Fungal Biology

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

Agriculturally Important Fungi for Sustainable Agriculture

Volume 2: Functional Annotation for Crop Protection

Springer

Fungal Biology

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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

Sustainable agriculture is the only solution in providing food security to feed the gigantic population, with resource limitation being a foremost challenge for the global community. Sustainable agriculture requires limited use of harmful chemical fertilizers and pesticides. Among diverse groups of microbes, soil and plant fungal communities play an important role in plant growth, development, and soil health. The beneficial fungal communities help to promote plant growth directly or indirectly via different plant growth-promoting mechanisms viz: releasing plant growth regulators; solubilization of phosphorus, potassium and zinc; biological nitrogen fixation or by producing siderophores, ammonia, HCN and other secondary metabolites. The plant growth promoting fungal communities with multifunctional PGP attributes could be used as biofertilizers and biocontrol agents replacing chemical fertilizers and pesticides in the environmental as eco-friendly agents for sustainable agriculture and environment. Fungal communities possess a huge sink of capability by which they act as bioprotectants and biostimulants as well as for mitigation of different abiotic stress in plants. The utilization of beneficial soil and plant fungal resources will surely support sustainable agriculture.

The present book on “Agriculturally Important Fungi for Sustainable Agriculture, Volume 2: Functional Annotation for Crop Protection” covers soil- and plant-associated fungal communities and their role in plant growth promotion, and crop productivity for sustainable agriculture. This book will be immensely useful to the biological sciences, especially to microbiologists, microbial biotechnologists, biochemists, researchers, and scientists dealing with fungal biotechnology. We have the honour that the leading scientists who have extensive, in-depth experience and expertise in plant-microbe interaction and fungal biotechnology took the time and made efforts to contribute these outstanding chapters. Each chapter is written by internationally recognized researchers and scientists so that the readers are given an up-to-date and detailed account of our knowledge of fungal biotechnology and its innumerable agricultural applications.

Sirmour, Himachal Pradesh, India — Ajar Nath Yadav
Lucknow, Uttar Pradesh, India — Shashank Mishra
Baru Sahib, Sirmour, India — Divjot Kour
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All the authors are sincerely acknowledged for contributing up-to-date information on agriculturally important fungi, their biodiversity and biotechnological applications for sustainable agriculture and environments. The editors are thankful to all the authors for their valuable contributions.

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. Editors wish 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 great interest to the scientists, graduates, undergraduates, and postdocs who are investigating fungal biology and biotechnology.

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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.

Chapter 1
Agriculturally Important Fungi for Crop Protection

Pavidharshini Selvasekaran and Ramalingam Chidambaram

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1.1 Introduction

Fungi are one of the most important pathogens of crop plants in agriculture and forestry but they are also used as potential biocontrol agents to prevent and control plant disease. In recent years, the development of fungi for biocontrol of diseases, pests, and weeds has received a significant amount of interest among the community of scientists and researchers (Rangel et al. 2018). Public concerns on the usage of pesticides in the agricultural field and their effect on the environment are increasing day by day. Many fungi are being developed and mass produced as a commercially available biocontrol agents and are used in agriculture to promote the growth of plant and increase plant defense mechanism (Vega et al. 2009) as well as to control plant disease (Costa et al. 2012), terrestrial weeds (Monteiro, AC, Machado 2012). These biocontrol agents can also control and reduce aquatic weeds, plant-parasitic nematodes (Siddiqui and Mahmood 1996), and insects (Alston et al. 2005; Li et al. 2010).

Recent study in agricultural system on the role of Arbuscular mycorrhiza suggests that they can improve salinity tolerance and drought tolerance of their host plant by increasing the nutrient uptake, accumulation of organic solutes, and reducing the oxidative stress as a result of enhanced activity of catalase, peroxidase, calmodulin, superoxide dismutase, and ascorbate peroxidase (Abdel Latef and Chaoxing 2014; Chandrasekaran et al. 2014; Huang et al. 2014). An important role in stress tolerance is enhanced by symbiotic mycorrhizal fungi in both forest and agricultural ecosystems by improving nutrient uptake and drought tolerance and restricting base cation leaching as well as by mitigating the toxic effects of aluminum and other heavy metals (Finlay 2008; Finlay et al. 2009; Yadav 2017, 2019b).

The non-mycorrhizal fungi such as *Trichoderma* are well known for mediating stress reactions in plants and have the potential to parasitize or antagonize plant pathogenic fungi by stimulating the defense response and increasing the plant growth (Druzhinina et al. 2011; Sharma et al. 2019). The other fungi species such as *Piriformospora indica* induce disease resistance, tolerate salt stress, and promote the growth of crops through their capacity of glutathione ascorbate cycle mediated antioxidation activity (Waller et al. 2005). The enhancement of plant growth utilizing plant bio-stimulants and to access novel molecules by exploiting the fungal stress response to be used in agriculture is of current interest (Calvo et al. 2014; Yadav 2018).

Endophytic microbes specifically endophytic fungi are those that have established an equilibrium with their host during the evolution and are recognized as a potential source of a wide variety of bioactive secondary metabolites (Rana et al. 2019a; Tan and Zou 2001; Sonaimuthu et al. 2010; Gangadevi and Muthumary 2008). Their relationship with the host plant can vary from bordering on the pathogen to symbiotic. They adopt a different type of symbiosis such as facultative saprobic, exploitative, parasitic, and mutualistic (Clay and Schardl 2002). In most cases, the plant hosts are benefited by asymptomatic relationship. However in few cases they may exhibit beneficial or pathogenic effects (Photita et al. 2001; Wei et al. 2007; Neubert et al. 2006) Few endophytic fungi exhibit mutualistic relationship with single plant species and not with the other plant species whereas some species have the potential to associate with wide range of plant host as well as association of endophyte with specific host tissue has also been reported (Hardoim et al. 2015; Yadav et al. 2020d). Fungal endophytes are ubiquitous and have been found in the majority of plant species that have been studied to date (Rana et al. 2019b; Yadav et al. 2019b). However, the literature available on the association between few plant host and endophytic fungi is limited and has to be explored further (Brundrett 2007).

Endophytic fungi by secreting selected secondary metabolites have found to be associated with the plants to promote growth (Dai et al. 2008), protect from insects and disease (Wilkinson et al. 2000; Tanaka et al. 2005), and improve stress resistance (Lewis 2004). These secondary metabolites produced by endophytic fungi also have been identified as the source of antidiabetic, insecticidal, anticancer, immunosuppressive, and biocontrol compounds. These novel compounds help as remedies with their valuable biological and chemical characteristics for the health problems of plants, animals, and humans. The fungal endophytes have been represented as "chemical synthesizer inside the plant" because of the production of a variety of these useful chemical compounds (Yadav et al. 2020b, c).

Fungal diversity on earth is contributed significantly by endophytic fungi (Photita et al. 2001). Their biological distribution and diversity are massive in tropical rainforest and temperate zone. The detection of novel compounds from this group of fungi is extensively studied to investigate their potential to be used in pharmaceutical, medical, industrial, and agricultural sectors. A noteworthy discovery is the use of these compounds in agriculture as a biocontrol agent (Mane and Vedamurthy 2018). Fungal endophytes contribute to the fitness of plants by enabling the adaption of plant host to abiotic and biotic stresses. They establish a symbiotic relationship between their hosts and confer disease and pest resistance to host by enhancing their fitness, increasing the growth to resist stresses to the maximum extent, and promote the production of secondary metabolites (Gautam and Avasthi 2019; Rastegari et al. 2020a). Therefore, the use of fungi for the purpose of sustainable agriculture is of major interest.

1.2 The Role of Fungi as Biofertilizers

Biofertilizers are an important source of essential nutrients for plants and crops. They are inexpensive and eco-friendly. They play a vital role in improving the nutrient status of soil, increase soil fertility, and, thus, crop productivity. Biofertilizers are the formulation of living microbes including bacteria, actinomycetes, and fungi (Kour et al. 2020d). They can be applied directly to plant roots, soil, seed, and seedlings. Due to their inherent biological activity of the microorganisms, they help in mobilization and accessibility of nutrients (Pal et al. 2015). Fungal biofertilizers can be applied alone or in combination to the natural fields and can be beneficial directly or indirectly to plant development, yield, and growth through various methods (Rai et al. 2013; Yadav et al. 2019c). The roots of herbs, trees, xerophytes, epiphytes, aquatics, shrubs, trees, aquatics, hydrophytes, and terrestrial plants are reported to develop mycorrhizal associations when grown with the insufficient availability of essential elements such as zinc, phosphorus, nitrogen, iron, sulfur, boron, and copper (Rastegari et al. 2020b; Singh and Yadav 2020).

Fungal biofertilizers that solubilize phosphate are the biological agents that are commonly employed for improving the growth and development of plants by enhancing the phosphorus uptake. The phosphate solubilizing property of fungi contributes significantly to the soil phosphate availability to plants. Several fungi have phosphate solubilizing property, the most common are *Saccharomycopsis schoenii*, *Cryptococcus luteolus*, *Trichosporon beigelii*, *Rhodotorula aurantiaca A*, *Kluyveromyces walti*, *Neosartorya fisheri var. fischeri*, *Candida montana*, *Penicillium purpurogenum var. rubrisclerotium*, and *Zygoascus hellenicus* (Birhanu et al. 2017). The fungi that solubilize phosphate belonging to the genera *Fusarium*, *Aspergillus*, *Penicillium* sp. are also found in the rhizospheric region of various plants.

The fungal genera of *Penicillium*, *Chaetomium*, and *Aspergillus* are of widespread occurrence (Yadav et al. 2018, 2019c). The commonly employed fungi for the production of biofertilizer are *Trichoderma* which is predominantly present in agricultural soils. The rhizosphere inhabited by *Trichoderma* species can also interact and parasitize with other fungi. These species have long been recognized as they enhance crop nutrition, nutrient acquisition, and augment plant productivity. The metabolites produced by these species serve as a fungicide against the fungal pathogens that cause disease (Harman et al. 2008; Chang 1986; Vinale et al. 2009). The utilization of *Trichoderma* as a culture filtrate and its inoculation in soil enhances biomass production and plant growth. The application of this fungus as a model organism is feasible as they are easy to cultivate under laboratory conditions for the evaluation of beneficial interaction between plants and microbes. They can be used as a novel tool to enhance the productivity of plants (Varma et al. 2012).

1.2.1 Advantages of Fungal Biofertilizers

- They are renewable sources of nutrients and sustain soil health.
- They increase the yield of grains by 20–40% and replace 40–50% of chemical fertilizers.
- They enhance plant growth by secreting growth-promoting hormones and also secrete antibiotic and fungi static substances. They do not have an adverse effect on soil fertility and plant growth.
- Phosphate solubilizing or phosphate mobilizing fungal biofertilizer converts insoluble soil phosphate into soluble soil phosphate due to the secretion of various organic acids. Under optimum condition, they can mobilize or solubilize about 40–50 kg phosphorus and results in a 20–30% increase in the crop yield.

- They enhance the uptake of P, Zn, S, and water leading to increased yield and uniform crop growth. They improve the hardiness of the stock transplant and enhance resistance to root disease.
- They liberate the substance that promotes growth, vitamins, and maintain soil fertility.
- They stabilize C:N ratio of soil and decompose the residues of the plant.
- Fungal biofertilizers act as an antagonist and help in the biocontrol of disease by suppressing the incidence of soil-borne pathogens.
- Fungal biofertilizer plays a significant role in the recycling of plant nutrients.
- Fungal biofertilizers are eco-friendly, non-pollutants as well as cost-effective (Table 1.1) (Pal et al. 2015)

1.3 The Role of Fungi as a Biocontrol Agent

Currently, the rapidly growing research area with a significant role in increased food production and plant yield is "biocontrol." The phenomenon of biocontrol agent helps to sustain the food crop quality and to reduce the risks that result from the increased utilization of hazardous chemicals and synthetic pesticides. The major factor responsible for 10–30% of annual crop productivity loss is plant disease. In spite of the development of water management practice, an agricultural practice that has posed to be the effective management of plant disease, new techniques in agronomy, the development of disease-resistant varieties, there are still pathogens for which the synthetic chemicals are broadly used for the management of the disease (Kour et al. 2019b; Yadav et al. 2020a). The attractive choice of using the biocontrol agent against different pathogens has emerged as the most common and significant factor responsible for the death of insects in a large populations (Villa et al. 2017). Several postharvest diseases are biologically balanced using fungal species that have antagonist properties. The worldwide scientist is attracted by this area of research. The components of the biocontrol system are influenced by various factors such as UV light, temperature, pH, as well as abiotic and biotic stresses (Kumar et al. 2019a, b; Yadav 2019a). The biocontrol agent preparation is significantly affected by various abiotic stress factors which lead to modification of functionality. Therefore, knowledge on the survivability of biocontrol agents under certain environmental conditions and the development of the procedure to make the biocontrol agent resist stress tolerance is required to maintain their commercial exploitation and effectiveness. The experimental studies on various biocontrol agents on different plant species have been studied to understand their reaction under varied environmental conditions (Sui et al. 2015) (Table 1.2).

Table 1.1 Fungal biofertilizers for crop protection and sustainable agriculture

List of agriculturally important fungal biofertilizer	Reference
Zinc solubilizing biofertilizer • Ericoid mycorrhiza (*oidiodendron maius*) • *Penicillium simplicissimum* • *Saccharomyces* spp. • *Aspergillus niger*	Martino et al. (2003) Franz et al. (1991) Martino et al. (2003) Wold and Suzuki (1976)
Potash solubilizing biofertilizer • *Aspergillus* spp. (*A. terreus*, *A. fumigatus*, *A. niger*) • Ectomycorrhizal fungi	Lian et al. (2008) Alves et al. (2010)
Phosphate mobilizing biofertilizer • Arbuscular mycorrhiza, *Glomus* spp. (*G. viscosum*, (*G. mosseae*/*G. cerebriforme*/*G. manihotis*/*G. aggregatum*, *G. intraradices*, *G. versiforme*, *G. deserticola*, *G. radiatum*, *G. globiferum*, *G. monosporum*, *G. microcarpum*, *G. halonatum*) • *Paraglomus*, *Geosiphon*, *Acaulospora* spp. (*A. delicata*, *A. foveate*, *Sclerocystis clavispora*, *A. scrobiculata*) • Archaeospora, *Scutellospora* spp. (*S. scutata*, *S. erythropa*, *S. calospora*) • Ectomycorrhiza (*Pisolithus tinctorius*, *Amanita* sp., *Tuber* sp., *Lactarius* sp., *Elaphomyces* sp., *Pisolithus* sp., *Piriformospora indica*, *Cenococcum* sp., *Rhizopogon* sp.) • *Entrophospora*, *Gerdemannia*, *Gigaspora* (*Gigaspora rosea*)	Adholeya et al. (2005) da Silva (2006) Rai et al. (2013) Anderson and Cairney (2007), Pal et al. (2015)
Phosphorus solubilizing biofertilizer • *Aspergillus* spp. (*A. tubingensis*/*A. niger*/*A. terreus*/*A. awamori*/*A. fumigatus*/*A. tubingensis*/*A. melleus*) • *Penicillium* spp. (*P. rubrum*/*P. expansum*/*P. citrinum*, *P. simplicissimum*/*P. frequentans*/*P. oxalicum*/*P. bilaji*/*P. albidum*/*P. italicum*) • *Trichoderma* spp. (*T. virens*/*T. asperellum*, *T. viride*/*T. harzianum*) • *Fusarium* spp. (*F. moniliforme*/*F. udam*) • *Mucor* spp. (*M. ramosissimus*/*M. mucedo*/*M. hiemalis*) • *Candida* spp. (*C. scotti*, *C. krissii*) • *Tritirachium* spp. (*T. album*/*T. egenum*)	Manoharachary et al. (2005) Menon and Mohan (2007) Burton and Knight (2005) Harman et al. (2004) Manoharachary et al. (2005) Of (2009) Pal et al. (2015)
Biofertilizer enriching compost • *Trichoderma* spp. (*T. virens*/*T. asperellum*, *T. viride*/*T. harzianum*) • *Aspergillus* spp. (*A. terreus*/*A. awamori*/*A. fumigatus*, *A. tubingensis*/*A. niger*) • *Pleurotus* spp. (*P. ostreatus*/*P. flabellatus*) • *Fusarium* spp. (*F. solani*/*F. oxysporum*) • *Chaetomium* spp. (*C. bostrychodes*, *C. olivaceum*)	Manoharachary et al. (2005) Singh and Singh (2008) Whitelaw (1999) Harman et al. (2004) Of (2009), Pal et al. (2015)

Table 1.2 Fungal communities as biocontrol agents against plant species

S. No.	Fungi	Plant species	Reference
1.	*Pichia guilliermondii*	*Glycine max*	
2.	*Pichia membranifaciens*	*Vitis vinifera*	Santos and Marquina (2004)
3.	*Candida oleophila*	*Vitis vinifera*	Porat et al. (2003)
4.	*Lentinus conatus*	*Arachis hypogaea*	Lakshmanan et al. (2008)
5.	*Penicillium roqueforti*; *Penicillium viridicatum*	*Allium cepa*	Khokhar et al. (2013)
6.	*Streptomyces lydicus* WYEC108	*P. sativum*	Yuan and Crawford (1995)
7.	*Trichoderma asperellum* Tv5SC, *T. harzianum* Th4d SC	*Helianthus annuus*, *Ricinus communis*	Prasad (2015)
8.	*Trichoderma virens* IMI-392430, *T. pseudokoningii* IMI-392431, *T. harzianum* IMI-392432, *T. harzianum* IMI-392433, *T. harzianum* IMI-392434	*Capsicum annuum*	Rahman et al. (2012)
9.	*Trichoderma koningii*, *Trichoderma harzianum*	*Pisum sativum*	Nelson et al. (1988)
10.	*Pichia angusta*	*Malus domestica*	Fiori et al. (2008)
11.	*Penicillium* sp. EU0013	*Solanum lycopersicum*; *Brassica oleracea*	Alam et al. (2011)
12.	*Leucosporidium scottii* At 17	*Malus domestica*	Vero et al. (2013)
13.	*Penicillium citrinum* VFI-51	*Sorghum bicolor*	Meesala and Subramaniam (2016)
14.	*Saccharomycopsis schoenii*	*Citrus X sinensis*	Hashem et al. (2012)
15.	*Penicillium adametzioides*	*Vitis vinifera*	Ahmed et al. (2015)

1.4 Fungal Endophytes

The efficient and new biological control agents used for the control of pathogens and insects and the bioremediation of the environment are fungal endophytes (Guo et al. 2008). The evidence shows that the fungal endophytes play a significant role in protecting the host from the disease, supporting plant health and plant physiology. Fungal endophytes obtain nutrition, propagation opportunities, protection and shelter from their host by internal plant tissue colonization. This symbiotic relationship helps the host by promoting the overall health and reducing environmental sensitivity. The best offer to the control of chemical disease is the use of endophytes (Yao et al. 2017). To control the plant diseases these biocontrol agents utilize direct and indirect strategies by promoting the accumulation of bioactive compounds, increasing tolerance against stress, and enhancing fitness. An in-depth understanding of the mechanism involved in the association of plants and fungal endophytes is of major interest to optimize the efficacy as well as for the registration of products that are used for plant protection (Rana et al. 2019a; Suman et al. 2016; Yadav et al. 2018). The possible mechanism that is considered to be adopted by the fungal endophytes against the pathogens may be mycoparasitism, induction, antibiosis, direct and indirect inhibition, competition, and improvement of host plant resistance (Yu et al. 2010; Nisa et al. 2015; Gautam and Avasthi 2019). The aspects that are involved in the control of disease by these biocontrol agents are discussed below.

1.4.1 Direct Mechanism

Recent studies have proved the ability of the fungal endophytes to protect the host plant from various diseases and damages due to the activity of plant pathogenic microorganisms. The fungal endophytes produce bioactive compounds which have the potential to inhibit the growth of pathogenic microorganism directly. Some researchers have proposed a few possible mechanisms by the use of fungal endophytes and their secondary metabolites to suppress the pathogens (Yadav et al. 2017b, c). However, the knowledge on the mechanism between plant, endophyte, and pathogen is to be explored further. In direct mechanism fungal endophytes secrete lytic enzymes and produce antibiotics or the pathogens are directly suppressed through antibiosis, mycoparasitism, and competition (Bamisile et al. 2018; Mejía et al. 2008; Ganley et al. 2008; Gautam and Avasthi 2019).

1.4.1.1 Mycoparasitism

Few endophytes exhibit hyper parasitism distinct from antibiosis and competition. The plant pathogenic fungi are often attacked by these fungi that act as mycoparasites either to inhibit or suppress their growth. One of the most popular examples of mycoparasitism is *Trichoderma*. Prior to making any contact, *Trichoderma* detects the fungal pathogen and the extracellular exochitinase is produced in lower levels and discharges the oligomers of cell wall from the target fungus (Harman et al. 2004). This mechanism initiates the *Trichoderma* to release toxic endochitinase that can degrade the target plant-fungal pathogen. The hyphae of the plant pathogens including *Rhizoctonia solani* is parasitized by the *Trichoderma* species (Grosch et al. 2006). A novel endophytic fungus *Acremonium strictum* isolated from *Dactylis glomerate* has been reported (Rivera-Varas et al. 2007) for the activity of mycoparasitism against *Helminthosporium solani*. In the process of mycoparasitism the binding of chemical compounds between the host fungus and mycoparasite occurs initially. One such example is binding of lecithin in the cell wall of the host fungi to the carbohydrate present in the cell wall of *Trichoderma*. Later the establishment of contact with the host fungus is inhabited by the hyphae of the mycoparasite. Several lytic enzymes are involved along with the mechanisms in the cell wall degradation of the host fungi (Cao et al. 2009). These findings have proven that the pest damage in the agricultural crops can be limited by the mycoparasitic activity of the endophytic fungi and can prove to be a potential alternative to the use of chemical pesticides (Gautam and Avasthi 2019).

1.4.1.2 Competition

One of the important methods used by the fungal endophytes against the proliferation and infection of the plant pathogen is competition. This process involves competition between the endophytic fungi and pathogens for space and few common resources (Mejía et al. 2008). Few endophytic organisms can control plant pathogens involving such mechanisms and they could be used as an effective biocontrol agent against the plant disease. The effect on traditional rice varieties by the most frequently isolated endophytic fungi on the growth of plant and incidence of blast disease was evaluated by Atugala and Deshappriya (2015). The study concluded that a range of mechanisms of antagonistic activity was utilized by the endophytic fungi including the competition for antibiosis, substrate, and mycoparasitism. Studies across the world (Atugala and Deshappriya 2015; Mejía et al. 2008; Richmond 2004) demonstrated the use of endophytic fungi as a management strategy against numerous harmful pathogens (Gautam and Avasthi 2019).

1.4.1.3 Antibiosis

A wide spectrum of secondary metabolites is produced by fungal endophytes with the ability to reduce the attacks from various pests and insects. These fungi possess antibacterial, antifungal as well as insecticidal properties that strongly inhibit the growth of plant pathogens and infectious microorganisms (Gautam et al. 2013). The single or multiple kinds of antibiotics which has been proven to be effective has been reported to be produced by single fungus including aromatic compounds, polypeptides, terpenoids, and alkaloids. Researchers (Mejía et al. 2008; Wei et al. 2007) have been carrying out the examination of antibiotic compounds produced by endophytic fungi and have proven that the plants inoculated with endophytic fungi induce the defense mechanism in the host plant. It has been determined that the cultures of endophytic fungi possess the antibiotic properties against several plant pathogens after a series of tests involving liquid broths of endophytic fungi. It was also reported by Atugala and Deshappriya (2015); Kim et al. (2007); Wessels (1999) that the proteins secreted by the species of endophytic fungi act as a protein related with pathogenicity to suppress the activity of plant pathogens by degrading the cell wall. Several studies reported that various chemical compounds are produced with the antibiotic property against pathogens by the fungal endophytes. The examination of the interaction between the endophytic fungi and *Puccinia recondite f.* sp. *tritici* was done by Dingle and McGee (2003) and found that the leaf rust disease caused by this fungus was suppressed by the fungal endophytes. An endophytic fungus *Phomopsis cassiae* isolated from *Cassia spectabilis* (Lu et al. 2000a) secretes a chemical compound 3,11,12-trihydroxycadalene which was found to be effective against *Cladosporium Cladosporioides* and *Cladosporium sphaerospermum*. The antifungal activities of 183 endophytic fungi isolated from 15 plant species from 15 locations in Korea against pathogens causing rice sheath blight disease, tomato gray mold disease, rice blast disease, wheat leaf rust disease, tomato late blight disease and barley powdery mildew diseases such as *Corticium sasakii*, *Botrytis cinerea*, *Magnaporthe grisea*, *P. recondita*, and *Blumeria graminis f.* sp. *hordei*, respectively, were evaluated by Park et al. (2003). In another study examination of woody angiosperm *Theobroma cacao* associated with fungal endophytes against foliar pathogen sp was done (Arnold et al. 2003) and the study revealed that inoculation of leaf tissues by the assemblage of endophytic fungi that are isolated from asymptomatic and infected host limited the damage caused by a significant foliar pathogen (Gautam and Avasthi 2019).

1.4.2 Indirect Mechanism

The association of plants with fungal endophytes has a direct impact on the growth and development of the host plant. The host performance is affected in terms of morphology, growth, physiology, and biochemistry. The important reason for the improvement of host health is due to the production of secondary metabolites by these fungi along with the establishment of a symbiotic relationship (Kaur et al. 2020; Singh et al. 2020; Yadav et al. 2019a). The association of endophytic mycobiota with the host plant is believed to be responsible for the fate of pathogen attack (Wei et al. 2007; Vyas and Bansal 2018). These beneficial microbes can decrease the disease incidence, plant stress, increase the efficiency of nitrogen fixation, improve the nutrient uptake, growth rate of the shoot and root, and improve resistance (Liu et al. 2001; Kuldau and Bacon 2008). These properties of fungal endophytes can be used to play an essential role in the field of food safety, agriculture, and maintenance of environmental equilibrium (Rana et al. 2020). The indirect mechanism adapted by fungal endophytes in the control of pest and disease is given below.

1.4.2.1 Production of Metabolites

In the adaption of plants to biotic and abiotic stresses, the plant-fungal symbiotic association plays an important role by the production of secondary metabolites (Yadav 2019a). The significant factor in the production of various metabolites is the association between plants and endophytic fungi. The environmental and eco-friendly approach to control various plant diseases is the use of endophytic fungi (Rana et al. 2019a, b). The host plant is benefited by the endophytic fungi as they

Table 1.3 Bioactive compounds produced by fungal endophytes

Fungal endophyte	Bioactive compounds	Reference
Cladosporium delicatulum	Plumbagin (5-hydroxyl-2-methylnaptalene-1,4-dione)	Venkateswarulu et al. (2018)
Balansia obtecta	Ergobalancine	Tintjer and Rudgers (2006)
Melanconium betulinum	3-hydroxypropionic acid	Chomcheon et al. (2005)
Phomopsis phaseoli	3-hydroxypropionic acid	Chomcheon et al. (2005)
Neotyphodium coenophialum	Ergovaline	Tintjer and Rudgers (2006)
Acremonium coenophialum	Chitinases	Gautam and Avasthi (2019)
Neotyphodium sp.	Ergonovine	Miles et al. (1996)
Fusarium redolens	Peimisine and imperialine-3β-D-glucoside	Pan et al. (2015)
Aspergillus fumigatus	fumiclavine, A, fumiclavine B, fumiclavine C and Chanoclavine aldehyde	Panaccione (2005)
Colletotrichum gloeosporioides	Piperine	Chithra et al. (2014)
Rhinocladiella sp., *Helminthosporium* sp., *Chalara* sp., *Phoma* sp., *Hypoxylon* sp., *Phomopsis* sp., *Xylaria* sp.	Bioactive cytochalasines	Isaka et al. (2001)
Xylaria sp. YX-28	7-amino-4-methylcoumarin	Xu et al. (2008)
Penicillium sp.	Berkeleydione	Davis et al. (2005)
Ampelomyces sp.	O-methyl alaternin and altersolanol A	Miller et al. (1998)
Morinia pestalozzioides	Moriniafungin	Gautam and Avasthi (2019)
Aspergillus niger	Aurasperone A, fonsecinone A, asperpyrone B, rubrofusarin B	Song et al. (2004)
Pestalotiopsis adusta	Pestalachlorides	Li et al. (2008)
Periconia sp.	Periconicin A	Kim et al. (2004)
Chaetomium chiversii C5-36-62	Radicicol	Turbyville et al. (2006)
Pestalotiopsis jester	Hydroxyjesterone, jesterone	Li and Strobel (2001)
Muscodor albus	1-Butano, 3-methylacetate	Strobel and Daisy (2003)
Pestalotiopsis microspora	Ambuic acid	Li and Strobel (2001)
Colletotrichum gloeosporioides	Colletotric acid	Zou et al. (2000)
Epichloe festucae	Cyclonerodiol, IAA, diacetamide, IEtOH, indole-3-carboxaldehyde, methylindole-3-carboxylate	Yue et al. (2000)

prevent the colonization of pathogenic organisms (Arnold et al. 2003). It has been reported that fungal endophytes secrete a few chemical compounds that inhibit the plant pathogenic fungi based on the experimental studies. The endophytes isolated from the medicinal plants have cytotoxic metabolites, a fungicidal and bactericidal activity which can produce secondary metabolites in the tissue of the host and kill the pathogens (Zhang et al. 2006). It has been reported that the endophytic fungi produce secondary metabolites to protect the host plant from disease and pest (Sudha et al. 2016). These bioactive compounds serve as mediators for specific communication and interaction with the host plant. The competition, fitness, and growth of the host plant are triggered by the endopytic fungi upon production of the secondary metabolites that inhibit the pathogens. These metabolites are categorized into flavonoids, quinones, chinones, saponins, xanthones, phenolic acid, alkaloids, tetralones, benzopyranones, tannins, and several others.

The research on the secondary metabolites and their antipathogenic effects produced by the endophytic fungi to explore their application as a biocontrol agent in various fields has been conducted worldwide. It was reported that *Fusarium* spp. E4 and E5 promoted the content of terpenoids and the growth of *Euphorbia pekinensis* (Gautam and Avasthi 2019). Another study reported (Strobel and Daisy 2003) the production of 25–28 volatile compounds by an endophytic fungi *Muscodor albus*, isolated from the branches of *Cinnamomum zeylanicum*. These volatile compounds are capable of inhibiting the selected bacteria and fungi. Another endophytic fungus *Muscodor crispans* of *Ananas ananassoides* produces a mixture of volatile compounds containing an antibacterial and antifungal property with inhibitory effect against pathogenic fungi such as *Botrytis cinerea*, *P. palmivora*, *Pythium ultimum*, *Fusarium culmorum*, *Alternaria helianthi*, *Rhizoctonia solani*, *Verticillium dahliae,* and bacteria including *Xanthomonas axonopodis* (Yuan et al. 2017). Currently, researchers are investigating the endophytic fungi production of secondary metabolites which can inhibit the insects (Gautam and Avasthi 2019) (Table 1.3).

1.4.2.2 Growth of Root and Shoot

In the process of plant growth, the plant host and mutualistic organisms producing compounds that regulate the growth of the plant and antimicrobial substances are asymptomatically colonized by the endophytic fungi to enhance the competitiveness, growth, and fitness of the host in nature (Sudha et al. 2016). These fungi help the host plant in phosphate solubilization whereas the plant provides food and shelter. These fungi also help to enhance the uptake of phosphorus, nitrogen fixation, production of siderophores including several other plant hormones such as gibberellins, auxin, ethylene, abscisins, and IAA which are important for the regulation of plant growth (Boddey et al. 2003; Firáková et al. 2007). Hamayun et al. (2009) examined the endophyte *Cladosporium sphaerospermum* isolated from *Glycine max* for the production of bioactive molecules that promote plant growth. The study revealed that *Cladosporium sphaerospermum* produces GA3, GA4, and GA7 growth hormones that are associated with inducing the plant growth in soybean and rice. It was reported (Khan et al. 2013) that the endophytic fungi *Fusarium* *tricinctum* and *Alternaria alternata* produce the derivatives of indole acetic acid that promote the plant growth. In another study by Li and Zhang (2015) an apestalotin analogue was characterized by *Pestalotiopsis microspora*. The research revealed that the germination rate of Distylium chinense was significantly increased by *Pestalotin* a study conducted on the root colonizing endophytic fungus *Piriformospora indica*, by Johnson et al. (2014) revealed that the association of fungi with the root modulates the growth-promoting phytohormones, develops the host plant, and enhances the uptake of essential nutrients and translocation. The height and weight of plants along with other growth-promoting parameters such as weight of roots and shoots are also influenced through the colonization with the endophytic fungi (Lopez and Sword 2015). It is known that the plant growth can be actively or passively developed by the endophytic fungi through various mechanisms such as biochemical and molecular mechanisms. However, the mechanisms underlying the habitat adapted symbiotic relationship and high stress tolerance of plant remains unknown (Gautam and Avasthi 2019).

1.4.2.3 Improvement of Physiological Function

The mechanism of plant defense against the phytopathogenic organisms is promoted by the fungal endophytes through the enhancement of plant growth. The host plant can survive various biotic and abiotic stresses by colonization with endophytes. In many studies, the enhancement of physiological processes of the host plans was noted (Yong et al. 2009). The phytohormones that may influence physiological functions of plants produced by fungal endophytes are also demonstrated in many studies. The defense response of the host plant is found to be enhanced by the fungal endophytes. However, more energy is required to increase defense responses. The endophytic colonization of the host plant improves the uptake of nitrogen, phosphorus, and other essential nutrients and enhances the metabolic activity such as physiological functions and increases the growth of plant (Bolton 2009). The compounds that interfere in the cell division of plant are also produced by the endophytic fungi. The substances like IAA that are known to regulate plant processes are produced by an endophytic fungus, *Colletotrichum* sp. in *Artemisia annua* (Lu et al. 2000b).

Dai et al. (2008) studied the influence of the *Fusarium* sp. an endophytic fungus on the growth of *Euphorbia pekinensis* and the extract obtained from this fungus functions as an auxin. The growth of the host plant is influenced due to this phytohormone effect. Nitrogen fixation is one of the important functions performed by the endophytic fungi to their host. The impact of *Phomopsis liquidambaris* on N dynamics in rice was investigated by Yang et al. (2015) and it was found that the available nitrate and ammonium present in the rhizosphere soil of the endophytic fungi under low N conditions significantly infect rice. The ability to suppress the soil nitrification by the endophytic fungi was also reported. The potential of *Brachiaria* species to increase the nitrification of soil was observed by Cardoso et al. (2017) due to the release of an inhibitory compound called brachialactone from the roots of the plant growing with the endophytic association.