suppressing defense responses in plants. In the coming years, we expect the elucidation of the molecular mechanisms sustaining the hormonal relations involving fungal produced ABA and plant defenses.

ABA application has been proposed as an effective tool for stress upliftment as it can provide tolerance to the stress conditions like salinity, frost, cold, and drought (Gomez et al. 2002; Nayyar et al. 2005; Bano et al. 2012; Li et al. 2014). In wheat, application of ABA improved the antioxidant system and relative water level in response to the oxidative damage caused by drought (Bano et al. 2012). During drought conditions in rice, ABA application can protect the photosynthetic activity, by up-regulating the expression of the specific set of genes like *OsPsbD1*, *OsPsbD2*, *OsNCED2*, *OsNCED3*, *OsNCED4, and OsNCED5* involved in induction of photosystem II. Along with the ethylene, ABA maintains the shoot and root growth in maize (Spollen et al. 2000). In potato, *Solanum tuberosum*, ABA application improved the stress tolerance by significantly increasing the antioxidant enzyme peroxidase activity (Mora-Herrera and Lopez-Delgado 2007). Improved nitric oxide synthesis was reported due to ABA application, which resulted in increased plant growth, nutrient uptake, and nitrogen fixation under salt stress (Khadri et al. 2006). In citrus plants, exogenous application of ABA inhibited accumulation of sodium and chloride (Cabot et al. 2009).

In any case, exogenous ABA could likewise build the susceptibility of the host to a specific pathogen, for instance, it enhances the susceptibility of a resistant cultivar of barley to *Erysiphe graminis* (Edwards 1983) and tobacco to *Peronospora tabacina* (Salt et al. 1986). In *Ceratocystis fimbriata*, a pathogen of sweet potato and rubber trees, exogenous application of ABA advanced the fungal development. In *M. oryzae*, ABA builds the germination and development of appressoria for plant cell wall lysis to permit intrusion (Spence and Bais 2015) and furthermore represses the

SA-dependent defense response (Jiang et al. 2010). ABA influences JA biosynthesis and the initiation of barriers against oomycete *Pythium irregulare*.

7.3.5 Ethylene

Ethylene is a vaporous compound initially detected during maturation of fruits (Bleecker and Kende 2000). It is also known to be produced as the first phytohormone in response to injury, mechanical stress, and disease like symptoms in plants, e.g., tissue swelling, chlorosis, and bending of plants (Pierik et al. 2006). Ethylene regulates several plant developmental and environmental as well as pathogen responses. It is produced as an effective growth regulator at low dosage (Fukuda et al. 1993). It also invigorates leaf abscission, fall, and senescence. It displays impact on cell wall degrading compounds, the cellulases, ~ (1,3) glucanases, and catalysts which impact the degrees of hydroxylproline rich proteins thereby directly influencing the integrity of cell walls. It additionally advances germination, flowering while inhibits root and shoot growth (Bleecker and Kende 2000). In *Arabidopsis*, along with jasmonic acids, it prompts guard against necrotrophic pathogens (De Vleesschauwer et al. 2014). As opposed to being the chief controller, it is considered to adjust the resistance pathways, including those directed by jasmonic and salicylic acid.

Methionine acts as the sole precursor for ethylene biosynthesis in plants and microbes (Adams and Yang 1979). Maize rhizospheric bacteria and fungi have been reported to be capable of deriving ethylene from methionine (Arshad and Frankenberger 1991). In plants and fungi, methionine is transformed into L-aminocyclopropane1carboxylic acid (ACC) via ACC-synthase enzymes to synthesize the ethylene (Esser et al. 2002). Several pathways exist in fungi for its production depending on the growth medium (Esser et al. 2002; Strzelczyk et al. 1994). Fungi can likewise deliver ethylene from 2-keto-4-methylthiobutyric acid, synthesized from methionine or from 2-oxoglutarate (Van Bockhaven et al. 2015a). It was first reported to be produced by *Penicillium digitatum* by Dasilva et al. (1974). Different fungal groups whether in vegetative or resting forms and different lifestyles can produce this hormone, for example, *B. cinerea* (parasitic) and *F. oxysporum* (symbiotic) (Arshad and Frankenberger 1991). Ethylene and certain precursors like ethephon and ACC affect the germination of spore and hyphal development of the pathogenic fungi (*Alternaria alternata* and *B. cinerea*), and harmonious parasites (*Gigaspora ramisporophora* and *G. mosseae*) (Chague et al. 2006) suggesting that fungi might be able to sense these compounds. Higher concentration of this hormone results in the retarded growth (Ishii et al. 1996). Along these lines, ethylene seems to accept a noteworthy job in signal transduction of plant pathogen correspondence. During plant-contagious pathogen communications, the hormone level shows increased amounts close to the beginning of the association (Broekaert et al. 2006). Plant tissues contaminated by parasites show extended degrees of ethylene because of harming achieved by invasion and infectious assault.

Ethylene induces conidial germination, hyphal extension, and different appressoria course of action in *Colletotrichum*, thus enabling fungi to infect and harmonize time to fit with development stage of the host plant (Kolattukudy et al. 1995). The incitement of ageing and senescence in plants caused by ethylene may affect the susceptibility of plants to fungal intrusions. In this way, ethylene appears to assume a significant control in signal transduction of plant pathogen communication. During plant–fungal pathogen interactions, the hormone level shows increments toward the start of the interaction (Broekaert et al. 2006). Arshad and Frankenberger (1991) have reported that fungal soil isolates like *Acremonium falciforme* function as dynamic producers of ET. Plant tissues infected by fungi show expanded degrees of ethylene as a result of tissue injury brought about by infiltration and contagious attack.

Many reports for the fungal pathogen that acts by increasing the ethylene concentration are available. For example, in soybean, fungal pathogen *Phytophthora megasperma* f. sp. *glycinea* is known to enhance the biosynthesis of ET (Reinhardt et al. 1991) at very early stage after the infection that induces appearance of aging symptoms of plant disease like foliar chlorosis, petiolar fall, tissue distortion, foliar abscission, and necrosis (Pegg 1984). Similarly, *Verticillium* wilt in hops is associated with leaf drop, epinasty, and premature senescence, symptoms attributed to increased levels of ethylene in plants (Isaac 1992). Pegg and Cronshaw (1976) described the alleviation of symptoms of *V. alboatrum* in tomato caused by ethylene. Appressoria in tomato is caused due to *Colletotrichum* sp. pathogen (Flaishman and Kolattukudy 1994) as a result of ethylene production during the fruit ripening.

It is likewise seen that the rise in ethylene levels after *Verticillium* infection may actuate higher disease resistance in infected plants by following up of other metabolic pathways. Similarly, the effects of *Sclerotinia* root rot (Isaac 1992) and bitter rot in apples (Lockhart et al. 1968) get lowered and the phytoalexin-pisatin synthesis is increased in pea as resistance mechanism against pathogen (Chalutz and Strahmann 1969) that improves the defence response against pathogen. Production of ethylene by necrotrophic fungal pathogen, *Cochliobolus miyabeanus* increases susceptibility in rice, suggesting a virulent role of the fungal ethylene. However, inhibitor of fungal ET biosynthesis (2,2bipyridyl) abolished fungal ET production and thus exhibited lack of virulence (Van Bockhaven et al. 2015b). ET signaling impacts plant development by influencing parasitic colonization on the roots. DNA microarray-based gene expression analysis uncovered a differential enlistment of genes identified with ET blend and motioning in grain roots colonized by endophytic fungus *P. indica* (Schäfer et al. 2009).

On account of mycorrhiza, the role of ET depends on the type of symbiotic interaction. It was proposed that a restraint of the ethylene pathway and thus production by AM fungi is required to permit the foundation of advantageous interaction (Zsogon et al. 2008). To support this, another report on secretion of SP7 protein (secreted protein 7) by AM fungus *Glomus intraradices* has been documented. The SP7 protein interferes with the ethylene response factor to suppress signaling (Kloppholz et al. 2011). Truffles *Tuber borchii* and *Tuber melanosporum* produce ethylene to induce morphological alterations in the host root (Splivallo et al. 2009) depicting the role of ET in fungal virulence.

More recently, freshwater green algae *Spirogyra pratensis* was reported to possess an ethylene sensing system similar to land plants. These reports suggest that fungi could have been adapted a mechanism that could sense the ethylene produced by plant to establish the specialized structures for penetration and infection (Van de Poel et al. 2016). However, omics research should be carried out to explore, how these fungi perceive the ethylene signals, the mechanism behind fungal ethylene production should be identified and the its role in the agricultural practices should be discerned.

7.3.6 Other Small Phenolic and Lipid-Derivative Phytohormones

Certain small molecular weight phenol and other lipid-derivative molecules are synthesized in the plants in response to an array of biotic and abiotic stresses. Among these, salicylic acid (2-hydroxy benzoic acid, acronymed SA), a low molecular weight phenolic compound, involved in endogenous signaling mediates defense responses in plants against bio and hemibiotropic pathogens (Zhang and Xiao 2015), occurs in basal concentrations that may vary from low to hundred fold among different plant species (Raskin 1992). However, SA has also been explored to serve roles in several processes other than the elicitation of defense response during pathogen attack and stress conditions. These processes involve general growth and development of plants such as negative regulation of seed germination, establishment of seedling, nodulation in legumes, and fruit yield in fruit crops besides physiological events including flowering, leaf morphogenesis, elicitation of enzymes involved in cell wall relaxation and cell expansion, cellular respiration, and expression of senescence-related genes (Dempsey and Klessig 2017). Further, SA can also modulate both production and signaling of other plant hormones primarily including auxin, ethylene, and jasmonates (Yusuf et al. 2013).

Plants also produce a range of lipid-derivative phytohormones in response to stress conditions including brassinosteroids, strigolactones, and oxylipins such as jasmonates. Jasmonic acid (an cyclopentanone oxylipin) and its derivatives, jasmonates, are required to accomplish several physiological functions in plants such as breakage of dormancy followed by seed germination, pigment formation, fruit ripening, development of flower and even seed, nectar production in flowers, elicitation for synthesis of antioxidant enzymes, activation of aging and programmed plant death-senescence, indication of wounds and attack by herbivores, induction of systemic resistance in plant for defense against environmental stresses, initiation of synthesis of secondary metabolites in plants and many other (Tsavkelova et al. 2006; Egamberdieva et al. 2017; Leach et al. 2017). Further, jasmonates are also facilitate colonization and invasion of plant roots by symbiotic diazotrophs including different types of rhizobia through activated expression of *nod* genes in *Bradyrhizobium japonicum* and *Rhizobium leguminosarum* (Rosas et al. 1998).

Salicylic acid is biosynthesized in plant tissues through shikimate biosynthetic pathway dichotomized as two pathways, isochorismate and phenylalanine ammonia-lyase pathway (Yusuf et al. 2013). Therefore, it involves synthesis of two intermediary compounds isochorismate and chorismate from shikimate. While reports on biosynthesis pathway for SA production by fungi are not known till date though SA synthesis by two fungal genera, *Moniliophthora perniciosa* (Chaves and Gianfagna 2006; Kilaru et al. 2007) and *Oudemansiella mucida* (Zouchová et al. 1982) have been documented. Ismail et al. (2019) have reported synthesis of salicylic acid (95 µg mL^{-1}) from culture filtrates of an endophytic fungus, *Aspergillus flavus* isolated from wild *Euphorbia indica* plant. The other derivatives of SA such as 6-methyl salicylic acid which are precursors for the synthesis of fungal toxins, namely patulin are also produced (Fonseca et al. 2017).

In plants, jasmonates are produced in the chloroplast membrane from alpha-linolenic acid via lipid peroxidation involving the action of phospholipases (Ahmad et al. 2016). Several reports in 1970–1971 and 1991–1993 have documented that jasmonic acid, methyl jasmonic acid, iso-jasmonic acid, and other derivatives are produced in culture filtrates of several fungal genera particularly pathogenic fungi such as *Fusarium oxysporum* (Miersch et al. 1999), *Lasiodiplodia theobromae* (Dhandhukia and Thakkar 2007, 2008; Andolfi et al. 2014; Eng et al. 2016), and *Gibberella fujikuroi* (Miersch et al. 1993), polyphyletic endophytic fungi (Nicoletti and Fiorentino 2015), and basidiomycetes fungal genera *Collybia*, *Coprinus*, *Mycena,* and *Trametes versicolor* (Eng et al. 2018). The bio-catalytic enzymes of the octadecanoid pathway are involved in the synthesis of jasmonic acid and its derivatives from α-linolenic acid (Miersch et al. 1999; Eng et al. 2018). In fungi, a lipoxygenase enzyme system produces as well as accumulates jasmonates similar to plant system (Fonseca et al. 2017).

Jasmonates or their derivatives are required by the necrotrophic fungi to weaken the plant host defense responses during infection or may facilitate increased penetration of fungal hyphae in the plant tissue (Fonseca et al. 2017). Further, fungal JA-derivatives may also function as reserve pool of inactive JA that can be converted to active conformation as and when the fungi desires to induce death of host plant tissues followed by necrosis (Andolfi et al. 2014; Chini et al. 2018). Therefore, the researchers are now skeptical regarding the exact role of jasmonates in plant defense response cascades (Yan and Xie 2015). Physiologically, jasmonates exhibit a similar negative impact on the growth of fungi if applied epitomized as inhibition of the processes of spore germination and mycelial growth (Moosa et al. 2019). The relative significance of synthesis of salicylic acid by fungi and its role in their growth and development are not known till now. However, exogenous application of salicylic acid can inhibit spore germination and hyphal growth of several fungi (Panahirad et al. 2014; Abass 2017; Moosa et al. 2019). Contrarily, reports on supplementation of media with SA (300 µM) documented 50-fold increase in production of secondary metabolite, taxol, in mycelia of endophytic fungus *Pestalotiopsis microspora* (Subban et al. 2019). Similar but lower enhancements in taxol producing ability of yew tree endophytic fungal genera of *Paraconiothyrium variabile* and *Epicoccum nigrum* (Somjaipeng et al. 2016). Under natural conditions, the relevance of fungal production of JA and/or SA may be anticipated to help in manipulation of the host plant hormonal pathways during various stages of fungal pathogen invasion (Kilaru et al. 2007) or by exhibiting a direct positive effect on enhancing the fungal growth under lab conditions (Chaves and Gianfagna 2006; Chanclud and Morel 2016).

Application of fungal cell free extracts containing high amounts of salicylic and/or jasmonic acid as seed priming agent, soil/sand dressing, or foliar spray can improve the applied plants to withstand the diverse stress conditions such as thermal or high temperature, drought, and pathogen attack stress. As methyl jasmonate and salicylic acid are long-distance inducers of systemic acquired resistance (SAR), exogenously applied JA/SA can travel via apoplast of the phloem tissue (Maruri-López et al. 2019). Ismail et al. (2019) have observed improved tolerance to thermal stress (incubation temperature of 40°C) in seedlings of soybean and sunflower which demonstrated low levels of stress induced compounds or products by seed inoculation with IAA and SA producing *Aspergillus flavus* fungus. However, a synergistic positive effect observed as improved photosynthesis rate, chlorophyll content and biomass of *Capsicum annum* occurred on application of salicylic acid (10^{-6} M) along with inoculation of an endophytic fungus, *Penicillium resedanum* LK6, in response to PEG (15%) induced osmotic stress (Khan et al. 2013).

7.4 Conclusion and Future Prospects

Fungi are multicellular eukaryotes having versatile physiological and metabolic characteristics which aid these microbes to undergo diverse type of interactions with other uni- to multicellular organisms (Qi et al. 2018; Han and Kahmann 2019; Kalia and Singh 2019). Fungi can synthesize and secrete diverse types of signal compounds, phytohormones, or phytohormone like substances (analogues or derivatives) which help them to manipulate the host plant physiology to beneficiate fungal virulence (invasion across plants tissues) or for establishment of a symbiotic/mutualistic interaction with the host (Leach et al. 2017; Han and Kahmann 2019). However, the role, fate, and dynamics of mechanisms of action of the fungal phytohormones (FPHs) on the fungus synthesizing/secreting these FPHs and on other non-secreting fungi in soil, on and in the plant tissues is yet not understood (Fonseca et al. 2017). Enormous published reports have documented the importance and benefits of seed/foliar/root application of pre-formed solutions of phytohormones (Ahmad et al. 2016; Egamberdieva et al. 2017). As the plant–microbe interactions involve microbial secretome affecting host activities and vice versa under certain specific set of conditions, the FPH studies find better relevance considering the aberrant and extreme climate change patterns and may help in elucidation of the role and the quantum of impact of microbial generated phytohormones on microbes and the host plants. The plant probiotic, growth promoting, and even protecting bio-agents may impart tolerance to host plants or make it stress-ready through diverse pathways. One of the mechanism is through optimization of either balanced secretion of the phytohormones or these microbes may impart benefits to the host plant by modulating the phytohormones, their derivatives—the phytohormone mimics and the receptors for perception and triggering of the signal transduction events to address the biochemical and physiological changes occurring due to a variety of abiotic and biotic stress conditions (Busby et al. 2017; Leach et al. 2017). These experimental data can then be evaluated under field conditions on test crop plants to validate the protective or eliciting potentials.

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Chapter 8
Phytohormones Producing Fungal Communities: Metabolic Engineering for Abiotic Stress Tolerance in Crops

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8.1 Introduction

Agriculture forms the backbone of Indian sub-continent and provides food to millions across the globe. With the rising statistics of population, sustainable agriculture aims to increase agricultural production through employing better agricultural practices and improvement of quality of food products. However, agricultural productivity has been seriously affected by environmentally induced stress conditions, leading to approx. 50% losses in agricultural output, subject to varying climatic conditions (Jeyakumar, World Development Report, 2010). Additionally, the phenomena of global warming and rise in temperature worldwide have direct consequences on the quality and crop yield (Xu 2016; Helaly 2017). Several strategies, namely tissue culture methods, plant breeding, genetic engineering, etc. have been employed to enhance crop yield and productivity in adverse environmental conditions (Helaly 2017) (Fig. 8.1).

Plants are dynamic systems which are exposed to environmental stresses (abiotic and biotic), which threatens their growth and productivity (Suman et al. 2016; Yadav et al. 2016). Plants have evolved adaptive mechanisms to deal with such environmental challenges which include molecular, cellular, and physiological responses, respectively (Rejeb et al. 2014). Therefore, an understanding of how the plants respond to such stresses and their defense mechanisms would considerably reduce agricultural losses. The exposure of plants to biotic stress (together with pathogen attack, namely bacteria, viruses, and fungi) creates excessive pressure on plant survival (Mordecai 2011) while stress induced by abiotic factors namely heat, cold, metal toxicity, drought, salinity, etc. hampers growth and severe agricultural losses (Wang et al. 2003). There are several biotic agents which infect the plants and cause various plant diseases through mechanisms, namely viruses cause local lesions, plant chlorosis, stunted growth, insects damage the plants through feeding on the plants, parasitic fungi produce toxins and kill host, among other pathogenic mechanisms (Gimenez et al. 2018). There are several plant signaling pathways which

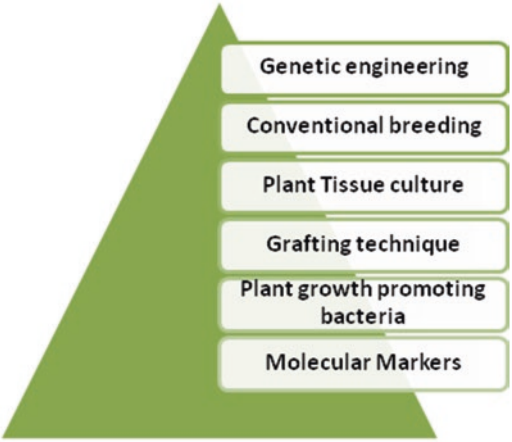

Fig. 8.1 Scientific methods and techniques for introducing abiotic stress tolerance in agricultural crops

operate in both biotic and abiotic stress mechanisms and include the function of transcription factors, phytohormones, and reactive oxygen species, respectively (Rejeb et al. 2014). During the course of evolution, plants have evolved adaptive mechanisms to survive against such environmental challenges. In fact, studies have suggested that the plant resistance to abiotic and biotic stresses is induced by such pressure; however, the susceptibility to different stresses may vary according to different plant species (Suzuki et al. 2014).

While dealing with environmental challenges, plants have evolved defense mechanism to counteract the adverse effects, production of phytohormones being a prominent one. Plant hormones or phytohormones, namely auxins, cytokinins, abscisic acid, jasmonic acid, ethylene, etc. play an important role in plant growth and abiotic stress tolerance besides mutualistic association with various fungal species (Rana et al. 2019a, b; Verma et al. 2017; Yadav et al. 2018a; Tian et al. 2017; Inahashi et al. 2018; Mathur et al. 2018). Several microbial associations (namely bacterial and fungal) colonize the roots of the plants and confer multiple benefits, namely plant growth and development, tolerance to abiotic stresses (drought, high/low temperature, salinity) and biotic stresses (nematodes and pathogens), respectively (Kour et al. 2019b, 2020b; Verma et al. 2017). Production of phytohormones by plants and their interplay contributes to various functions, namely plant stress tolerance is conferred by systemic response through abscisic acid, jasmonic acid among others while plant growth is linked to production of auxins, gibberellins, etc. (Gill et al. 2016).

Metabolic engineering of crops to produce better varieties with abiotic stress tolerance, is gaining momentum (Kour et al. 2019c; Yadav et al. 2019). In the present scenario, phytohormones and their interplay in conferring stress tolerance to transgenic crops has been extensively investigated and explored by researchers all over the world. The chapter provides a comprehensive analysis of fungal species producing phytohormones and their signaling mechanisms. Moreover, the chapter further discusses the major contributions of these plant–microbe associations in plant growth promotion and in conferring abiotic stress tolerance in plants. Highlighting the significance of genetic engineering of crops for improvement and production of better plant varieties as well as the associated challenges with crop production, are discussed.

8.2 Plant Response to Biotic and Abiotic Stress

8.2.1 Biotic Stress Factors

Biotic stress is caused by living organism like bacteria, virus, fungi, insects, and even other plants. When a plant is damaged by the living organism, it causes stress to the plant, as a result, it affects the growth and regulation of the life cycle. The biotic stress affecting plants depends on the climatic responses like its habitat or how it is able to tolerate the particular stress. Biotic stress is a broad term and it projects several challenges, such as the greater difficulty to understand the complex biotic stress mechanisms in an experimental context (Fig. 8.2).

8.2.1.1 Causative Factors of Biotic Stresses

Insects

It is observed in nature that the insects chew the plant leaves, as a result it reduces the leaf area of the plants and some insects chew roots which hampers the absorption of water intake into the plants, adversely affecting the photosynthetic process in the plant.

Virus and Fungi

The biotic stresses affect photosynthesis, reduction in the rate of photosynthesis per leaf area infected by the virus. Moreover, the water transport and photosynthesis is hampered by inducing stomatal closure, caused by vascular-wilt fungi (Balachandran et al. 1997).

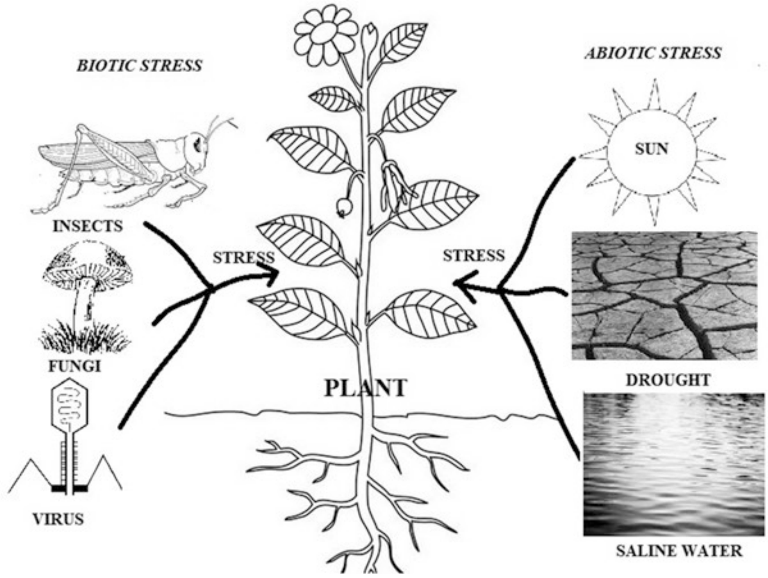

Fig. 8.2 Diagrammatic representation of the various causes of biotic and abiotic stresses in plants

8.2.1.2 Plant Response to Biotic Stress

Since the origin of life, evolutionary studies have shown that plants co-evolved with parasites. This co-evolutionary process has induced several defense mechanisms/adaptations to plants against pathogens. This defense system developed into the plant includes physical and chemical adaptations, this response is only activated at the time of pathogen attack. For example, a plant utilizes high metal ion concentration from soil to reduce stress like situation; by these protective physiological pathways severe metal toxicity safeguard metal ion distribution throughout the plant. These defense mechanisms are avoidable unless it is beneficial to the plants. As the same time, pathogens and pest become resistant to this mechanism. To understand biotic stress resistance, we should study range of scale, from the molecular to the community level (Roberts 2013).

Plants Responses Towards Insects

The defense mechanism of the plant towards the insects is well elucidated. Since millions of year ago plant has evolved defense mechanisms towards the insects through their saliva. The saliva of the insect's triggers the responses in the plants that are known as elicitors or herbivore-associated molecular patterns (HAMPs) (Lincoln et al. 2015). HAMPs trigger the defense mechanism into the plants and minimize the harm to the other parts of the plant. Plant have a defense mechanism by using salicylic acid pathway, which is also used in infection stress, when defending itself against phloem feeders. Plants perform many defense functions towards the insect's gut and digestive system. This whole function is performed by the help of proteinase inhibitor action. This proteinase inhibitor inhibits the protein digestion of the insect; it binds to the active site of the protein such as trypsin and chymotrypsin. This whole mechanism is performed against insects in biotic stress.

Calcium ions have an important role in plants defense response. The fatty acid amides are present in insect saliva, these amides induce the mitogen-activated protein kinases (MAPKs). When these genes activated, they activate the jasmonic acid pathway. The jasmonic acid pathway is also known as the Octadecanoid pathway. This pathway helps to activate defense genes in plants. As a result there is production of jasmonic acid, a phytohormone through this pathway.

Plants Responses Towards Pathogens

Plants have a special defense against the microbes and involves the detection of microorganism-associated molecular patterns (MAMPs) (Spoel and Dong 2012). The common MAMPs include nucleic acid which detects specialized pattern recognition receptors of virus and bacterial membrane (Boller and He 2009). Another detection method includes the plant immune receptors to detect molecules released into the plant cell by pathogens. Plants detect those signals in infected cell which induces an effector-triggered immunity (ETI), it is a type-f innate immunity (Tsuda and Katagiri 2010).

The pattern recognition immunity (PTI) and effector-triggered immunity (ETI) result in a multiple defense mechanism which includes the chemical signaling compound. The plant increases the salicylic acid (SA) production which is induced by pathogenic infection. The increase in SA results into the activation of the pathogenesis related (PR) genes which make plant resistant towards the biotrophic and hemibiotrophic pathogens. Similarly, there is increase in jasmonic acid near the pathogen infected area, which leads to the defense mechanism by jasmonate ZIM domains (JAZ) protein and increase JA defense genes.

8.2.2 Abiotic Stress Affecting Plants

The stress arising by the non-living factors to a living organism is called abiotic stress. The abiotic stress depends upon the conditions which causes unfavorable effect on the organism. Abiotic stress is the natural process of every ecosystem, and it depends on the various conditions occurring in the environment. Abiotic stress is a problem which is concern for the growth and productivity of plants. An abiotic stress is responsible for huge losses and induce stress on the plants, such as drought, salinity, and extreme temperatures (Yadav et al. 2020a, b). Photosynthesis in plants is one of the process greatly affected by abiotic stress in plants. The stress reduces the photosynthesis which will affect the capacity of plants directly connected with reduction of yield. Thus, the plant responses and adaptation mechanims to save their photosynthesis can help in developing new crop plants with more robust photosynthetic machinery capacity for high yields and even under stressed environments.

8.2.2.1 Plant Response Towards Abiotic Stress

Plant Response Towards Drought

Drought is the major factor that effects crop growth and yield all around the world (Kour et al. 2019c, 2020a). Limited water available for crop evokes adaptive physiological responses regulated by changes in expression of numerous stress-responsible genes (Yang et al. 2016). There are some groups of transcription factors (TFs) of protein that binds to the specific regulatory DNA elements which are present as gene promoters of initiation sites, repressing or activating target gene expression. In recent years, researches have shown that temporal and spatial modulation of stress (which is related to TFs) provides an efficient way for plants to deal with unfavorable growth conditions. TFs showing a drought reaction was recognized and characterized in a wide range of crops. Over-expression of several target genes shows stress-responsive TFs leading to improved survival rate under water limitation in plants (Nuruzzaman et al. 2010).

Plant Response Towards Salinity

Salinity stress gives rises to two types of stress situations in plants: (1) osmotic stress and (2) ionic imbalance (Hossain and Dietz 2016). Osmotic stress is a water deficiency like condition and creates drought-like responses which are closure of stomata, reduced CO_2 fixation, over-reduction of ETC, and stimulation of photorespiration, which leads to the generation of stress conditions. Studies have shown that the salt stress have been found to give rise to respiratory ETC in the mitochondria, this activity of plasma membrane-bound respiratory burst oxidase homolog (RBOH) and apoplastic diamine oxidase (Ben Rejeb et al. 2015).

Plant Response Towards High Temperature

Day by day, there is rise in atmospheric CO_2 concentrations, and heat stress defines a more widespread problem. Normally, when the temperature exceeds the ambient temperature by 10–15 °C, it is referred to as heat shock or heat stress (Wahid et al. 2007). Transient high temperature projects a negative impact on the plant growth and development thus it also limits the productivity (Song et al. 2014). The heat stress is damaging to the photosynthetic system and as a result it reduces yields (Feng et al. 2014). PSII complex is the most heat-intolerant part of the photosynthetic apparatus on the light reaction side of photosynthesis. Oxygen-evolving complex (OEC), PSII reaction center, and the light-capturing complexes are the primary components that are damaged by high temperature (Mathur et al. 2014)

Plant Response Towards High Light Intensity

Light is the important factor or fundamental for the process of photosynthesis. However, on the other hand, light intensities above the light saturation point of photosynthesis are harmful to plants and termed as high light stress (Lichtenthaler and Burkart 1999). Light induced drop in photosynthetic rate is generally referred as photo-inhibition. High light mainly affects the PSII complex, which are the initiation site for linear electron flow and oxygen evolution from water. The degree of PSII photo-inhibition is a measure of the difference between its rate of photodamage and repair (Takahashi and Badger 2011). Multiple mechanisms of PSII photoinhibition occur at the same time under high light stress. The process, which dominates in photoinhibition, depends on the intensity and quality of light. The process of photo-inhibition during high light will affect the plant and induce stress.

Plants Response Towards Phytohormones

The studies have suggested that plant responses to many abiotic stresses such as drought, high temperature, chilling, and salinity stress is due to the variation in the levels of abscisic acid (ABA) (Leng et al. 2014) which results in stress in plants caused by photohormones. ABA plays a key role in the adaptation of plants to various stresses by initiating different signaling pathways (Bücker-Neto et al. 2017). The higher amount of accumulation of ABA triggers a signaling cascade in guard cells leading to efflux of K+ ions from guard cells resulting in decreased turgor pressure and afterward stomata closure (Lim et al. 2015). The biosynthesis of osmoprotectants, late embryogenesis abundant proteins, dehydrins, and other defense proteins involved by the ABA assists plants in altered copy by inducing the expression of many gene encoding enzymes (Sah et al. 2016). Moreover, there is absorption of ABA in leaves leading to cell wall extensibility, root hydraulic transmission, and tissue turgidity. It also induces the feedback inhibition of photosynthesis by accumulating carbohydrates and reduces the concentration of photosynthetic enzymes (Vishwakarma et al. 2017).

8.3 Fungal Communities and Production of Phytohormones

The environmental challenges, particularly the abiotic stresses, adversely affect plant growth by altering physiological and morphological processes, leading to changes in cellular pathways (Egamberdieva et al. 2017). Abiotic stresses, namely drought, salinity, chilling/freezing, and heat are detrimental to plant growth, highlighting a potential alarming concern to food security worldwide.

Plants have evolved complex defense mechanisms to counteract the effects and adapt to fluctuating climatic conditions. Phytohormones are growth regulators which play crucial roles in various biological processes, thereby affecting plant metabolism. Recent researches have highlighted that plant–microbial associations and phytohormone produced by root-associated microbes enhance abiotic stress tolerance in plants, suggesting these as an important targets for metabolic engineering (Kour et al. 2019a, b). The microbes present in the rhizopheric zone derive nutrients from the associated plant and in turn produce biological compounds (including phytohormones), enhancing plant growth, nutrient uptake, and tolerance to biotic and abiotic stresses (Grover et al. 2013; Cho et al. 2015; Yadav et al. 2018a, c). The plant growth promoting rhizobacteria (PGPRs) improves plant protection and growth by employing several biological functions, namely cell wall degrading enzymes, nitrogen fixation, osmoprotectants synthesis, among other processes (Berg et al. 2013; Wang et al. 2016; Verma et al. 2019; Yadav 2017; Yadav and Yadav 2018). Studies have showed the increase in plant tolerance to stress due to phytohormones produced by rhizospheric microbes (Etesami et al. 2015). The microbial synthesized phytohormones influence growth compounds and their metabolism and alteration in morphology of plant root, subject to exposure to abiotic stress (Spaepen et al. 2008), respectively. The fungal associations with plants, namely fungal endophytes and mycorrhizas are beneficial for plant development and abiotic stress tolerance in plants (Rana et al. 2019a; Suman et al. 2016; Yadav et al. 2017, 2018b).

8.3.1 Rhizospheric Microbes and Abiotic Stress Tolerance

The statistics suggests variations in climatic conditions and its effect on agricultural production and abiotic stress conditions forms a key concern. Studies have suggested that different fungal species form symbiotic associations with approx. 80% land plants and live inside plant tissues, known as fungal endophytes (Rodriguez et al. 2009; Khan et al. 2015).The beneficial association highlights plant's adaptation to stress conditions, exhibiting tolerance to intense solar radiations, extreme temperatures, and desiccation (Verma et al. 2017; Yadav 2018; Yadav et al. 2020b; Selosse and Le Tacon 1998). The mutualistic association of fungus with plant species highlights a significant aspect and fungal endophytes confer plant resistance to pathogens and salinity, drought and temperature stresses (Rodriguez et al. 2009). Moreover, the fungal endophytes execute a significant function in enhancing drought tolerance in plants by altering multiple biochemical and physiological processes (Malinowski and Belesky 2000).

The fungal endophytes are classified into two groups, namely class 1: Clavicipitaceous endophytes and class 2: Nonclavicipitaceous endophytes. Clavicipitaceous endophytes form associations with grasses, are present in shoots, and exhibit intercellular infections (Rodriguez et al. 2009). Studies have shown that class 1 endophytes protects the plant from metal and drought tolerance, besides herbivory by insects and mammals (Koulman et al. 2007; Malinowski and Belesky 2000), Class 2: Nonclavicipitaceous endophytes (found with ferns, conifers, and angiosperms), these induce tolerance to plants inhabiting extreme environments (Rodriguez et al. 2009). Additionally, class 3 (found in shoots) and class 4 endophytes (present in roots) are less explored classes of fungal endophytes and are relatively less explored for their role in abiotic stress tolerance in plants.

There are several mechanisms by which fungal endophytes enhance abiotic stress tolerance in plants, namely by production of reactive oxygen species (ROS) and Osmotic adjustment (biochemical mechanism), respectively. Studies have shown production of ROS in drought conditions (Gill and Tuteja 2010).The highly reactive metabolite functions as signaling molecules and regulates biological processes such as plant growth, cell cycle, response to abiotic stress, by monitoring gene expression (Gill and Tuteja 2010). A study discussed the induction of Abscisic acid hormone during water stress which further lead to production of ROS (Cai et al. 2015) and plants produce scavenging enzymes namely peroxidase (POD), catalase (CAT), superoxide dismutase (SOD), among various others to combat ROS levels (Cai et al. 2015; Shi et al. 2012). A biochemical mechanism, Osmotic adjustment has been described as a method to combat salt and drought stress in plants. It refers to osmotic adjustments to maintain uptake of water and metabolic processes (Sanders and Arndt 2012) by increasing levels of soluble sugars, loline alkaloids, amino acids, which in turn improves cell hydration and turgidity (Sanders and Arndt 2012).

Rhizospheric zone of the plant represents the area where different bacteria and fungi colonize the roots of the plant and form a mutualistic association with them.

The associated fungi derive nutrition from the plant and in turn produce phytohormones and metabolites, accelerating plant growth and adaptation against abiotic stress factors, namely heat, salinity, and drought (Mendes et al. 2011; Firakova et al. 2007). An interesting example is monotypic fungus, *Piriformospora indica* found to be associated with more than 150 plant species namely *Glycine max*, *Zea mays*, *Pisum sativum,* and other plants (Kumar et al. 2017). It is typically a plant growth promoting fungus which colonizes the roots of higher plants and increases growth promotion, uptake of nutrients, and tolerance to environmental stresses (Unnikumar et al. 2013).

Another significant plant–fungal association is represented by Arbuscular mycorrhizal fungi (AMF), which plays an important biological role in plant protection. These act as biological fertilizers and constitute an integral component of organic farming, promoting agricultural output. The AMF promotes the uptake of nutrients (K, N, P, Mg) and micronutrients, heavy metal and salinity tolerance and protection against pathogens (Smith and Read 1997), respectively. Moreover, such mycorrhizal interactions are present in both cultivated and wild plants except for the members of the family Cyperaceae and Brassicaceae do not form such associations (Kumar et al. 2017). Table 8.1 provides a comprehensive account of the Plant–fungal associations and production of phytohormones.

8.4 Role of Phytohormones in Abiotic Stress Mechanism

8.4.1 Gibberellins

Plant hormones regulate the plant growth and development, through responses towards the changing environmental conditions. By changing the production, distribution of this hormone, we can regulate and coordinate both growth or stress tolerance to promote survival or escape from environmental stress. Gibberellins or Gibberellic Acid (GA) growth hormone is responsible for abiotic stress regulation (Rastegari et al. 2020a, b). With the decline in the GA levels, the plant is exposed to several stress like cold, salt and osmotic stress. Similarly, the increase in the level of GA, the plant is protected by the responses of shaping and submergence. Several studies suggested that the GA signaling is linked with the stress tolerance in plants. The transcription regulation of GA metabolism regulates the GA pathway, while the interaction of the GA signaling molecule DELLA with components of the signaling pathway for the stress hormone jasmonic acid suggests some additional mechanisms by which GA signaling may integrate multiple hormone signaling pathways.

8.4.1.1 GA Response to Abiotic Stress

GA induce plant growth and response to abiotic stress linked with the DELLA protein (Achard et al. 2008a). In *A. thaliana* seedlings, there is an exposure of salinity triggered reduction in endogenous bioactive GAs with DELLA accumulation

Table 8.1 A comprehensive account of the plant–fungal associations and production of phytohormones

S. no.	Fungal species	Family	Host plant	Phytohormone production	Effect on plant	References
1.	*Gibberella fujikuroi*	Nectriaceae	*Oryza sativa*	GA	Growth increase	Bomke and Tudzynski (2009)
2.	*Piriformospora indica*	Sebacinaceae	*Hordeum vulgare*	IAA	—	Hilbert et al. (2012)
3.	*Scolecobasidium tshawytschae*	Dematiaceae	Soybean cultivar Daewonkong	GA	Growth promotion	Hamayun et al. (2009)
4.	*Aspergillus fumigatus*	Trichocomaceae	*Glycine max*	GA	Salt stress tolerance	Khan et al. (2011)
5.	*Trichoderma asperellum*	Hypocreaceae	*Cucumis sativus*	IAA, ABA, GA	Increased Iron uptake	Zhao et al. (2014)
6.	*Porostereum spadiceum* AGH786	Phanerochaetaceae	*Glycine max*	GA	Salinity tolerance	Hamayun et al. (2017)
7.	*Phoma glomerata* LWL2 *Penicillium* sp. LWL3	— Trichocomaceae	*Waito-C* and Dongjin-beyo rice	IAA, GA	Drought and salinity tolerance	Waqas et al. (2012)
8.	*Aspergillus japonicus* EuR-26	Aspergillaceae	*Euphorbia indica L.*	SA, IAA	Heat stress tolerance	Ismail et al. (2018)
9.	*Penicillium ruqueforti* Thom.	Trichocomaceae	*Triticum aestivum*	IAA	Heavy metal tolerance	Ikram et al. (2018)
10.	*Paecilomyces formosus* LWL1	Trichocomaceae	*Japonica* rice cultivar Dongjin	ABA, JA	Heat stress	Waqas et al. (2015)
11.	*Funneliformis mosseae* *Rhizophagus intraradices*	Glomeraceae	*Solanum lycopersicum*	ABA	Water stress	Chitarra et al. (2016)

(Achard et al. 2006). The growth of *A. thaliana* was inhibited by salt stress, these included reduction in root growth and reduced leaf production rate, and delayed flowering time (Achard et al. 2006). There is another link between the DELLA function and survival of salt stress. GA deficient biosynthetic mutant ga1-3, improves the survival of severe salt stress, with the quadruple-della mutant. The growth parameters and salt tolerance in a range of Della mutants indicated a strong association between plant height, flowering time transition, and susceptibility to severe salt stress, suggesting that DELLA proteins may restrain growth and enhance stress tolerance through a common mechanism (Achard et al. 2008b). There were similar responses of *A. thaliana* seedlings to cold stress triggering a reduction in bioactive GA, promoting DELLA accumulation, and resulting in DELLA-mediated growth restriction (Achard et al. 2008a).

8.4.1.2 GA Stress Tolerance

The DELLA protein function to restrict growth under abiotic stress demonstrating a positive effect on stress tolerance. The range of Della mutants in *A. thaliana* shows that DELLA function and associated growth restraint under non-stressed conditions, correlated well with reduced susceptibility to severe salt stress. The antioxidant system is an important DELLA-mediated response towards the stress. DELLA activity was found to restrain the reactive oxygen species (ROS), which are known to accumulate in salt-treated plants. At high levels, ROS triggers plant cell death, a response that is also delayed by DELLA. In rice, a similar link between maintained levels of SLR1 and reduced levels of oxidative stress for Sub1A lines exposed to drought dehydration and flooding, was observed (Fukao et al. 2011). Cell proliferation is known to be regulated by DELLA, and DELLA accumulation triggers mitotic exit on exposure to mild osmotic stress (Claeys et al. 2012). By the following mechanisms, the GA confers the stress tolerance to the plant. The DELLA protein plays a pivotal role in the stress tolerance in the plants.

8.4.2 Abscisic Acid

Abscisic acid (ABA) is phytohormone acting towards the stresses like heavy metal, drought, heat stress, salinity, temperature and radiation. It is used in many developmental processes like seed germination, seed dormancy, and closure of stomata. ABA acts by changing the level of gene and subsequent analysis of *cis*- and *trans*-acting regulatory elements of responsive promoters. It interacts with signaling molecules in stress responses and development of seeds. Moreover, various stress-responsive genes can be susceptible or tolerant by taking into account their coordinated activities. There are no of transcription factors available for the regulating the expression of ABA responsive gene by acting together with respective cis-acting elements. For an understanding of the stress tolerance mechanims in plants, it is important to understand the mechanism behind it.

8.4.2.1 Mechanism of ABA Under Abiotic Stress

The increase in the de novo biosynthesis of ABA is due to the rise in abiotic stress which is important to inhibit its degradation and is stimulated by stress. Gene recognized for ABA biosynthesis is ZEP and expressed in many plant species. ZEP gene is associated with the basal expression in leaves (Xiong et al. 2002). The level of ABA biosynthesis through ZEP gene is regulated not only in different plant portions and development phases, but also in different plant species. The ZEP gene in *Arabidopsis* has a same basal transcript level in non-stressful conditions as in tobacco and tomato plants. These changes in the expression of ZEP genes are partially related to basal transcript levels which also covers stress inducibility of genes as identified in different experiments. However, ABA biosynthetic genes expressions (NCED, AtAAO3, MCSU, and AtSDR1) are less debatable. The ABA biosynthesis is notably achieved after cleavage in the rate-limiting step, and thus expression of NCED gene(s) has received a significant attention. NCED gene is found to be over-expressed in drought stress condition in maize (Tan et al. 1997), tomato (Burbidge et al. 1999), bean (Qin and Zeevaart 1999), among others. A remarkable rise in NCED transcript levels has been reported following 15–30 min of leaf disentanglement or induced dehydration (Xiong and Zhu 2003), providing an evidence for the instant activation of NCED genes. Since ABA biosynthesis mechanism upregulates considerably in response to stress, it can be deduced that protein levels of the related genes increase with the transcript levels, which were similarly noticed in NCED gene (Xiong and Zhu 2003).

The product ABA of the biosynthesis pathway negatively regulates the ABA accumulation *via* triggering its catabolic enzymes (Cutler et al. 2010). The cytochrome P450 enzyme activity and ABA 8′- hydroxylase activity carries out the primary step of ABA degradation and regulated by exogenous ABA accumulation. Since the product of NCED gene regulates the rate-limiting step in the ABA biosynthesis pathway, the information regarding the control of this gene product by ABA is very limited in terms of auto-regulation of ABA biosynthesis.

8.4.3 Cytokinins

Cytokinin is a multi-branched plant hormone that functions in plant development, in addition to stress reactions. Moreover, it plays an important role in assimilation, transport, and monitoring reactions to changes in levels of both macronutrients (nitrogen, phosphorus, potassium, sulfur) and micronutrients (boron, iron, silicon, selenium). The cytokinin’s impact on plant’s xenobiotic and its cooperation with light, temperature, dry season, and salinity signals was discussed.

8.4.3.1 Cytokinins in Drought and Salinity Tolerance

Drought and salinity stress hampers crop harvest and productivity on a worldwide scale (Daryanto et al. 2016). Investigations on regular variations in Arabidopsis demonstrated that dry season may influence plants when they are not developmentally adjusted to it (Clauw et al. 2015). Plants respond to water-restricting conditions by reducing their cytokinin levels, chiefly through the balance of cytokinin digestion in *Arabidopsis*, crawling bentgrass, soybean, tobacco, and sunflower (Xu and Huang 2009) as well as the cytokinin receptors' (Tran et al. 2007). The negative controllers of cytokinin signaling AHP6 and ARR5 contributes in this process (Huang et al. 2018). Fitting balance of cytokinin digestion and flagging has been known to improve drought and salt resistance for a long duration (Ghanem et al. 2011), and components may add to cytokinin-mediated tolerance to water deficiency. These are protection of the photosynthetic apparatus, improvement in water balance, and adjustment of plant development.

8.4.3.2 Role of Cytokinins in Plant Growth

As cytokinins have key functions in root and shoot development, it helps in development and structural qualities that are required for resistance of water-constraining conditions. Cytokinins are notable to diminish root to shoot hypocotyl proportions (Werner et al. 2010), and one of the methodologies for upgrading plants dry spell resistance is to diminish cytokinin levels, so as to change root morphology and improve root biomass (Pospisilova et al. 2016). Root-explicit over-expression of CKX may likewise upgrade root development, supplement take-up, and dry spell resistance, just as improving recuperation after dry season pressure (Pospisilova et al. 2016) without unfriendly impacts on shoot development. So also, one of the lacks of hydration responsive component restricting variables in *Malus* (MdDREB6.2) enacts the declaration of MdCKX, for the most part in roots, and over-expression of this factor can improve dry spell resilience (Liao et al. 2017). A few studies demonstrate that quantitative as well as subjective attributes of root tissues could be significant factors in cytokinin-controlled reactions to water-restricting conditions, including the separation of vascular tissue (Jang and Choi 2018) and lignification (Pospisilova et al. 2016).

8.4.4 Auxins

In most abiotic stress conditions, including salinity and water shortage, the formative plasticity of the plant root is directed by the phytohormone auxin. Changes in auxin are frequently credited to changes in shoot-inferred long-separation auxin stream. Studies suggested that short-separation auxin transport from nearby capacity and neighborhood auxin biosynthesis, conjugation, and oxidation during abiotic stress. Moreover, studies examined current understanding on auxin transport in stress conditions, and consequently auxin transport and indole-3-acidic corrosive (IAA) impact possible auxin collection and flagging.

8.4.4.1 Auxin Signaling

Over the most recent 10 years, investigations on *Arabidopsis* and other plant species have recognized a noteworthy auxin signaling pathway. A couple of methodical outlines of auxin discernment and signaling have been distributed (Retzer et al. 2014). To summarize, three proteins TIR1/AFBs (Transport Inhibitor Response 1/ Auxin Signaling F-Box Proteins), ABP1(Auxin Binding Protein1) and SKP2A (S-Phase Kinase-Associated Protein 2A) have been perceived so far as auxin receptors and every one of them intercedes auxin flagging falls that assume a differing administrative job in plant development and improvement. The TIR1 is the primary generally acknowledged auxin receptor. It exists as a feature of a protein complex, the TIR1/AFB proteins which are subunits of the SKP1–Cul1–F-box (SCF)—type E3 ligase called SCFTIR1/AFB. Under the conditions, where auxin levels are low or even missing, Aux/IAA protein repressors tie to ARFs (Auxin-Responsive Factors), and quell their transcriptional movement. Whenever accessible, auxin goes about as a "sub-atomic paste" to advance connection between the auxin co-receptor, TIR1/AFB and repressor Aux/IAA, bringing about the last's debasement and along these lines initiating ARF interpretation factors and the downstream flagging parts. The tir1 freaks demonstrated an assortment of development imperfections including hypocotyl stretching and horizontal root arrangement, showing that TIR1 is required for ordinary reaction to auxin (Wang and Estelle 2014).

8.4.4.2 Auxin Signaling Under Stress Conditions

It is possible that the auxin signaling pathway likewise functions in plant response to abiotic stress. The decreased plant development during stress condition. Development is generally the consequence of weakened auxin flagging. Constriction can happen at a few levels, including auxin homeostatic procedures that outcome with less accessible dynamic auxin, deactivation of receptors, and the flagging parts at transcriptional or post-transcriptional levels. One segment incorporated into post-transcriptional guideline is miRNAs (microRNAs). The miRNAs are little administrative RNAs, which assume basic jobs during plant development and improvement by contrarily managing quality articulation at post-transcriptional level. These non-coding little RNAs (miRNAs) restrain quality articulation post-transcriptionally by focusing on related mRNAs for either debasement or translational restraint. Throughout the years, various miRNAs that target plant qualities have been accounted for.

A large number of miRNAs are accounted to react to ecological pressure signals (Sunkar et al. 2007) and some of them obviously direct auxin signaling segments

(Sanan-Mishra et al. 2013). Specifically, miR393, miR397b, and miR402, whose anticipated targets are mRNAs encoding auxin receptor TIR1, LACCASE, and DEMETER-LIKE PROTEIN3, separately, were upregulated in cold, salt, and ABA in *A. thaliana*, *Oryza sativa*, *Zea mays* and *Phaseolus vulgaris* (Dharmasiri and Estelle 2002). There is a theory that the concealment of auxin flagging may be one of the plant techniques to upgrade their resistance to stresses. As definitely known, a gentle salt pressure brings about an extraordinary decrease of parallel root extension and an expansion in horizontal root numbers, while higher salt levels totally hinder root prolongation. Because of salt pressure, horizontal root numbers were decreased in auxin signaling freaks axr1, axr4, and tir1 (Wang et al. 2009) affirming the significant job of this flagging components in stress reaction. Salt and osmotic burdens lead to a suppression of TIR1 and AFB2 receptors (Sunkar et al. 2007).

The tir1afb2 *Arabidopsis* freak demonstrated expanded resistance to salt stress in contrast with wild type (Iglesias et al. 2010). Strikingly, it contained less H_2O_2 and superoxide anion and expanded cancer prevention agent chemical, showing expanded resilience to oxidative pressure. Consequently, the auxin receptor intercedes plant versatile development under salt pressure (Iglesias et al. 2010). Likewise, the study demonstrated that down regulation of TIR1/AFB2-intervened auxin flagging was managed post-transcriptionally by miR393 which was upregulated upon expanded saltiness. Conversely, the mir393ab freak showed expanded degrees of responsive oxygen species (ROS) because of diminished ascorbate peroxidase (APX) enzymatic movement. In view of those discoveries, researchers proposed a speculative model to clarify how salt pressure may smother auxin motioning by coordinating pressure signals, redox state and physiological development reactions during acclimation to salinity in *Arabidopsis*. *Arabidopsis* plants overexpressing miR393 (that down directs the outflow of the AFB3 auxin receptor), showed bargained essential root and parallel root development in light of healthful pressure (Kinoshita et al. 2012).

Besides, extra miRNA, called miRNA167a has been distinguished in *Arabidopsis* as a significant controller of root design changes in osmotic pressure and dry season resistance. IAR3 mRNA has been recognized as another objective of miR167a. As of now referenced, IAR3 is auxin amidohydrolase which hydrolyzes an idle type of auxin (IAA-Ala) by discharging bioactive IAA. Arrangement correlation uncovered that the miR167-IAR3 connection seems, to be developmentally regulated in higher dicot and monocot plant species (Kinoshita et al. 2012). Similar creators distinguished that miR167a levels diminished, though IAR3 mRNA levels expanded under pressure conditions. Conversely with the wild kind, iar3 freaks collected diminished IAA levels and did not show high osmotic pressure incited root engineering changes. Transgenic plants communicating a cleavage-safe type of IAR3 mRNA gathered abnormal amounts of IAR3 transcript and demonstrated expanded parallel root improvement contrasted and transgenic plants communicating wild-type IAR3. It was resolved that an expansion in grain miR160a during warmth stress significantly downregulates the articulation level of the auxin reaction translation factors ARF17 and ARF13. ARF8 mRNA is additionally unequivocally downregulated under warmth stress and it is anticipated as an objective of miR167h

(Kruszka et al. 2014). What's more, a combinatorial methodology of high-throughput sequencing in wheat approved ARF10 as objective succession of miRNA160 (Pandey et al. 2014). Auxin responsive variables ARF8, ARF13 and ARF17 are among others in charge of guideline of shoot morphology and root design.

8.5 Metabolic Engineering for Abiotic Stress Tolerance in Plants

The global trends in population explosion and an increase in food consumption, projects an urgent need to increase food supply through agriculture. The statistics suggests that for nutritional subsistence of 2.3 billion people (the projected population rise by 2050), agricultural production has to be increased by 70% (Tilman et al. 2011). Besides, environmental adversities such as abiotic stresses contribute to substantial agricultural losses, leading to low economical returns. Therefore, studies into understanding the complex mechanism how plants adapt to these adverse conditions form an integral aspect of research (Wani et al. 2016).

Abiotic stresses withhold a prime challenge for developing world and its ever increasing population, and continue to account for substantial agricultural losses. Environmental conditions namely heat, cold, salinity, drought, radiations constitutes abiotic stresses, which hampers plant growth and development (Yadav et al. 2015c, 2018a, d). How a particular condition affects the plant depends on the developmental stages, the duration of exposure as well as the plant species (Feller and Vaseva 2014). Some plant species and their genotypes are more susceptible or tolerant to abiotic stresses than others. Drought defines the most serious of all abiotic stress, negatively affecting plant growth, photosynthetic process, integrity of membranes, etc. and influencing various physiological processes (Sanghera et al. 2011; Pathak et al. 2014). With global warming and changing climatic conditions, groundwater resources are depleting and very little water is available for crop cultivation. Moreover, a condition like drought severely hampers growth and development of plants, leading to extensive losses. Besides drought, salinity stress adversely affects agricultural crops.

Genetic manipulation of food crops has been extensively explored as an efficient strategy to improve crop yield and productivity. Deciphering whole genomes and identification of gene families modulation during abiotic stress, has made significant contributions in increasing agricultural yields and conferring abiotic stress tolerance to plants. However, conventional breeding methods have been less successful, subject to complex mechanism and their interplay in abiotic stress responses. In the present time, phytohormones production in plants and their functional role in key biological processes highlight a potential method to produce abiotic stress tolerant crops, respectively (Verma et al. 2015, 2016; Yadav et al. 2015a, b). Phytohormones are produced in low concentration and regulate cell-signaling pathways during abiotic stress responses in plants (Kazan 2015). Literature has suggested the role of abscisic acid in abiotic stress, affecting various processes namely plant development, regulation of growth, seed dormancy, closing of stomata, among others (Li et al. 2010). Additionally, several phytohormones have demonstrated protective effect in plants, particularly in abiotic stress acclimatization by monitoring plant growth, nutrition, activating signaling pathways. These hormones are produced in low quantities and are transported to various plant organs and play pivotal functions in plant response to environmental stimuli (Fahad et al. 2015).

Genetic engineering approaches in conferring abiotic stress tolerance in plants, has emerged as the prospective method of choice for increasing crop productivity. Moreover, phytohormones regulate plant development and response to environmental stresses, thus constituting a key target for metabolic engineering in crops. For example, genetic manipulations of plants for abscisic acid biosynthetic enzymes and their role in abiotic stress tolerance have been extensively studied (Jewell et al. 2010). For example, a study showed that over-expression of an ABA associated stress in *Arabidopsis thaliana* increased osmotic stress tolerance in the plant (Park et al. 2008). A similar research on genetic engineering of dehydration-responsive element binding (DREB) genes in *Lycopersicum esculentum* enhanced tolerance to water-deficit stress (Lee et al. 2003). Table 8.2 provides a detailed summary of genetic manipulations of phytohormones from different plant sources and their role in abiotic stress tolerance.

Table 8.2 A detailed summary of genetic manipulations of phytohormones from different plant sources and their role in abiotic stress tolerance

S. no.	Plant hormone	Associated gene	Function(s)	Improvement in transgenic plant	References
1.	Auxin	IPT	Biosynthesis of cytokinin	Increased growth under salt stress in tomato	Ghanem et al. (2011)
2.	Auxin	YUCCA6	IPA/Auxin biosynthesis	Tolerance to drought stress	Ke et al. (2015)
3.	Abscisic acid	MsZEP	ABA biosynthesis	Drought and salt tolerance	Zhang et al. (2015)
4.	Ethylene	ACC synthase	Biosynthesis of ethylene	Transgenic maize showing drought tolerance	Habben et al. (2014)
5.	Cytokinin	CKX	Cytokinin dehydrogenase	Drought tolerance in *A. thaliana*	Werner et al. (2010)
6.	Abscisic acid	AtLOS5	Biosynthesis of ABA	Tolerance to salinity stress	Zhang et al. (2016)
7.	Brassinosteroids	AtHSD1	Biosynthesis of BRs	Salinity tolerance and increased growth	Li et al. (2007)
8.	Cytokinin	SlIPT3	—	Transgenic tomato showing salinity tolerance	Žižková et al. (2015)

8.6 Conclusion and Future Prospects

Agricultural crops are exposed to environmental stress conditions, having an adverse impact on crop yield and agricultural productivity. Scientific methods and high throughout technologies have made substantial contributions in addressing the concern, however, met with limited success. Phytohormone engineering constitutes a key area for enhancing abiotic stress tolerance in plants, leading towards sustainable agriculture. Additionally, the advancement in genomic technologies have led to the identification of abiotic stress-responsive genes and their metabolic pathways providing better understanding of the abiotic stress tolerance in plants. The symbiotic association of plants with microbes (particularly fungi), namely fungal endophytes and arbuscular mycorrhiza, confers distinct advantages to plant species, respectively. Genetic manipulation of phytohormones (produced by fungal communities) and creation of transgenic plants with tolerance to abiotic stress put forth a prospective solution to counteract adverse climatic conditions and increase agricultural production.

In the present scenario, increasing agricultural output employing genetic engineering strategies highlights a prospective solution to growing nutritional demands throughout the world. Genetic manipulations of phytohormones for enhancing abiotic stress tolerance has been gaining momentum and provide key insights into understanding the plant mechanisms to combat environmental stress conditions. However, the area of phytohormone engineering in plants withholds several challenges in delineating complex signaling pathways and mechanisms occurring in abiotic stress conditions. Whole genome sequencing projects have unraveled huge genomic information "Big Data" and annotation of complete genomes is underway, offering insights into an organism genome and interplay of associated gene/protein families. In research, extensive investigation of gene and their biosynthetic pathways in genomic level is required, for example a research investigation focusing on how a phytohormone, for instance, IAA is biosynthesized in plants and the different gene families functionally involved in its biosynthesis is to be discovered. Since phytohormones play a significant role in conferring abiotic stress tolerance in plants, their genetic manipulations offer a promising approach to increase crop yield and production. Another potential challenge accounts for engineering staple food crops, namely rice, wheat, corn, and creation of stable transgenic plants, which does not pose health hazards. Although the genomic technologies highlight a significant method, however, it still has to undergo a long way for completely addressing the growing nutrition problem worldwide.

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Chapter 9
Fungal Biofertilizers for Sustainable Agricultural Productivity

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9.1 Introduction

The use of beneficial microbes as biofertilizers has become an increasing area of research in agriculture and life sciences owing to the role they play in food security and sustainable agro crop production. These microorganisms are diverse and constitute the most important biological community structure in the soil ecosystem. Most often, their interactions and activities lead to increase in crop yield, earth geochemical stability, climatic and biogeochemical cycles (Tringe et al. 2005; Hansel et al. 2008). According to Odoh et al. (2019a), these microorganisms live in a coordinated and complex ecosystem arrangement within which exist influences from living and non-living features. Recent studies however have shown the applicability of engineered species in medicine such as antibiotic resistance genes (Cycon et al. 2019) and microbial pigments in food industry (Sen et al. 2019). This is thought to improve understanding of species behavioral pattern, complexity, and mechanisms of action (Kumar 2016; Ahmad et al. 2011). According to Bhardwaj et al. (2014), some of the eco-friendly and soil microbiology advances have inspired a wide range of applications of plant growth promoting rhizobacteria (PGPRs), endo- and ecto-mycorrhizal fungi, and other microbial agents to improve nutrient uptake. In their work, they also identified increased plant growth and tolerance to abiotic and biotic stress owing to biofertilizers addition (Bhardwaj et al. 2014; Clark et al. 2009). Elsewhere, Pathak et al. (2017) opined that fungal–fungal (tropical plant and their foliar endophytes) and bacterial–fungal (arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria) associations enhance turnover of soil organic matters and also aiding mobilization of nutrients for plants growth through the fixation of nitrogen (N) in leguminous crops (Franco et al. 2011; Nuti and Giovannetti 2015). This however underlines the growing interest and study in fungal biotechnology and explores its inherent potentials in sustainable agriculture (Berruti et al. 2016).

9.2 Fungal Interactions, Operations, and Mechanisms

Mycological studies have shown that fungi live in a wide range of environmental niches/habitats and carry out processes such as nutrient cycling and decomposition of organic matters. Their vital role in agrobiology and biotechnological advances has been well documented. According to Zeilinger-Migsich and Mukherjee (2014), these fungi through nutritional versatility, mechanisms, and biochemical processes interact with other organisms (bacteria, plants, and animals) in their natural habitat. At both intra- and inter-specific interactions, these microbial agents communicate within the population using chemical language typically for signaling. In principle, these signaling molecules influence certain behavioral changes and responses such as propagation or alterations in growth and development, and pathogenicity. In many cases, the specificity and functions of these interactions are not well understood and the attractive mechanisms involved largely unknown (Zeilinger-Migsich and Mukherjee 2014).

9.2.1 Fungal–Fungal Interactions (FFI)

Microbial symbiotic interactions in a single habitat involve associations of symbionts performing roles as mutual consortia against other consortia. This interaction though widespread occurs in a cryptic fashion (Van Bael et al. 2011). During this process, leaf-cutting ants and their symbiotic fungi maintain an obligate symbiosis with each other. Following a series of systematic steps, plant leaves are cut and transported to the nest where they are cleaned up, processed, and utilized as substrate. In return, the fungal agents utilize the leaf material by converting its biomass to carbon source for the larvae and worker ant's population. This is however achievable owing to the activities of the underground chambers of fungal residence (Van Bael et al. 2011). Most importantly, this mechanism undermine the behavior of leaf-cutter ant including plant endophytes fungi. Similarly, they also synthesize organic compounds with antimicrobial and insect repellent properties (Borges et al. 2009). This compounds thus provide avenue for microbial competition within community, while altering the chemical and adaptive defense system (Pettit 2009). In addition, Van Bael et al. (2011) identified some associative roles of endophytes on leaves (e.g., drought tolerance) and how it enhances deposition of lignin in plants cell wall.

9.2.2 Bacterial–Fungal Interactions (BFI)

Ecological studies have revealed that bacteria and fungi co-habit through their assemblage into complex and dynamic co-evolving groups. These communities, for instance fungal and bacteria, are found in practically in all ecosystems (Peleg et al. 2010; Scherlach et al. 2013). Interactions between these microbes play a huge role as they are considered vital players in driving activities such as biochemical cycles and contributing significantly to plants and animals pathogens (Deveau et al. 2018). For centuries, these agents have been utilized for food production and processing (Odoh et al. 2017), pharmaceutics and antibiotics synthesis, biotechnology and production of metabolites (Frey-Klett et al. 2011). Elsewhere, BFI by-products are exploited for enhanced agricultural, environmental, and forestry management (Frey-Klett et al. 2011; Odoh et al. 2019a, b). In characterizing BFI, understanding of microbiomes using molecular tools, chemical and microbial ecology, genomics, and biophysics are essential (Bergelson et al. 2019; Thompson et al. 2017). Frey-klett et al. (2011) in their work suggested a shift from disordered poly-microbial communities to a highly specific symbiotic association of fungal hyphae and bacterial cells, following their complexities.

Arbuscular mycorrhizal fungi (AMF) and bacteria (plant growth promoting rhizobacteria—PGPR) association has been reported to promote crop growth (Pathak et al. 2017). According to Philippot et al. (2013), *Bacillus* sp., *Pseudomonas* sp (PGPR) and AMF interaction proffers strong viability and causes significant improvement in field study when used singly or in combined application (Pathak et al. 2017). Although this association has positive influence on crop yield, it also enhances soil nutritional status and soil microbial biodata. Elsewhere, studies have shown that PGPR and AMF are key bioinoculants with potential for halting dependence on agrochemicals, thus aiding sustainable agricultural practices (Pathak et al. 2017; Franco et al. 2011). PGPR boost plant growth directly (growth promoting hormones) and indirectly (synthesis of antimicrobial substances) (Deshwal and Kumar 2013; Zheng et al. 2018). As aid to the process of mycorrhization, mycorrhizal helping bacteria (MHB) and PGPR symbiotically interact with mycorrhizal fungi, and mycorrhizal roots for nutrient uptake. Studies have revealed that rhizospheric AMF and PGPR elicit systemic host immune responses for plant resistance (Zamioudis and Pieterse 2012; Singh 2018), just as experimental evidence has proven that co-inoculants of AMF and PGPR give synergistic advantage to crop growth especially in nutrient limited agricultural soil (Gouda et al. 2018).

9.3 Fungal Biofertilizers: Its Importance and Functions

In recent time, application of fungal species to arable land to improve soil quality has been gaining prominence and is very promising (Bagyaraj and Ashwin 2017; Frąc et al. 2015). It is a process where fungal biological composition made up of microbes colonizes the immediate plant roots region (rhizosphere) to promote growth. This bio-phenomenon usually increases the efficient distribution of essential nutrients to the target crops while also maintaining soil inhabitants, owing to their ability to adopt various forms in response to unfavorable conditions. Kumar et al. (2018) in their work reported that these fungi could be used in seeds, applied on plants surfaces or in the soil to stimulate growth. They have also been implicated to continuously help in the release of nutrients through their metabolism (Mazid et al. 2011; Malusa et al. 2012), thus forming a central component of Integrated Nutrient Management (INM) system needed in sustainability of agriculture and environmental practices (Kumar et al. 2018).

Some of the common microorganisms usually used as biofertilizers or in it composition are nitrogen fixing agents (N-fixer) (Rana et al. 2019a, b; Verma et al.

2019), plant growth promoting rhizobacteria (PGPRs) (Verma et al. 2016; Yadav et al. 2015, 2018a), potassium (Kour et al. 2020; Verma et al. 2017a), phosphorus solubilizers (Yadav et al. 2017a), cyanobacteria, and endo- and ecto-mycorrhizal fungi (Itelima et al. 2018; López-Bucio et al. 2015). Intrinsically, these organisms possess ability to produce a wide variety of extracellular enzymes for the breakdown of organic matter (Frąc et al. 2018). On the other hand, the bioagent improves plants vigor and tolerance to abiotic and biotic factors while serving as an eco-friendly and cost-effective alternative (Itelima et al. 2018; Rouphael et al. 2015). Žifčáková et al. (2016)) in their report maintained that fungi biofertilizers contribute in no little way to the soil decomposing components and regulate the balance of carbon and other nutrients. Besides plays a key maintaining the soil primary and secondary nutrients requirement—through potassium and phosphate solubilization, nitrogen fixation and mineralization; biofertilizers (Fig. 9.1), also help in the biodegradation of organic matter and pollutants in the soil environment (Odoh et al. 2019b; Sinha et al. 2014; Adesemoye and Kloepper 2009).

9.4 Fungal Biofertilizers and Agriculture

Biofertilizers are composition of microbial group (fungi, algae, and bacteria) with capacity of addition nutrients to soil, fixing nitrogen, and solubilization minerals for plants usage. They are environmentally friendly, cost effective, and renewable source of plant nutrients that have gained acceptance over chemical fertilizers (Kour et al. 2020; Verma et al. 2019; Yadav et al. 2020c). These bio-based materials play an important role in maintaining soil fertility, nutritional enrichment, and sustenance of healthy soil for generations (Mishra et al. 2015; Fuentes-Ramirez and Caballero-Mellado 2005). Their inoculants just as seen in Table 9.1 improve crop yield by enhancing a number of biochemical processes leading to increase in uptake of nutrients, stimulation of plant growth hormones, antibiosis, and decomposition of organic residues (Odoh et al. 2019a, b). With history of fungal biofertilizer utilization, there has been an increasing call in recent time to understand their application and role as biocontrol agents. This capacity according to Ajmal et al. (2018) lies in the fungi specie inherent aptitude in promoting crop growth and reducing reliance on synthetic chemical products.

Mycorrhizas are unique microbes which form mutual symbiotic relationships with plant roots. They interact with these plants and enhance uptake of phosphorus (P), nitrogen (N), zinc (Zn), copper (Cu), iron (Fe), sulfur (S), and boron (B). Some of the important plants with mutualistic interaction with mycorrhiza spp. include herbs, shrubs, trees, xerophytes, epiphytes, and hydrophytes (Rai et al. 2013). Few of the most studied and main mycorrhizae of interest include arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM). Of late, there has been increasing call for the use of this mainstream inoculant and the genetically engineering of the dominant mycorrhiza to improve yield and induce resistance against stress. Ectomycorrhizal (ECM) fungi increase plants tolerance to abiotic stress. Besides

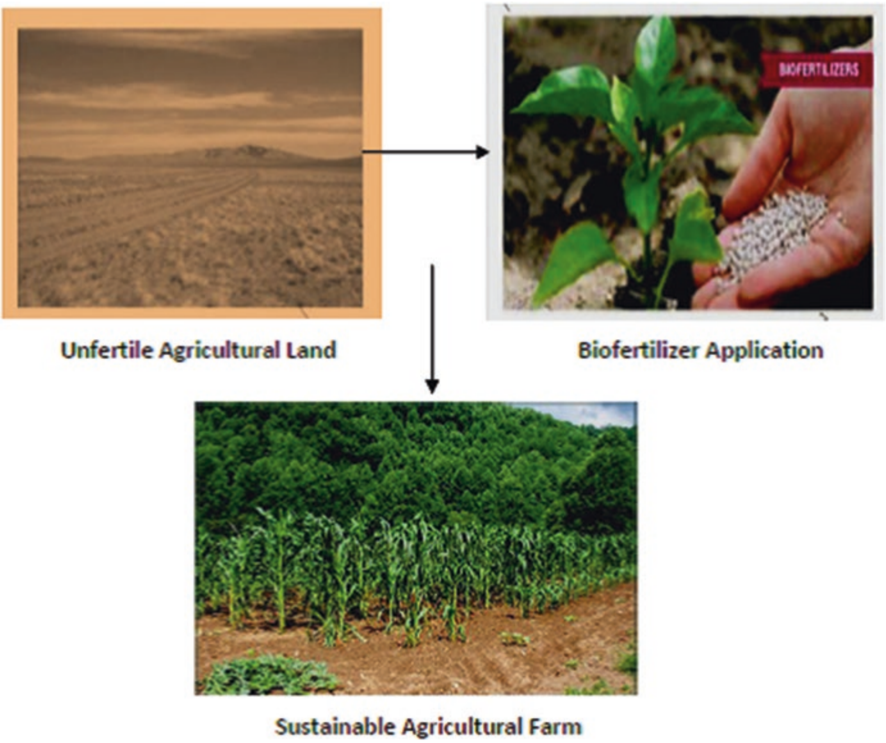

Fig. 9.1 Schematic representation of biofertilizer application

decreasing the level of toxins in the soil, and reducing the extremes of soil pH they also shield plant roots from biological related stresses (Odoh et al. 2019a, b). Arbuscular mycorrhizae (endomycorrhizae) are phosphate scavengers which expedite the recruitment of soluble phosphate from soil aquifer. Since mycorrhizal fungi are more efficient in the uptake of specific nutrients like P, Ca, Zn, S, N, B and are resistant against soil-borne pathogens, interest in the use of these fungal agents as biofertilizers has been on the increase (Odoh 2017; Sumita et al. 2015; Aggani 2013). In addition, as important members of the soil microbial community, arbuscular mycorrhizal fungi (AMF) play a key role in plant growth promotion, plant protection, and soil quality improvements. Also, besides being widely spread in agricultural systems, they have received wide acceptance as organic farming manure, especially in regions where quest for sustainable crop production is prioritized.

Table 9.1 Some fungi used as biofertilizers and their mode of action

Biofertilizer agents	Mode of actions/functions	Microbial specie
Fusarium spp	Enrich compost biofertilizers Degrade plant residues and maintaining C: N balance in the soil	*Fusarium solani and F*. Oxysporum
Trichoderma spp	Enhance compost degradation	*Trichoderma harzianum* + *Aspergillus* + *Penicillium*
Mycorrhizal fungi	Reduced the impact of environmental stress Improve the plant health status while enhanced optimum mineral	*Glomus intraradices*
Aspergillus spp	Solubilizing unavailable phosphate for plant use through the secretion of organic acid It improves soil quality with subsequent uses	*Aspergillus niger*
Penicillium spp	Supplies of essential minerals (P, Mn, Zn, Fe, Co, Cu, and Mo) to the plants Inducement of abiotic stress resistance in young seeding Protect the plants from fungal pathogens	*P. bilaji, P. italicum, P. albidum, P. frequentans, P. simplicissimum, P. rubrum, P. expansum, P. oxalicum, P. citrinum*
Chaetomium spp.	Enhances compost degradation	*C. bostrychodes, C. olivaceum*
Gliocladium spp	Reduce the incidence of damping-off disease	*Gliocladium catenulatum*
Tritirachium spp	Organic acids secretion for mineral dissolution	*T. album, T. egenum*

9.4.1 Trichoderma *spp*

Trichoderma is a fungal genus commonly found in most habitats. They are predominantly found in root and soil ecosystems and considered as ubiquitous saprobes. *Trichoderma* spp. can be easily isolated from decaying wood soil and organic materials (Rosa et al. 2012). Studies have shown a number of successfully reduced plant diseases through their highly effective antagonistic and mycoparasitic activity (Kour et al. 2019; Sharma et al. 2019; Verma et al. 2017b). Some *Trichoderma* strains interact with their plants host, increasing directly their growth potential and imposing resistance against diseases and abiotic stresses (Rosa et al. 2012*)*. Some of the fungal disease causing agents acted upon by Trichoderma (Trichoderma harzianum

T-22) include *Rhizoctonia spp.*, *Pythium spp.*, *Botrytis cinerea*, *Pythium*, *Rhizoctonia*, and *Fusarium spp.* As an agent with mycofungicides properties, Trichoderma spp. has been engineered overtime to successfully support crops such as potato, corn, tomato, peanut, beans, cotton, and soybean (Sneha et al. 2018). They are considered an excellent competitor within the rhizosphere because they exercise resistance against soil unfavorable conditions and high efficiency in harnessing soil nutrients while also being hostile to phytopathogens (Chandrashekrappa and Basalingappa 2018).

9.4.2 Chaetomium *spp*

Chaetomium species are found mostly in soil and organic compost. It is a mycofungicide agent used mostly for protective and curative purposes. According to Dhingra et al. (2003), *Ch. Bostrychodes* and *Ch. olivaceum* have been used severally as biofertilizers for compost enrichment. Most interesting also is that the product of *Chaetomium* species has in recent time been used as fungal biofertilizers. A good example is seen in Ketomium, a bioproduct formulated from *Ch. Globosum* and *Ch. cupreum* which serves as plant growth stimulants (Jehangir et al. 2017). As a unique strategy, *Chaetomium* spp. have developed ability to enable the suppression of bacteria and other fungi growth through competition, mycoparasitism, and antibiosis (Marwah et al. 2007). *Chaetomium globosum* and *Ch. cupreum* control most importantly root rot disease in black pepper, citrus, soybean stem, and strawberry with tendency of reducing sugar beet damping-off diseases (Dhingra et al. 2003; Zarafi and Dauda 2019).

9.4.3 Penicillium *spp*

Penicillium spp. are phosphorus solubilizing agent. They act as biofertilizers by enriching compost and soil quality (Sharma et al. 2013). Some of the important species in this genus are *P. bilaji*, *P. italicum*, *P. simplicissimum, P. oxalicum*, *P. frequentans,* and *P. rubrum* (Yadav et al. 2018b). They act as zinc solubilizers, e.g., *Penicillium simplicissimum and Penicillium sp* in combination with *Aspergillus awamori* are used as phosphate mobilizing biofertilizers. Mishra et al. (2013), in their finding suggested that combination of *Penicillium* and *Trichoderma* increases the development of wheat and soybean under nursery condition. Some commercial products formulated with *Penicillium spp* (*Penicillium bilaiae*) enhance accumulation of phosphorus (P) and increase yield in canola (*Brassica napus*) (Chang and Yang 2009; Chandrashekrappa and Basalingappa 2018). In their works, they suggest these fungi (*Penicillium radicum* and *P. italicum*) to be of phosphate-solubilizing taxa, with *Penicillium radicum* serving as a good plant growth promoter in wheat roots. Elsewhere, *P. italicum* from the rhizosphere soil also has ability to solubilize tricalcium phosphate (TCP) and promoting efficient soybean growth and production (Ram et al. 2015), while *Penicillium* spp. serves as phosphate solubilizer and general plant growth stimulator (Sumita et al. 2015).

9.4.4 Aspergillus *spp*

These are fungi that help in unlocking the soil phosphate complexes. This is accomplished through the synthesis of an organic acid, which dissolves the phosphate in the soil for plant uptake (Zarafi and Dauda 2019). A good example is *Aspergillus niger;* this agent facilitates plant growth through root formation (biopromoter). It improves soil quality and can be used to produce zinc solubilizing biofertilizers. An example of the biofertilizers made from *Aspergillus niger* includes “Ambiphos”; it secretes organic acids, which aid in dissolving unavailable phosphate into soluble form and make it available for plants use. In addition, Ligno Biocom post culture is also a good biofertilizers made from *Aspergillus awamori,* this serves as an enhancer for compost degradation (Sumita et al. 2015). Most importantly, these fungi genera (*A. flavus*, *A. tubingensis*, *A. awamori*, *A. terreus, A. fumigates*, *A. niger,* and *A. melleus*) are able to solubilize inorganic phosphate through the production of citric acid, gluconic acid, glycolic acid, oxalic acids, and succinic acid. *Aspergillus fumigatus* which most often isolated from compost has been reported to be potassium releasing fungus (Barroso et al. 2006, Akintokun et al. 2007, Lian et al. 2008, Sharma et al. 2013). Aspergillus spp. are also considered as microphos biofertilizers because of their ability to release phosphate from the bounded and insoluble state (Jehangir et al. 2017).

9.4.5 Gliocladium *spp*

Gliocladium species are common soil saprobes. They are parasites to many plant pathogens such as *Sporidesmium sclerotiorum* and *Fusarium* spp. It attacks the fungal host by direct hyphal contact and forms pseudoappressoria. Engineered strain of *Gliocladium catenulatum* (Strain JI446) has also been used as a wettable powder applied in soils, roots, and foliage to reduce the incidence of damping-off disease in the greenhouse (Viterbo et al. 2007; Youssef and Eissa 2014). *Gliocladium virens* has been used as a biological control agent against a wide range of soil-borne pathogens such as Pythium and Rhizoctonia under greenhouse and field conditions. It also produces antibiotic metabolites such as gliotoxin which has anti-bacterial, anti-fungal, anti-viral, and anti-tumor activities. A good example is *Gliocladium catenulatum*-JI446, a commercialized bioagent that has been used to reduce the impact of damping-off disease caused by *Pythium ultimum* and Rhizoctonia solani (Punja and Utkhede 2004; Kaewchai et al. 2009; Nissipaul et al. 2017).

9.5 Biology of Fungal Biofertilizers

The use of fungal biofertilizers in sustainable agriculture has been gaining prominence in recent times, not only because it allows for effective utilization of mineral elements such as nitrogen and phosphorus (Alori et al. 2017), but also enhances mineral acquisition, transportation as well as acting as an efficient biocontrol agent. Fungal mycorrhizal symbiosis is arguably the most important symbiosis because of its agricultural importance (Yadav et al. 2019a, b, c). It involves the application of a wide range of fungi as biofertilizers. In real term, these plant species form mycorrhizal associations by acting as a critical linkage between soil and plant roots. This association is usually characterized by the movement of fungal acquired nutrients to plants and the movement of plant produced carbon to fungus (Johri et al. 2015). The fungal mycelium that extends from the root surfaces into the soil matrix captures nutrients from soil solution while the minuscule diameter of the fungal hyphae increases the surface area for absorption, thus increasing its ability for nutrient acquisition and utilization. Interestingly, these occurs when mycorrhizal fungi colonizes plant root systems; just as seen in the endo (arbuscular), ecto, ectendo, arbutoid, ericoid, monotropoid, and orchidaceous mycorrhizae (Table 9.2).

Endomycorrhizae These are a group of fungi that provide biological protection against soil-borne diseases and are associated with most agricultural crops and horticultural soils (Frąc et al. 2018). They occur in most ecosystems of the world and are found in many important crop species such as wheat, maize, rice, grape, soybean, and cotton and also in horticultural species like roses and petunias. Commonest among them is arbuscular mycorrhizal fungi (AMF). Bagyaraj and Ashwin (2017), in their work, reported significant increases in crop yield following inoculation with AMF which aid in stimulating key effects such as root development, improved soil structure, increased nutrient uptake, and mobility of ions. Besides enhancing plant tolerance to stresses, endomycorrhizae improves the general well-being of plants.

Ectomycorrhizae (ECM) The fungi in this group are characterized by the formation of a thick mantle structure within the intercellular spaces of root cortex. They also form sheath around the feeder root, thus acting as an interface for nutrient uptake (Bücking et al. 2012). They are surrounded by living cells in the host roots leading to the development of an extensive network called Hartig net. This Hartig net acts as both storage and transport organ for phosphorus. Most importantly, ectomycorrhizae are common in members of the families of Pinaceae, Fagaceae, Betulaceae, Salicaceae and Myrtaceae.

Table 9.2 Mycorrhizal fungi and their attributes (Jagnaseni et al. 2016)

Mycorrhizal type	Fungal taxa	Plant taxa	Intracellular colonization	Fungal sheath	Vesicle
Arbuscular	Glomeromycota	Bryophyte Pteridophyta gymnosperms angiosperms	Present	Absent	Present or absent
Ecto	Basidiomycota Ascomycota Zygomycota	Gymnosperms angiosperms	Absent	Present	Absent
Ectendo	Basidiomycota Ascomycota	Gymnosperms angiosperms	Present	Present or Absent	Absent
Arbutoid	Basidiomycota	Ericales	Present	Present or Absent	Absent
Monotropoid	Basidiomycota	Monotropoideae	Present	Present	Absent
Ericoid	Ascomycota	Ericales gymnosperms	Present	Absent	Absent
Orchidaceous	Basidiomycota	Orchids	Present	Absent	Absent

9.5.1 Fungal Biofertilizers Enhance Mineral Acquisition and Transport

The primary goal of AMF inoculation is to increase and enhance mineral acquisition and transport. Clark (1997), in his work observed increased plant acquisition of mineral nutrients upon AMF addition. During seasonal variation (dry season), soil structure and porosity determine soil water retention ability. As a result, this agent "AMF" influences hormonal flow and changes information from plant roots to shoots, and affects stomatal responses when soil water potential is lowered (Odoh et al. 2019a, b). In the work of Jagnaseni et al. (2016), they maintained that mycorrhizal associations increase nutrient uptake during water stress through hydraulic conductivity in the roots. They occur as the hyphal sheath, Hartig net, and extraradical mycelium. These fungal mantles represent a significant apoplastic barrier creating a closed interfacial apoplast, thus enabling nutrient transfer (Bücking 2011; Bücking et al. 2012).

Upon application, the differential expression of plant and fungal uptake transporters in the mycorrhizal interface plays a role in the development of a strong concentration gradient across the mycorrhizal interface. Elsewhere, high affinity phosphorus (P) and nitrogen (N) transporters of ECM and AM fungi are expressed in the ericoid mycorrhiza (ERM), but down-regulated in the intraradical mycelium (IRM). This favors the active absorption of nutrients by the ERM, but reduces nutrients re-absorption process in IRM (Willmann et al. 2007; Fellbaum et al. 2012; Bücking and Kafle 2015). Consequently, AM and ECM fungi store significant amounts of P as poly P where they are assumed to play an important role in the transport of P and N from the ERM to the IRM (Bücking and Kafle 2015), unlike in hydrolysis of poly P where IRM would release Pi and Arg into the fungal cytoplasm to facilitate the efflux catabolic product of the urea cycle into the mycorrhizal interface. In general, AM and ECM fungi regulate nutrient transport in host cells via accumulation of poly P while inducing carbon supply in host plant, a process that also triggers polyp hydrolysis (Cruz et al. 2007; Bücking and Kafle 2015).

9.5.2 Fungal Biofertilizers Enhanced Nitrogen Fixation

Soil nitrogen is considered a valuable nutrient for plant growth. It is also one of the most essential micronutrients for food production. They exist in the form of ammonium, nitrate, and amino acids. Bücking and Kafle (2015) in their research reported that the ERM of AM and ECM fungi takes up inorganic N sources (ammonium [NH^{4+}] or nitrate [NO^{3-}]) from the soil. Through protein transporter named AMT1, nitrogen is taken up by plants as ammonium. During glutamine synthetase formation, this ammonium in combination with glutamate forms glutamine in the extraradical mycelium. Interestingly, NH^{4+} has been described as the preferred N source of mycorrhizal fungi, because its uptake is energetically more efficient than the uptake of NO^{3-}. In *Hebeloma cylindrosporum,* AMT1 and AMT2 are expressed as NH^{4+} transporters and regulated by exogenous NH^{4+} supply. The expression of both transporters is up-regulated under low NH^{4+} supply conditions, but down-regulated in response to an exogenous supply of NH^{4+}. More importantly, low affinity NH^{4+} transporter (AMT3) also enables the fungus to maintain a basal level of N uptake and assimilation at high exogenous supply conditions (Bücking et al. 2012; Wipf et al. 2019). Advanced studies on N transport in the AM symbiosis propose breakdown of Arg in the IRM followed by subsequent transfer to the host using the mycorrhizal interface (Fellbaum et al. 2012).

9.5.3 Fungal Biofertilizers Enhanced Phosphate Solubilization

Phosphorus (P) is an extremely immobile element present in the soil. It is very vital for plant growth. One of the major roles of vascular-arbuscular (VA) fungi is the supply of phosphorus to plant roots via phosphate transporters in the hyphal membrane (Rastegari et al. 2020a, b). This enables the fungi to provide phosphorus as poly P pool to the plants. The mycorrhizal hyphae present outside the root of the host plant known as the networks of filamentous, extraradical hyphae of AM fungi help in the uptake of freely available phosphates. Generally, the fungal hyphae extend beyond the host root to enable greater soil volume contact for phosphate acquisition. This fungus (AM fungi) hydrolyzes organic phosphates to soluble forms for plant use. This uptake is done using the phosphate transporter of the Pht1 family. According to Vergara et al. 2019, this fungus has two separate uptake systems for phosphorus: (a) a high affinity system that works against an electrochemical potential gradient. This takes up the Pi from the soil via proton cotransport and (b) a low affinity system which facilitates the diffusion of Pi across the fungal plasma membrane. The expression of these transporters is often regulated by responses to externally available P concentration and P demand of the fungus (Johri et al. 2015).

9.5.4 Fungal Biofertilizers as an Efficient Biocontrol Agent

Biological control agents are referred to as organisms that suppress plant diseases. In other words, they are considered as the utilization of introduced or resident living organisms such as fungi to reduce pressure and effects exerted by plant pathogens or suppressing reproduction of their kinds (Khokhar et al. 2012; Yadav et al. 2020a, b). Various fungal biofertilizers possess this ability, for example, *Trichoderma harzianum*—a species with biocontrol potential against *Botrytis cineria*, *Fusarium*, *Pythium,* and *Rhizoctonia* (Redda et al. 2018); *Chaetomium globosum* and C. *cupreum*,—having biocontrol activity against root rot disease caused by *Fusarium*, *Phytophthora,* and *Pythium* (Aggarwal 2015); *Coniothyrium minitans*—a mycoparasite of Sclerotinia and *Fusarium oxysporum* (Smolińska and Kowalska 2018). Besides inducing biocontrol, mycorrhizal associations also protect plants against heavy metal toxicity (copper, zinc, iron, manganese, cadmium, nickel, etc). Ectomycorrhizal fungi protect trees by accumulating and immobilizing these toxic metals in the mycorrhizal mantle (Odoh 2017). Also, this association enhances detoxification mechanisms through extracellular heavy metal chelation (e.g., glycoprotein glomalin), binding of heavy metals to rhizodermal cell walls, and distorting heavy metal uptake mechanism. In addition, fungal biofertilizers also act as biocontrol agents (BCA) by competing for nutrients and space or by producing metabolites that impede spore germination (fungi stasis), kill the cells (antibiosis), or modify the rhizosphere (acidifying the soil) so as to prevent pathogens multiplication (Khokhar et al. 2012).

In mycoparasitism, biocontrol may result from a direct interaction between the pathogen itself and the BCA as they rely on the recognition, binding, and enzymatic disruption of the host fungus cell wall (Abdallah et al. 2018).

9.6 Sustainable Agricultural Productions

Sustainable agriculture is an eco-friendly approach in agricultural practices where negative impacts or activities on environment are limited. There is no doubt that agricultural practices such as excessive tilling of the soil, deforestation, bush burning, and indiscriminate use of agrochemicals all contribute to environmental degradation. Sustainable agriculture in a nutshell is aimed at employing agricultural practices and techniques that are less harmful to the soil and have minimal use of non-renewable resources (Figueiredo et al. 2017). To meet the global need and demand for food sufficiency, suitable agriculture would require systematic and efficient use of biological inoculants (bacteria or fungi) to increase the mobilization of key nutrients especially pests and disease control while improving general plant productivity (Owen et al. 2015). According to Sivasakthivelan and Saranraj (2013), these biological inoculants are composed of live beneficial microorganisms needed for plant development unlike their chemical counterparts.

9.7 Role of Fungi in Sustainable Agro-Practices

The use of fungi as agents to improve soil fertility, water uptake, nutrient availability, induce environmental stress tolerance, biocontrol as well as in limiting the use of agrochemicals has long been identified (Hatami and Ahangarani 2016; Figueiredo et al. 2017; Odoh et al. 2019a). It has been well established that plants rely solely on these interactions in their root zone to survive. Among the many functions performed by these microbial consortiums include transformation of plant nutrients such as nitrogen and phosphorus, and promotion of plant growth and productivity (De La Peña and Loyola-Vargas 2014). Fungal agents act as inhibitors or antagonizers of phytopathogens (biocontrollers), promote plant growth (biostimulants), activate mineral nutrients, and fix atmospheric nitrogen (biofertilizers) as part of sustainable agricultural practices (Odoh et al. 2019a). Arbuscular mycorrhizal fungi (AMF), a group of soil fungi that live in symbiosis with most agricultural crops, have the ability to mobilize mineral nutrients from soil for their plant hosts. According to the study carried out by Koller et al. (2013), arbuscular mycorrhizal fungi colonize the cortical cells of vascular plants where arbuscular structures are developed, which allow for the exchange of nutrients among the symbionts. Baum et al. (2015) in their works also noted that fungi by means of their hyphal growth have the capacity to extend the volume of soil that can be accessed by plant roots for uptake and movement of water and nutrients.

9.7.1 Fungal Biofertilizers as an Alternative to Chemical Fertilizers

Fungal biofertilizers are renewable source of plant rhizospheric nutrients that could serve as a close alternative to chemical fertilizers (Kannaiyan 2002). The use of fungal biofertilizers can help to curb the excessive use of synthetic fertilizers, which when used indiscriminately causes detrimental effects to the environment and human health (Singh and Yadav 2020; Yadav et al. 2017a, b; Odoh et al. 2019b).

Chemical fertilizers are non-renewable. They deplete soils organic matter and make them prone to erosion. It also causes imbalance in the soil salinity leading to chemical run-offs. Fungal biofertilizers on the other hand are natural and provide the host plant with water, nutrients, and protection against pathogens. Fungal biofertilizers include plant growth stimulating fungi (*Trichoderma*), mycorrhizal fungi (ectomycorrhiza and arbuscular mycorrhizae), enzyme-producing fungi for compost production, and P/k-solubilizing fungi. Mycorrhiza fungal biofertilizers also known as vesicular arbuscular mycorrhiza (VAM) help in retaining moisture around the root region and increase resistivity towards different root and soil pathogens unlike the chemical fertilizers (Sadhana 2014). In a study conducted by Zhang et al. (2018), *Trichoderma* biofertilizers were shown to increase soil antifungal compounds that suppressed pathogenic fungi and allowed for improved grassland biomass. This suggests that *Trichoderma* biofertilizers could be an important tool for sustainable management of soils and plants productivity.

9.7.2 Benefits of Fungal Biofertilizers in Sustainable Agriculture

A number of fungal biofertilizers are produced from cultures of fungi with proven capacity for improvement of soil fertility and increase in crop yield. These bioinoculants such as endophytic fungi (*Penicillium, Aspergillus*, *Piriformospora,* and *Curvularia*) solubilize and mineralize phosphorus (Rai et al. 2013; Mehta et al. 2019). One of the most fundamental fungi for sustainable agricultural production—arbuscular mycorrhizal fungi—increases the availability of nutrients through their mycelia network and allows for efficient absorption of nutrient by plants. Pal et al. (2014) noted that when mycorrhiza are used as biofertilizers they enhance uptake of phosphate, zinc, and water leading to improved hardiness and uniform growth of transplanted stock. The arbuscular mycorrhizal fungi also improve soil structure and control plant diseases thus implying that plants colonized by these microbes grow better than those without them (Tripathi et al. 2017). However, for phosphate solubilization, endophytes are the major contributors. Here, they colonize plants without inducing symptoms of disease making it a more aggressive colonizer of plant root than non-endophytic microbes. These endophytes convert soluble soil phosphate into soluble forms through the secretion of organic acids with concomitant changes in the texture, structure, and water holding capacity of the soil.

9.8 Current Status and Global Trend of Fungal Biofertilizers Usage

The use of fungi as biofertilizers is not entirely new. It is indeed an old biotechnological application with record of proven success across the globe. Over the years, over 65% of research and experiments involving fungal biofertilization are conducted or carried out in greenhouses and 24% in open fields with varying abiotic conditions (Berruti et al. 2016). One of the major fungi that have successfully been used as bioinoculant is *Glomus* sp. Isolated from tropical soil of Taiwan, two species of AM were used by Young et al. (1986), in a bench scale experiment to observe the effect of inoculation of AM fungi on the yield and mineral phosphate utilization of soybean plant. Elsewhere, researchers have conducted experiment by growing Papaya seedlings in pot containing an average of 150 spores of AM fungi (*Glomus aggregatum, Glomus etunicatum, Glomus clarum, Glomus mosseae,* and *Acaulospora scrobiculata*) (Cheng and Chung 2004; Chiu et al. 2004). These plants grew faster and with a wider root system than that of the control.

Despite the benefits associated with the use of fungal biofertilizers in crop production, its usage in sub-Saharan Africa is still low compared to Asia, Europe, and America. Europe and Latin America are currently the top consumers of biofertilizers due to the rigorous and tight regulations imposed on chemical fertilizers. This is followed by Asia-pacific which controlled 34% of the market as at 2011 (Raja 2013). The European biofertilizers market as at 2017 is valued at USD 335.9 million and is expected to grow by at least10.2% by the year 2023. At the moment, farmers in Europe are constantly being encouraged to use biofertilizers to replace completely or partly the use of chemical fertilizers. One of the constraints associated with the utilization of biofertilizers according to Lucy et al. (2004) includes nonspecific host–inoculant relationships, different physical and chemical edaphic conditions, poor competitive ability with autochthonous strains, and a deficiency of adequate formulations of the live strain.

In the tropics, factors such as technology, funding, government regulation, and lack of sensitization have impeded the full exploitation of biofertilizer as the best alternative in agriculture. In areas faced with severe abiotic stress such as drought, e.g., (Sudan) mycorrhizal fungi biofertilizers are employed to enhance the host plants osmotic adjusting ability. In East Africa, there is a low demand and use of biofertilizers in agricultural productions. This is in contrast to countries such as Brazil, India, China, and Japan, with proven government support and where almost all crops are produced with the aid of biofertilizers (Schutte-Geldermann 2013; Douds et al. 2000). In Canada, for instance, the Canadian Food Inspection Agency (CFIA) has well-defined procedure accepted by the industry for the production and registration of biofertilizers. Conversely, in countries like Nigeria, Kenya, and Ethiopia, its application has not been clearly defined as assessment has shown presence of contaminants and absence of active ingredients in its biofertilizers and other agricultural bioproduct formulations (Jefwa et al. 2014; Masso et al. 2014) (Table 9.3).

9.9 Formation of Fungal Biofertilizers

Fungi biofertilizer is formulated either in liquid or in solid state. Often time, these bioproducts are packaged as dry biomass (dusts, granules, and briquettes) and suspension (water based and emulsions). The granules are discrete masses containing an inert carrier like charcoal, lignite, clay minerals (vermiculite, bentonite), starch polymers, dry fertilizers, and ground plant residues. In some cases, the choice of carrier depends on absorption, hardness, bulk density, and product disintegration rate in water. During formulation, these microbial bioagents get coated with various materials to slow and control the rate of their release. In the solid-based state however, their shelf-life is within 6 months as they are not tolerant to UV rays and temperatures more than 30 °C. Usually, the population density of these microbes ranging from 10^8 CFU/ml, this reduces with time (10^6 CFU/mL) at fourth month, reaching almost nil at the end of sixth month. Again, the improper sterilization of carrier material and their handling such as mixing the organism with carrier and packing serve as source of contaminations. Because of this, the inoculant packet could not hold desired biofertilizers organism for longer time and has not become effective and popular among the farmers in some climes. Furthermore, the quality of the biofertilizers gets deteriorated with longer and unsafe storage conditions. These have in many ways contributed to the limitation associated with biofertilizers application and in some cases where it could not be able to give viable results in the field.

Owing to these challenges, the liquid formulation of organisms with a count of 10^9 CFU/ml (*Azospirillum* and *Phosphobacteria*) was developed to avoid drawbacks of biofertilizers and to increase the quality and shelf-life of bioinoculants. Here, preservatives are added with the microbial cultures and packed in bottles with improved shelf-life of about 2 years. According to Pal et al. (2015), the application

Table 9.3 Summary of the biofertilizers commonly used in different countries and the associated crop plants

Country	Fungal biofertilizer	Crop grown	References
USA	Arbuscular mycorrhizal fungi	Rice	Bernaola et al. (2018)
Bangladesh	Vesicular arbuscular mycorrhizae	Soybean	Das and Dang (2010)
India	Vesicular arbuscular mycorrhizae	*Stevia rebaudiana*	Das and Dang (2010)
Egypt	Vesicular arbuscular mycorrhizae	Sweet fennel	Zaki et al. (2010)
Iran	Phosphate solubilizing + *Trichoderma* fungi	Canola	Mohammed (2010)
Nigeria	Arbuscular mycorrhizal fungi (*Glomus intraradices*)	Rice	Oladele and Awodun (2014)
Mexico	*Rhizophagus intraradices*	Rice	Orona-Castro et al. (2013)
Brazil	*Cunninghamella elegans*	Melon	Oliveira et al. (2014)
Colombia	*Penicillium janthinellum*	Rice	Moreno-Sarmiento et al. (2007)

of 1 ml of liquid biofertilizers is equivalent to the application of 1 kg of 5 months old carrier based biofertilizers. Increasing research has often suggested amendment of carrier materials to increase effectiveness of the biofertilizers (Itelima et al. 2018). These carriers are the delivery vehicle of live biofertilizers from the factory to the field which upon application turns into organic, inorganic, and/or synthetic materials in the environment (Mahanty et al. 2016). Bashan et al. (2014) in their work reported that carriers have tremendous importance in delivering the right number of viable cells in good physiological condition. It also provides a short-term protective niche to the biofertilizers in soil, either physically via the provision of a protective surface of pore space or nutritionally via the provision of a specific substrate (Arora et al. 2010); hence a good carrier should be non-toxic, high moisture absorption capability, easy to process and free of lump-forming materials, easy to sterilize, available in adequate amounts, cost-effective with good pH buffering capacity (Mahanty et al. 2016).

9.10 Mode of Application of Bio-fertilizers

Below are several ways biofertilizers can be applied:

- Seed inoculation with powder formulations
- Dry biofertilizers mixed with the seeds in the seed hopper
- Sprinkle method (a small amount of water mixed with seeds before peat powder is added and mixed)
- Slurry method (the biofertilizer is suspended in water then added to the seeds and mixed)
- Seed pelleting
- Biofertilizers and adhesive are applied as slurry to seeds and coated with ground material like lime
- Peat suspension in water sprayed into the furrow during sowing
- Seed treatment or seed inoculation
- Soil application
- Seedling root dip (Bashan 1998).

9.11 Prospects and Challenges of Fungal Biofertilizers Usage

One of the most important limitations of biofertilizers is seen in their nutrient content when compared to inorganic fertilizers as a number of works have reported deficiency symptoms associated with plants grown in biofertilizer treated soils (Itelima et al. 2018). However, this challenge is curbed by the addition of substances such as bone meal (rich in phosphorus), wood ash (rich in potassium), or other substances of natural origin such as phosphate rock to enrich the fertilizer (Itelima et al.

2018). Also, the use of nutrient rich organic materials such as palm wastes (rich in potassium) and wood ash (rich in potassium also) in making biofertilizers serves as a good remedy. Mahimairaja et al. (2008) stated that the addition of phosphorus to wastes makes the biofertilizers more balanced and reduces nitrogen losses. Notably also are the limitations associated with the storage conditions of biofertilizers; this goes a long way in affecting its efficacy. Biofertilizers should be stored in cold storage conditions away from heat and the polythene used in packaging should be of low density grade and thickness of about 50–75 microns (Mishra and Dadhich 2010). As good as they are (biofertilizers), sometimes they do bring about the expected outcome owing to exposure to high temperatures and other harsh environmental conditions. Other constraints limiting the use of biofertilizers technology may include human resource, unavailability of suitable strains, and unavailability of suitable carrier (Ritika and Uptal 2014; Ritika and Uptal 2014). Chen (2006) has identified some bottlenecks for effective biofertilizer inoculation.

- *Unavailability of suitable strains*: This is one of the major constraints in the production of biofertilizers because only suitable strains have ability to survive both in the broth and in the inoculants carrier.
- *Unavailability of suitable carrier*: If suitable carrier material is not available, it becomes difficult to maintain the shelf-life of the biofertilizer. In terms of suitability of carrier, the order is peat, lignite, charcoal, farmyard manure, soil, and rice bran.
- *Lack of awareness among farmers*: Farmers are mostly not aware of biofertilizers and their usefulness in increasing crop yields. They are unaware of the damages caused on the ecosystem by continuous application of inorganic fertilizer and increasing bioaccumulation of toxic materials in plants.
- *Skills and technical knowhow*: This is another problem. This is because the unskilled and inadequate staff farmers are not given proper instructions about the application. This however affects in general terms the success of biofertilizers.
- *Environmental constraints*: Soil characteristics like salinity, acidity, drought, water logging, and a number of climatic conditions affect the use of biofertilizers.

9.12 Conclusion and Future Prospects

Biofertilizers are an environment friendly alternative to chemical fertilizers that have gained prominence in agricultural application in the last few decades. These products are formulated using different microbial genera and consortium. Most popular among them are fungi. Fungi biofertilizers decrease the occurrence of plant diseases by inhibiting their (pathogens) growth and suppressing a number of their biological processes. Besides increasing the soil nutrient uptake and producing bioactive compounds, they also produce hormones and enzymes which stimulate plant growth. Biofertilizers, though affected by some environmental conditions, limited shelf-life, and slow action as compared to chemical fertilizers are still a worthwhile alternative to the latter because of its many advantages. Among the fungal biofertilizers, mycorrhizal biofertilizers products greatly appeal to the agro industry mainly due to its versatility and use of environment friendly technology. Further research in the field, supported by advanced technology, will enhance biofertilizers use worldwide as well as its profitability for the small and marginal farmers.

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Chapter 10
Role of Algae–Fungi Relationship in Sustainable Agriculture

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Contents

10.1 Introduction

Global climate change, extreme weather conditions, and changes in precipitation pattern have had profound consequences on freshwater supplies, crop productivity, and soil health, thus compromising availability of food to feed the rapidly growing population. Moreover, the livelihood of millions of people who are dependent on agricultural based practices for income has been adversely affected (FAO,

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Sustainable development goals). This calls for robust scientifically proven sustainable agricultural approach based on integrated cropping methods and microbial application to mitigate climate change.

The ubiquitous occurrence of microbes is due to their ability to survive under wide range of environmental conditions from low nutrient concentrations to high salinity, from hot and cold deserts to hot springs and snow and under osmotic stress to UV irradiation (Godinho et al. 2013; Gonçalves et al. 2011; Abdel-Raouf et al. 2012). The dynamic microbiome of plant rhizosphere is the main site where chemical and biological interaction takes place between the microbes of the soil and higher plants (Sahu et al. 2018). They assimilate nutrients by various enzyme catalyzed processes in order to improve soil organic matter and maintain the cycling of various minerals like C, N, P, K, Fe, B, and S. The inherent ability of cyanobacteria to form symbioses and fix nitrogen in soil as symbiotic associations with ferns (*Azolla-Anabaena*) or as ecological obligate symbionts with fungi as lichens, besides aiding land restoration, water holding capacity, aquaculture, wastewater treatment, and produce secondary metabolites has been a boon to microbial biotechnology.

10.2 Lichens

Lichens as pioneer species are known to disintegrate and colonize bare rock and initiate formation of soil, thereby paving way for ecological succession (Cooper 1953). Most of the lichenized fungi belong to Ascomycota and few from Basidiomycota in association with either green algal species or cyanobacteria (Tschermak-Woess 1988; Hawksworth et al. 1995; Honegger 1996a, b; Oksanen 2006; Lewis and McCourt 2004).

They are equipped to tolerate desiccation and extreme habitat conditions and can scavenge free radicals due to the presence of oxidoreducatase enzymes like peroxidases and laccases as studied in Peltigeralean lichens (Laufer et al. 2006; Liers et al. 2011; Beckett et al. 2013a, b). These enzymes also act as allelochemics, protecting the Peltigeralean lichens from the detrimental phenolic compounds produced by other organisms (Armstrong and Welch 2007; Beckett et al. 2013a, b).

Lichens are also known as biomonitors of environmental pollution and accumulation of heavy metal sand is known to produce substances with cation chelation properties (Oksanen 2006; Garty 2001; Lawrey 1993). The symbiont together produces an array of bioactive metabolites like dibenzofurans, depsidones, anthraquinones, xanthones, usnic acids, pulvinic acids, atranorin, and other phenolic substances which have antimicrobial, antifungal, antimutagenic, antibiotic as well as allelopathic and anti-herbivoral properties.

10.3 Azolla-Anabaena

The symbiotic association between a free floating heterosporous water fern, *Azolla* and cyanobacterium, *Anabaena* found globally in tropical and temperate regions has high economic value. It has largely been used in agriculture as a potential biofertilizer with outstanding capability of fixing atmospheric nitrogen and rapid decomposition of biomass besides being used as for production of biogas, weed control, manure; poultry feed and fodder (Wagner 1997; Alalade and Iyayi 2006).

Incorporation of *Azolla* in water logged paddy fields along with rice increases its yield by 14–40% (Kannaiyan et al. 1983). Its application shows significant enhancement in the biological health of soil, microbial activity, and soil fertility (Singh et al. 2007). Few species of *Azolla*, like *A. microphylla* has been extensively used in phytoremediation and reclamation of heavy metals from polluted water bodies (Arora and Saxena 2005; Umali et al. 2006).

10.4 Role of Cyanobacteria in Nitrogen Fixation

Blue Green Algae is one of the most important nitrogen fixing biological agents which is ecofriendly, fuel independent, cost-effective, and more efficient than N-rich chemical fertilizers (Halperin et al. 1981; Rodrigo and Eberto 2007; Abdel-Raouf et al. 2012). Cyanobacterial inoculants have largely been used to enhance N2 fixation in paddy fields in rice cultivation (Singh 1961; Nayak et al. 2004) besides other crops like barley, oats, tomato, radish, cotton, sugarcane, maize, chili, lettuce (Thajuddin and Subramanian 2005).

It has been reported that cultures of 250g dry mass ha^{-1} of *Tolypothrix tenuis* when added to rice fields increased the yield by 19.5% as compared to 16.6% when 25 kg ha^{-1} Ammonium sulfate was used (Aboul-Fadl et al. 1967; Abdel-Raouf et al. 2012). Nitrogenase catalyzed fixation of N2 in these organisms takes place in specialized cells known as heterocyst since the enzyme is highly sensitive to oxygen. Heterocyst lack both photosystem II and the activity of Ribulose bisphosphate carboxylase, hence they are incapable of producing oxygen as well as fixing carbon dioxide.

Filamentous cyanobacteria sense the nitrogen status of the soil and consequently 5–10% of the vegetative cells transform into heterocyst in response to the heterocyst differentiating signals. The nitrogenase protein complex comprises of two subunits, dinitrogenase encoded by *nif*D and *nif*K genes and dinitrogenase reductase encoded by *nif*H genes. This endergonic reduction of nitrogen to ammonia requires ATP in the form of metabolic energy. Certain heterocysted genera of commercial importance are *Anabaena*, *Aphanizomenon*, *Gloeotrichia*, *Nostoc,* and *Nodularia* (Table 10.1).

Table 10.1 Cyanobacterial based fertilizers

Species	Formulation	Used for	References
Spirulina platensis	Intact cells (Spirufert®-bio fertilizer) Intact cells and wastewater remediation	Foliar treatment on eggplant; Enhancing plant dry weight of leafy vegetables	Osornio-Berthet et al. (2017), Wuang et al. (2016)
Consortium ZOB1	Intact cells	Biostimulator for plants	Zayadan et al. (2014)
Anabaena, Cylindrospermum, Nostoc, Tolypothrix	Intact cells for Nitrogen fixation and as a growth promoting substance	Wetland rice cultivation	Ashok et al. (2017)
Frankia Hsli10	Biofertilizer for saline soils		Srivastava and Mishra (2014)

10.5 Plant Growth Promoting Substances

Plant growth regulating substances produced by cyanobacteria, microalgae as well as macroalgae and seaweeds include auxin like substance (Verma et al. 2016) (Venkataraman 1981; Crouch and Van Staden 1993), cytokinin like (Stirk and Van Staden 1997a, b), gibberellic like (Shen-Rui and Shen 1997), toxins, enzyme activators (Yadav et al. 2016; Senn 1987), and other organic acids (Yadav et al. 2015, 2019a). Auxinic like activity is detected from extracts of cyanobacterium *Nostoc muscorum* on paddy fields and seedlings of *Panicum miliaceum* and seed germination stimulation in wheat, sorghum, maize, and lentil (Adam 1999). Gibberellic like activity has been reported in *Phormidium foveolarum* (Gupta and Agarwal 1973; Abdel-Raouf et al. 2012). Cyanobacterial filtrates of *Anabaena oryzae, Nostoc calcicola, Microchaete tenera,* or *Cylindrospermum muscicola* have shown to increase root and shoot length of rice seedlings (Mohamed 2001). Algal exudates from *N. piscinale* and *N. muscorum* increase rate of germination, total proteins, and soluble sugar content (Mohamed 2001).

Root growth promoting activity by seaweed extracts was observed (Biddington and Dearman 1983; Khan et al. 2009). Presence of glycine betaines in seaweed extracts of *Ascophyllum nodosum* has shown to increase the chlorophyll content in tomato leaves by inhibiting chlorophyll degradation (Whapham et al. 1993). Seaweeds contain a range of compounds like kahydrin, alginic acid, betaines, microelements, and vitamins which synergistically act as growth promoters (Agarwal et al. 2016).

Seaweed extracts increase as well as enhance the development of fruit formation of tomato plants. Their application has also shown to enrich the fatty acid content of olive oil in linolenic and oleic acid (Craigie 2011). Application of extract of *Rosenvingea intricata* has shown to enhance pigment content, number of leaves as well as stimulate lateral root formation in *Abelmoschus esculentus* (Craigie 2011). Application of seaweed extracts from *Gracilaria debilis, Sargassum liebmanni,* *Sargassum vulgare*, and *Ulva fasicata* at low concentration has been reported to increase germination, root length as well as overall growth in *Lens esculenta* (Mendoza-Morales et al. 2019). Besides the most potent commercial growth stimulants derived from *A. nodosum, Laminaria* spp*, Ecklonia maxima, Sargassum* spp, *and Durvillaea* spp.*,* it has been recently shown that extracts from *Ulva fasicata,Gracilaria caudate,* and *Palisada perforata* also have significant increase in growth and yield of *Pisum sativum* (Duarte et al. 2018).

Reports from Ali et al. (2019) showed that foliar application of 0.5% *Ascophyllum nodosum* showed significant increase in overall growth like change in height of the plant, number of leaves, plant dry biomass, length of root and chlorophyll content and photosynthetic potential in tomato and sweet pepper crops besides reducing the disease incidence caused by pathogens *Xanthomonas campestris pv. vesicatoria* and *Alternaria solani* in the tropics.

10.6 Role of Secondary Metabolites Derived from Algae

Marine macro as well as microalgae contains a myriad of bioactive metabolites like mannitol, polysaccharides, oligosaccharides, laminarin, alginic acid, antioxidants, phytohormones, quinones, alkaloids, and vitamins, besides lipids, pigments and accessory pigments which have a wide range of biological role. Extracts of these compounds prepared in different organic and inorganic solvents have shown positive results as phytopathogen biocontrol agents (Abdel-Raouf et al. 2012), as a source of valuable elicitors inducing systemic acquired resistance (Agarwal et al. 2016), as commercial antioxidants and biostimulant.

10.6.1 Role as Biocontrol Agents

Studies show that the antibacterial properties of algal extracts are accredited mainly to the diverse sets of saturated and unsaturated fatty acids, phenols, and polyphenols. Extracts of and extracellular products of *Nostoc muscorum* inhibit the growth of *Sclerotinia sclerotiorum* and *Rhizoctonia solani*, causal agents of damping-off (Zaccaro et al. 1991; Abdel-Raouf et al. 2012). Noscomin from *Nostoc* commune has shown increased antibacterial activity against *Bacillus cereus, Staphylococcus epidermidis, Escherichia* coli than standard drugs. Also extracts from *Anabaena* showed antibacterial properties against vancomycin-resistant *S. aureus* (Bhateja et al. 2006). Norbietane diterpenoid from *Microcoleus lacustris* and carbamidocyclophanes from *Nostoc* sp.CAVN10 showed inhibitory action against *S. aureus* and fatty acids like coriolic acid and α-dimorphecolic acid from *Oscillatoria redekei* showed similar effect on *B. subtilis* and *S. aureus*.

10.6.2 Antibacterial Potential

Antibacterial action of *Sargassum swartzii* (methanolic extract) has been reported against *Pseudomonas syringae*, which causes leaf spot disease on *Gymnema sylvestre* (Kumar et al. 2008) and *Xanthomonas oryzae* pv. *oryzae* causing bacterial blight of rice (Arunkumar et al. 2005). *Agrobacterium tumefaciens* causing Crown gall disease in tomato plants have shown drastic reduction when extracts from *Cystoseira myriophylloides* and *Fucus spiralis* were applied (Esserti et al. 2017). Also extract of *Padina gymnospora* prepared in methanol has high proportion of palmitic acid which showed inhibitory activity against *Ralston solanacearum* (Ibraheem et al. 2017). Nonpolar extracts from *Chlorella vulgaris, Isochrysis galbana,* and *Microchloropsis gaditana* showed inhibitory activity against gram positive bacterium *Enterococcus faecium* and *Staphylococcus aureus* (Ronga et al. 2019). Diatoms like *Skeletonema costatum* and *Phaeodactylum cornatum* produce metabolites which have antibacterial properties against pathogens like *Staphylococcus aureus* and *Vibrio anguillarum* (Naviner et al. 1999; Desbois et al. 2008). Recent studies have even shown that benthic diatoms like *Nitzschia* and *Navicula* are capable of inhibiting growth of *Vibrio alginolyticus, V. campbellii, and V. harveyi* which are pathogenic to mollusks, crustaceans, and fish.

10.6.3 Antifungal Potential

Algal polysaccharides like carrageenan and other oligosaccharides are known to be the cause of resistance against a variety of pathogens (Vera et al. 2012; Agarwal et al. 2016).κCarrageenan has been shown to elicit antifungal protein β-1,3-glucan hydrolase in cultures of *Rubus fruticosus* (Patier et al. 1995) and induce antimicrobial metabolites like phytoalexins in *Hypnea musciformis* on peas, chickpeas, carrots, and potatoes (Arman and Qader 2012; Bi et al. 2008; Agarwal et al. 2016). Studies also showed that sap of *Kappaphycus alvarezii* increased the Salicylic acid levels in order to enhance systemic acquired resistance by amplifying the transcription of defense related PR genes and upregulation of Pti4, an Ethylene responsive factor, in tomato plants against the soil borne fungus causing charcoal rot, *Macrophomina phaseolina* (Agarwal et al. 2016).

Fungicidal alkaloids from *Tolypothrix tjipanasensis* showed moderate activity against *Candida albicans, Trichophyton mentagrophytes, and Aspergillus flavus*. Fungicidal compound calophycin produced by *Calothrix fusca* was operational against *Aspergillus oryzae, Candida albicans, Penicillium notatum, and Saccharomyces cerevisiae*. A complex mixture of antimicrobial peptide, called Hormothamnin A, from the cyanophyte *Hormothamnion enteromorphoides* showed antifungal and antibacterial activity against an array of microbes. In vivo utilization of *Spatoglossum variable* shows significant activity against *Fusarium solani* and

Macrophomina phaseolina, known to cause the root rot in eggplant and watermelon (Matsum and Nakai) and stimulate growth as well.

Studies from (Tuney et al. 2006) showed that abstracts of *Cystoseira mediterranea* and *Ulva armoricana* prepared in different solvents had strong antifungal activity. Extracts from *Ascophyllum nodosum* enhanced resistance against *Phytophthora capsici* on pepper (Lizzi et al. 1998), *Alternaria radicina* and foliar blights on carrots, and *Didymella applanata* on cucumber (Jayaraj et al. 2011). The biologiaclly active derivatives of phenolic compounds and flavonoids of *Sargassum vulgare* prepared in methanol have been shown to possess strong antifungal action against *Pythium aphanidermatum* (Ammar et al. 2017).

10.6.4 Antiviral Potential

Research has shown that macroalgae bioactive compounds have a wide array of antiviral effects (Pulz and Gross 2004; Zaid et al. 2016). Sulfated polysaccharides are known to block viral adsorption on plant cell membranes (Sano 1999; Pardee et al. 2004) and alginates with concentration as low as 10mg/mL inhibit potato virus X (PVX)(Pardee et al. 2004). Compounds like Betaines, dictyodial, dictyol C, and Dictyol H derived from brown alga *Dictyota ciliolate* and Vitamin C, omega 3-fatty acids and peptides from red marine algae have prominent antiviral activities.

Anti-TMV activity has been found in the κ and β carrageenans extracted from *Tichocarpus crinitus* (Nagorskaia et al. 2008) and lectins isolated from *Ulva pertusa* (Wang et al. 2004; Liu et al. 2005).

10.6.5 Anti-nematodal Potential

Lyophilized biomass of *Spatoglossum variabile, Polycladia indica, and Maelanothamnus afahusaini*, when sprayed on watermelon and eggplant, reduced the infection caused by root knot nematode, *Meloidogyne incognita* (Baloch et al. 2013). Betaines derived from *Ascophyllum nodosum* caused similar reduction in infection by *M. javanica and M. incognita* on tomato plants as commercial chemical nematicide, carbofuran (Wu et al. 1998). Root damage by *M. incognita* in tomato plants was greatly reduced on application of seaweed extract, Keplak 66 derived from *Ecklonia maxima* (Featonby-Smith and Van Staden 1983). Recent studies have shown that extracts from these seaweeds also affect the hatching of eggs and sensory perception of root knot nematodes like *M. chitwoodi and M. hapla* (Ngala et al. 2016).

10.6.6 Biopesticidal

To combat and reduce the risk associated with use of synthetic insecticides both on environment, agriculture, and human health, considerable research has been done on implementing ecofriendly biopesticides from algal, bacterial, and fungal communities (Rastegari et al. 2020a, b; Yadav et al. 2020; Singh and Yadav 2020). Marine macroalgal extracts have insecticidal properties which are employed in Integrated Pest Management practices (Manilal et al. 2009; Sahayaraj and Kalidas 2011; Asha et al. 2012). Crude algal extracts from *Caulerpa scalpelliformis, Padina pavonica; Sargassum tenerrimum and Ulva fasicata and U. lactuca* show insecticidal activity against Hemipteran cotton insect pest *Dysdercus* spp (Sahayaraj and Kalidas 2011). Seaweed *Padina pavonica* had nymphicidal and ovicidal impact on *D. cingulatus* (Sahayaraj and Kalidas 2011). Extracts from *Polcamium cartilagineum* and *P. violaceum* showed insecticidal activity against tobacco horn worm, as well as on tomato moth, *Tuta absolute* and green bug, *Schizaphis graminum*, and sucking pest like *Aphis fabae* (Sanmartin et al. 1991). Volatile oils extracted from *Actinotrichia fragilis, Liagora ceranoides, and Colopmenia sinuosa* showed insecticidal activity against *O. Mercator and T. castaneum.*

10.6.7 Antioxidative Properties

Array of bioactive compounds in the form of pigments and storage compounds is present in microalgae which exhibit beneficial roles like antioxidant, anticancer anti-inflammatory, anti-obesity, and anti-angiogenic properties. Accessory pigments in the form of carotenoids and xanthophylls are the most efficient quencher of ROS, singlet molecular oxygen, peroxyl radical, and lipid peroxidation. Carotene, which is the precursor of provitamin A, acts as the stimulator of gap junctional communication and also protects the cell from oxidative damage, is produced naturally in almost all algal strains.

Application of β carotene rich *Dunaliela* has been shown to inhibit LDL oxidation in diabetic patients and influences cellular level of plasma triglycerides, cholesterol, and HDL and reduces occurrence of antherosclerosis. Phytoene and phytofluene also protect cells against UV and oxidative damage and reduce incidence of degenerative diseases. Keto-carotenoid, Astaxanthin produced commercially by *Haematococcus pluvialis* and *Chlorella zofingiensis* has very strong antioxidative activities against cancer, metabolic syndrome, and diabetic nephropathy and neurodegenerative diseases (Table 10.2).

Lutein produced from *Muriellopsis* and *Scendesmus* is an important component of Macula lutea. Fucoxanthin inhibits intracellular ROS formation, reduces nitric oxide levels, and regulates cascade of events under anti-proliferative and anti-inflammatory activities. Flavonoids, tocopherols, Vitamin E, and other phenolic compounds together with the production of cobalamin, ascorbic acid, Butylated

Table 10.2 Agriculturally important seaweed derived products (modified from Khan et al. 2009)

Name of the product	Name of seaweed	Company name	Used as	Formulation
Acadian®	*Ascophyllum nodusum*	Acadian Agritech, Canada	Plant growth enhancer	Soil drench as well as foliar spray
Acid Buf	*Lithothamnium calacerum*	Chance & Hunt Limited, United Kingdom	Animal Feed (Efficient rumen buffer)	To reduce anti-nutritional effects of Phytate
Agri Gro Ultra	*Ascophyllum nodusum*	Agri Gro Marketing Inc.	Plant growth enhancer	
Tri-Kelp™	*Three seaweeds (Laminaria, Sargassum, and Ascophyllum nodosum.)*	Nutri-Tech Solutions P/K (NTS), Australia	Fertilizer enhancer and Plant growth enhancer, Improve water retention	Freeze dried powder
AgroKelp	*Macrocystis pyrifera*	Algas y Bioderivados Marinos, S.A. de C.V., Mexico	Plant growth enhancer	Diluted preparation
Alg-A-Mic™	*Ascophyllum nodusum*	BioBizz World Wide Organics	Plant growth enhancer	Prepared by extracting through cold pressing
Bio-Genesis™ High Tide™	*Ascophyllum nodusum*	Green Air Products, Inc, Oregon	Plant growth enhancer	Applied at root zone/Foliar in very less quantities (has 6% Humic acid)
Biovita	*Ascophyllum nodusum*	PI Industries	Stimulant for plant growth and Natural Fertilizer	Liquid preparation
Emerald RMA	Red marine algae	Dolphin Sea Vegetable company, USA	Health product	Iodine supplement
Espoma	*Ascophyllum nodusum*	The Espoma company	Plant growth enhancer	Instant application mixed with water
Guarantee®	*Ascophyllum nodusum*	MaineStream Organics	Plant growth enhancer	Stress tolerance
Kelp Meal	*Ascophyllum nodusum*	Acadian Seaplants Ltd., Canada	Plant growth enhancer	
Kelpak	*Ecklonia maxima*	BASF, Germany	Plant growth enhancer	Also aims at pest control
Kelpro	*Ascophyllum nodusum*	Techniprocess Biologicos, S.A. de C. V	Plant growth enhancer	
Maxicrop	*Ascophyllum nodusum*	Maxicrop, USA	Plant growth enhancer	Foliar as well as aqueous preparation

(continued)

Table 10.2 (continued)

Name of the product	Name of seaweed	Company name	Used as	Formulation
Nitrozime	*Ascophyllum nodusum*	Hydrodynamics International Inc. Michigan	Plant growth enhancer	Naturally occurring trace elements and macronutrients
Profert®	*Durviella antarctica*	BASF	Plant biostimulant	
Seasol®	*Durviella potatorum*	Seasol International Pty Ltd, Australia	Plant growth stimulant	Also induces stress tolerance
Stimplex	*Ascophyllum nodusum*	Acadian Agritech, Canada	Plant growth enhancer	
Synergy	*Ascophyllum nodusum*	Green Air Products, Inc., Oregon	Plant growth enhancer and induces systemic resistance	Complex metabolic precursors

Table 10.3 Important metabolites and their role derived from microalgae (Modified from Sathasivam et al. 2019)

Metabolite	Microalgae	Uses
Mycosporine like amino acids	*Chlamydomonas nivalis, Scenedesmus*	UV screening agent
Lipophilic and phenolic antioxidant	*Botryococcus braunii, Chlamydomonas nivalis*	Antioxidative and antimicrobial property
B carotene and Astaxanthin	*Dunaliella salina, Haematococcus pluvialis*	Food supplement, additive
Cantaxanthin	*C. nivalis, Chlorella vulgaris*	antioxidant
Fucoxanthin	*Nitzschia spp, Phaeodactylum tricornutum, Isochrysis galbana*	Antioxidant
Zeaxanthin	*Dunaliella salina*	Neutralize free radicals
Glutathione	*Dunaliella salina*	Detoxify metals
PUFA (EPA, DHA, Arachidonic acid)	*Phaeodactylum tricornutum, Nannochloropsis, Odontella aurita*	Nutritional supplements, aquaculture feeds
Vitamin B12, Auxin like 3 methyl indole	*Cylindrospermum, Tolypothrix tenius, Nostoc, Hapalosiphon fontinalis*	Plant growth promoting substance

hydroxytoluene, and glutathione are few of the most potent metabolites present in algal species which have been used in food industry, as an additive and as photoprotective agents in cosmetics.

Production of long chain Polyunsaturated fatty acids (LC-PUFA) like γ-linolenic acid (GLA), Eicosapentaenoic acid (EPA C20:5), and docosahexaenoic acid (DHA, 22:6 omega3) plays a pivotal role in cellular and tissue metabolism, in regulating membrane fluidity, transport of electron and oxygen, thereby reducing the levels of triglycerides and cholesterol in order to control heart diseases and antherosclerosis (Funk 2001; Sathasivam et al. 2019). These essential fatty acids are an important formulation in infant food for correct brain and eye development and are parallely used in the treatment of arthritis, depression, schizophrenia, Parkinson's disease, zinc deficiency, and others (Kerby et al. 1987; Sathasivam et al. 2019) (Table 10.3).

10.7 Significance of Mycorrhizal Associations

Mycorrhizal symbiosis has a prominent impact on the structure of plant communities, resource distribution and plant–plant interaction. It can also regulate ecological succession of plants (Koziol and Bever 2016), impact the response to habitat fragmentation and changes in land use (Smith et al. 1999; Maltz et al. 2017) besides influencing the ability of invasive species to colonize and outcompete the local ones (Nuñez et al. 2009).

The arbuscular mycorrhizal fungus like the one from phylum Glomeromycota is one of the ancient plant root symbionts (Bonfante and Genre 2010; Zhu et al. 2018) wherein it provides soil nutrients to the host in exchange for carbohydrates from the plant (Hodge et al. 2010; Zhu et al. 2018). A more complex interaction would involve multiple species of mycorrhizal fungi (Ecto and AMF) inhabiting a single host or roots of two or more plants sharing a common network (Yadav et al. 2019b). Also different mycorrhizal families are efficient in providing different resource and purpose like Gigasporaceae involved in nutrient acquisition and Glomeraceae in plant protection against pathogens.

AMF promotes uptake of phosphorous and plays a vital role in biogeochemical cycling of nitrogen (Hodge et al. 2010; Zhu et al. 2018) by improving the nitrogen use efficiency of the crop and minimizing the detrimental impact of using nitrogen fertilizers (Verzeaux et al. 2017; Hirel et al. 2011). Tripartite symbioses between legumes, rhizobiacae, and AMF have the potential to develop a more efficient nutrient uptake and transfer process than conventional tillage and cropping systems (Varennes and Goss. 2007; Verzeaux et al. 2017).

Plants colonized by AMF are not only able to deliver enough nitrogen for optimal growth and development of the plant (Govindarajulu 2005) but also aid in the transfer of amino acids like asparagine and arginine with the help of multiple transporters as in the case of *Sorghum bicolor* (Whiteside et al. 2012). However, the extent of successful and efficient AMF symbiosis depends on a few factors like:

1. Density of the viable propagules presents within the rooting zone;
2. The biochemical communication and interaction between the plant and hyphae; and
3. Diversity of the AMF communities (Verzeaux et al. 2017).

Weed and AMF interaction could also provide a new alternative to weed management by altering the abundance of mycotrophic host weeds and non-host ones and thereby reducing their impact and overall crop losses (Jordan et al. 2000). The growth and branching of the hyphae and spore germination are strongly influenced by the composition of the root exudate, root architecture, the soil structure, and the physiological status of the host plant. For instance, the release of metabolites like Strigolactones by compatible host plants attracts as well as stimulates the growth and colonizing ability of AMF (Akiyama et al. 2005).

As multiple fungi can simultaneously colonize different plants, studies have shown that the presence of *Rhizophagus intaradices* and *Claroideoglomus claroideum* together increased the productivity of plants like *Medicago truncatula* and *Allium porrum* by many fold. Thus this plant fungal symbiotic association has potential profitable large scale agronomic importance.

10.8 Role of Endophytic Fungus as Biocontrol Agents

Endophytic microbes are organisms that live in association within internal tissues of the plants thus protecting the plant through antibiosis, parasitism and competition and improving resistance to stress (Rana et al. 2019a, b; Suman et al. 2016). Endophytes are the warehouse of secondary metabolites which have anticancer, antidiabetic, antioxidative, immunosuppressive, and insecticidal properties (Verma et al. 2017). Endophytic community is divided into Passenger, facultative, and obligate endophytes (Hardoim et al. 2015) of which the latter is the most prominent which either live under the epidermal cell layers or within the intercellular spaces of the tissues and are unable to colonize any other habitat. Fungal endophytes induce abiotic and biotic stress tolerance, germination, and shoot growth, prevent from plant pathogens as a significant biocontrol agent against pests, insects, nematodes, and help in phytoremediation (Kumar et al. 2019a, b; Zea and Devi 2017; Xie et al. 2018). Induction of propagules from *Aspergillus terreus* and *Penicillium citrinum* has been shown to improve both biomass yield as well as disease resistance against *Sclerotium rolfsii*, in sunflower plants (Zea and Devi 2017). Studies from (Gao et al. 2010) have shown that fungal endophyte, *Cassia spectabilis*produces a large group of bioactive compounds from polypeptides to terpenoids and cadinane sesquiterpenes, harboring *Phomopis cassia*, shows very strong antifungal activity against *Cladosporium sphaerospermum* (Tables 10.4 and 10.5).

10.9 Fungal and Algal association: Lichens

Lichens are known to be the classic example of an adaptive and mutual beneficial association between heterotrophic fungus and photosynthetic algal species. Selectivity and specificity (Galun and Bubrick 1984; Beck et al. 1998, 2002) which involves one-to-one interaction between the partners is a very crucial aspect in determining the fungal–algal association besides habitat and ecological specialization (Yahr et al. 2004; Muggia et al. 2013; Singh et al. 2017). However, proving whether the underlying factor in the evolutionary origin of such novel symbioses is a result of co-speciation or coevolution or simply an event of ecological encounter

Table 10.4 Bioactive compounds and their role derived from endophytic fungus

Fungal endophyte	Bioactive compounds	Application	References
Balansia obtecta	Ergobalancine	Protection from herbivores	Tintjer and Rudgers (2006)
Aspergiluus fumigatus	Chanoclavine aldehyde, fumiclavine A, B, C	Against insect Pest	Panaccione (2005)
Phomopsis; Helmintospormium	Bioactive cytochalasines	Inhibit cell division, glucose transport and many other	Isaka et al. (2001) and Wagenaar et al. (2000)
Penicillium sp.	Berkeleydione	Antimicrobial	Davis et al. (2005)
Aspergillius niger	Rubrofusarin, asperpyrone B	Antimicrobial	Song et al. (2004)
Epichloe festucae	IAA, methylindole-3-carboxylate, diacetamide, indole-3-carboxaldehyde	Inhibition of chestnut blight	Yue et al. (2000)
Colletotrichum gleosporides	Colletotric acid, piperine	Antifungal	Zou et al. (2000) and Chithra et al. (2014)
Cladosporium delicatulum	Plumbagin		Venkateswarulu et al. (2018)
Fusarium redolens	Peimisine and imperialine-3β-D-glucoside	Therapeutic	Pan et al. (2015)
Phomopsis phaseoli	3-hydroxypropionic acid	Adhesives, Biodiesel production	Chomcheon et al. (2005)

is really difficult. Studies have shown that nutrient exchange of carbon and nitrogen between synthetic consortia of *Chlamydomonas reinhardtii* and a diverse group of ascomcyete fungi was due to the latent capacity of ecological interaction between the species than any evolutionary relationship (Hom and Murray 2014; Du et al. 2019). Other studies have demonstrated that how a long lived bipartite interaction was the reason for nitrogen starved alga to respond favorably towards fungal counterpart (Simon et al. 2017). Similarly, non-lichenized interaction between *Rhizidium phycophilum* and green alga *Bracteacoccus* showed that the association was based basically on solute exchange (Picard et al. 2013; Du et al. 2019). Such synthetic associations however lack morphological complexities at cellular as well as organism level (Hom and Murray 2014).

It has also been reported that the photobiont is generalist species and shows selectivity at community level hence have the ability to associate with several lichen forming fungi found in allopatry (Rikkinen et al. 2002; Dal Grande et al. 2014a, 2014b). This was shown in several studies where green algal symbionts like *Trebouxia* (Beck et al. 1998), *Astereochloris* (Peksa and Skaloud 2011), and *Dictyochloropsis* (Dal Grande et al. 2014a, b) associated with different lichen forming fungi (Singh et al. 2017). The phototrophic population occupies the above ground space for exchange of gases facilitated by the fungal partner (Honegger 1991) which in turn enables the lichen to adapt to shady, moist, and stable habitats of rainforests (Green and Lange 1990).

Table 10.5 Antifungal activities of fungal endophytes

Fungal Endophyte	Target plant	Causative agent	Disease/ condition caused	References
Trichoderma viride	*Spilanthes paniculata*	*Alternaria solani, Colletotrichum capsici, Fusarium solani, Pythium aphanidermatum*	Affects roots	Talapatra et al. (2017)
Aspergillus flavipes	*Steviare baudiana*	*Sclerotinia sclerotiorum*	Wilting and necrosis	Verma et al. (2014)
Penicillium spp	Musa spp.	*Fusarium oxysporum F.sp.*	Panama disease	Ting et al. (2010)
Cylindrocarpon sp.	*Phargmites australis*	*Rhizoctonia solani, Rhizoctonia cerealis*	Root rot	Ronga et al. (2019)
Penicillium simplicissimum	Cotton roots	*Verticillium dahlia*	Wilt of cotton	Yuan et al. (2017)
Trichoderma citrinoviride	*Panax ginseng*	*Rhizoctonia solani, Botrytis cinerea, Alternaria panax, Cylindrocarpon destructans*	Red skin root-rust rot disease	Park et al. (2019)
Rhizopycnis vagum	*Zingiber officinale*	*Rhizoctonia solani, Colletotrichum acutatum, Phytophthora infestans*		Anisha et al. (2018)
Trichoderma asperellum	Lettuce leaves	*Curvularia aeria(leaf spot fungi)*	Leaf Spot	Baiyee et al. (2019)
Penicillium commune, Aspergillus oryzae	*Monarda citriodora*	*Sclerotinia sp.*		Katoch and Pull (2017)
Epicoccum nigrum	Sugarcane	*Fusarium verticillioides, Ceratocystis paradoxa*	Pokkha boeng disease	Luiza and Sebastianes (2012)

Lichens, besides higher plants are known to regulate biogeocenoses by controlling soil formation, weathering of rocks, and flow of energy and matter. Phytocenotic studies have shown how epilithic lichens like *Alectoria, Dryas, Cobresia* play an integral part in stabilizing communities in high mountain belt of Siberia (Sedelnikova and Sedelniko 2009). Some prominent historical documentation also shows how the abundance of lichens on the Pribilof Islands, South of Bering Sea, prompted the establishment of reindeer, *Rangifer tarandus*, in 1911. Moreover, the differential depletion of the lichens population due to grazing pressure paved the way for introduction of vascular plants like lupines, wild celery and sedges that is greening of the landscape as well as modulated the climate and pioneered the community structure (Klein and Shulski 2011).

Since the maritime Antarctic region has similar habitat and less severe environmental conditions like the boreal-Arctic zones of Northern Hemisphere they harbor similar lichen communities (Lindsay 1978). The ecologically prominent ones which play an intriguing role in nutrient cycling, soil formation and weathering and successional processes are *Usnea*, *Bryoria, Physica, Sphaerophorus, Caloplaca, and Rinodina* (Rudolph 1977; Smith 1972; Lindsay 1978). These lichens besides having very high tolerance are able to withstand drought and low nutrient availability and hence appear to be the major colonizers which pioneer the succession towards climax community. Studies suggest that many endemic and cold adapted macroalgae of Antarctica associates with various dominant indigenous and complex fungal communities which enables both of them to survive in extreme conditions as well serve as a prospective reservoir of novel products (Godinho et al. 2013). On the other hand, several experiments and observations state that lichens play a vital part both in weathering of rock and protecting the soil top layer from erosion (Mottershead and Lucas 2000). Its biochemical weathering potential has also been studied by evaluating the iron chelation capacity of the whole lichen like *Cladonia squamosa* by the enzymes such as squamatic acid on the solution (Rudolph 1977).

Peltigeralean lichens encompass variety of redox enzymes which in high stress micro niches aid in formation and biodegradation of soil organic matter (Beckett et al. 2013a, b). They produce redox enzymes like peroxidases (Liers et al. 2011), cellulases and phenolic oxidases (Laufer et al. 2006). Laccases and tyrosinases are multicopper enzymes (Solomon et al. 2001) which catalyze oxidation of aromatic substrates into semiquinones (Thurston 1994) and conversion of monophenols to diphenols and diphenols to o-quinones (Halaouli et al. 2006), respectively. Peroxidases are haem containing proteins catalyze oxidation of various compounds in presence of hydrogen peroxide (Welinder 1992). These oxidoreductase enzymes help to defend the lichens against both biotic and abiotic stresses (Laufer et al. 2006; Beckett et al. 2013a, b).

Latest literature have even shown the bioflocculation of *Nannochloropsis oceania* with fungus *Mortierella*, enhanced the production of TAGs and PUFAs like Arachidonic acid and eicosapentenoic acid to a great extent under optimized growth conditions showing another aspect of fungal and algal interactions (Du et al. 2019). The lichens are well-known to produce a range of bioactive compounds with distinct roles as antibiotic, anti-herbivore, allelopathic, and other miscellaneous purposes. The antibiotic potential of lichen substance was first reported by Burkholder et al. followed by numerous clinical preparations against different microorganisms. Most of the lichen species possess an array of substances like vulpinic acid, lichesterinic acid, depsidones which are effective against many microbes. Since they can coexist with different species of plant kingdom, their intraspecific and interspecific interactions confer added advantage to adapt to any habitat.

Lichen secondary metabolites derived either from acetyl polymalonyl pathway, Shikimic acid pathway or mevalonic acid pathways have antioxidative properties (Shukla et al. 2010). Polysaccharides and fatty acids extracted from *Cladonia foliacea, Dermatocarpon miniatum, Everinia, and Neofuscella* have been shown to even possess antiviral, anti-tumor, and immune stimulatory properties (Ola Fsdottir and Ingó Lfsdottir 2001; Mischenko et al. 1984; Shukla et al. 2010) (Table 10.6).

Pharmaceutically important compounds of lichen extracts which have been identified as potential therapeutic agents show anti-inflammatory, antipyretic, analgesic, and anti-proliferative properties (Shawuti and Abbas 2007; Zambare and Christopher 2012). Extracts of *Parmelia sulcata* prepared in range of solvents have been shown to have strong antibacterial activities against *Aeromonas, Bacillus, Listeria, Staphylococcus* (Candan et al. 2007). *Cetraria aculeate* also had remarkable effects against a number of gram positive and gram negative bacteria (Türk et al. 2003).

Table 10.6 Bioactive substances from lichens

Lichen species	Characteristic compound	Role	References
Cladoniaceae			
Cladonia	Usnic acid, Atranorin	Antibiotic, antimycobacterial	Vartia (1973) and Falk et al. (2008)
Heterodea muelleri	Usnic acid, Diffractic acid, Barbatic acid	UV-C stress and cold temperature stress	Hager et al. (2008)
Stictaceae			
Pseudocyphellaria glabra and *P.homoeophylla*	Usnic acid	Antimicrobial, antiviral and cytotoxic	Perry et al. (1999)
Lobariaceae			
Lobaria pulmonaria	Depsidones and melanins	Light screening pigments	McEvoy et al. (2007)
Pseudophellaria nudata	Phenolics, depsides, triterpenes		Cuellar et al. (2008)
Parmeliaceae			
Alectoria ochroleuca	Vulpinic acid and usnic acid	Antifungal	Lauterwein et al. (1995)
Cetraria islandica	Fumaroprotocetraric acid	Inhibits HIV-I reverse transcriptase	Pengsuparp et al. (1995)
Evernia prunastrii	Orcinol, orsellic acid	Perfumery	Heide et al. (1975)
Parmelia sp.	Orcinol type depside, orsellinic acid derivative, 3-D-glucopyranoside		Saraswathy et al. (1990)
Peltigera apthosa	Tenuiorin, methyl orsellinate		Maass (1975)
Protousnea poeppigii	Isodivaricatic acid, usnic acid	Antifungal and antiprotozoal	Schmeda-Hirschmann et al. (2007)
Protousnea	Resorcinol derivative	Tyrosinase inhibition	Kinoshita et al. (1994)
Ramalinaceae			
Ramalina almquisii	D-Protolichesterinic acid	Anti-tumor	Hirayama et al. 1980
R.farinacea	Usnic acid, Norstictic acid	Antimicrobial	Tay et al. (2004)
Teloschistaceae			
Caloplaca species	anthraquinone	Broad spectrum antifungal and antibacterial properties	Manojlovic et al. (2005)
Umbilicariaceae			
Umbilicaria mammulata	Secondary metabolites	Low temperature stress	Stocker-wörgötter (2001)
Usneaceae			
Usnea campestris	Usnic acid	Antifungal and Antibacterial	Gutkind et al. (1981)

Antifungal agents identified from acetone and methanolic extracts of *Lasallia pustulata, Parmelia sulcata, and Umbilicaria crustulosa* were effective against *Aspergillus* and *Penicillium*, besides other fungus (Rankovic et al. 2007). Also lichen extracts of *Evernia prunastri, Hypogymnia physodes, and Cladonia portentosa* prepared in acetone have significant inhibitory effect on almost 8 phytopathogenic fungus like *Pythium ultimum, Phytophthora infestans, Rhizoctonia solani, Botrytis cinerea, Colletotrichum lindemuthianum, Fusarium solani, Stagonspora nodorum, Ustilago maydis* (Halama and Van 2004; Zambare and Christopher 2012) (Table 10.7).

Anti-tumor activity of lichen extracts being effective on tumor cells-melanoma B16, P388 Leukemia, K-562 Leukemia has been studied for many years (Hirayama et al. 1980; Takai et al. 1979; Khanuja et al. 2007). Anticancer effect of bisanthra-

Table 10.7 Antimicrobial potential of Lichens (edited from Zambare and Christopher 2012)

Antimicrobial property	Lichen	Bioactive compound	Test organism
Antibacterial activity against gram positive bacteria	*Cladonia foliacaea*	Usnic acid, Atranorin	*B.cereus, B. subtilis*
	Usnea ghattensis	Usnic acid	*B. licheniformis, B. subtilis, Staphylococcus aureus*
	Parmelia caperata	Protocetraric acid	*B. mycoides, B. subtilis, Staphylococcus aureus*
	Everniastrum cirrhatum	Atranorin	*B. cereus, B. subtilis, Listeria Monocytogenes, Saphylococcus aureus,*
	Cladonia furcata	Fumarprotocetraric acid	*B. mycoides, B. subtilis, staphylococcus aureus*
Antibacterial activity against Gram negative bacteria	*Cladonia foliacea*		*Aeromonas hydrophila,*
	Cetraria islandica	Protolichesterinic	*Helicobacter pylori*
	Parmelia caperata		*E. coli*
	Cladonia furcata	Fumaroprotocetraric acid	*E. coli, E netrobacter cloacea*
Antifungal activity	*Cladonia furcata*	Fumaroprotocetraric acid	*Aspergillus flavus; Botrytis cinerae; Candida albicans; Fusarium oxysporum; Mucor mucedo, Penicillium purpurescens; Trichoderma harsianum*
	Parmelia caperata	Protocetraric acid	*A. flavus; A. fumigates; Fusarium oxysporum; Mucor mucedo; Penicillium purpurescens; Trichoderma harsianum*
	Everniastrum cirrhatum	Atranorin	*A. fumigates, A. niger*
	Evernia prunastri	Lichenic acid	*Stagonospora nodorum; Phytophthora infestans; Rhizoctonia solani*

quinone glycosides, depsidone pannarin, usnic acid and lacanoric acid are few of the potent metabolites derived from a number of lichen species against an array of carcinomas and cell lines.

Many lichen compounds have been screened which shows different cytotoxic effects targeting apoptotic pathway, telomerase activity and cell cycle regulation (Lin et al. 2003). Extracts of lichens have insecticidal impact on *Spodoptera ornithogalli and S. littoralis* (Khanuja et al. 2007). Antioxidative agents like the phenolic compounds inhibit and prevent the reactive oxygen species generation and in turn their degenerative effect. The total antioxidant potential of few lichen extracts has been estimated based on the DPPH radical scavenging activity, total reducing power and superoxide anion scavenging ability has been reported by number of researchers (Zambare and Christopher 2012).

Extensive field studies have even shown that lichens are sensitive indicators of air pollutants and their occurrence itself is related to the degree and concentration of different contaminants (Nash and Gries 1991). Urbanization has affected the balance of the ecosystem as well as the lichen habitats with increasing concentration of pollutants like sulfur dioxide, hydrogen fluoride, PAN and acid rain. On being exposed to these pollutants, lichens suffer from enzyme deactivation and formation of free radicals. However, number of species with differential abilities to withstand these conditions has been thoroughly studied and reported (Nash and Gries 1991) (Fig. 10.1).

10.9.1 Lichens of Commercial Importance in India

Studies show that lichen extracts from *Parmelia nilgherrensis, Parmelia nepalensis, Usnea lucea* collected from various parts of India find their applications as spices, medicines, dyes, perfumes, animal feed and monitors of environment health (Shah 2014). Four grades of commercial products based on their field of application have been identified in Indian state, Uttarakhand, derived from different species of lichen (Table 10.8).

10.10 Conclusion and Future Prospects

Lichens occurring ubiquitously in most of the world's ecosystems play a unique role as effective colonizers, Nitrogen fixers, and interceptors of wet and dry deposition, as major carbon sequestering models, indicators of pollutants and soil bioremediator and enhancers of plant growth. Extensive study on Algal and Fungal interactions has been reported as an interesting phylogenetic relation which compares the endemic taxa involved, its complexity, biological mechanism, potential of metabolites produced, and adaptability. Though this bio-trophic interaction shows high specificity, studies have shown that combined effect of the metabolites produced by both the partners together has vast and varied applications than when individually.

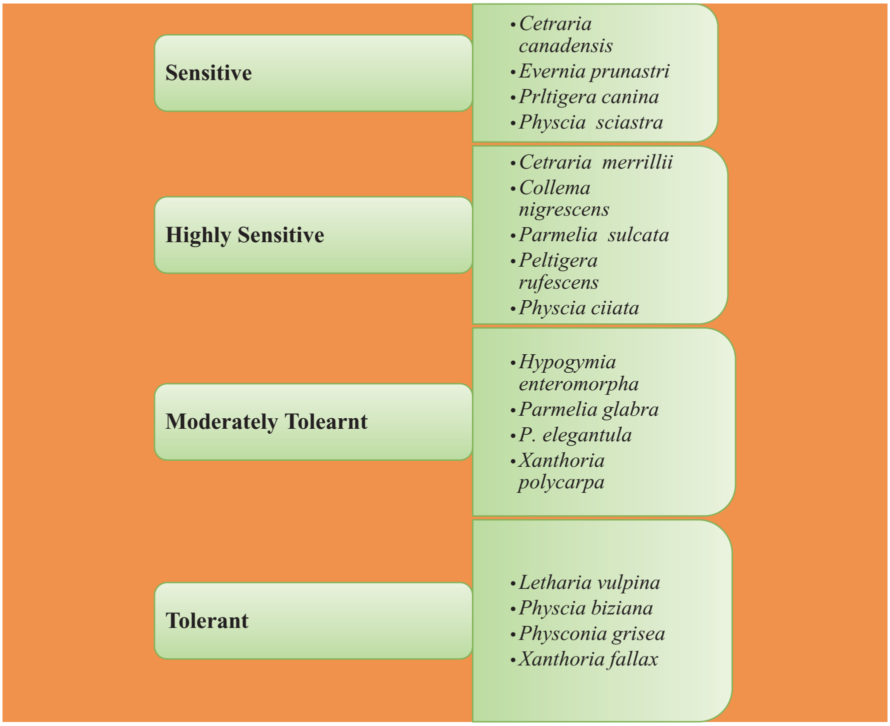

Fig. 10.1 Lichens tolerant and sensitive to air pollution

Table 10.8 Commercial Lichens of different grades (modified from Shah 2014)

Grade	Species	Uses
I	*Parmotrema nilgherrase* (Nyl.) Hale (*Parmelia nilgherrensis* Nyl.)	For extraction of resinoids and high grade perfumery
II	*Parmotrema nilgherrense* (Nyl.)Hale *Everniastrum nepalense* (Taylor) Hale (*Parmelia nepalensis* Taylor) *Everniastrum cirrhatum* (Fr.) Hale (*Parmelia cirrhata* Fr.)	For use in indigenous perfumery and native medicines
III	*Parmotrema nilgherrense* (Nyl.) Hale *Everniastrum nepalense*(Taylor) Hale *Everniastrum cirrhatum* (Fr.) Hale	For indigenous pharmaceutical and condiment powders
IV	*Usnea baileyi* (Strilon) Zahlbr *Usnea subsordida* Strilon	Flavoring ingredient in tobacco and as an ingredient of “Sacrificial” fire material

Large scale industrial production of metabolites and its derivatives however require better collection and extraction techniques besides more optimized and scale-up harvesting methods. In silico and in vitro synthetic systems for studying the evolution of symbiosis would also open new prospects of combination of different species and possibilities of pyramiding multiple aspects.

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Chapter 11
Fungi as a Biological Tool for Sustainable Agriculture

Monika Thakur

Contents

11.1 Introduction

Sustainable agriculture is an integrated system of farming technique having site specific applications over a long period. It is the study of relationships and interactions between plants and their physical environment. In sustainable agricultural

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systems, the soil microflora is one of the most important ecosystem processes and is affected by nutrient availability and disease suppression (Rastegari et al. 2020; Singh and Yadav 2020; Yadav et al. 2020). The rising demand for environmentally friendly, organic, and sustainable agricultural practices is driving the application on the use of beneficial biological products. The use of fungi in agriculture sector is potentially useful for improved plant health and growth, water uptake, nutrient availability, stress tolerance, and biocontrol. Fungi also play a fundamental role in multifarious physiological processes including mineral and water uptake, photosynthesis, stomatal movement, and biosynthesis of compounds termed bio-stimulants, auxins, lignan, and ethylene to enhance the ability of plants to establish and cope up the environmental stresses such as drought, salinity, heat, cold, and heavy metals (Hatami and Ahangarani 2016).

Sustainability in agriculture involves:

- building and maintaining healthy soil,
- managing water,
- minimizing air, water, and environmental pollution,
- promoting biodiversity.

Many in the agricultural communities have adopted sustainable agriculture concept. Sustainability has become an integral component of different initiative by the government, and it is beginning to be woven into agricultural policy. Slowly and progressively there have been certain positive changes in the system as:

- satisfy human food and fiber needs;
- enhance environmental quality and natural resources;
- natural biological cycles and controls;
- sustain the economic viability of farm operations;
- enhance the quality of life for farmers and society.

In the current scenario, the climatic conditions are changing at a very faster pace. These changes include global rise in temperature and atmospheric pollution which adversely affects the agricultural productivity. To mitigate the problems arising from the present climatic conditions and to ensure food security, sustainable agricultural practices are need of the hour. The pollution has significant deleterious consequences on the sustainable agriculture ecosystem. In the past few years, the agricultural system is getting more and more polluted and remediation of these pollutants again is a challenging task.

11.2 Fungi: Biological Tool for Sustainable Agriculture

Microorganism (both bacteria and fungi) plays a significant role as a biological tool for establishment of sustainable agricultural system (Thakur 2014). Watanabe (2001) reported that naturally occurring microbial consortia (bacteria/fungi) have been utilized in a variety of bioremediation processes. Fungi are widespread in environment having rapid adaptability and diverse metabolic activities in agricultural systems. In the soil, the fungal cultures can sustain under diverse environmental conditions in the maintenance and functioning of ecosystem because of their decomposing behavior. The beneficial fungi play an important role in improving plant growth, increasing plant yield, and involvement in biotic and abiotic stress tolerance, hazardous materials remediation, sustainable crop production, and food safety. Singh et al. (2019) also discussed the use of fungi in mycoremediation and mycocontrol. The chapter highlights the role of fungi as a biological tool for a sustainable agricultural system. The fungi can be involved in three different manners to attain sustainability in the ecosystem mentioned below:

- Mycoremediation,
- Mycocontrol—mycoherbicides, mycoinsecticides, and
- Mycorrhizal fungi.

11.3 Mycoremediation

Bioremediation is an attractive technology that utilizes the metabolic potential of microorganisms in order to clean up the environmental pollutants (Asgher et al. 2008; Haritash and Kaushik 2009). Mycoremediation is a form of bioremediation that uses native fungi and fungal mycelium applied to surface soils to remove and degrade contaminants (Thomas et al. 2009). During the last two decades, the mycologists have used various fungal species (mycelium) in the degradation of organic compounds (Singh 2006). Mycoremediation is an innovative biotechnological application that uses living fungus for in situ and ex situ cleanup and management of contaminated sites. Purohit et al. (2018) also mentioned the same as an attractive technology in which fungi are used to break down or degrade hazardous toxic substances into less toxic or nontoxic forms. Mycoremediation is an economically and environmentally sound alternative for bioremediation (Thakur 2014). It restores the value of depleted and polluted land.

11.3.1 Role of Fungi in Mycoremediation

Fungi are major decomposers of various complex polymers as—cellulose, hemicelluloses, and lignin. (Thomas et al. 2009). Loske et al. (1990) reported the eight main contaminants of polluted soils which have been degraded by the use of fungi:

- Polycyclic aromatic hydrocarbons (PAHs)
- Polychlorinated biphenyls (PCBs)
- Dioxines

- Petroleum hydrocarbons
- Halogenated organic compounds
- Dyes
- Pesticides
- Heavy metal toxicity and its sources

11.3.2 Process of Mycoremediation

Mushroom uses different types of methods to decontaminate polluted sites and make the environment sustainable by three different processes as biodegradation, biosorption, and bioconversion.

11.3.2.1 Biodegradation

The biodegradation mechanism is a complex process there is change of the complex molecule to its mineral constituents. This process leads to complete mineralization of complex compounds to simple ones like CO_2, H_2O, NO_3, and other inorganic compounds by living organisms. Table 11.1 enlists the mushroom species can

Table 11.1 Role of mushroom species as mycoremediators for pollutants

S. no.	Mushroom species	Role as mycoremediator	References
1	*Pleurotus ostreatus*	Mushroom species degraded the plastic grew on it (oxo-biodegradable plastic)	da Luz et al. (2013) and Thakur (2019)
2	*Lentinula edodes*	Mushroom species degraded 2,4-dichlorophenol (DCP) by using vanillin as an activator	Tsujiyama et al. (2013) and Thakur (2019)
3	*Pleurotus pulmonarius*	Radioactive cellulosic-based waste: Waste containing mushroom mycelium was solidified with cement and then this solidified waste acts as first barrier against the release of radio-contaminants from the site	Eskander et al. (2012) and Thakur (2019)
4	*Auricularia sp.*, *Schizophyllum commune,* and *Polyporus* sp	Malachite green dye was degraded in 10 days	Rajput et al. (2011) and Thakur (2019)
5	*Pleurotus pulmonarius*	Mushroom species help in the degradation of crude oil	Thakur (2019)
6	*Coriolus versicolor*	Mushroom possesses the ability to degrade PAH with the help of lignin-modifying enzymes laccase, manganese-dependent peroxidase (MnP), and lignin peroxidase (LiP)	Thakur (2019)

produce various extracellular enzymes (peroxidases; ligninase—lignin peroxidase, manganese-dependent peroxidase and laccase; cellulases; pectinases; xylanases and oxidases) and act as mycoremediators (Thakur 2019).

11.3.2.2 Biosorption

Biosorption is the process for the removal of pollutants from the environment with the help of mushroom species. This process has been considered as an alternative to the remediation of industrial effluents. It is a process based on the sorption of metallic ions/pollutants/xenobiotics from effluent by live or dried biomass which often exhibits a marked tolerance towards metals and other adverse conditions (Thakur 2019). Table 11.2 enlists the mushroom species playing an important role in biosorption of pollutants.

11.3.2.3 Bioconversion

In this process there has been conversion of industrial waste into some mushroom species. The lignocellulosic waste, generated by industries, can be used for cultivation of mushrooms. Various mushroom species cultivated on industrial and agro-industrial wastes are given in Table 11.3 (Kulshreshtha et al. 2010, 2013, 2014; Thakur 2019).

Table 11.2 Removal of pollutant s by biomass of mushroom using biosorption process

S. no	Mushroom spp.	Pollutants and mushroom species role	References
1	*Agaricus bisporus*, *Lactarius piperatus*	Cadmium (II) ions*:* Mushroom species showed higher removal efficiency on Cd (II) ions	Nagy et al. (2013)
2	*Fomes fasciatus*	Copper (II): Mushroom is efficient in biosorption of Cu (II) ions	Sutherland and Venkobachar (2013)
3	*Pleurotus platypus*, *Agaricus bisporus*, *Calocybe indica*	Copper, zinc, iron, cadmium, lead, nickle: Mushroom species are efficient biosorbent for the removal of these ions from aqueous waste	Lamrood and Ralegankar (2013)
4	*Flammulina velutipes*	Copper: Mushroom fruiting body used as biosorbent for removing copper ions from aqueous waste	Luo et al. (2013)
5	*Pleurotus tuber-regium*	Heavy metals: Mushroom species bio-absorb the pollutant (heavy metals) from the soil artificially contaminated with some heavy metals	Oyetayo et al. (2012)
6	*Pleurotus ostreatus*	Cadmium: Mushroom species bio-absorb the cadmium ions in the substrate	Tay et al. (2011)
7	*Pleurotus sajor-caju*	Mushrooms bio-absorb the heavy metals	Jibran and Milsee Mol (2011)

Table 11.3 Bioconversion of waste by mushroom species

S. no.	Mushroom species	Waste material	Mushroom cultivation	References
1	*Pleurotus citrinopileatus*	Handmade paper, cardboard, and industrial waste	Successfully cultivated. Basidiocarps possessed good nutrient content and no genotoxicity	Kulshreshtha et al. (2013)
2	*Pleurotus ostreatus*	Sawdust of different woods	Biomass of mushroom produced in submerged liquid culture was analyzed	Akinyele et al. (2012)
3	*Volvariella volvacea*	Agro-industrial residues such as cassava, sugar beet pulp, wheat bran and apple, pear pomace	Enzyme activities were measured during the fermentation of substrates	Akinyele et al. (2011)
4	*Pleurotus florida*	Handmade paper, cardboard, and industrial waste	Successfully cultivated. Basidiocarps possessed normal morphology and no genotoxicity	Kulshreshtha et al. (2010)
5	*Pleurotus*	Cotton waste, rice straw, cocoyam peels, and sawdusts of *Mansonia altissima, Boscia angustifolia,* and *Khaya ivorensis*	Successfully cultivated with good crude protein, fat, and carbohydrate contents in fruiting bodies	Kuforiji and Fasidi (2009)
6	*Pleurotus eous* and *Lentinus connatus*	Paddy straw, sorghum stalk, and banana pseudostem	Waste successfully bio-converted by mushroom with good biological efficiency	Rani et al. (2008)
7	*Pleurotus tuber-regium*	*Terminalia superba, Mansonia altissima, Holoptelea grandis,* and *Milicia excelsa*	Mushroom species grow on trees	Jonathan et al. (2008)
8	*Pleurotus tuber-regium*	Cotton waste, sawdust of *Khaya ivorensis,* and rice straw	Sclerotia propagated on groundnut shells and cocoyam peels with lipase and phenoloxidase; cellulase, carboxy-methylcellulase enzymatic activities	Kuforiji and Fasidi (2008)
9	*Lentinula edodes*	Eucalyptus waste	Successfully convert this waste and qualitative and quantitative changes were also measured	Brienzo et al. (2007)
10	*Lentinula edodes*	Mushroom fruiting bodies were grown on the vineyard pruning, barley straw, and wheat straw	Bioconversion of waste having highest biological efficiency, yield, and shortest production cycle	Gaitán-Hernández et al. (2006)
11	*Lentinula tigrinus*	Wheat straw	Characterize the production of lingo-cellulosic enzymes and bio-convert the wheat straw into fruiting bodies	Lechner and Papinutti (2006)

(continued)

Table 11.3 (continued)

S. no.	Mushroom species	Waste material	Mushroom cultivation	References
12	*V. volvacea*	Banana leaves	Efficient bioconversion with good yield into the fruiting bodies	Belewu and Belewu (2005)

11.3.3 Mushrooms and Mycoremediation

Mushrooms (mostly basidiomycetes) are among the most powerful decomposers in nature, secreting strong extracellular enzymes due to their aggressive growth and biomass production (Elekes and Busuioc 2010). They have always been known for their nutritive and medicinal benefit, but many scientists as reported that they can be used to evaluate the level of environmental pollution and to remediate the metal polluted soil (Sesli and Tuzen 1999; Ouzouni et al. 2009; Tišma et al. 2010). The enzymes secreted by the fruiting bodies include lignin peroxidases (LiP), manganese peroxidase (MnP), and laccase, help in decomposition of pollutants. Many researchers have worked on mycoremediation and this technology has been applied to oil spills, contaminated and polluted soil, industrial chemicals, contaminated water, and even farm waste (Bennet et al. 2001; Alexander 1994; Ashoka et al. 2002; Adenipekun and Lawal 2012). Some specific examples of macrofungi mycelium especially white-rot fungus used for mycoremediation are mentioned in Table 11.4 and Fig. 11.1.

11.3.4 Advantages of Mycoremediation

This process has many advantages over other commercialized technologies on the removal of contaminants from the soil. Some have been listed below:

- Public acceptance
- Natural and environment friendly
- Safety
- Simple and quiet
- Low maintenance
- Reusable end products
- Low cost
- Flexibility
- Fast

Table 11.4 Mushroom species with their role in mycoremediation

S. no.	Fungi	Use in mycoremediation	References
1	*Phanerochaete chrysosporium*	Successful in degrading toxic substances such as aromatic hydrocarbons, chlorination organics, insecticides, pesticides, nitrogen aromatics, and laccases	Bumpus et al. (1985), Aitken and Irvine (1989), Barr and Aust (1994), Nigam et al. (1995), Sasek and Cajthaml (2005), Leonardi et al. (2007), Adenipekun and Lawal (2012), and Thakur (2014)
2	*Lentinus edodes*	Degrade pentachlorophenol (PCP)	Adenipekun and Lawal (2012) and Thakur (2014)
3	*Lentinus tigrinus*	Mycoremediate chlorobenzoic acids (CBA)	Stella et al. (2012)
4	*Lentinus squarrosulus* (Mont.) Singer	Mineralize soil contaminated with various concentrations of crude oil	Adenipekun and Fasidi (2005), Adenipekun and Isikhuemhen (2008), and Clementina and Omoanghe (2008)
5	*Pleurotus ostreatus* (Jacq. Fr.) P. Kumm	Degrade a variety of polycyclic aromatic hydrocarbons (PAH) in non-sterile soil both in the presence and in the absence of cadmium and mercury	Sack and Gunther (1993), Bojan et al. (1999), Sykes (2002), Okparanma et al. (2011), Baldrian et al. (2000), Eggen and Majcherczyk (1998), Eggen and Sveum (1999), and Bhattacharya et al. (2012)
6	*Pleurotus tuber-regium* (Fries) Singer	Ability to ameliorate crude oil polluted soil	Isikhuemhen et al. (2003) and Adenipekun et al. (2011a, 2012)
7	*Pleurotus pulmonarius*	Significant decrease in the lead, copper, manganese, and nickel contents of the soils	Adenipekun et al. (2011b)
8	*Trametes versicolor*	Better degradation of hydrocarbons, produces three ligninolytic enzymes with efficient degradation capacity on lignin, polycyclic aromatic hydrocarbons, polychlorinated biphenyl mixture, and a number of synthetic dyes	Morgan et al. (1991), Tanaka et al. (1999), Gadd (2001), Novotny et al. (2004)
9	*Bjerkandera adusta*	Degradation of PAHs	Adenipekun and Lawal (2012) and Pozdnyakova (2012)
10	*Irpex lacteus*	Degradation of PAHs	Bhatt et al. (2002) and Adenipekun and Lawal (2012)

11.3.5 Constraints for Mycoremediation

There have been certain constraints with the process also, as the research has shown that mushroom species like *P. ostreatus* and *P. chrysosoporium* have emerged as model systems for studying bioremediation. But, still the process know-how is still

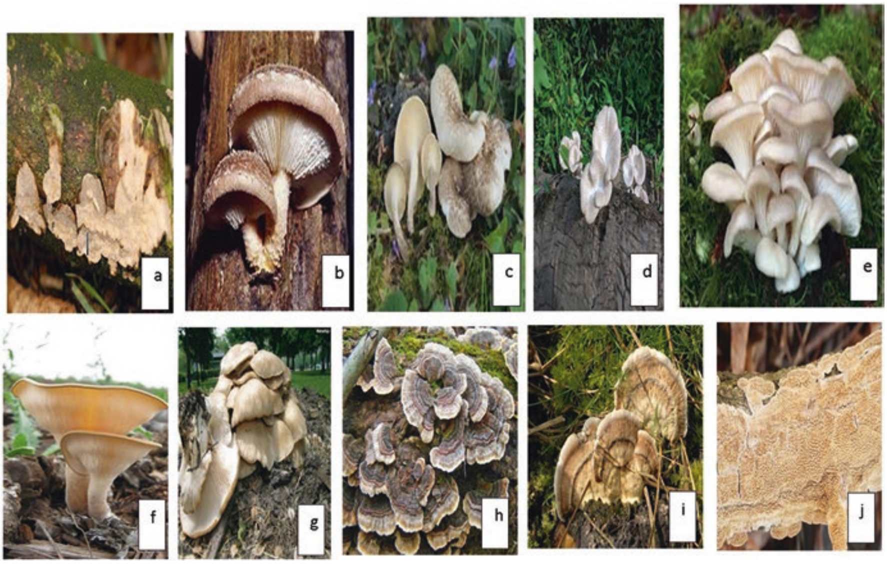

Fig. 11.1 Macrofungi used in mycoremediation. (**a**) *Phanerochaete chrysosporium*, (**b**) *Lentinus edodes*, (**c**) *Lentinus tigrinus*, (**d**) *Lentinus squarrosulus* (Mont.) Singer, (**e**) *Pleurotus ostreatus* (Jacq. Fr.) P. Kumm; (**f**) *Pleurotus tuber-regium* (Fries) Singer, (**g**) *Pleurotus pulmonarius*; (**h**) *Trametes versicolor*; (**i**) *Bjerkandera adusta*; (**j**) *Irpex lacteus*

a mystery on how this white-rot fungus removes pollutants. Major constraint of this process was *Phanerochaete chrysosporium* as the major work on mycoremediation is on this fungus only. The ability is generally attributed to lignin-degrading enzymes system of this fungus. Similar degrading abilities have also been described by many other species of white-rot fungus but of not that very successful. Sasek (2003) also mentioned that the performance of white-rot fungus in soil bioremediation depends upon other physical factors. Boopathy (2005) and Thakur (2014) discussed some of the challenges faced as:

- Fungal species has the inability to compete with native microbes in soils. Bacteria could either inhibit the growth of fungi or in combination with fungi enhance degradation of pollutant.
- Nutrient requirement of the fungus has to be completely understood so as to enable it to thrive at a contaminated site.
- Mushroom mycelium should not be used as a starter species.
- Legal issues involved in this process. There are several patents specifically granted for matching fungus against a toxin. This is a major hindrance in preventing wide-scale fungal clean-up of toxins from the polluted site.
- Lack of experienced mushroom cultivators in outdoor trials is a problem in mycoremediation. This lacking has affected the success of several trials.

11.4 Biocontrol

The concept of use of fungal species as a biocontrol agent was developed in the late 1800s to early 1900s. Very few studies have been conducted on utilization of fungi in controlling insects and weeds as the chemical sprays in the form of insecticides and weedicides are very cheap and readily available in market. However, in the last decades, there is an upsurge of the problems with the focus on various toxic carcinogenic compounds in many chemical sprays, slow and gradual resistance in organisms and their slow biodegradability in the environment have brought about a renaissance in the use of various biocontrol agents. These chemical insecticides and weedicides are also slowly and steadily degrading the agricultural system. In the current scenario, the problem is to be tackled now only otherwise, the whole agricultural ecosystem will be disturbed and will be of no longer use. There biocontrol agents in fungi are used in two ways: mycoinsecticides and mycoherbicides.

11.4.1 Mycoinsecticides

The use of fungi in controlling insect growth and development is *Mycoinsecticide*. The fungal strains have the ability to penetrate the cuticle of insects. Although there have been many species of fungi that are pathogenic to insects (exception of some Basidiomycota and Deuteromycota), but very few have been studied, and only six have been registered for pest control (Table 11.5). However, before the potential of fungal species as insect controlling agents is exploited, lot of research must be carried on the same.

11.4.2 Insect Biological Control Fungi

Most fungal species that are parasitic on insect have been studied belong to the Entomophthorales (Zygomycota). In utilizing fungi as biological control agents against insects, the following three categories of treatment have been established:

Table 11.5 Fungi as mycoinsecticide

S. no.	Name of fungi	Insects
1	*Entomophaga maimaiga*	*Lymantria dispar* (gypsy moth)
2	*Beauveria bassiana*	Dendrolimus (the pine moth)
3	*Erynia* sp.	*Hypera postica* (the alfalfa weevil)
4	*Cordyceps militaris*	Insects and arachnids
5	*Coelomomyces* sp.	Mosquito larvae

- *Permanent introduction of a fungal strain* to an area with a host population. This method is one of the least costly and labor intensive methods, involving periodic release of fungal spores, in order to maintain a high density of the biocontrol fungus.
- *Inoculative augmentation* involves releasing the pathogen in the field where it will control the insect pathogen. This method is applicable for annual problem of crops.
- *Conservation with environmental establishments* involves the modification of the host environment to enhance the probability that the fungus will infect and eliminate the host. The environment might be modified and established to maintain a constantly wet environment in order to favor fungal growth.

11.4.3 Advantages of Using Fungi for Biocontrol

Use of fungi as mycoinsecticide is a very fruitful idea. They are safer in comparison to chemical insecticides as some of them are also banned for this reason. But, the concept is still to be explored lot of research is to be done on many other fungal species. There have been many benefits for use of fungi as biocontrol agents. Some have been listed below:

- do not pose a health hazard to people and domestic animals,
- ubiquitous nature of fungi,
- genetic diversity,
- ability to directly infect the host insect by penetrating the cuticle of the insects.

11.4.4 Mycoherbicides

The use of fungi to control weedy plants again is a natural process. On the other hand, the use of chemical herbicides will be a great threaten to the health of the organisms. A mycoherbicide is an herbicide based on fungal strains. As a biological agent, these “mycoherbicides” work by producing toxic compounds that dissolve the cell walls of targeted plants (weeds). Unlike traditional herbicides, mycoherbicides can reproduce themselves and stay in the soil for many years to destroy the re-growing weed crops.

Some of the fungal species used are listed below:

- *Alternaria destruens*
- *Chondrostereum purpureum*
- *Colletotrichum acutatum*
- *Colletotrichum gloeosporioides*
- *Cylindrobasidiumlaeve*
- *Phytophthora palmivora*
- *Puccinia canaliculata*

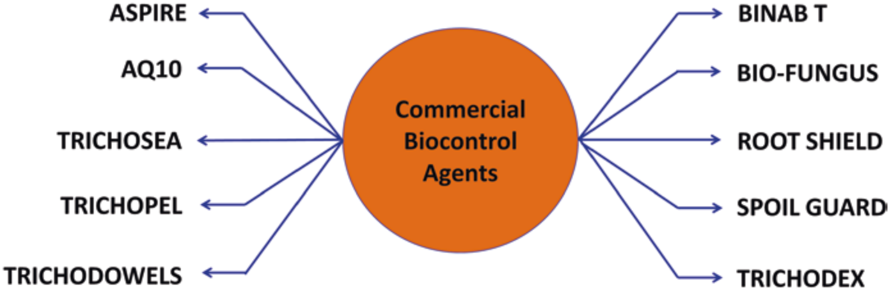

Fig. 11.2 Commercial mycoherbicides and mycoinsecticides

- *Puccinia thalaspeos*
- *Sclerotinia minor*

11.4.5 Commercial Mycoherbicides and Mycoinsecticides

There are presently only a few mycoherbicides and mycoinsecticides that are available and have limited success. The most common species of fungi used in this type of biocontrol is *Trichoderma harzianum*. However, a number of mycofungicides are available commercially mentioned below (Fig. 11.2).

11.5 Mycorrhiza Fungi (MF)

Mycorrhiza is an enormous, useful, and untapped resource for sustainable management of soil ecosystem. It is a heterogeneous group of fungi that is primarily associated with roots of many plants. The word mycorrhiza is derived from classical Greek word for "mushroom" and "root." In the mycorrhizal association, the underground mycelium is in contact with the plant roots and does not cause any harm to the plant, thus shows a symbiotic relationship (Hart and Trevors 2005). Out of these associations, one group of root obligate mycorrhiza provides the host plant with water, nutrients, and most importantly protects from pathogens, known as Arbuscular Mycorrhizal Fungi (AMF).

This association helps in improving the nutrient supply like nitrogen and phosphorus to the plants and in turn, the fungus gets 20% of the fixed carbon (Basu et al. 2018). In the last two decadeds, the use of chemical fertilizers in agriculture has substantially increased globally, but because of excessive use of fertilizers is leaving bad to worse impacts on the soil and water body environment. Therefore, the concept of using mycorrhizal fungi as a biofertilizer, in terms of cost effectiveness, energy saving and as environment friendly, is a promising perspective (Kour et al. 2020; Yadav et al. 2017). The significance of MF in augmenting food production is far and wide; therefore these can be used with the concept of sustainable agricultural systems. AMF are the root-symbionts which obtain their nutrients from the plant and provide mineral (like N, P, K, Ca, S, and Zn) to the host plant. AMF has suppressing abilities against soil borne pathogens (root feeding nematodes and fungi), infecting various crops and thus the productivity of crops is increased.

Various benefits attributed to the plant through mycorrhizal symbiosis are listed below:

- increases plant tolerance to various biotic and abiotic stresses (including alkalinity, toxicities associated with mining operations, heavy metals, and mineral imbalances).
- potential use as biofertilizer and replaces the fertilizer requirements and reduces the needs of current levels of chemical fertilizer,
- plays a vital role in changing the ecology of a given site and mycorrhiza promotes mineral cycling and are key component of efficient and closed nutrient cycle of natural ecosystems.

11.5.1 Advantages of Mycorrhiza in Sustainable Agriculture System

- role of mycorrhiza in improving the plant health by improving the nutrient supply, hormone biosynthesis,
- acquired systemic resistance against pathogens in plants,
- alleviation of abiotic stress in plants by mycorrhiza,
- prospects in sustainable agriculture,
- models highlighting plant-mycorrhizal signaling and their role in providing protection against biotic/abiotic stresses.

11.5.2 AMF as a Multifaceted Potential Tool for Sustainable Agriculture System

AMF is a multifaceted potential tool in sustainable agricultural systems (Hart and Trevors 2005; Abbasi et al. 2015). They can be used a biofertilizers and biocontrol agents. Some of them have been enlisted below:

- *Nutrient uptake*: AMF mycelium increases the uptake of nutrients (P, N, S, Cu, K, Zn, Mg, Na, Mn, Fe, Al, etc.) and trace elements (Clark and Zeta 2000; Smith et al. 2004).
- *Mineralization of organic nutrients*: AMF mycelium also shown to uptake the N and P directly from decomposing sources (Hodge et al. 2001; Tarafdar and Marschner 1994).

- *Drought resistance*: AMF mycelium improves host water relations (Auge 2001).
- *Seedling establishments*: The AM seedlings have more access to resources than others (van der Heijden et al. 2004).
- *Pathogen resistance*: AMF spear to reduce disease symptoms for some plant diseases such as root rot, wilt, damping off, and yellowing disease (Whipps 2004).
- *Increased herbivore resistance*: AMF have shown their increased tolerance to herbivore through increased responses (Kula et al. 2005).
- *Increases pollination*: AMF plants are more attractive to pollinators due to improve nutritional status (Wolfe et al. 2005).
- *Heavy metal tolerance*: AMF buffers host from toxic exposure (Gaur and Adholeya 2004).
- *Increased soil stability*: AMF increases soil stability (Rillig 2004).

11.6 Conclusion and Future Research Challenges

Fungi can be used as a tool to reduce waste materials in contaminated soils via non-specific enzymes activity. Mycoremediation is not a magical miracle, but an effective and powerful tool to remediate and further help in attaining sustainable ecosystems. Myco-facilitation can help to transform a degraded location into a thriving ecosystem with increased diversity. Despite the known facts under use of fungi in achieving sustainable ecosystems, fungal strains have not been fully exploited for the bioremediation of such polluted environments. In this review, the mycoremediation, mycocontrol, and mycorrhizal associations are described and their potential for attaining sustainable agricultural systems has also been discussed. More extensive research needs to be carried out on the potential of mushrooms and fungal species in the area of mycorrhizal technology. Therefore, the present chapter aims to study the role of fungi by mycoremediation, mycocontrol, and as mycorrhizal fungi for the crop improvement and important biological tool for sustainable agricultural systems. The potential of fungal mycelium is still underexploited in sustainable agricultural systems and further can be explored.

Recent advancements with the addition of potential fungal strains to the soil and the enhancement of the indigenous microbial population have proven to be successful. Whether the fungal mycelium is native or newly introduced to the site, the process of destroying contaminants is important and critical for understanding. Lot of work is focused on strategic development to make agriculture a sustainable system. Further, the application of this technology in large scale projects will demand much more work to streamline the methodologies. But extensive research needs to be pursued as removing toxic chemicals and making agricultural system sustainable is a big challenge. Researchers also feel that this complete process is expected to be faster and more cost effective than other remediation technologies once it is commercialized. The use of fungi for remediation would allow commercial concern to offer inexpensive, safe products to their customers. There is one more challenge as greenhouse emission in agricultural system for which AM fungi also act and they reduce release of greenhouse gasses associated with agriculture as CO_2 and N_2O. If the underexploited potential of fungus mycelium is further exploited, it will go a long way and come as the most efficient biological tool in sustainable agriculture system.

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Chapter 12
Agriculturally Important Fungi for Crop Productivity: Current Research and Future Challenges

Ajar Nath Yadav, Divjot Kour, Tanvir Kaur, Rubi Devi, and Neelam Yadav

Contents

This book contains current knowledge about agriculturally important fungi for crop productivity. The diverse groups of fungal communities are the key components of soil-plant systems, where they are engaged in an intense network of rhizosphere/endophytic/phyllospheric interactions. The rhizospheric, endophytic, and epiphytic fungi with plant growth promoting (PGP) attributes have emerged as an important and promising tool for sustainable agriculture. These PGP fungi could be used as biofertilizers/bioinoculants in place of chemical fertilizers for sustainable agriculture. The aim of the present book is to collect and compile the current developments in the understanding of the rhizospheric, endophytic, and epiphytic fungal diversity associated with plants and others habitats. The book encompasses current knowledge of agriculturally important fungi (AIF) and their potential biotechnological applications for crop productivity. The book will be highly useful to the faculty, researchers, and students associated with microbiology, biotechnology, agriculture, molecular biology, environmental biology, and related subjects.

One of the fast growing segments of the biological sciences, biotechnology, is dealing with genetic engineering of living organisms or their components for producing useful products thus, has a wide range of uses in sustainable agriculture. The genetic resources of animals, plants, and microbes comprise a significant basis for

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all research based on biotechnology and new products creation. The biotechnology molecular tools have accelerated precision breeding by cloning and desired genes transfer from one to another species. Agricultural practices are now being implemented worldwide and a variety of methods are being exercised to meet sustainable, ecological, and economic development, with the aim of increasing the yield simultaneously protecting the biosphere (Kour et al. 2020b; Rastegari et al. 2020a; Verma et al. 2017; Yadav et al. 2015).

The rising demand for food with the population increase has been a major concern worldwide. The pressure to fulfill the demands the growing population and reduce the hunger problems has led to the advancement of novel scientific technologies and agronomic practices (Kour et al. 2020b). Microbial biotechnology is an imperative field playing a significant role in promoting human nutrition, food security, preservation, and protection of animals and plants ultimately the overall fundamental research in the agriculture (Rastegari et al. 2020b; Yadav et al. 2020d). Microbial biotechnology is greatly contributing to sustainable agriculture by dropping the dependence on agrochemicals and more utilization of bioresources. In coming decades, the major focus to achieve sustainability will be on beneficial microbes. Microbes are expected to pave way for the next agricultural green revolution and will surely be the great option for better sustainable organic farming practices (Yadav et al. 2020b, c). Taking into account the potential of microbial inoculants in terms of supplying nutrients, bio-control activities, and environment cleaning, they need to be more and more encouraged for implementation in agriculture so that productive agro-ecosystem could be achieved in future (Arora et al. 2020).

Plants association with microbes can be very well enlighten by plant growth promoting fungi. The beneficial fungi play a vital role in plant growth and yield improvement through different mechanisms of plant growth promotion including the solubilization of different insoluble and unavailable nutrients and different plant growth regulators production. Fungi also take part in alleviating the adverse abiotic stress effects and food safety (Ansari et al. 2013; Rabie and Almadini 2005). They also bind to particles of soil thereby increasing the soil water holding capacity by providing the excellent soil's porosity (Augé et al. 2001). Several reports demonstrate the paramount importance of the interaction between fungi and plants for sustainable plant production (Smith et al. 2009; Yadav et al. 2019d, e).

Beneficial fungi are chief players in the natural agro-ecosystem as they avail important ecosystem services such as the acquisition of the nutrients, organic matter recycling, and protection against plant pests (Pozo et al. 2009; Ramos-Zapata et al. 2012). A shift to a world of fungi have consequences for carbon cycling as fungal decomposers have developed pathways to degrade recalcitrant structural compounds unique to terrestrial vascular plants such as lignin (Yuste et al. 2011). The usage of organic components of the soil, leaf litter, woody debris, and animal remains, there are numerous ways in which fungi can interact with the mineral component of the soil. In the mutualistic symbiotic relation with algae, lichens produce lichenic acid, which aids in solubilization of rock and protosoils formation. Once there is true soil fungi formation it make a vital contribution to the soil aggregates formation and stability. The ecological significance of *Phanerochaete velutina*, *Perisporiopsis lat-*

eritia, and *Pleurotus* sp. can be elucidated by their role in dead vegetation recycling via conversion of hard wood to usable forms (Chaverri and Gazis 2010). As a component of the ecosystem, fungi itself is also available as food source to be consumed by animals as they contain high amounts of proteins and vitamins. Fungi also provide benefits to plants. Mycorrhizal associations ubiquitous in nature are important components of ecosystem nutrient cycling processes (Cairney and Meharg 2002) and the association also benefits plants by increasing the efficiency of plant nutrition. An ample amount of data strongly supports that plants cultivated with certain species of fungi result into significant uptake of nutrient and higher nutritional grade of crop plants (Yaseen et al. 2011). Fungi such as *Penicillium*, *Piriformospora indica,* and *Trichoderma* have been reported to be efficient as bio-control agents and productivity increase (Sharma et al. 2019; Yadav et al. 2018).

Fungi are the chief inhabitant of soil as well as of plant habitat and play an essential role in ecosystem. They are the chief decomposers that help in stabilization of soil. In agriculture, fungi influence the nutrition, growth, and health of plant. Also, association of fungi with plant helps in defending against plant pathogens that indirectly promotes plant growth. So, use of fungi as a biofertilizers in agriculture plays an essential role in plant development by availing several minerals, and growth regulators like auxin and gibberellins (Kour et al. 2019c; Verma et al. 2017).

Nutrition is one of the factors on which growth and health of the plant mainly depend upon. Now days, nutrition of crops mainly sustain upon chemical fertilizers. These chemical based fertilizers are taken up by crop plants only one half the doze applied. The chemical based fertilizers affect the fertility of soil and also causing pollution in the environment. Biofertilizers are the best substitute to chemical based products for providing nutrition to plants in ecofriendly way (Verma et al. 2015, 2016; Yadav et al. 2016). Fungi biofertilizers used in agriculture provide several nutrients including macronutrients like phosphorus, nitrogen, potassium, and micronutrients like zinc, iron, copper, and magnesium (Suman et al. 2016; Yadav et al. 2019b). Along with providing nutrition fungal biofertilizers also reduces loss of soil nutrients (Cavagnaro et al. 2015). There are many reports which confirm that fungi especially arbuscular mycorrhizal fungi (AMF) association with plants enhances plant growth by providing nutrition. *Glomus etunicatum* and *Glomus mosseae* individually and consortia of *G. mosseae, G. etunicatum, Glomus clarum,* and *Glomus caledonium* were evaluated on the seedling of cucumber and found that there was significant increase in seedling survival, yield, phosphorous, and zinc concentration in the shoot of cucumber plant (Ortas 2010). In another study, AMF, *Glomus intraradices* individually and in combination with PGPR like *Bacillus polymixa*, *Pseudomonas putida*, and *Azotobacter chroococcum* were found to enhance biomass, NPK uptake, stevioside, and chlorophyll of *Stevia rebaudiana* (Vafadar et al. 2014). In a report, AMF, namely *Mortierella elongate, Ceratobasidiaceae* sp., *Alternaria embellisia*, *Dactylonectria torresensis*, *Tetracladium maxilliforme*, *Cadophora*, *S. indica, C. tofieldiae, Oidiodendron maius, and Rhynchosporium secalis* isolated from *Arabis alpina* (Brassicaceae) were observed, and found plant growth enhancement and increase in P uptake (Almario et al. 2017).

Plant growth regulators are the organic compounds that play essential role enhancing in plant growth and development. These are also called biostimulants or bioinhibitors, which may stimulate or inhibits plant cells metabolism (Yadav 2018; Yadav et al. 2019a). Agriculture depend on chemical fertilizers and pesticides to increased crop production. Plant growth regulators are normally active in plants at very small concentrations. They are classified in to main five groups such as auxins, abscisic acid, cytokinin, gibberellins, and ethylene. Ethylene is the plant growth regulators that were firstly identified. It is naturally occurring drugs, which helps to improve pineapple flower production. They were also produced synthetically which mimic like plant hormones occurring naturally, since then the plant growth regulators usage has been growing significantly and has become a modern agriculture major components. Auxins have been primarily regulated growth during enlargement of the cell. They can perform like a both stimulators and inhibitors of growth, and caused various parts of plants (root stem and bud) to response differently. For example, the auxins as herbicides, induced cell enlargement at a low contrition level, whereas at higher concentrations almost always increase ethylene production (George et al. 2008). They delays or it is even toxic to cells. Additionally, auxins promote cell differentiation, plant cuttings root formation, and the development of xylem and phloem tissues. Cell elongation and division in plant shoot is regulated by gibberellins. Cytokinin acts in cell enlargement, plant division, senescence, and amino acid transportation. Ethylene accumulated in the tissue culture vessels can then inhibit the development and growth of many plants tissue culture. Instead, ethylene can have an effect on the transport and metabolism of auxins.

Iron is the fourth most abundant element on earth's crust, and it is necessary for every living organism's growth and development processes. It regulates biosynthesis of aromatic, antibiotic, cytochrome, porphyrin, pigment, nucleic acid, siderophore, toxin, and vitamin (Saha et al. 2016). Iron occurs in two state in aqueous solution, namely Fe^{2+} and Fe^{3+}, however, plants and microorganism cannot use Fe^{3+} form because they form insoluble oxide and hydroxides, thus reducing bioavailability (Aeron et al. 2011; Zuo and Zhang 2011)**.** Fungal origin siderophores are iron chelating, linear to cyclic secondary oligomeric metabolites with high affinity (Speckbacher and Zeilinger 2018). Siderophores are essential metabolites that respond to oxidative stress in various fungi, including *Tricoderma virens*, *Gibberella zeae*, *Cochliobolus heterostrophus*, *Aspergillus fumigates*, *Aspergillus nidulans* and they also play a major role in conidial germination and sexual development (Kour et al. 2019b; Rana et al. 2019a; Verma et al. 2017).

Agriculture is foremost vulnerable sectors to climate change which greatly hampers the crops growth and productivity. The rising incidence of biotic and abiotic stresses has become a major challenge and cause for the stagnation of crop yield. There is a greater need to develop cost effective strategies for abiotic stress conditions management. In this regard, fungi are gaining a greater interest for management of the abiotic stress conditions through different mechanisms. The osmolytes like proline, glycine betaine and sugars accumulation plays an significant role in lowering the osmotic potential in leaves for growth and adaption of plant under water deficit conditions (Kour et al. 2019a, 2020a). Proline as a compatible solute is known to maintain osmotic turgor under stress, stabilize macromolecules and helps in free radical detoxification. Further, it also acts as a sink of carbon and nitrogen for use after relief of stress (Grover et al. 2014). The extent of glycine betaine accumulation is directly linked to extent to stress tolerance (Yadav 2015). Glycine betaine is known to stabilize the enzymes quaternary structures and complex proteins. It also maintains the highly ordered state of membranes at salt concentrations and non-physiological temperatures (Chen and Murata 2008).

Some reports have well demonstrated the raise in the osmolytes concentration and stress tolerance with inoculation of the fungi. Yooyongwech et al. (2013) investigated the growth performance of *Macadamia tetraphylla* with treatment of AMF under water deficit conditions and enhanced accumulation of proline and soluble sugar was observed. The study of Ahmad et al. (2015) reported the proline content and other growth parameters increase with inoculation of *Trichoderma harzianum* and alleviation of salinity stress in Indian mustard. The study of Kumar et al. (2017) also reported the increase of proline content in maize under high salt concentration with treatment of *Trichoderma* sp. The study of Liu et al. (2017) showed higher concentrations of soluble sugars and proline in *Vaccinium ashei* and *Vaccinium corymbosum* treated with *Glomus mosseae* and exposed to cold stress. Thus, osmotic regulation helps cell development and plant growth under stress conditions.

Relative water content in the leaves of plant is another important criterion for plant water status measurement as it plays a significant role in the metabolic activity in plant tissues. Lower relative content of water reflects turgor loss involved in limited expansion of cell and thus reduced growth of plant (Barnawal et al. 2019; Castillo et al. 2013). The rise in RWC could be an efficient approach for stress tolerance. The study of Zhu et al. (2011) demonstrated increase in relative water content, other growth and physiological parameters of maize plants treated with *Glomus etunicatum* under high temperature stress. The increase in relative water content along with other physiological parameters was reported by Zhang et al. (2016) in wheat inoculated with *Trichoderma longibrachiatum* under salinity stress.

Another major consequence of stress is reactive oxygen species (ROS) production including superoxide radical, hydrogen peroxide, and hydroxyl radical (Cruz 2008). The reactive oxygen species production affects the plants metabolic activities via oxidative damage to lipids and proteins ultimately leading to the death of cell (Hasanuzzaman et al. 2013). To reduce the harmful effects of ROS, fungal associations have developed a mechanism including ROS scavenging enzymes such as ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), peroxidase (POX), and superoxide dismutase (SOD). Wu (2011) demonstrated increased superoxide dismutase and catalase activities in *Poncirus trifoliate* with *Glomus mosseae* at high temperature. Gusain et al. (2014) reported higher catalase, superoxide dismutase, and peroxidase activities in rice with inoculation of *Trichoderma harzianum* and *Fusarium pallidoroseum* under water stress conditions. Ganjeali et al. (2018) investigated the effect of inoculation of *Glomus mosseae* on common bean under drought stress and plants on harvesting showed increased superoxide dismutase, polyphenol oxidase, and peroxidase activities.

Plant stresses, weather biotic (plant pathogens) or abiotic (temperature, light, drought, salinity, metals) are the most important limiting factor for the plants growth (Malyan et al. 2019; Yadav et al. 2019c, 2020a). In response to environmental stresses, plant modifies its metabolism and physiology that produces several range of defensive proteins and stress ethylene (Glick et al. 2007). The increase of ethylene level often damages the plant and inhibits its growth. The high ethylene level in plant also may lead to plant death. In aid to lower the level of ethylene, plant growth promoting fungi produces an enzyme named 1-aminocyclopropane-1-carboxylate (ACC) deaminase. This enzyme is a precursor of ethylene and cleaves ACC into α-ketobutyrate and ammonia that helps in decreasing the ethylene concentration, impact of a variety of environmental stresses and its effect on plants and promotes its growth (Nascimento et al. 2014). There are very few reports that are available of fungi that produce ACC deaminase. In one of the reports, *Trichoderma asperellum* was reported for having enzymatic activity of ACC deaminase that can be used in promotions of plant growth (Viterbo et al. 2010). In another report, *Trichoderma longibrachiatum* was producing ACC deaminase and this strain was evaluated on wheat plant and results were showing the alleviation of stresses (Zhang et al. 2019). Another species of *Trichoderma,* i.e. *Trichoderma harzianum* was also reported for producing ACC deaminase enzyme and promotes the growth of soybean on evaluation (Zhang et al. 2017).

The utilization of plant growth promoting fungi as bioinoculants could be an essential components of an integrated nutrient management system. There is a need to focus more on plant and its associated fungal communities and their activities in diverse ecological niches. More and more availability of information will lead to novel agricultural technologies development. The widespread acceptance of such technologies will improve overall plants growth and development which will result in higher yields, maintain soil structure and fertility, reduce the use of agrochemicals, and will also protect the plants from different pathogens (Singh and Yadav 2020; Yadav et al. 2020a). The attack of pathogens leads to inestimable crop losses in many developing regions. Soil suppressiveness of plant diseases could be an important consideration which should be continuously studied for identifying and exploiting the benefits from the specific resident organisms involved (Verma et al. 2018; Weller and Thomashow 1993). These bioresources will also be useful for stressed environments like saline, drought, high and low temperature, heavy metal, alkalinity, and acidity. Thus, the detailed and better understanding of such beneficial communities will surely help in utilization of bioresources in increasing productivity in developing regions and the knowledge may have universal applications across all regions of the world (Adesemoye and Egamberdieva 2013; Kaur et al. 2017).

The development of novel and ecofriendly agricultural services is a key issue in present-day era of demanding population and climate change. In fact, the abiotic stresses prevailing in environment is a key factor affecting the agricultural productivity (Rana et al. 2019b; Verma et al. 2019). On the other hand, the use of agro chemicals to improve yields is another major challenge to be sorted out as the excess use in greatly affecting the environment. Fungal populations in diverse niches play a very essential role in growth of plant and regulation under normal as well as the stress conditions. They greatly influence the fertility of the soil, help in acquisition of the nutrients, and overcome stress conditions. The amelioration of stress conditions in plants through the fungi use needs to be explored more and have to be studied on sound grounds of biochemical, molecular, and physiological parameters (Saxena et al. 2016; Yadav et al. 2017). Thus, better understanding of plant–fungal interactions is important for complete utility of such associations for sustainability. Further, the use of omics approaches such as genomics, metabolomics metagenomics, metaproteomics, metatranscriptomics, and proteomics will further aid in broad vision of such interactions. Eventually, after the detailed studies the application of fungi in agro systems will reduce the cost as well as use of chemical fertilizers, restore the soil's natural fertility, and will also protect against abiotic and biotic stresses.

This book will be useful not only to the researchers, but also to each and every stakeholder that contributes toward evergreen agriculture. The enriched efforts of contributors and editorial team have resulted in a volume, which systematically describes to different issues, and applications of fungal communities in sustainable agriculture and environments. Needless to mention, that maybe, such volumes will be needed to place the biofertilizers and biopesticides technology in field to its potential, but this particular book stands on its merit for the information and contents, which will be useful to all.

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