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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All editors would like to thank their families who were very patient and supportive during this journey. Our sincere thanks to the whole Springer team who was directly or indirectly involved in the compilation of this book. We are grateful to the many people who helped to bring this book to light. The editors would like to thank Mr. Eric Stannard, Senior Editor, Botany, Springer; Dr. Vijai Kumar Gupta, and Prof Maria G. Tuohy, Series editor, Fungal Biology Springer; Ms. Saveetha Balasundaram, Project Coordinator, Springer for generous assistance, constant support, and patience in initializing the volume.

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-vinylguaiacol. 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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