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

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.

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Lucknow, Uttar Pradesh, India	Shashank Mishra
Baru Sahib, Sirmour, India	Divjot Kour
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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. 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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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 59 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 05 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.

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Chapter 1
Agriculturally Important Fungi for Crop Protection

Pavidharshini Selvasekaran and Ramalingam Chidambaram

Contents

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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.

1.4.2.4 Plant Stress Reduction

The endophytic fungi were found to enhance the tolerance of plants to abiotic stresses in addition to increasing the fitness, competitiveness, and growth of the host plants (Aly et al. 2011). The endophytic colonization of fungi supports and protects plants to tolerate the environment under high stress such as high temperature, salt, and drought (Rodriguez et al. 2008). The fitness of the plants such as *Dichanthelium lanuginosum* is increased by the presence of endophytic fungi in the areas with high soil temperature. The endophytic fungi promote tolerance against water stress, salt stress, and high soil temperature (Bartels et al. 2002). Therefore, such symbiosis is considered of great significance in helping the plants to tolerate and adapt globe climatic change (Selim 2012).

Such beneficial potential of endophytic fungi on plants has increased interest to improve the production of crop plants by the use of endophytic microbes (Kour et al. 2020c). However, the mechanism of the symbiotic interaction resulting in the ability of the plant to tolerate high stress is not studied in depth. The colonization of fungal endophytes with the tissues of the plant enhances the ability to adapt stresses based on habitat (Murphy et al. 2015). The grasses obtained from coastal beaches in the United States such as *Dicanthium lanuginosum* and *Leymus mollis* were reported to grow in geothermal soils due to their symbiotic relationship with fungal endophytes *Curvularia protuberata* and *Fusarium culmorum*, respectively, which confers tolerance towards heat and salt (Rodriguez et al. 2008; Gautam and Avasthi 2019).

1.4.2.5 An Improvement of Plant Resistance

The endophytic fungi also possess the capability to induce disease resistance. Several mechanisms behind these resistances were proposed such as improved nutrient uptake, root growth, and nitrogen fixation. The decrease in the plant stress has a direct impact on the growth as well as the development of the host plants and enables them to resist the phytopathogens (Sudha et al. 2016; Bae et al. 2009). The toxic compounds produced by certain plants with endophytic colonization are reported to be effective as a pest repellent (Akello et al. 2007). The process of competition and production of biocidal compounds or phytoalexins can improve the resistance of the host plants colonized with the fungal endophytes and their molecular studies showed significant changes in the metabolism of the plant such as biochemical production which induces the mechanism of defense and resistance against the pathogen. During the endophytism certain protein that acts as pathogenicity related proteins is produced that are reported to suppress the activity of plant pathogen (Li et al. 2004). The promotion of plant growth enhanced by the fungal endophytes is another benefit that enhances the capacity of the plant to develop resistance against various pathogens. The study on the ability of fungal endophytes to induce resistance among host plants was done by many researchers. The barley plants are reported to be resistant against *Blumeria graminis*, *Fusarium culmorum*, leaf and vascular pathogens that are inoculated with *Piriformospora indica*. They also exhibited an increase in tolerance towards salt stress. The endophytic fungi such as *Colletotrichum* sp. and *Cryptosporiopsis cf. quercina* are reported to be effective against various phytopathogens such as *Gaeumannomyces graminis*, *Rhizoctonia cerealis*, *Pyricularia oryzae*, and *Phytophthora capsici* (Lu et al. 2000b). The *Festuca rubra* L., when inoculated with the endophyte *Epichloe festucae* the induced resistance was observed against *Sclerotinia homoeocarpa* which causes dollar spot disease (Clarke et al. 2006).

1.4.3 The Advantages of Fungal Endophytes Over Chemical Methods

- The genetic resistance against numerous plant pathogens is developed by colonization with fungal endophytes. Hence, the requirement for the use of chemical pesticides to prevent and control numerous foliar phytopathogens that have a high rate of sporulation is reduced. They are well suited for widespread dissemination as airborne propagules.
- The beneficial microbes are affected by the use of synthetic chemicals although they inhibit pathogens. During the treatment with pesticide, the effective root nodule formation with the nitrogen-fixing bacteria is decreased and inhibited. This proves endophytic fungi as a potential alternative over synthetic chemicals.
- The systemic fungicide increases the chance of fungicide resistance by pathogens though they help in the control of plant pathogens. The fungal endophytes manage these pathogens in a better way and reduce the development of resistance by pathogens.
- The requirement of farmers on the synthetic chemical is reduced by the use of fungal endophytes thereby reducing the exposure of user and environment to the synthetic chemicals that are harmful.
- The use of endophytic fungi as a biocontrol agent, an eco-friendly and cost-effective method when compared to all the other methods. The cultivation of eco-friendly fungi, their handling is easy and environmentally friendly (Gautam and Avasthi 2019).

1.5 Arbuscular Mycorrhizae and Its Role in Agriculture

The term mycorrhizae was derived from the Greek words mycos and rhiza which means fungus and root, respectively (Wang and Qiu 2006). Mycorrhiza is categorized into arbuscular, ectendo, ecto, ericoid, abutoid, monotropoid, and orchid mycorrhiza. One of the most effective microorganisms involved in the stabilization of soil structure is Arbuscular mycorrhiza (SWABY 1949; Miller and Jastrow 2000). They are economically important types of microorganisms and are exploited commercially in forestry and agriculture. Arbuscular mycorrhiza is a monophyletic lineage of obligate mycobionts (Schwarzott et al. 2001). They form symbiotic associations with plant roots belonging to phylum *Glomeromycota* (Owen et al. 2015). About 80–90% of extant plant species are mycorrhizal as phylum is an ancient form of symbiosis in plants. Mycorrhiza penetrates the root cell walls of plants and develops arbuscules, hypae, and vesicles (intra-radical structures) in the cortical cells of the host and hyphae and spores (extra radical structures) in soil. Bidirectional flux characterizes the mutualistic association whereas the acquisition of soil nutrients in phytobiont is enhanced by mycobiont while the phytobiont provides carbon sources (photo assimilates) to the mycobiont (Buscot et al. 2000; Brundrett 2009). The ability of Arbuscular fungi to form hyphae for nutrient uptake with highly favorable surface area to volume ratio and to secrete enzymes and organic acids is due to the mutualistic association (Owen et al. 2015).

The interaction between plants and microbes has a major impact on the functioning of the plant and ecology of the plant community (Boon et al. 2014; Vimal et al. 2017). Mycorrhiza along with plant root hairs increases soil-root contact area as they are the vital components at the soil–root interface through their extra radical hyphae. Hence, they improve plant nutrient uptake mainly phosphate (Jakobsen et al. 2005; Bucher 2007), iron (Treeby and Bag 1992), calcium (Azcón and Barea 1992), manganese, nitrogen, and zinc. Arbuscular mycorrhiza is also beneficial to improve the nutrient acquisition of plants in soils with a low fertility rate. They serve as a substitute for reduced fertilizer input and lead to sustainable agriculture (Galvez et al. 2001).

The beneficial attributes to host by Arbuscular mycorrhiza include:

- Increased plant tolerance to salinity, drought, and metal pollution (abiotic stress) and pathogenic infection, herbivory (biotic stress) (Augé 2004)
- Increases plant growth and development by improving the rooting of micropropagated plantlets.
- They contribute to plant nutrition acquisition by influencing the chemical and microbial ecology of the mycorrhizosphere (Azcón and Barea 1992)
- In a disturbed ecosystem, they help to improve energy flow, nutrient cycling, and plant establishment.
- The symbiosis by Arbuscular mycorrhiza fungi helps to stimulate the synthesis of secondary plant metabolites which are essential for the plants to tolerate environmental induced stresses and beneficial to human beings through their antioxidant activity and protective nutrient compounds.
- They enhance plant diversity as they interconnect several individual and unrelated plant species
- Arbuscular mycorrhiza enhances the soil bioremediation as they are involved in phytoremediation-use of plants for the uptake of pollutants. They are beneficial in revegetation and restoration of contaminated and disturbed areas as they help in alleviating toxicity of metals to plants by reducing the translocation of metal from the root to shoot.

- Arbuscular mycorrhizal fungal hyphae improve the soil stability, water retention, and binding property through the extra radical mycelial network and secretion of glomalin which is a hydrophobic proteinaceous substance.

1.6 *Penicillium* and Its Role as Plant Growth Promotion

Penicillium as an ascomycetous fungus is a genus which is significant for the production of food and drug in the environment. In the human body, the antibiotic penicillin produced by *Penicillium* restricts the spreading of certain bacteria. *Penicillium* belongs phylogenetically to *Trichocomaceae* and is an anamorph genus (Berbee et al. 1995; Samson 2016). The name *Penicillium* is derived from the word penicillus which means little brush. It has been reported that *Penicillium* spp. intermingles with the roots of plants and crops to enhance their growth (Shivanna et al. 1994; Khan et al. 2008). Several plant hormones such as gibberellins (GA), indole-3-acetic acid (IAA) are secreted by this fungus and are involved in phosphate solubilization (Khan et al. 2008, 2011; Radhakrishnan et al. 2013).

Penicillium species are widely spread in nature across various soil environments such as dessert soil, cultivated soil, beach soil, forest soil, and marine habitats (Chandanie et al. 2006). *Penicillium* species are of great interest to researchers as they secrete herbicides, insecticides, antibiotics, mycotoxins, antioxidants, anticancer compounds, and extracellular enzymes (Munns and Tester 2008). The production of phytohormones such as gibberellins, auxin, cytokinin, solubilization of minerals and antagonism against phytopathogens are the key mechanism involved in promoting plant growth by *Penicillium* species (Volpin et al. 1995). The phosphorus uptake, growth, and yield of several crops such as pomegranate, sesame, and wheat are promoted by the inoculation of *Penicillium* species with PGP in soil. The upregulation of IAA which is a plant growth-promoting phytohormone during stress conditions promotes plant growth (Faeth and Fagan 2002).

It has been reported that under oxidative stress *Sesamum indicum L.* treated with *Penicillium* showed a significant increase in IAA. The species of *Penicillium* and *Phoma glomerata* produce gibberellins and IAA to promote the growth of the host plant under the condition of abiotic stress. The phytohormone gibberellins regulate various physiological processes such as fruit set, floral development, flowering, seed germination, and shoot growth (Khan et al. 2011). The level of GA is increased in host plants with the help of the endophytic *Penicillium* population under abiotic stresses such as heat, heavy metals, and salinity. The production of GA by various species of *Penicillium* has been reported such as *P. funiculosum* under drought and salinity (Waqas et al. 2012), *P. janthinellum* LK5 under the stress of cadmium toxicity (Khan et al. 2013), and *P. resedanum* under drought, heat, and salinity (Khan et al. 2013).

1.6.1 The Role of **Penicillium** *Under Abiotic Conditions*

The tolerance of host plants against various pathogens and metal toxicity is provided by *Penicillium*. The tolerance in host plants against metal toxicity can be enhanced by different strains of *Penicillium*. The strains of *Penicillium simplicissimum* and *Penicillium janthinellum* synthesize citric acid and are known to reduce zinc and aluminum toxicity (Zhang et al. 2002). Similarly, the cadmium content is reduced by the strains of *Penicillium* species obtained from the polluted industrial sediments (Massaccesi et al. 2002). Studies on the potential of *Solanum lycopersicum* against cadmium toxicity proved that the metal toxicity can be mitigated by *Penicillium* species by the synthesis of enzymes and various other bioactive metabolites. Plants under cadmium stress are addressed through the complexation and compartmentation (Mazid et al. 2011). Sulfur is one of the most significant nutrients for plants along with a component of glutathione which is considered to be active in the detoxification of heavy metals (Howden et al. 1995). Under the exposure to cadmium and *Pencillium*, the glutathione and the sulfur content of the root increased. The sulfur content is enhanced by treatment with *Penicillium* that increases the synthesis of glutathione required for the synthesis of phytochelatin (Rüegsegger et al. 1990). The calcium content under cadmium stress increases by the treatment of *Penicillium*.

In the plant growth, calcium plays an essential role and is a key molecule in the signal transduction under biotic and abiotic stress conditions (White and Broadley 2003). The plants need to reduce the peroxidation of lipids in the cell membrane and enhance their capacity to intake nutrients and antioxidant activities to reduce the effects of metal toxicity and to increase the plant yield (Siddiqui et al. 2011). The potential of antioxidant activity of plants against cadmium is stimulated by the *Penicillium janthinellum* and lowers the content of cadmium in roots as well as protects the plant from electrolytic leakage induced by cadmium. The plant generates ROS due to the membrane damage caused by the cadmium injury and releases the product MDA resulting in from the breakdown of aldehydic lipid in the membrane. The plants treated with *Penicillium* during cadmium stress have significantly less MDA indicating less injury to the functional membrane. Studies have shown that osmotic stress is induced by drought and salinity stress which is transmitted through the abscisic acid-dependent and the abscisic acid-independent pathways (Mauch-Mani and Mauch 2005; Cao et al. 2014). It has been observed that the synthesis of abscisic acid is low under stress and fungal treatment (Hause et al. 2007; Jahromi et al. 2008). The minimum effort is required by plants for the synthesis of abscisic acid and to control the movement of the guard cell under stress conditions as the water balance in the plant can be improved by *Penicillium* treatment. The exposure of the plant to stresses like cold and drought significantly increases the expression of the RAB18 gene while the heat shock suppresses the gene. However, in *Penicillium*-treated and salinity-stressed plant the mRNA of RAB18 accumulation is noted.

Table 1.4 The role of *Penicillium* species against abiotic stress

Penicillium species	Abiotic stress	Steps in stress mitigation	Plant source	Reference
P. funiculosum	*Copper* Salinity	Potassium plays a significant role in the oxidative stress response and helps the synthesis of glutathione associated with the stress tolerance. Increased level of calcium, potassium, and phosphorus Lower content of abscisic acid and higher content of GA and IAA. The vegetative growth through GA is promoted by fungal association whereas IAA promotes the plant growth regulation	Soybean Soybean	Khan et al. (2011) Khan and Lee (2013)
Penicillium sp. LWL3	Drought and salinity	The higher level of gibberellin and indole acetic acid is exhibited by the culture filtrates of Penicillium. The host plant had increased plant height, shoot length, increased biomass and chlorophyll content	Cucumber	Waqas et al. (2012)
P. resedanum LK6	Osmotic stress	Lower level of superoxide anion formation and lipid peroxidation and higher levels of catalase, peroxidase, glutathione, and polyphenol indicated lower injury of membrane in plants associated with Penicillium as the plants had minimum lipid peroxidation and electrolytic leakage	Capsicum annuum	Khan et al. (2013)
P. minioluteum LHL09	Salinity	Increase in the secretion of GA4 and GA7 and decrease in the production of abscisic acid	Soyabean	Mazid et al. (2011)
Penicillium spp.	Salinity	Sesame seeds treated with Penicillium had increased root growth of seedling due to the amino acid present in the culture medium	Arachis hypogaea	Radhakrishnan et al. (2013)
P. janthinellum	Cadmium	Plants inoculated with Penicillium had higher stomatal conductance. Higher content of catalase, glutathione, and ABA. Elimination of ROS during the response of plant to Cd stress involves the enzyme catalase	Tomato	Khan and Lee (2013)

The interaction of fungi and the production of phytohormone GA might have activated the expression of RAB18 (Ghelis et al. 2000). Similarly, the same results had been noted by the exogenous abscisic acid-induced RAB18 in the abscisic acid mutant of *Arabidopsis thaliana* (Ghelis et al. 2000). In plants treated with *Penicillium* the upregulation of RAB18 under salinity stress is due to the anionic channel activation during stomatal closure as confirmed by the increased ionic flux (Bray et al. 2000). The accumulation of abscisic acid is correlated with the increased

Table 1.5 The mechanism involved in the suppression of plant pathogens by *Trichoderma* species

Trichoderma sp.	Biocontrol factors	Target organism	Disease
T. virens "Q" strain	Induction of plant phytoalexin by antibiotic compound, gliovirin	*Pythium*/*Rhizopus oryzae*	Cotton seedling disease
BAFC 742, *T. harzianum*	Chitinase and β-1,3-Glucanase	*BAFC2232*, *Sclerotinia sclerotianum*	Fungal-soybean plant
T. harzianum T-203, *T. virens* isolate GL3 and GL21	Antibiotics gliotoxin and gliovirin and other inhibitory metabolites	*Pythium ultimum*, *Rhizoctonia solani*, *Meloidogyne incognita*	Damping-off of cucumber
T. harzianum 25, *T. viride*	Antibiotics and anthraquinones	*Serpula lacrymans*	Fungal wood decay
T. pseudokoningii, *T. harzianum*, *T. virens*, *T. lignorum*, *T. hamatum*	Unknown inhibitory substance, metabolites, antibiotics, extracellular or action of lytic enzyme	*Rhizoctonia solani*	Damping-off of bean
T. viridae, *T. harzianum*	Cellulolytic, proteolytic, lipolytic and pectinolytic enzyme. Unknown antibiotic compounds such as peptides and cyclic polypeptides	*Aspergillus flavus* and *Fusarium moniliforme*	Fungal seed associated
T. harzianum 1051, *T. harzianum* 39.1	N-acetylglucosaminidase, chitinase, total cellulase, endoglucanase,aryl-β-glucosidase, protease, and amylase	*Crinipellis perniciosa*	Witches' broom disease of cocoa

electrolytic flux which causes a reduction in the elongation of shoot, rate of photosynthesis, chlorophyll content, leaf area, development of flower and fruit. The treatment of plants with endophytic fungi *P. janthinellum* mitigates the negative effect as the plants synthesize abscisic acid in smaller amounts to deal with the stressful condition. This mechanism of growth promotion is related to the effects of exogenous GA3 treatment under stress (Hamayun et al. 2010; Iqbal and Ashraf 2013) (Table 1.4).

1.7 *Trichoderma* for Sustainable Agriculture

The species of *Trichoderma* suppresses the severity of disease by antagonizing the pathogens and improves the growth of the plant through different modes of actions through the combination of mechanisms such as the production of cell wall degrading enzymes, antibiotics, competition for growth production and key nutrients, stimulation of mechanism of plant defense, parasitism of host fungus, and induced systematic systemic resistance (Jayalakshmi et al. 2009).

1.7.1 Mycoparasitism

Mycoparasitism is an effective mechanism and has long been involved in the suppression of pathogenic fungi by *Trichoderma* species (Vinale et al. 2013). The process of mycoparasitism is complex involving chemotrophic growth on the host by the antagonist, host recognition by the mycoparasite, attachment, and coiling of pathogen hyphae, excretion of extracellular enzymes followed by lysis and exploitation of host (Chet et al. 1990). The suppression of *R. solani* by *T. lignorum* was reported. The hyphal cell walls of the pathogen are lysed by enzymes such as

Table 1.6 Volatile compounds and antibiotics produced by *Trichoderma* species

Volatile compounds	Reference
B-1,3-glucanase	Khan and Mohiddin (2018)
Alamethicin, paracelsin, trichotoxin	Lumsden (1989)
Succinic acid, heptelidic acid	Howell et al. (1993)
6-n-Pentyl-2H-pyran-2one,6-n-pentyl-2H-pyran-2-one	Claydon et al. (1991)
Trichorzianines, propionic acid, trichoviridin, 3-(3-isocyano-6-oxabicyclo(3,10)hex-2-eh-5yl)	Baldwin et al. (1981)
Chitin-1-4-b-chitobiosidase n-acetyl, b-d-glucosaminase, endochitinase	Khan and Mohiddin (2018)
Harzianolide(3-(2-hydroxyl-propyl))-4(hexa-2′-dienyl-2(5H00 furanone	
Harzianum A	Malmierca et al. (2012)
Harzianone Limonene	Miao et al. (2012) Nemčovič et al. (2008)
Pachybasin	Liu et al. (2009)
Koninginin F	Song et al. (2010)
Trichodermin	Watts et al. (1988)
Trichoviridin Trichodermol	Marquez et al. (1983) Reino et al. (2008)
Trichosetin	Marfori et al. (2002)
Viridin, gliotoxin	Haggag and Mohamed (2002)
Chitobiase	Khan and Mohiddin (2018)
Chitinase	Köhl et al. (2019)
Protease	Köhl et al. (2019)
Viridol, 9-epi-viridol	Phuwapraisirisan et al. (2006)
Isomenthone, isopentyl acetate, menthone	Polizzi et al. (2011)
Octadecyl ester, arachidic acid, butyl ester, phenol, isopropyl myristate, acetic acid, acetone, bicyclohepatan-2-ol, butanoic acid, phenol, lindane, isopropyl ester, carbolic acid, 1-methylethyl ester	Siddiquee et al. (2012)

proteases, chitinases, β-1,3-glucanases during the activity of mycoparasitism (De La Cruz et al. 1992). The degradation of the cell wall, inhibition of mycelium growth, and spore germination of pathogenic plant fungi are associated with the properties of the enzyme, β-1,3-glucanases (Lin et al. 2007). The degradation of the pathogen cell wall and hyphal membranes and cell walls are reported (Grandgirard et al. 2002) to be associated with proteases produced by *T. harzianum* T-39. The hydrolytic enzymes, exogalacturonase, and endopolygalacturonase produced by *Botrytis cinerea* that reduces the severity of gray mold can be deactivated by the proteases. The mycoparasitic activity of *Trichoderma* species against plant pathogenic fungi was reported by Kotze et al. (2011) (Table 1.5).

1.7.2 Antibiosis

The term antibiosis is defined as the process of inhibition and destruction of the microorganisms by the action of specific or non-specific substances and by the production of growth inhibiting antibiotics (Haggag and Mohamed 2007). Several species of *Trichoderma* and various other biological agents produce enormous antibiotics (Handelsman and Stabb 1996). The species of *Trichoderma* are also known to produce extracellular enzymes that are involved in biocontrol of plant pathogenic fungi (Monte 2001). It has been reported that *T. lignorum* produces a toxic substance called gliotoxin lethal to *R. solani* and *Sclerotinia americana*. But later it was found that gliotoxin was produced by *Gliocladium virens* and not *T. lignorum* (Webster and Lomas 1964). It has also been reported that the culture filtrate of *T. harzianum* inhibits the growth of *F. longipes* and *F. solani* by 74% and 60%, respectively.

The produced toxins suppressed the disease development by affecting the spore germination (fungistasis) and causing mortality to the cells (antibiosis). *Trichoderma* species produces antibiotics such as harzianic acid (Vinale et al. 2013), viridian (Zafari et al. 2008), gliotoxin (Anitha and Murugesan 2005), viridiol (Phuwapraisirisan et al. 2006), alamethicins (Aidemark et al. 2010), and several others (Goulard et al. 1995). The process of action of these antibiotics is synergized by combining with the enzymes that degrade the cell wall and by producing a strong inhibitory effect on the pathogens (Vinale et al. 2008). *T. harzianum* produces Trichotoxin A50 that is reported (Suwan et al. 2000) to inhibit the growth of mycelium and sporangium produced by *P. palmivora*. (Table 1.6) enlists the volatile compounds and antibiotics produced by *Trichoderma* species.

1.7.3 Competition and Competence of Rhizosphere

An excellent competitor for nutritional resources and space is the species of *Trichoderma*. The displacement of the pathogen can be achieved by the competition between pathogens and the biocontrol agents. These species compete for food, essential elements in soil with other fungi. They modify the rhizosphere through acidification of soil and inhibit the growth of pathogens (Benítez et al. 2004). *Trichoderma* species are either added to the soil directly or as seed treatments and grow spontaneously along with the developing root system thereby protecting the plant against pathogens (Howell et al. 2000). The colonization of *Chondrostereum purpureum*, the pathogen of plum trees was suppressed by *T. viride* (Corke and Hunter 1979). The determination of the antagonism expressed by various strains of *Trichoderma* spp against *F. oxysporum* and several other plant pathogens involves competition for carbon (Sivan 1989). The Fusarium species on several different crops were controlled by *T. harzianum* T-35 through nutrient competition and colonization of the rhizosphere (Viterbo et al. 2007). In the rhizosphere of cotton, the competition for carbon is involved in the suppression of *F. oxysporum* f. sp. melonis (Sivan 1989).

1.7.4 Enzyme Production

Trichoderma species produces several different enzymes that play an important role in the disease suppression and growth promotion of plant (Mohiddin et al. 2010). The polysaccharides, glucans, and chitin that provide rigidity to fungal cell walls are broken by the enzymes produced by *Trichoderma* species and destroy the integrity of the cell wall. Metcalf and Wilson (2001) reported that endo and exochitinases produced by *T. Koningii* (Tr%) help in the penetration and destruction of the plant pathogen cells without harming the tissue of the plant. *Trichoderma* species also produce various hydrolytic enzymes such as β-1,3-glucanase, chitinase, and proteases as well as volatile and non-volatile antibiotics (Elad 1983). Elad and Kapat (1999) reported that the biocontrol of *B. cinerea* by the *T. harzianum* (T39) is due to the proteases that are produced by the *T. harzianum*. These proteases inactivate the production of hydrolytic enzymes by *B. cinerea*. The solution of protease produced by the biocontrol fungus partially deactivates the hydrolytic enzymes when applied to the bean leaves and reduces the severity of disease by 70–100%.

1.7.5 Enhancement of Host Defense Response

The important mechanism of disease suppression by *Trichoderma* spp. is the stimulation of host defense response (Harman 2006). The induction of resistance mechanisms such as hypersensitive response induced systematic resistance and systematic acquired resistance protects the plants from pathogens when the strains of *Trichoderma* are added to the rhizosphere (Haggag 2008). Induced resistance has been observed by De Meyer et al. (1998); Koike et al. (2001) with an unidentified *Trichoderma* sp. on cucumber, *T. harzainum* on bean, and *T. virens* on cotton. The seedlings of cotton treated with the strains of *T. virens* (Howell et al. 2000) had a higher level of compounds such as terpenoids that are related to the mechanism of defense and higher peroxidase activity in the roots of the host plant. The peroxidase activity induced by *T. virens* has also been reported (Howell et al. 2000) in the seedlings of cotton more than in the control experiment. The production of phytoalexin in the cells of grapevine (Calderón et al. 1993) is elicited by ethylene-inducing xylanase produced by the *T. viride*. The stimulation of significantly higher terpenoid levels in cotton was noted in the culture filtrates of few effective strains of *T. virens* and the elicitors are mostly glycoproteins or proteins (Hanson and Howell 2004). The root inoculation of the cucumber seedling which is 7-day old in an aseptic hydroponic system with *T. harzianum* has been reported (Yedidia et al. 1999) to induce the response of defense in the leaves and roots of the treated plants.

The activation of systematic acquired resistance in plants correlates with the expression of pathogenesis-related genes such as acidic and basic β-1,3-glucanase and chitinase which acts against the cell wall of plant pathogen (Ferreira et al. 2007). The systematic resistance induced by *Trichoderma* species in plants is phenotypically similar to that of systematic acquired resistance (Yedidia et al. 2000). The cellulase and xylanase derived from *Trichoderma* are well known in inducing the biosynthesis of ethylene (Martinez et al. 2001). The high activity of phenylalanine ammonia lyase, polyphenoloxidase, peroxidase, and total phenolics has been recorded in the plants that are pretreated with *Trichoderma*, *Bacillus*, and *Pseudomonas* (Khan and Mohiddin 2018).

1.7.6 Growth Promotion of Host Plants

The growth of plants can be stimulated, enhanced, and improved by the *Trichoderma* species. It has been reported (Chang 1986) that seed germination of pepper was induced two days earlier in soil treated with *T. harzianum* than in the untreated soil. The flowering and the blooms increased in the plant *Chrysanthemums* and the weight as well as height was greater in either raw or steamed soil treated with *T. harzianum* (Baker 1984). These responses were noted consistently with population densities of *T. harzianum* greater than 108 cfu/g soil irrespective of the application form. Dry matter of bean plants was increased by *Trichoderma koningii* at

106–108 conidia/g of soil (Baker 1984). Sivan (1989) speculated that the growth promotion of plant may be due to the activity of the biocontrol fungus that reduces the concentration of plant growth inhibitory substances or increase the concentration of compounds that are related to the defense mechanism of plant. Thus, the growth promotion of plants may be due to the production of growth-promoting hormones or increased nutrient uptake by the plants (Sivan 1989).

The application of *Trichoderma* species can strengthen the defense mechanism of plants. It has been reported (Rabeendran et al. 2000) that by dipping transplants in spore suspensions (10^7 conidia/mL) of *T. tomentosum* and *T. longipile* can increase the surface area (58–71%), dry weight of root (100–158%), dry weight of shoot (91–102%) of cabbage. In a field trial, yield of lettuce treated with *T. longipile* 6Sr4 increased significantly. The lateral root production and biomass production were stimulated by *Trichoderma virens* (Contreras-Cornejo et al. 2009). The infectivity on bean plants by *R. solani* (Bakarat et al. 2007) was reduced by the conidial suspension of *Trichoderma* isolates at 3 × 107 cfu and increased the growth. The increase in fresh weight, dry weight, and plant height by 133%, 217%, and 160% was noted respectively. Moreover, after 14 and 28 days the reduction of 60%–40% of disease was recorded (Yobo et al. 2009). Okoth et al. (2011) reported the rise in maize seed germination as a result of coating with *Trichoderma*.

1.7.7 Phosphate Solubilization

The major nutrient required for the growth and development of the plant is phosphorus. It is present in an unutilized form in the soil. They are converted by phosphate solubilizing microorganisms to be utilized by plants (Kour et al. 2020a, b, 2019a). In recent years species of *Trichoderma* have also been reported to solubilize phosphorus. A clear zone of phosphate solubilization was recorded by Saraf et al. (2013) after 3 days of inoculation with *Trichoderma* isolate MJ3 on the Pikovskaya agar

Table 1.7 Total percentage increase in the yield of various crops after the treatment with *Trichoderma* species

Crop	Percentage of yield	Reference
Potato	65	Drahansky et al. (2016)
Cotton	320	Harman et al. (2004)
Chickpea	124	Khan and Mohiddin (2018)
Mustard	110	Haque et al. (2012)
Maize	82	Sankar and Sharma (2001)
Mung bean	40	Dubey (2003)
Strawberry	90	Porras et al. (2007)
Black pepper	180	Ayub et al. (2010)
Tomato	150	Dutta and Das (2002)
Rice	87	Barari (2016)

media. The 14 strains of *Trichoderma* species isolated from the rhizosphere of the forest tree such as deodar, bamboo, guava, pinus, and oak for their potential of in vitro solubilized phosphate in the culture broth containing tricalcium phosphate as the sole source of phosphate (Khan et al. 2008). The maximum amount of phosphate solubilization was shown by *Trichoderma* isolate DRT followed by *T. harzianum* after 96 h incubation period at 30 °C (Kapri and Tewari 2010). The phosphate solubilization under the environment of low temperature was induced by fungal root endophytes with maximum solubilization by *T. pseudokongingii*. Similarly, the solubilization of phosphorus from ten isolates of *Trichoderma* species derived from the rhizosphere has been reported (Saravanakumar et al. 2013).

In the evaluation of plant growth promotion among the 12 fungal endophytes, *Chaetomium globosum*, *Fusarium fusarioides*, *mucor* species, and *Aspergillus versicolour* showed the production of HCN. Rawatand studied *T. virens* (SE6 and KT28), *Aspergillus flavus* (BRT11), *T. viride* (KT6) for their potential of plant growth promotion and indicated that only three isolates, SE6, KT6, and BRT11 showed the production of HCN (Rawat and Tewari 2011). During the isolation of six *Trichoderma* isolates for the potential of in vitro plant growth promotion only *Trichoderma* produced HCN. Colonization of root by the strains of *Trichoderma* frequently enhances the growth and development of root, abiotic stress resistance, productivity of the crop, uptake, and use of nutrients. After the addition of *T. hamatum* or *T. koningii* the productivity of crops in fields increased up to 300%.

The experiments that were carried out by treating the seeds with *Trichoderma* spores in greenhouses significantly showed greater yield. When the plant seeds were separated from *Trichoderma* by a cellophane membrane, they showed an equal degree of yield enhancement. This indicates the production of growth factors from *Trichoderma* that enhances seed germination, growth of the plant, and the yield. Besides having the inhibitory effect on the germ tube elongation and conidial germination of *Botrytis cinerea*, the *T. harzianum* T39 also reduces the production and activity of the pectolytic enzymes. The reduction in the activity of pectolytic enzymes can increase the accumulation of pectic enzymes that is oligogalacturonides. The host plant defense can be elicited by these sugars, thus checking the development of the disease. Chet et al. concluded that the promotion of plant growth may be due to the increased uptake of nutrients and the production of plant hormones (Khan and Mohiddin 2018) (Table 1.7).

1.7.8 Drought Tolerance

One of the major environmental stresses that affect the growth of plant and crop production is drought (Kour et al. 2020c). In traditional agricultural practice, the effectiveness of the use of chemical or synthetic fertilizers is also significantly affected by drought (Saba 2012). Improvement in the stimulation of plant growth and soil fertility in the dry and drought areas is one of the major issues that farmers have been facing for decades. Few species such as *T. harzianum*, *T.*

longibrachiatum, *T. viride*, *T. hamatum*, and *T. koningii* are efficient biocontrol agents that can inhibit the growth of pathogens in the soil, thereby improving the overall health of the plant. *Trichoderma* species also help in sustaining the plants under drought conditions which are considered as biological methods. The interaction of the plant with *Trichoderma* species increases the yield, development, and stress tolerance in various conditions. These species occur almost in all the ecosystems and constitute one of the parts on the microflora of the rhizosphere. The alleviation of damage is induced by *Trichoderma* through reactive oxygen species, improvement in the efficiency of water use, and phytohormone secretion that enhances the growth of plants under drought stress (Khan and Mohiddin 2018).

Trichoderma is considered a virulent organism that stimulates the growth of plant under the suboptimal conditions. The plant symbionts help in either inducing plants to scavenge ROS or by preventing the production of ROS under abiotic stress. Symbiotic plants spend significantly less water when compared to the non-symbiotic plants. Tomato and rice with the *Trichoderma* species used less fluid than the non-symbiotic plants. *Trichoderma* protects the plants against ROS by increasing the ROS scavenging capacity. The antioxidative enzymes such as peroxidase, superoxide dismutase, glutathione-reductase, and glutathione-S-transferase as well as other detoxifying enzymes present in leaves increase due to the inoculation of roots with *Trichoderma* species. The superoxide dismutase converts the toxic superoxide to hydrogen peroxide and oxygen through the dismutation reaction. The application of *T. atroviride* ID20G increases the fresh and dry weight of the roots of maize under the drought stress.

Besides inducing the antioxidant enzyme activity, the fungal strains also increased the carotenoid and chlorophyll content of the seedlings. The colonization of root by *T. atroviride* ID20G prevented the increase in lipid peroxidation and also reversed the changes in the contents of pigment and efficiency of photosystem caused by drought. The seeds that are subjected to oxidative stress restored vigor after treatment with the *Trichoderma* T22. Furthermore, in cucumber plants, the peroxidase gene was primed after inoculation with *Trichoderma* species. In tomato seeds, the percentage of germination increased after the application of *T. harzianum* T22 under osmotic conditions. An increase in the content of lipid peroxide in young seedlings was reported in a study with an increase in the water potential of the media whereas the seedlings that are treated with T22 have significantly less lipid peroxide than the untreated seedlings (Khan and Mohiddin 2018).

1.8 *Piriformospora indica*

The endophytic Agaricomycetes fungus *Piriformospora indica* owing to its exceptional ability to efficiently promote the growth of plant, protection, and tolerance to stress has received significant attention over the past few decades and mimics the capabilities of *Arbuscular Mycorrhizae*. This is an axenically cultivable fungus exhibiting the versatility for hosting and colonizing plant species through direct manipulation of plant hormones-signaling pathway during mutualism. The root colonization by *Piriformospora indica* promotes plant performance and enhances the proliferation of root by the production of indole-3-acetic acid. The production of indole-3-acetic acid also improves the nutrient acquisition and improves the growth and productivity of the crop. Through the signal transduction pathway, this fungus can induce local and systemic resistance to viral and fungal plant disease. The plant stress tolerance is conferred through the stimulation of components involved in the defense mechanisms and expressing the genes related to stress by the *P. indica*. Therefore, micro-propagated plantlets can be biotized by this fungus as well as the transplantation shock can be overcome. *P. indica* can also be involved in various symbiotic relationships such as symbiosis of tripartite and promotes the rhizobacteria thereby enhancing the population dynamics of plant growth. Hence, *Piriformospora indica* has the potential to be utilized as a bio protector, bioregulator, biofertilizer, biotization agent, and plant growth promoter.

1.8.1 Acquisition of Phosphorus

Phosphorus is one of the important essential nutrients. The phosphorus present in the soil cannot be directly accessed by the plants as the phosphorus is in the form of scarcely soluble complexes. Hence, the deficiency of phosphorus impedes the production of crops throughout the world. It was reported that the uptake of radiolabeled phosphorous from the culture media was mediated by the *Piriformospora indica*. The acid phosphatases are also produced by this fungus in significant amounts which helps the host plants to access insoluble, condensed, and complex forms of phosphate in the soil (Yadav et al. 2010). Isolation of high-affinity phosphate transporter, identification and characterization of their functional property from the root endophytic fungus *P. indica* revealed that the phosphate transporter is essential for the transport of phosphate to the host plants (Johri et al. 2015). The mechanism behind the transport of phosphate from fungus to plant is still not clear but the hypothesis states that it might occur at the plant-fungus interface. This process requires two transporters. The first transporter to enable the phosphate efflux from the fungus and the second transporter to mediate the uptake of phosphate by the plants (Rausch and Bucher 2002). The reports concerning the involvement of *P. indica* in the transfer of phosphate are contradictory. It has been reported that the phosphate uptake in *Arabidopsis* seedling is enhanced by *Piriformospora indica* 2–3 times higher (Shahollari et al. 2005). It has been reported by Yadav et al. (2010) on the influence of phosphate on the biomass of *Z. mays* plant that was colonized with *P. indica*. Increased biomass and total phenolic content were observed in the plants colonized with *P. indica* of wild type as compared with non-colonized (Yadav et al. 2010). The growth-promoting activity of *P. indica* was observed to be higher under the condition of low phosphate as compared with the condition under high phosphate. Hence it has been concluded that *P. indica* can be a potential agent for utilization in sustainable agriculture to improve the production of the crop in lands deficient with phosphate (Gill et al. 2016).

1.8.2 Acquisition of Other Nutrients

The growth and development of the plant are restricted due to the deficiency of other nutrients such as nitrogen and zinc (Rana et al. 2019c). The plants uptake nitrogen either in the form of nitrate or ammonium (Esseling and Emons 2004; Kour et al. 2020d; Yadav et al. 2017a). It was reported by Sherameti et al. (2005) that *Arabidopsis* seedling and *Nicotiana tabaccum* when co-cultivated with *P. indica* is accompanied by the transfer of N from the Petri plates containing agar to the seedlings. This effect is activated by the enzyme that plays a significant role in the acquisition of nitrate, NADH-dependent nitrate reductase. It has been proposed that the growth-promoting effect of *P. indica* is accompanied by the enzymes that are involved in the metabolism of nitrate and starch (Gill et al. 2016).

1.8.3 Plant Growth and Development

The growth, development, and yield of many crops, horticulture, and other medicinal plants were increased by the *P. indica* (Varma et al. 2012). In several crops seed germination and development induced by this fungus have been reported (Pham et al. 2008; Kumar et al. 2009; Vadassery et al. 2008). The enhanced seed development and production have been reported in *A. thaliana* as a result of microdomains present in the plasma membrane such as *pii*-2 and AT5g16590. The *H. vulgare* seeds inoculated with *P. indica* showed higher viability (Harrach et al. 2013). The germinated seeds under adverse conditions showed a higher survival rate when immersed in the homogenate containing *P. indica*. In vascular plants, the early seed germination is facilitated by the filtrate of *P. indica*. The seed oil yield from the *Helianthus annuus* was evidenced to be influenced by the culture filtrate of *P. indica* (Bagde et al. 2011). As a result of root colonization by *P. indica* the members of angiosperms, gymnosperms, bryophytes, and pteridophytes were reported to have higher seed yield. In medicinal plants the inoculation and colonization role of *P. indica* has been seen as utmost significance (Hock 2012).

In medicinal plants, the colonization by *P. indica* has been reported including *Lantana camara*, *Coleus forskohlii*, *Linum album*, *Bacopa monnieri*, *Ocimum sanctum*, *Stevia rebaudiana*, *Chlorophytum borivilianum*, *Artemisia annua*, *Withania somnifera*,, *Linum album*, *Spilanthes calva*, *Trigonella foenumgraecum* (Kumar et al. 2009; Das et al. 2014; Sharma and Agrawal 2013). In *C. forskohlii* increased content of secondary metabolites and chemical compounds have been reported due to the colonization of roots by *P. indica* (Das et al. 2014). The hypertrophy *B. monnieri nuclei* and the growth, the level of bacoside endogenous, and antioxidant activity are enhanced by *P. indica* (Prasad et al. 2013). The properties of medicinal plants such as *H. annuus*, *A. elegans*, *A. indica* were increased by their colonization with *P. indica* (Bagde et al. 2011). In the cell culture of L. album the inoculation of *P. indica* improved the anticancer drug podophyllotoxin. In the herbaceous plant such as *A. annua and S. rebaudiana* their leaf area and biomass were enhanced when cultivated with *P. indica*. The medicinal plants namely *W. somnifera* and *S. calva* were reported to have a positive impact on their growth in a field trial when inoculated with *P. indica* (Rai et al. 2001). In *W. somnifera and A. annua the* productivity of biomass was enhanced by in vitro co-cultivation with the filtrate of *P. indica* (Baishya et al. 2015). In view of the colonization role of *P. indica* in crop plants, it has been reported that the enhanced growth and production of biomass have been observed in *Ridax procumbans*, *Oryza sativa*, *Phaseolus vulgaris*, *Saccharum officinarum*, *Zea mays*, *Abrus precatorius* (Varma et al. 2012). The plant root growth is promoted by *P. indica* due to their role in the production of auxin as well as their interaction with ethylene signaling. They stimulate the synthesis of the secondary metabolites such as betulinic acid, ursolic acid, oleanolic acid in the suspension culture of *L. camara*. Further, this fungus can be used as a biopriming agent due to its symbiotic effect on the overall growth of plant biomass (Gill et al. 2016).

1.8.4 Role in the Tolerance of Biotic and Abiotic Stress

There has been an extensive report on the ability of *Piriformospora indica* to increase the tolerance capacity of plants against various abiotic stress including heavy metal toxicity, salinity, and low temperature. In *Triticum aestivum and Arabidopsis* seedlings, the colonization with *P. indica* mediated tolerance against high salinity and drought stress, respectively (Zarea et al. 2012; Sherameti et al. 2008). The activation of genes that are related to defense mechanisms such as LOX2, PR, and ERFI are reported (Zarea et al. 2012) to be activated by colonization with *P. indica*. The interaction of *P. indica* with the roots of *A. thaliana* can be used as a unique model system to study the symbiotic relationship. The ability to deliver molecules such as effectors has been evolved by the mutualistic fungi *P. indica* to enhance and manipulate the microbial infection and host metabolism, respectively. These molecules play an important role in the establishment as well as the maintenance of symbiosis in endo and ectomycorrhiza and allow the manipulation of plant defense response (Vahabi et al. 2015a).

The antioxidant defense enzymes such as monodehydroascorbate reductase and dehydroascorbate reductase including other components related to the ROS scavenging system have been reported to be modulated by the *P. indica* (Vadassery et al. 2008). The upregulation of various enzymes involved in the ROS metabolism of the plants exposed to salinity is mediated by *P. indica* colonization. The tolerance of plants against various abiotic stresses such as heat, salinity, drought, and heavy metal was conferred by the inoculation of *P. indica*. In addition to protection against abiotic stresses, *P. indica* also provides protection against various biotic stresses

Table 1.8 The role *Piriformospora indica* in major crops under biotic stress

Host plant	Beneficial roles	Reference
H. vulgare	Provides protection against *Rhizoctonia solani* which causes root rot.	Qiang et al. (2012)
A. thaliana	Significant reduction in the development of disease caused by *Verticillium dahlia* Protection against *Alternaria brassicae* which causes leaf blight Protection against *V. dahlia* which causes Verticillium wilt Provides protection against *Rhizoctonia solani and Verticillium longisporum* which causes root rot and Verticillium wilt	Sun et al. (2014) Vahabi et al. (2015b) Sun et al. (2014) Knecht et al. (2010)
L. esculentum	Provides protection against *Thielaviopsis basicola and Fusarium oxysporum* that causes black root rot and Fusarium wilt	Qiang et al. (2012)
	Provides protection against *V. dahlia and* Pepino mosaic virus which causes Verticillium wilt and yellow leaf mosaic	Fakhro et al. (2010)
Triticum aestivum	Protection against head blight disease caused by *Fusarium*	Rabiey et al. (2015)

Table 1.9 The role of *Piriformospora indica* in major crops under abiotic stress

Host plant	Beneficial roles	Reference
T. aestivum	Mitigation of stress caused by Zinc deficiency Increase in stress tolerance again st cadmium	Abadi and Sepehri (2016) Shahabivand et al. (2012)
Oryza sativa	Increase in salinity stress	Jogawat et al. (2013)
Hordeum vulgare	Increase the tolerance against salinity stress by increasing the ratio of foliar potassium/sodium	Alikhani et al. (2013)
Solanum lycopersicum	Tolerance against osmotic stress and toxicity of chloride	Gill et al. (2016)
Sesamum indicum	Increases the growth as well as tolerance against drought stress	Gill et al. (2016)
Nicotiana tabacum	Increased cadmium tolerance	Hui et al. (2015)
H. vulgare	Tolerance against low temperature stress and increase in the yield of crop Enhanced tolerance against drought stress Enhanced salinity tolerance and increase in the biomass of aerial plants	Gill et al. (2016) Ghabooli et al. (2013) (Gill et al. (2016)

such as pathogenic fungi, bacteria, and virus. The genes encoding the enzymes responsible for the synthesis of ascorbate in *Arabidopsis* are due to the greater colonization by *P. indica.*

Research Van Wees et al. (2008) concerning the greenhouse study of *Solanum lycopersicum* Mill inoculated with the culture filtrates of *P. indica* showed a significant increase in their growth under osmotic stress and chloride toxicity. The

Table 1.10 The role of *Piriformospora indica* in major crops under normal conditions

Host plants	Beneficial roles of *P. indica*	Reference
Centella asiatica	Increase in the fresh weight of plant, root, and leaf number	Gill et al. (2016)
Hordeum vulgare	Increase in the viability and survival of seeds as well as vegetative and yield of grain	Harrach et al. (2013)
Populus and Jatropha	Early germination of seeds as well as increase in formation of seed and the yield	Prasad et al. (2013)
Brassica campestris	Increase in the fresh weight of root and shoot	Sun et al. (2010)
Oryza sativa	Improvement and increase in the length of root and shoot along with their dry weight	Jogawat et al. (2013)
Tridax procumbens	Increase in the fresh and dry weight and the length of root and shoot	Gill et al. (2016)
Nicotiana attenuata	Increase in the length of stalk, number of flowers, weight of seed and fresh weight of fruit	Gill et al. (2016)
Cyclamen persicum	Increase in the number of leaves and flowers	Ghanem et al. (2014)
Lycopersicon esculentum	Increase in the growth of seedling	Anith et al. (2015)
Foeniculum vulgare	Increase in the height of the plant, dry weight of the root and shoot	Gill et al. (2016)
Vegetable crops	Induced germination and formation of the seed. Increased seed value and yield of crops	Prasad et al. (2013)
Helianthus annuus	Increase in the yield of seed with high content of oil and lipid biosynthesis	Bagde et al. (2011)

mechanism underlying the development of resistance by *P. indica* has already been studied for abiotic and biotic stresses in plants colonized with rhizobacteria but very less research has been done on the mechanism underlying the resistance induced by *P. indica* against various abiotic and biotic stresses. The observation on the interaction that is beneficial between the host plant and fungus has been reported to upregulate various genes that are related to the mechanism of defense including PR genes involved in pathogenesis and ethylene signaling genes (ERF1) in pathogen attack (Molitor et al. 2011). The plant *H. vulgare* is protected from *Fusarium culmorum* and *Blumeria graminis* which cause root damage and shoot infection, respectively (Molitor et al. 2011). The activity of antagonism by the endophytic fungus, *P. indica* directly inhibits various root pathogens except for *F. culmorum* (Waller et al. 2005), *F. oxysporum* (Saba 2012), *and P. herpotrichoides* (Serfling et al. 2007). The resistance of host plants against various root pathogens was also reported to be associated with the root colonization of *P. indica*. The crop plants result in better vegetative and generative development as they are defended against various viral and fungal pathogens.

To the economically important agricultural and horticultural crops, the *Piriformospora indica* has been found to possess the potential as a bio protective agent. The resistance against fungal disease is increased in plants by the utilization of *P. indica*. It has been reported (Molitor et al. 2011) that the *H. vulgare* plants, when colonized with the *P. indica*, became free from the fungal pathogen such as *F. culmorum.* The plants treated with the *P. indica* were protected against root pathogens such as *Cochliobolus sativus* fungus (Oelmüller et al. 2009). The systemic resistance against the biotrophic leaf pathogen such as *B. graminis* f. sp. *hordei in H. vulgare* roots was developed by colonization with *P. indica* (Waller et al. 2005). This fungus has also been involved in the biocontrol of take-all diseases of *T. aestivum and Fusarium* wilt disease of lentil. Therefore from the reports, *P. indica* is a multifunctional agent providing service such as nutrient uptake, stress tolerance, disease resistance, and promotion of growth (Gill et al. 2016) (Tables 1.8, 1.9, and 1.10).

1.9 Notable Research on the Role of Fungi in Agriculture

- Mittal et al. (2008) evaluated the growth and seed production of *Cicer arietinum* in the pot experiments under greenhouse conditions by the impact of six phosphate solubilizing fungi including four strains of *Penicillium citrinum* and two strains of *Aspergillus awamori.* Result of the study showed an increase in seed number, seed weight, and shoot height in the inoculated plants and higher in the plants inoculated with the strains of *Aspergillus awamori.*
- Kapri and Tewari (2010) evaluated *Cicer arietinum* after the application of inoculation containing P-solubilizing *Trichoderma* sp. and found that it increased all the growth parameters such as fresh and dry weight of shoot and root, length of shoot and root in phosphate deficient soil.
- Promwee et al. (2014) observed when *Hevea brasiliensis* was inoculated with phosphorus solubilizing fungus *Trichoderma harzianum* and rock phosphate it resulted in increased fresh and dry weight of shoot and root, circumstances of the stem, leaf number, and height of the plant compared with the control containing only the rock phosphate.
- Saxena et al. (2015) evaluated the combined effect of the phosphorus solubilizing *Aspergillus niger and Bacillus* sp. on the growth, development, and yield of *Cicer arietinum.* The result of the study indicated an increased growth of the plants with dual inoculations than with single inoculation or uninoculated plants.
- Priyadharsini and Muthukumar (2017) evaluated *Curvularia geniculata* by inoculation with *Cajanus cajan* and reported that the inoculated plants showed better growth because of the role of fungus in solubilization of phosphorus and production of IAA
- Zhou et al. (2018) observed in the studies involving *Alternaria* sp. increased the biomass of dry root and accumulation of secondary metabolites of *Salvia miltiorrhiza* and the seedlings of the plant showed increase in fresh as well as dry weight as well as enhancement in the total phenolic content, lithospermic acids A and B. The study concluded that this fungus stimulates the growth of root as well as production of secondary metabolites.

- The influence of Arbuscular mycorrhizal fungus including *Glomus intraradices* and *Glomus mosseae* with or without the presence of nitrogen fixer, solubilizers of phosphate and potassium on the soil properties, and growth of maize was evaluated by Wu et al. (2005). The result was concluded as the application of *Glomus mosseae* increased the biomass yield and height of the seedling as the inoculum increased the total P, N, K, and organic matter in the soil.
- Saravanan et al. (2011) reported fungal genera such as *Penicillium simplicissimum*, *Absidia cylindrospora*, *Aspergillus niger*, *Absidia glauca*, *and Absidia spinosa* with the potential to solubilize the insoluble zinc.
- Saravanan et al. (2011) reported various Ericoid mycorrhizae such as *Suillus bovinus*, *Beauveria caledonica*, *Suillus luteus*, *Hymenoscyphus ericae*, *Paxillus involutus*, and *Oidiodendron maius* with the potential to solubilize insoluble zinc.
- Martino et al. (2003) demonstrated the potential of *Oidiodendron maius* to solubilize insoluble inorganic zinc compounds
- Altomare et al. (1999) evaluated the capability of *Trichoderma harzianum* a plant growth-promoting and biocontrol agent to solubilize in vitro some insoluble and sparingly soluble minerals. The observed result was solubilization of metallic zinc, $MnO_{2,}$ and rock phosphate.
- Anastasiou et al. (2014) isolated *Penicillium dalea*, *Aspergillus terreus*, *Aspergillus oryzae* possessing the capacity to solubilize manganese from the low-grade manganese mine tailing.

1.10 Conclusion and Future Perspective

The growth development and use of synthetic pesticides and fertilizers have significantly enhanced the protection of crops but their use also has disadvantages such as environmental related problems such as drought, salinity, and pathogen resistance. Further, these chemicals are not successful in different crop fields to sustain the production of crops. Green technology such as the use of beneficial fungi may pose to be a significant alternative to these chemicals. Among various beneficial fungi *Arbuscular mycorrhiza*, *Trichoderma*, *Penicillium*, fungal endophytes, and *Piriformospora indica* have the potential to deal with the various stresses such as drought, nutrient deficiency, soil salinity, and disease tolerance. The beneficial role of these fungi is being studied by researchers. On the contrary, the majority of the crop growers have remained unaware of the utility of these fungi. Hence, requires the spread of awareness among the farmers' community. Further continuous research is required to identify and isolate an efficient fungus with the multifarious characteristics of disease suppression and growth promotion.

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Chapter 2
Role of Fungi in Adaptation of Agricultural Crops to Abiotic Stresses

Fatma A. Abo Nouh and Ahmed M. Abdel-Azeem

Contents

2.1 Introduction

Agriculture is considered to be one of the most vulnerable sectors to climate change. Crop production, particularly in tropical regions is facing increasing stresses caused due to natural and anthropogenic factors. Stress in plants refers to external

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conditions that adversely affect growth, development, or productivity of plants (Verma et al. 2013). Stresses trigger a wide range of plant responses like altered gene expression, cellular metabolism, changes in growth rates, crop yields, etc. (Kour et al. 2019b). A plant stress usually reflects some sudden changes in environmental condition. Plant stress can be divided into two primary categories namely abiotic stress and biotic stress (Yadav et al. 2017a). Abiotic stress imposed on plants by environment may be either physical or chemical, while biotic stress exposed to the crop plants is a biological unit like diseases, insects, etc. (Verma et al. 2013). Plants in natural systems and crop lands are simultaneously exposed to both biotic and abiotic stresses. Abiotic stresses such as drought (water stress), excessive watering (water logging), extreme temperatures (cold, frost, and heat), salinity, and mineral toxicity negatively impact growth, development, yield, and seed quality of crops and other plants (Yadav et al. 2020c). Abiotic stress tolerance plays a vital role in determining crop productivity and distribution of plant species across the environment (Boyer 1982; Chaves et al. 2003). These factors are likely to cause serious negative impacts on crop growth and yields and impose severe pressure on our land and water resources (Grover et al. 2011). Environmental stresses such as drought, extreme temperatures, salinity, or chemical toxicity bring serious consequences to crop production, causing collectively more than 50% yield losses worldwide (Wang and Frei 2011). Due to global climate change, abiotic stresses are expected to become more widespread in the coming decades and will pose serious threats to global food security (Ashmore et al. 2006; Battisti and Naylor 2009). Among the environmental stresses, water stress commonly, known as “drought,” is considered as one of the major challenges to crop production worldwide (Yue et al. 2006; Kour et al. 2020a, 2020b, c). If the crop is subjected to stress, particularly drought during its early stage of growth, germination and seedling establishment are severely arrested mainly owing to low water uptake, low energy supply, and hindered enzyme functions (Okcu et al. 2005; Kour et al. 2019a). Oxidative stress, which frequently accompanies high temperature, salinity, or drought stress may cause denaturation of functional and structural proteins (Smirnoff 1998). Plant responses to abiotic stresses are complex, involving signal reception and transduction followed by genetic and physiological responses. It is perceived that all plants are capable of perceiving and responding to stress (Bartels and Sunkar 2005).

Some biochemical processes which are common to all plant stress responses are: the production of osmolytes, altering water movement, and scavenging reactive oxygen species (ROS) (Singh et al. 2011).

The interaction of microbes with the plant can be traced back to the origin of plants. Fossil records indicate that fungi have been associated with plants since at least 400 MYA and might have played an important role in the movement of plants from an aquatic arena to comparatively dry terrestrial habitats (Rodriguez et al. 2008). The most well-known plant–microbe interaction is the mutualism between mycorrhizal fungi and plants where both partners generally benefit from each other (Verma et al. 2017a, b). However, under natural settings, plants form relationships with endophytic fungi which can be beneficial or harmful for the partners depending on host types and natural and environmental situations (Dastogeer and Wylie

2017). Nasim (2010) showed that the growth and health of colonized plants are improved and they obtain increased protection against biotic and abiotic stresses detrimental to their survival. Among the sustainable efforts, the role of root-associated microbes especially arbuscular mycorrhizal (AM) fungi in imparting stress tolerance has been exploited by many researchers in the recent years (Evelin et al. 2009; Garg and Singla 2012; Garg and Pandey 2015). Mycorrhizal symbioses are ubiquitous system of green technology. In these symbioses, the fungal mycelia scavenge through soil for resources (often phosphorus or nitrogen) and provide these resources to plants in exchange of organic carbon. The associations are mutualistic most often but sometimes exist as parasitism depending upon fungal nature (Prasad 2017). They are ubiquitous soilborne fungi, whose origin and divergence date back to over 450 million years (Gutjahr and Parniske 2013).

Besides mycorrhizal endophytes, non-mycorrhizal endophytes (hereafter referred to as endophytes) have been recovered from most plants. Fungal endophytes are microfungi that internally infect living plant tissues without causing disease or any harm to plants, and live in mutualistic association with plants for at least a part of their life cycle (Rana et al. 2019a; Rodriguez et al. 2009; Lugtenberg et al. 2016; Jain and Pundir 2017; Lata et al. 2018; Chhipa and Deshmukh 2019). The existence of fungal endophytes from fossil records suggests that endophyte–host associations may have evolved from the time of development of first higher plants on earth (Dastogeer and Wylie 2017). The plant provides nutrition to the endophytes, while in return endophytes help in adaption to abiotic conditions like nutrients limitation, salination and extreme pH, drought, temperature variation, and protection from pathogens, insects, and nematodes (Chhipa and Deshmukh 2019; Abo Nouh 2019; Yadav et al. 2015a, b; Verma et al. 2016)

2.2 Abiotic Stress Effect on Agriculture Crops

Fundamentally, plants require energy (light), water, carbon, and mineral nutrients for growth. Abiotic stress is defined as environmental conditions that reduce growth and yield below optimum levels. Plant responses to abiotic stresses are dynamic and complex (Skirycz and Inze 2010); they are both elastic (reversible) and plastic (irreversible). The plant responses to stress are dependent on the tissue or organ affected by the stress (Cramer et al. 2011). Abiotic stresses, such as drought, salinity, extreme temperatures (heat and cold), heavy metal toxicity, and oxidative stress are serious threats to agriculture and result in the deterioration of the environment (Singh et al. 2011; Saxena et al. 2016; Yadav 2017, 2019; Yadav and Yadav 2018). A global water shortage due to significant climatic changes is the leading cause of these abiotic stresses including drought, extreme temperatures, and salinity (Redman et al. 2011; Hussain et al. 2018). Abiotic stress is the primary cause of crop loss worldwide, reducing average yields for most major crop plants by more than 50% (Boyer 1982). Abiotic stress leads to a series of morphological, physiological, biochemical, and molecular changes that adversely affect plant growth and productivity (Yadav 2017;

Wang et al. 2001). Drought, salinity, and extreme temperatures, which are often interconnected, result in oxidative burst and cellular damage (Kaur et al. 2020; Rana et al. 2020; Yadav et al. 2019b). For example, water stress and salinization, which are apparent osmotic stress, disrupt the ion distribution and metabolism in the cell (Raghuwanshi 2018). A plant's first line of defense against abiotic stress is in its roots. One of the primary responses to abiotic stress such as high salinity is the disruption of the Na^+/K^+ ratio in the cytoplasm of the plant cell. The phytohormone abscisic acid (ABA) plays an important role during plant adaptation to environmental stress such as high salinity, drought, low temperature, or mechanical wounding (Gull et al. 2019). Among abiotic stresses, drought stress, soil salinity, and accumulation of heavy metals (HM) in the soil are one of the major grounds of diminished plant performance and restrained crop yield worldwide (López-Ráez 2016). In response, plants modify their root morphology, ultrastructure (Fusconi and Berta 2012), which may modulate their physiology and biochemistry to limit stress-induced damages and/or facilitate the repair of damaged systems (Latef et al. 2016).

2.2.1 Salt

Salinity is defined as the presence of excessive amounts of soluble salts that hinder or affect the normal functions of plant growth (Yadav et al. 2020b). Worldwide, more than 45 million hectares of irrigated land have been damaged by salt, and 1.5 million hectares are taken out of production each year as a result of high salinity levels in the soil (Munns and Tester 2008). It was found that salinity stress resulted in decrease of water content, accumulation of hydrogen peroxide, and electrolyte release in plants (Mandhania et al. 2006). Throughout the world about 45 million hectares of irrigated land is affected by salt (Munns and Tester 2008). Salt stress affects plants in numerous ways such as ion toxicity, nutritional disorders, physiological drought, oxidative stress, modification of metabolic processes, membrane incompetence, and reduction of cell division (Zhu 2007).

At low salt concentrations, yields are mildly affected or not affected at all (Maggio et al. 2001). When a plant is exposed to high salt at germination it causes physiological drought and reduction in leaf expansion. The osmotic effects of salinity stress can be observed immediately after salt application and are believed to continue for the duration of exposure, resulting in inhibited cell expansion and cell division, as well as stomatal closure (Munns 2002). If plants are exposed for long time to salinity, plants face ionic stress, which can direct to premature senescence of adult leaves, and thus a reduction in the photosynthetic area available to support continued growth (Cramer and Nowak 1992). High salt concentration in soil affects plants in two ways such as high concentrations of salts in the soil upset the ability of roots to extract water, and high concentrations of salts within the plant itself can be toxic, resulting in an inhibition of many physiological and biochemical processes such as nutrient uptake and assimilation (Batool et al. 2014). During the onset and development of salt stress within a plant, all the major processes such as photosynthesis, protein synthesis, and energy and lipid metabolism are affected (Carillo et al. 2011; Singh et al. 2020; Yadav et al. 2020a).

2.2.2 Drought

Agricultural drought indicates an extended dry period that results in crop stress and crop yield. It causes the dehydration of cells and osmotic imbalance (Mahajan and Tuteja 2005). Water stress may occur either due to excess of water (i.e., flooding) or water-deficit (i.e., drought stress) conditions (Kour et al. 2020a, 2019b; Rana et al. 2019b). In the latter condition, the absence of adequate water table which is required for normal plant growth, development, and reproducibility results in drought/water stress (Latef et al. 2016). Severe droughts occur periodically in several major food-producing countries, having far-reaching impacts on global food production and supply. Drought is the most significant abiotic stress, adversely affecting the productivity and distribution of crop plants worldwide. For example, drought alone affects up to 45% of the global agricultural land (Hussain et al. 2018). Plants reduce their growth of shoots under drought conditions and reduce their metabolic demands. After that protective compounds are synthesized by plants under drought by mobilizing metabolites required for their osmotic adjustment (Gull et al. 2019; Yadav et al. 2018a, b).

2.2.3 Temperature

Greaves (1996) defines suboptimal temperature stress as any reduction in growth or induced metabolic, cellular, or tissue injury that results in limitations to the genetically determined yield potential, caused as a direct result of exposure to temperatures above or below the thermal thresholds for optimal biochemical and physiological activity or morphological development. High temperature stress causes extensive denaturation and aggregation of cellular proteins, which lead to cell death (Singh et al. 2011; Verma et al. 2019; Yadav et al. 2019a). Heat stress significantly affects plant growth and development by imparting loss of plant vigor and inhibition of seed germination, retarded growth rate, decreased biomass production, wilting and burning of leaves and reproductive organs, abscission and senescence of leaves, damage as well as discoloration of fruit, reduction in yield and cell death, and enhanced oxidative stress (Begum et al. 2019). The Intergovernmental Panel on Climate Change (IPCC 2007) reported that global temperatures are predicted to increase by 1.8–3.6 °C by the end of this century due to climate changes (Hussain et al. 2018). Increase in temperature throughout the globe has become a great concern, which not only affects the growth of plants but their productivity as well especially in agricultural crops plants. When plants encounter heat stress the percentage of seed germination, photosynthetic efficiency, and yield declines (Gull et al. 2019). Low temperature stress causes impairment of metabolic processes, by alterations in membrane properties, changes in structure of proteins, and interactions between macromolecules as well as inhibition of enzymatic reactions (Verma et al. 2019; Yadav et al. 2018c; Singh et al. 2011).

2.2.4 Flood

Flooding may be defined as any situation of excess water. Sudden inundation following high rainfall events also poses a severe physiological stress on crops. The effect of water logging of roots and lower stems are apparent as a range of symptoms on the shoots, including rapid wilting and severe physiological disruption (Latef et al. 2016). There are two typical kinds of flood. One is short duration over a few weeks and not very deep, termed a "flash flood" and the other is deep flooding that lasts for a long time, called as "deep-water flood." Flash floods are unexpected and uncontrollable, and its flooding water level can reach 50 cm in the rain fed lowlands of the humid and semi-humid tropics of South and Southeast Asia. In these areas, flash floods at the seedling stage of rice cause severely reduced yields of rice grain (Hattori et al. 2011).

2.2.5 Heavy Metals

Accumulation of toxic metals such as cadmium (Cd), lead (Pb), arsenic (As), and mercury (Hg) in the soil or within plants is considered as another abiotic stress that negatively affects environmental health and threatens ecosystem sustainable food production/sustainability. Such HMs are produced by various natural activities as well as by different anthropogenic activities such as metal smelting, use and drainage of chemical agro-products (e.g., fertilizers and pesticides), mining tail dumping, and burning of fossil fuels (Wang and Chen 2006). Heavy metal like Cu is taken up by plant cell by specific transport systems. "Free" Cu is extremely dangerous because it will reduce molecular oxygen leading to increased formation of superoxide, hydrogen peroxide, and hydroxyl radicals switching normal metabolism to programmed cell death (Singh et al. 2011). At elevated levels, HMs have been documented to cause several morphological, physiological, biochemical, and structural changes in plants including inhibition of seed germination, decrease in root elongation, growth inhibition, disturbance in cellular homeostasis, suppression of photosynthesis rate, leaf chlorosis, and premature leaf senescence (Benavides et al. 2005; Kour et al. 2020d; Yadav et al. 2020d). In addition, toxic metals have been reported to get translocated to different plant parts where they interfere with active sites of many enzymes including phosphatase, ATPase, and enzymatic antioxidants (Latef et al. 2016), thereby destroying protein structures and replacing crucial elements resulting in deficiency symptoms (Bhandari and Garg 2017).

2.3 Fungal Symbiont

There are two major classes of fungal symbionts associated with plants: (1) Endophytic fungi, which reside entirely within plant tissues and may be associated with roots, stems, and/or leaves; and (2) Mycorrhizal fungi that reside only in roots but extend out into the rhizosphere (Singh et al. 2011; Rana et al. 2019b). Based on the survey conducted in the last 20 years on endophytes, it is thought that the majority, if not all plants, have one or more types of these endophytes and numerous endophytic species; in some cases, above a hundred can be found in a certain plant species (Arnold 2007). Rodriguez et al. (2009) classified the endophytes under two major groups, viz. clavicipitaceous and non-clavicipitaceous on the basis of phylogeny and life history traits. Clavicipitaceous fungal endophytes are limited to certain grasses, while non-clavicipitaceous ones have a broad host range including both nonvascular and vascular plant species. In addition, recent reviews propose that members of the non-clavicipitaceous group can be segregated into three subgroups on the basis of host range, type of tissue infected, pattern spread, in planta infection and the establishment, diversity, and benefits given to hosts (Rodriguez et al. 2009; Dastogeer and Wylie 2017). Endophytic fungi which are predominantly ascomycetous are ubiquitous and have been isolated from all groups of plants starting from the lower forms like mosses and ferns to the higher ones including the conifers and the angiosperm plants (Arnold 2007), as they have been recovered from plants adapted to a wide range of ecosystems that include hot deserts, Arctic tundra, mangroves, temperate and tropical forests, grasslands and savannahs, croplands (Lugtenberg et al. 2016), and extreme arctic, alpine, and xeric environments (Ali et al. 2018).

Colonization by endophytic fungi promotes plant growth by protecting against several fungal and bacterial borne diseases, assisting in the uptake of available phosphorus or improving the ecological adaptation abilities of the host by providing tolerance to counteract against biotic and abiotic stresses (Schulz et al. 1999; Schulz and Boyle 2005; Yadav et al. 2017a, b). Endophytic fungi have been classified into Clavicipitales, with few hosts within the monocots, and non-clavicipitaceous species inhabiting both monocots and eudicots (Carroll 1988), which probably represent the majority of microbial symbionts which interact with plants, with a great diversity occurring both at taxonomical and at functional levels (Jain and Pundir 2017). Class 2 endophytes have a broad host range of both monocot and eudicot plants, are the largest group of fungal symbionts, are readily culturable on artificial media, and are thought to colonize all plants in natural ecosystems (Rodriguez et al. 2008). Class 2 endophytes confer stress tolerance to host species and play a significant role in the survival of at least some plants in high-stress environments (Rodriguez et al. 2004). For example, class 2 endophytes confer heat tolerance to plants growing in geothermal soils (Redman et al. 2002), the extent of tree leaf colonization by endophytes correlates with the ability to resist pathogens (Arnold et al. 2003), and endophytes confer drought tolerance to multiple host species (Waller et al. 2005).

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 vesicular mycorrhiza (AM) and vesicular-arbuscular mycorrhizas (VAM). These are members of Zygomycetes, Ascomycetes, and Basidiomycetes classes of fungi kingdom (Prasad 2017). The term symbiosis in mycorrhiza association is used to describe their highly interdependent or obligatory mutualistic relationships with the plants where the host plant receives mineral nutrients and in turn fungus harness photosynthetically derived carbon compounds (Prasad 2015). AMF, belonging to the phylum Glomeromycota (Schüβler et al. 2001) 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) (Gutjahr and Parniske 2013). Mycorrhizal symbionts have long been investigated and considered as the primary mutualistic fungal symbionts associated with plant roots (Diouf et al. 2003). AMF found in rhizosphere and associated with several vascular plants have tremendous contribution in sustainable agriculture as well as agricultural ecosystems management (Prasad 2017). 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 2000). AMF also benefit plants by increasing nutrient water uptake, resistance against phytopathogens, adaptation to a variety of environmental stresses such as drought, heat, salinity and heavy metal contamination, production of growth hormones and certain enzymes, and even in the uptake of radioactive elements (Prasad 2017). AMF are ecologically significant to the majority of vascular plants. It is quite easier to separate the list of mycorrhizae from others (Harley and Smith 1983).

2.4 Fungal Symbiosis

Symbiosis, defined as the permanent association between two or more specifically distinct organisms, at least during a part of the life cycle, is known to be a ubiquitous and important aspect of life on Earth (Kour et al. 2019b). Evolutionarily, plants require some specialized microbial partners in order to adapt to certain ecological niches and maintain their normal growth and development (Yuan et al. 2010; Rana et al. 2019c). There are several outcomes of symbiotic interactions defined by the fitness benefits realized by each partner (Lewis and Clements 1986). Benefits to fungal symbionts can be positive (mutualism, commensalism, and parasitism), neutral (amensalism and neutralism), or negative (competition). Benefits to host plants can also be positive (mutualism), neutral (commensalism and neutralism), or negative (parasitism, competition, and amensalism) (Rodriguez et al. 2008). While it is fairly straightforward to determine the impact of symbiosis on host fitness, it is more challenging to determine the benefits for fungal endophytes. Mutualistic benefits for endophytes may involve acquiring nutrients from hosts, abiotic and biotic stress avoidance and dissemination by seed transmission (Schardl et al. 2004; Schulz 2006). Commensal symbioses have no beneficial or detrimental effects on hosts whereas parasitic symbioses negatively affect host fitness by decreasing growth rates and/or fecundity, or inducing disease symptoms that may result in lethality (Redman et al. 2001).

Successful plant–fungal symbioses involve at least three events: penetration by the fungus into plant tissues; colonization of plant tissues by the invading fungus; expression of a fungal symbiotic lifestyle (Pieterse and Dicke 2007; Yadav et al. 2019d). It is assumed that some form of biochemical and/or genetic communication occurs between the symbionts and hosts that allow mutualists to confer physiological benefits to hosts (Singh et al. 2011). Rodriguez et al. (2008) however, current studies suggest that fungi may express different symbiotic lifestyles in response to host genotypes or environmental factors (Yadav et al. 2019c). For example, depending on the physiological status of plants, some mycorrhizal fungi may be mutualistic or parasitic (Johnson et al. 1997). One of the most interesting aspects of lifestyle expression is that the initial phases of infection and colonization by pathogens, mutualists, and commensals are identical for many fungi (Rodriguez et al. 2004). Thus, the mode of recognition and early signaling processes are crucial in understanding how a plant can differentiate between a beneficial and a detrimental microbe and express a lifestyle accordingly (Vadassery and Oelmüller 2009). A very early event in the interaction of pathogenic, mycorrhizal, or endophytic microbes with a plant cell is an increase in the intracellular calcium (Ca2+) levels within seconds or minutes after the recognition of the two partners. Ca2+ ion is a second messenger in numerous plants signaling pathways, coupling extracellular stimuli to intracellular and whole-plant responses. The cellular Ca2+ level is tightly regulated and even a small change in its concentration provides information for protein activation and signaling (Vadassery and Oelmüller 2009; Singh et al. 2011).

A diverse kind of relationships exists between the fungal endophytes and plant ranging from mutualistic (Redman et al. 2002), symbiotic, and commensal (Deckert et al. 2001) to pathogens (Schulz et al. 1998). However, the state of the interaction between endophyte and host may be transitory, and many factors could make changes in their mode of interaction (Schardl et al. 2004). For example, *Colletotrichum* spp. are classified as virulent pathogens, yet several species can express mutualistic lifestyles in non-disease hosts. Mutualistic benefits conferred by *Colletotrichum* spp. include disease resistance, growth enhancement, and/or drought tolerance (Redman et al. 2001; Singh et al. 2011). When *C. magna* is introduced into different tomato cultivars, the fungus may express mutualistic, commensal, or parasitic lifestyles. Whereas parasitic and mutualistic lifestyles are easily observed, commensal lifestyles are often designated when no host fitness benefit is observed. However, depending on the traits being assessed, the commensal designation may be misleading (Rodriguez and Redman 2008). For example, *C. gloeosporioides* was designated a pathogen of strawberry and a commensal of tomato because it conferred no disease protection (Redman et al. 2001); Nevertheless, *C. gloeosporioides* increased plant biomass and conferred drought tolerance to tomato plants and was therefore designated a mutualist (Rodriguez and Redman 2008).

2.4.1 Habitat-Adapted Symbioses

In fact, symbiotic fungi are responsible for the adaptation of plants to environmental stresses (Khan et al. 2012), and these tolerances can be transferred to agricultural plants (Rodriguez et al. 2008; Redman et al. 2011); these endophytes have been commercialized to improve agriculture in relation to climate changes, which involve increasing tolerance to drought and water stress and tolerance to high temperature and high salinity (Lugtenberg et al. 2016). The ability of endophytes recovered from grasses were applied to confer drought & water stress, high temperature and high salinity to genetically distant plants such as tomato (Chaw et al. 2004). The concept that fungal endophytes adapt to stress in a habitat-specific manner has been confirmed with different fungal and plant species, and different environmental stresses (Redman et al. 2002). This habitat-specific adaptation is defined as HA-symbiosis, and it is hypothesized that this allows plants to establish and survive in high-stress habitats (Rodriguez and Redman 2008). During performing laboratory and field studies of Class II endophytes from plants from geothermal soils, coastal beaches, and agricultural fields, Rodriguez and co-researchers observed a new ecological phenomenon and defined as habitat-adapted symbiosis. They have determined that endophytes from these habitats confer habitat-specific stress tolerance to plants. This habitat-specific phenomenon provides an intergenomic epigenetic mechanism for plant adaptation and survival in high-stress habitats (Rodriguez et al. 2008; Singh et al. 2011). For example, within the geothermal soils of Yellowstone National Park, WY, a plant species (*Dichanthelium lanuginosum*) has been studied and found to be colonized by one dominant endophyte (*Curvularia protuberata*). *C. protuberate* confers heat tolerance to the host plant, and neither the fungus nor the plant can survive separately from one another when exposed to heat stress >38 °C (Redman et al. 2002).

A comparative study of *C. protuberata* isolates from geothermal and nongeothermal plants revealed that the ability to confer heat tolerance was specific to isolates from geothermal plants, hence the ability to confer heat tolerance is a habitat-adapted phenomenon (Rodriguez et al. 2008). Another example, a native dunegrass (*Leymus mollis*) on coastal beaches of Puget Sound, WA, *L. mollis* which is colonized by one dominant fungal endophyte (*Fusarium culmorum*), *F. culmorum* confers salt tolerance to the host plant which cannot survive in coastal habitats without the habitat-adapted endophyte. A comparative evaluation of *F. culmorum* isolates from *L. mollis* and a noncoastal plant revealed that the ability to confer salt tolerance was specific to isolates from the coastal plants, indicating that the ability to confer salt tolerance is a habitat-adapted phenomenon (Rodriguez et al. 2008; Singh et al. 2011). Evaluation of *C. protuberata*, *F. culmorum*, and *C. magna* isolates further supports habitat-specific adaptation of endophytes: *C. protuberata* confers heat but not disease or salt tolerance; *F. culmorum* confers salt but not heat or disease tolerance; and *C. magna* confers disease but not heat or salt tolerance (Rodriguez et al. 2008).

2.5 Stress Tolerance Mechanisms

Symbiotically conferred stress tolerance involves at least two mechanisms: (1) activation of host stress response systems soon after exposure to stress, allowing the plants to avoid or mitigate the impacts of the stress (Redman et al. 1999) and (2) biosynthesis of antistress biochemicals by endophytes (Miller et al. 2002)

2.5.1 Osmotic Adjustment

Drought, heat, and salt stress affect plant–water relations triggering complex plant responses, which include increased production of osmolytes (Bray 1997). Osmotic potential is determined primarily by two components: solute potential and matrix potential, and it is likely that symbiotic fungi contribute to the matrix potential, which is particularly important in helping plants retain water and thereby enhance plant drought tolerance (Singh et al. 2011). Upon exposure to heat stress, nonsymbiotic panic grass and tomato plants significantly increased osmolyte concentrations as predicted. Increased osmolyte concentrations correlated with the development of subsequent wilting and desiccation symptoms prior to plant death (Rodriguez et al. 2008). In contrast, symbiotic plants either maintained the same (panic grass and Rutgers tomato), (Márquez et al. 2007) or lower (Tiger-Like tomato) (Rodriguez et al. 2008), osmolyte concentrations when compared to non-stressed controls. The differences in osmolyte patterns in tomato may be reflective of differences in the varieties (Rutgers versus Tiger-Like). Most investigations of Epichloe effects on stress tolerance focus on osmotic adjustment, water relations and drought recovery (Cheplick et al. 2000), accumulation of drought protective osmolytes in the grass tissues (Richardson et al. 1992), and photosynthetic rates under water or heat stress (Amalric et al. 1999). Under water stress, the tall fescue endophyte is also associated with a significant increase in cell wall elasticity as measured by bulk modulus tissue elasticity, and by turgid weight to dry weight ratio (TW/DW) (White et al. 1992); likewise, *Neotyphodium uncinatum* increases TW/DW in water-stressed meadow fescue (Rodriguez et al. 2008).

2.5.2 Water-Use Efficiency

Symbiotic plants consumed significantly less water than nonsymbiotic plants regardless of the colonizing endophyte. Panic grass, rice, tomato, and dunegrass plants all used significantly less fluid than nonsymbiotic plants (Singh et al. 2011). Since these symbiotic plants achieve increased biomass levels, decreased water consumption suggests more efficient water usage. Decreased water consumption and increased water-use efficiency may provide a unique mechanism for symbiotically conferred drought tolerance. Substantial (>50%) stand losses in tall fescue were reported after removing the endophyte from this grass (Read and camp 1986). These losses are typically associated with drought periods, and endophyte-infected tall fescue exhibits improved recovery after drought compared to endophyte-free tall fescue (Arachevaleta et al. 1989). It was suggested that grass endophytes, particularly *N. coenophialum* in tall fescue, affect plant–water relations, nutrient acquisition, as well as allocation and photosynthetic assimilation (Bacon 1993).

2.5.3 Osmotic Protection

Osmotic protection is more likely than stomatal conductance to be involved in drought protection in tall fescue, (Richardson et al. 1993) but reduced stomatal conductance might be important to conserving water in *Festuca arizonica–Neotyphodium* sp. interactions (Morse et al. 2002). Some speculation regarding osmoprotectants centers around the fungal loline alkaloids, which are abundant in those symbiota for which the endophyte has a documented and consistent positive effect on drought tolerance (Malinowski and Belesky 2000). Other potential osmoregulators and protectants are soluble sugars and sugar alcohols, produced by the endophyte, plant, or both (Richardson et al. 1992).

2.5.4 Reactive Oxygen Species (ROS)

A plant biochemical process common to all abiotic and biotic stresses is the accumulation of ROS. ROS are extremely toxic to biological cells causing oxidative damage to DNA, lipids, and proteins. On the other hand, ROS can act as signaling molecules for stress responses and generation of ROS is an early event in plant response to stress (Apel and Hirt 2004). Tanaka et al. (2006) Therefore, in a pathogenic or symbiotic association, both the plant and the microbe must be able to deal with a complex mixture of ROS coming from both sides. ROS are not necessarily harmful for the partners and, depending on the model considered, they can also help to signal and limit/control the interaction (Rouhier et al. 2008). Certainly, low ROS concentrations are known to be required for signaling, growth, and development, while high concentrations are detrimental to the cell and can damage various macromolecules. It is of primary importance for the development of plant–microbe interactions that ROS produced at the interface between the partners, that is, in the extracellular matrices, cell walls, and more generally the apoplast compartment (Rouhier et al. 2008).

Symbiotic and nonsymbiotic plants when exposed to ±stress (panic grass and tomato to heat stress and dunegrass and tomato to salt stress) revealed that in the absence of stress, both nonsymbiotic and symbiotic plant leaf tissues for all plants (panic grass, tomato, dunegrass) remained green indicating the absence of ROS generation and hence lack of stress response. In contrast, when exposed to stress, nonsymbiotic tissues bleached white indicating the generation of ROS while symbiotic tissues remained green. This suggests that endophytes either scavenge ROS or induce plants to more efficiently scavenge ROS, or prevent ROS production when exposed to abiotic stress (Singh et al. 2011).

2.5.5 Antioxidant Enzymes

It is a common belief that antioxidant enzymes play an important role in fungal symbiosis conferring abiotic stress tolerance. These enzymes include the low molecular-weight compounds are involved in the removal of ROS either directly (superoxide dismutases, catalases and ascorbate- or thioldependent peroxidases) or indirectly through the regeneration of the two major redox molecules in the cell, ascorbate and glutathione (glutathione reductases, dehydroascorbate reductases, and monodehydroascorbate reductases) (Rouhier et al. 2008). An interesting feature of the interplay between oxidants and antioxidants is that it occurs in all subcellular compartments including plastids and mitochondria, two sites of extensive ROS production (Navrot et al. 2007). Under salt stress conditions *P. indica* increases the tolerance of a salt-sensitive barley (Hordeum vulgare) cultivar to severe salt stress. *P. indica*-colonized plants contained higher ascorbate concentrations in roots compared with noncolonized plants, while the ratio of ascorbate vs. dehydroascorbate was not significantly altered and catalase, ascorbate peroxidase, glutathione reductase, dehydroascorbate reductase, and monodehydroascorbate reductase activities were increased (Waller et al. 2005; Singh et al. 2011).

2.6 Fungi Conferring Adaptation of Agriculture Crops to Abiotic Stress

Several studies have shown that endophytes may be profitable to plants harnessing in stressed conditions, like the presence of pollutants, heavy metals, organic compounds with chlorinated aromatic molecules, high salinity, elevated temperature, and drought, by basically controlling the oxidative stress (Raghuwanshi 2018). Class II endophytes confer heat tolerance to plants growing in geothermal soils (Redman et al. 2002), the extent of tree leaf colonization by endophytes correlates with the ability to resist pathogens (Arnold et al. 2003) and endophytes confer drought tolerance to multiple host species (Waller et al. 2005). Class I endophytes frequently increase plant biomass, confer drought tolerance, and produce chemicals that are toxic to animals and decrease herbivory (Singh et al. 2011). For example, Neotyphodium and Epichloë endophytes as grass symbionts which improved the plant's growth and its ability to resist biotic and abiotic stresses and found that volatile organic compounds have shown to be important in plant's response to stress factors (Jain and Pundir 2017). The plant's root colonized with *P. indica* showed tolerance in different abiotic stresses like extreme temperature, salinity, drought, and heavy metals (Chhipa and Deshmukh 2019). Mycorrhizal symbiosis is a key component in helping plants survive under adverse environmental conditions (Augé et al. 1992). AMF benefit plants by increasing nutrient water uptake, resistance against phytopathogens, and adaptation to a variety of environmental stresses such as drought, heat, salinity, and heavy metal contamination (Prasad 2017).

2.6.1 Salt Tolerance

Less availability of water to the agricultural fields and consequent increase in soil salinization have become a growing challenge in the agricultural sector in many parts of the world and are expected to raise due to climate change effects. Grass species growing on coastal areas harbor symbiotic fungal endophytes which strengthen them against salinity and heat (Rodriguez et al. 2008). These endophytes have been reported to induce salt tolerance in several noncoastal plants. *Leymus mollis* (dunegrass), plants harboring endophyte *Fusarium culmorum*, flourished on the coastal beaches of the USA, which are areas of high salinization. Salt-sensitive plants not growing in coastal areas were able to develop salt tolerance when inoculated with the endophyte *Fusarium culmorum* (Rodriguez et al. 2008). Redman et al. (2011) showed that some class 2 fungal endophytes can confer salt and drought tolerance to two commercial rice varieties which were not adapted to these stresses. Moreover, these endophytes reduced water consumption by 20–30% while increasing growth rate, reproductive yield, and biomass of greenhouse grown plants. Colonization of plants by *P. indica* shows salt tolerance, and this attribute is well demonstrated in tobacco (Nicotiana) and members of Poaceae family like barley (*Hordeum vulgare* L.), wheat (Triticum), and rice (*Oryza sativa*) which involve the detoxification of ROS by initiating production of antioxidants and enhancing the photosynthetic efficiency (Johnson et al. 2014).

Tolerance of the host *Festuca arundinacea* against a hydrocarbon mixture was enhanced by endophytic fungi Lewia (Cruz-Hernández et al. 2013). The endophytic fungi *Lewia* sp. has been isolated from *Limonium tetragonum* and *Phragmites australis*, which grow in high salt conditions (Khalmuratova et al. 2015). *Colletotrichum magna* and *C. protuberata* are well reported for water stress tolerance in wheat (*Triticum* sp.), tomato (*Solanum lycopersicum*), and watermelon (*Citrullus lanatus*) plants (Raghuwanshi 2018). *Penicillium* sp. and *Phoma glomerata* significantly increased plant biomass, related growth parameters, assimilation of essential nutrients such as potassium, calcium, magnesium, and reduced the sodium toxicity in cucumber plants under salinity and drought stress, when compared with control plants (Abo Nouh 2019). *Trichoderma* sp. and *P. indica* showed drought and salt tolerance in cacao, barley, and Chinese cabbage plant (Chhipa and Deshmukh 2019).

AMF fungi widely occur in salt stressed environment (Wang and Liu 2001). Recent literature suggest that AM fungi play a vital role in alleviating the effects of salinity (Al-Karaki et al. 2001a, b) and enhance the ability of the plants to cope with salt stress (Jahromi et al. 2008) by compensating nutritional imbalances imposed by salinization through improved nutrient acquisition, improving plant nutrient uptake (Asghari et al. 2005) and ion balance (Giri et al. 2007) protecting enzyme activity (Rabie and Almadini 2005) and facilitating water uptake (Ruiz-Lazano and Azcon 1995). Salt resistance was improved by AM colonization in maize (Feng et al. 2000), mung bean (Jindal et al. 1993), and clover (Ben Khaled et al. 2003) with the AM effect correlated with improved osmoregulation or proline accumulation. Also enhance relative water content in Zucchini leaves (Colla et al. 2008), water potential of maize plants (Feng et al. 2000), and chlorophyll concentration in the leaves of several plant species like *Sesbania aegyptiaca*, *S. grandiflora*, and *Lotus glaber* (Sannazzaro et al. 2006). Mycorrhizal maize plants had greater biomass than non-mycorrhizal plants under salt stress, thus implying that mycorrhizal plants grow better than non-mycorrhizal plants under saline conditions (Sheng et al. 2008). Similar trend were also reported in various other crops, e.g., tomato (Al-Karaki et al. 2001a, b), cotton (Feng and Zhang 2003), and barley (Mohammed et al. 2003). AMF-inoculated *Allium sativum* plants showed improved growth traits including leaf area index, and fresh and dry biomass under saline conditions (Borde et al. 2010).

2.6.2 Drought Tolerance

Fungal endophytes have been shown to provide fitness benefit to plants when exposed to water-limiting conditions. Perhaps the most widely documented example of endophyte-mediated drought stress tolerance in plants is the enhanced drought tolerance of tall fescue and perennial ryegrass due to infection of the endophyte *Neotyphodium coenophialum* (Dastogeer and Wylie 2017). Interestingly, all fungal endophytes conferred drought tolerance to plants regardless of the habitat of origin (Rodriguez et al. 2008). Kane (2011) studied the leaf-inhabiting endophyte *Neotyphodium lolii* to assess its potential benefits or harm in drought stress tolerance of native perennial ryegrass collections formerly obtained from the Mediterranean regions. The findings showed that endophyte colonization can help improve biotic stress tolerance such as drought in N. lolii (Cheplick 2006; Suman et al. 2016). *Curvularia protuberata* (Cp4666D) and *Fusarium culmorum* (FcRed1) isolates from geothermal soil and Costal Beach both conferred similar levels of drought tolerance in tomato (Rodriguez et al. 2008) and rice (Redman et al. 2011). Endophytes *Chaetomium globosum* and *Penicillium resedanum* isolated from *Capsicum annuum* plants promoted shoot length and biomass of the host plants subjected to drought stress (Khan et al. 2012). Drought-challenged tomato plants showed higher root and shoot biomass when inoculated with class 2 fungal endophytes, including *Alternaria* sp. and *Trichoderma harzianum* (Azad and Kaminskyj 2016). *Epichloë* species may enhance the eco-physiology of host plants and enable plants to counter abiotic stresses such as drought and metal contamination (Rodriguez et al. 2009). *Penicillium brevicompactum* isolated from wild barley species was helpful in drought tolerance improvement of barley plant in drought condition (Chhipa and Deshmukh 2019).

Extensive amount of research literature indicates that mycorrhizae often have a substantive impact on water movement into, through, and out of host plants, with consequent effects on plant tissue hydration and leaf physiology (Nasim 2010). They usually increase host growth rates during drought, by affecting nutrient acquisition and possibly hydration and typically water-use efficiency, which are influenced by the kind of fungi involved (Augé 2001). 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). Mycorrhizal plants may avoid drought to some extent through enhanced water uptake at low soil moisture levels. In onion, the effects seem to be conferred through improved phosphorus nutrition (Nelson and Safir 1982). An influence on host osmotic potential has been observed in wheat (Allen and Bosalis 1983). However, there is a strong evidence of drought stress alleviation by AMF in different crops such as wheat, barley, maize, soybean, strawberry, and onion (Ruiz-Lozano et al. 2015). Lavender plants inoculated with *Glomus intraradices* and *Glomus* sp. strain accumulated these compounds and exhibited high drought tolerance by improving water contents, root biomass, and N and P contents (Hussain et al. 2018). While working on sunflower plant exposed to drought stress, Gholamhoseini et al. (2013) stated that inoculation with *G. mosseae* improved availability of P, thus minimizing the impact of stress on seed oil percentage and oil yield. Zou et al. (2013) reported that when inoculated with *Funneliformis mosseae, Poncirus trifoliata* plants recorded lower tissue accumulation of this amino acid that related with improved plant growth and productivity under drought-stressed conditions.

2.6.3 Heat Tolerance

Several possible mechanisms could confer thermotolerance. In plants, the fungal endophytes produce cell wall melanin that may dissipate heat along the hyphae and/or complex with oxygen radicals generated during heat stress (Davidson et al. 1996). Rhizosphere fungus Paraphaeosphaeria quadriseptata enhanced plant heat stress tolerance of Arabidopsis thaliana (Grover et al. 2011). An endophytic fungi *Curvularia* sp. were reecovered from the *Dichanthelium lanuginosum* grown under geothermal soils. *C. protuberata* isolated from a monocot have ability to confer heat tolerance to tomato (a dicot) (Grover et al. 2011), also increased heat tolerance in wheat in terms of height, weight of grain, and germination of second-generation seeds (Lata et al. 2018). Under low temperature and higher nutrient input, *P. indica* triggers flowering earlier and increases grain yield indicating its potential as an effective endophyte promoting growth (Shrivastava and Verma 2014). Endophytic symbiont dark septate fungi (DSF) found in plants growing under stressed environments such as alpine habitats and arid grasslands have been reported to increase their resistance to drought and heat and facilitate the acquisition of nutrients (Grover et al. 2011).

Rhizosphere fungus *Paraphaeosphaeria quadriseptata* enhanced plant heat stress tolerance of *Arabidopsis thaliana* (McLellan et al. 2007). Generally, AMF-inoculated plants show better growth under heat stress than do the non-AMF inoculated ones (Begum et al. 2019). AMF can increase plant tolerance to cold stress. Moreover, a majority of reports state that various plants inoculated with AMF at low temperature grow better than non-AMF inoculated plants (Liu et al. 2013). AMF support plants in combating cold stress and eventually improve plant development (Begum et al. 2019). Maya and Matsubara (2013) have reported the association of AMF *Glomus fasciculatum* with plant growth and development leading to positive changes in growth under the conditions of high temperature. For example, during cold stress, AMF-inoculated plants showed an enhanced water conservation capacity as well as its use efficiency (Zhu et al. 2010). The role of AMF during cold stress has also been reported to alter protein content in tomato and other vegetables (Abdel Latef and Chaoxing 2011).

2.6.4 Flood Tolerance

AMF colonization by *Glomus intraradices* contributed substantially to the flood tolerance of *Pterocarpus officinalis* seedlings by improving plant growth and P acquisition in leaves. Flooding induced nodules both on adventitious roots and submerged parts of the stem (Grover et al. 2011). Mycorrhizal *Casuarina equisetifolia* seedlings could better adapt to flooding than noninoculated seedlings. This could be due to increased O2 diffusion and removal of ethanol through greater development of adventitious roots, aerenchymatous tissue, and hypertrophies lenticels on the root zone and submerged part of the stem (Rutto et al. 2002). The better tolerance of AM inoculated *A. trifolium* plants to flooding was mediated through an improvement of osmotic adjustment and proline in plant tissue (Neto et al. 2006).

2.6.5 Heavy Metals Tolerance

Studies have documented that the presence of HM in excess concentrations not only reduces spore germination, mycelia growth, degree of colonization, and sporulation of these fungi but also causes a significant impact on their ecology and diversity (Bhandari and Garg 2017). *Piriformospora indica* has been extensively reported to improve crop tolerance to a number of abiotic stresses including salinity, low temperature, and heavy metal toxicity (Gill et al. 2016). In a study made by the root-associated dark septate endophyte *Exophiala pisciphila* of Zea mays analyzed under increased soil Cd stress (0, 10, 50, 100 mg kg^{-1}) showed enhanced antioxidant enzyme activity (Lata et al. 2018).

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 Pandey 2015). 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). Studies have further depicted that spores isolated from polluted soils are more tolerant to and germinated better in HM-polluted soil in comparison to spores isolated from non-polluted soils (Gaur and Adholeya 2004). Consequently, AM fungi have been validated to lower the translocation of metals from roots to aerial organs (Garg and Kaur 2012). In one of the studies, Garg and Kaur (2012) demonstrated that in comparison with non-AM pigeon pea plants, colonization with *F. mosseae* led to significant immobilization of metals—Cd and Zn in roots—thus leading to lower translocation of toxic ions in above-ground plant organs in mycorrhizal-stressed plants. Similarly, colonization with *R. intraradices* restricted large amount of Pb in roots of woody legume *Robinia pseudoacacia*, thus preventing future damage to above-ground parts (Bhandari and Garg 2017). AMF association with wheat positively increased nutrient uptake under aluminum stress. Also in rice, AMF were very effective in lowering the levels of Cd in both the vacuoles and cell wall (Begum et al. 2019).

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Chapter 3
Arbuscular Mycorrhizae Associations and Role in Mitigation of Drought Stress in Plants

Deepika Goyal, Sushma Mishra, and Prem Kumar Dantu

Contents

3.1 Introduction

Now a days, we are suffering with a problem climate change which is causing drought in large areas of the earth (Sheffield et al. 2012). Drought is one of the most destructive abiotic stresses being faced by plants and it has widely attracted the attention of agricultural scientists and biotechnologists. Drought is a major concerned agriculture problem and reduces or limits plant growth and productivity (Kour et al. 2020b). A large piece of agricultural land is affected by drought and it adversely affects human society, economical rate, etc. (Disante et al. 2011; Mishra and Singh 2010). Drought stress limits water content available in soil, reduces cell size, membrane integrity, produces reactive oxygen species, and promotes leaf senescence causing reduction in crop productivity (Kour et al. 2020a; Tiwari et al. 2015). Apart from morphological changes there are some molecular changes in drought stressed plants such as increase in ethylene production (stress-responsive

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phytohormone), reduction in chlorophyll content, and inhibition in photosynthetic rate (Lata and Prasad 2011). Drought elevates accumulation of free radicals that induce change in membrane function, protein conformation, and lipid peroxidation leading to cell death (Tiwari et al. 2016; Yadav et al. 2020c, d, e). It is being believed by some scientists there will be increase in drought as time passes out due to climate change. Drought stress is among the most destructive abiotic stress that increased in intensity over the past decades affecting world's food security (Kour et al. 2019; Singh and Yadav 2020). Drought stress may range from moderate and short to extremely severe and prolonged duration, restricting the crop yields (Austin 1989; Pereira and Chaves 1995). Drought is expected to cause serious plant growth problems for more than 50% of the arable lands by 2050 (Ashraf 1994; Vinocur and Altman 2005; Kasim et al. 2013). Under drought stress plants adapt themselves through physiological, biochemical, and molecular responses (Ito et al. 2006) and control water status by adjustment of root hydraulic conduction, reduced transpiration, and stomatal closure (Parent et al. 2009). A change in plant stress-responsive genes is found by transcriptomic and proteomic approaches (Hirayama and Shinozaki 2010; Deshmukh et al. 2014; Liu et al. 2015). Some genes are found upregulated whereas others are found downregulated.

In molecular responses of drought, plants synthesize some specific proteins to impart drought tolerance such as LEA (late embryogenesis abundant), DSP (Desiccation stress protein), and dehydrins (Fig. 3.1). In addition, mycorrhizal association is a symbiotic non-pathogenic relationship between plant roots and fungal hyphae (Osonubi et al. 1991; Sieverding et al. 1991). In this mutualistic association, the fungi gain carbon compounds and other nutritional supplements from the roots of plants, and in return, provide the plant with macro and micronutrients such as nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), copper (Cu), and zinc (Zn) from the soil. The importance of mycorrhizae association in both agricultural and ecological systems had earlier been widely recognized (Mosse 1978; Osonubi et al. 1991). The increased plant growth by vesicular arbuscular mycorrhizae (VAM)

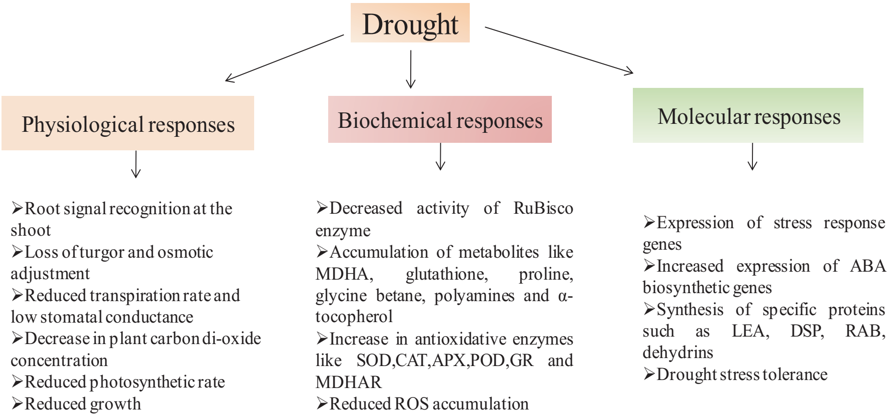

Fig. 3.1 Plant's physiological, biochemical, and molecular responses towards drought stress

association is usually due to increased mineral elements uptake by the hyphae from the soil, improved water relations and pest resistance of host plants (Farahani et al. 2008; Olawuyi et al. 2011a, b, 2012). VAM provided tolerance to a variety of abiotic stresses (Wilcox et al. 1990) and increased resistance to soil pathogens (Odebode et al. 1998; Pozo et al. 2002; Olawuyi et al. 2014a, b). Mycorrhizae can also resist drought in many plants under stress conditions; therefore, the plants infected with VAM are less likely to wilt under drought affected conditions as compared to non-inoculated plants (Lindermann and Hendrix 1982; Olawuyi et al. 2011a, b, 2014a, b).

3.2 Background of Arbuscular Mycorrhizal Fungi

Arbuscular mycorrhizal fungi are soil-borne fungi that alleviate abiotic stress and improve plant growth and yield (Sun et al. 2018). Most of the AMF belong to the sub-phylum Glomeromycotina, of the phylum Mucoromycota (Spatafora et al. 2016). AM fungi are classified in four orders namely, Glomerales, Archaeosporales, Paraglomerales, and Diversisporales and these orders include 25 genera (Redecker et al. 2013). Mycorrhizae are obligate biotrophs and ingest carbon compounds (Bago et al. 2000) and lipids to sustain their life cycle (Jiang et al. 2017). AMF provide drought tolerance to plants and act as safety-valve against fungal pathogens (Smith and Read 2008; Jung et al. 2012). In this way, Mycorrhizae are playing a vital role to maintain energy system and global harmony (Yadav et al. 2019a, b, c). They act as biofertilizers and improve crop productivity under adverse conditions also (Gianinazzi et al. 2010).

3.3 Arbuscular Mycorrhizal Fungi as a Biofertilizer

Biofertilizers are a mixture of naturally occurring substances which increase crop productivity without harming environment. Biofertilizers improve soil health and plant growth and development (Kour et al. 2020c; Sadhana 2014; Yadav et al. 2020a). From a long ago many researches are being conducted on AMF and myriad benefits are observed on soil health and crop productivity. Therefore, it is considered that AMF could be used as bio-fertilizer as a substitute of inorganic fertilizers due to their application can lower the quantitative use of chemical fertilizer input especially of phosphorus (Ortas 2012). Continuous exposure of herbicides, inorganic fertilizers, and fungicides has caused ecological imbalance and many threats to soil, plants, and human health, through their harmful effect on the quality of food products, soil composition, and aquatic bodies. It is believed that AMF can lower down the application of chemical fertilizers up to 50% for best agricultural production, but this estimate depends on the type of plant species and the prevalent stressful regimes (Rana et al. 2019; Yadav et al. 2020b). AMF are being used in various applications such as to provide resistance to plants against various abiotic stress and biotic stress along with used as biofertilizers (Fig. 3.2).

3.4 Mechanisms Used by AMF to Provide Drought Tolerance to Plants

There are certain mechanisms which explain how AMF provide resistance to plants against drought stress such as (1) adjustment of hormonal balance (Estrada-Luna and Davies Jr 2003), (2) enhancement of plant water status by improving hydraulic conductivity through an increase of water absorption by the external hyphae of VAM (Augé et al. 2007), (3) osmotic adjustment (Porcel and Ruiz-Lozano, 2004), (4) increase in antioxidant activity (Goicoechea et al. 2005), and (5) higher nutrients absorption (Al-Karaki 2006). This chapter describes these potential mechanisms adopted by mycorrhizae to alleviate drought stress being challenged by plants, and to improve yield and productivity of crops (Fig. 3.3).

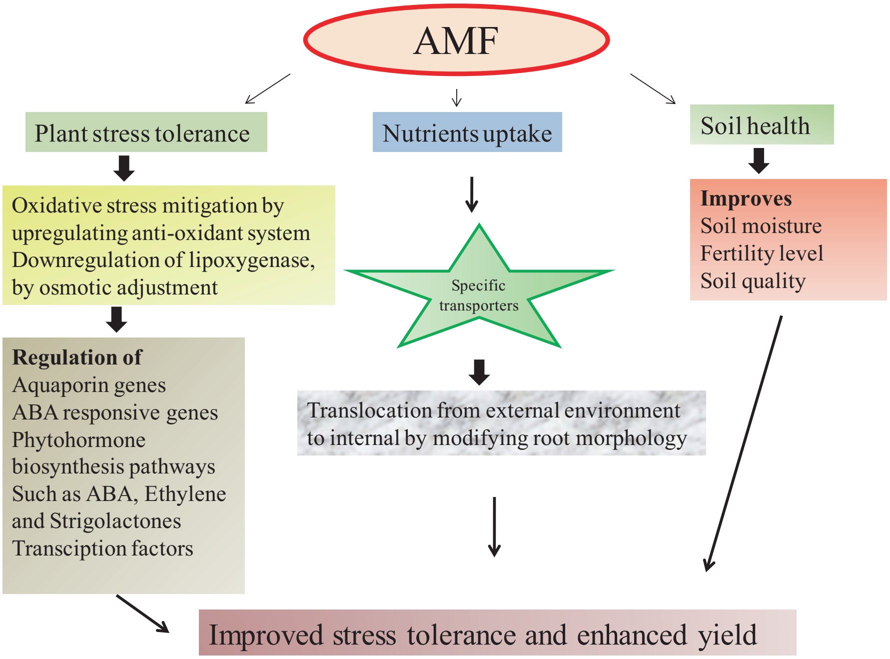

Fig. 3.2 Diagrammatic representation of application of mycorrhizae in improving plant growth and imparting tolerance against abiotic stress

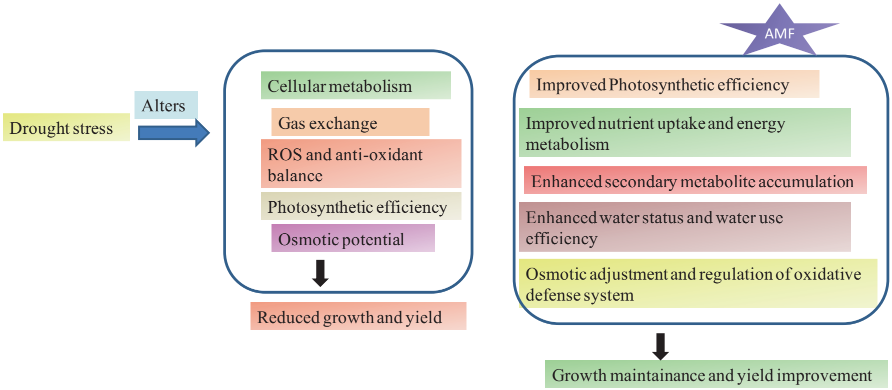

Fig. 3.3 Various mechanisms adopted by VAM fungi to provide drought tolerance to plants

3.4.1 Modification of Hormonal Balances

Under drought stress, AMF build changes in content of isoprenoids in leaves of tomato plants (*Solanum lycopersicum* L.), increasing the level of essential isoprenoids instead of nonessential isoprenoids (Asensio et al. 2012). This increase in production of essential isoprenoids is due to increasing requirement and biosynthesis of compounds derived from carotenoids such as ABA and strigolactones in mycorrhizal plants (Asensio et al. 2012). ABA, strigolactones, and jasmonic acid are the plant hormones where change in level is recorded in mycorrhizal plants under water-deficit conditions (Ludwig-Müller 2010).

3.4.1.1 Abscisic Acid and Strigolactones

Till today, it is quite complex to understand mycorrhizal interaction in plants due to their contrasting effects on ABA concentrations in plants under drought stress. Beneficial effects of symbiosis include increase of transpiration and water absorption by roots (Augé 2001) and lowering concentrations of ABA (Aroca et al. 2013). On the other hand, in tomato concentration of ABA increases under drought stress (Asensio et al. 2012). This change in hormonal levels is due to AMF genotype and the host plant (Ludwig-Müller 2010); it is found through various studies that, under drought stress, the mutualistic association with AMF regulates the ABA content (Table 3.1) (Estrada-Luna and Davies Jr 2003). ABA is primary requirement of AMF for sustainability and colonization, in host plant especially in water-deficit stress (Ludwig-Müller 2010). In fact, in tomato, ABA increases the susceptibility of plants to AMF colonization and appears to play an indispensable role in the development and functionality of arbuscules (Herrera-Medina et al. 2007). A significant correlation has been found between ABA production and strigolactones (Aroca et al. 2013). Strigolactones are reported as a new class of phytohormones regulating

Table 3.1 Recent studies showing the effect of AMF on plants subjected to a drought stress

Stress	Host species	Fungus species	Observed responses	References
Drought	*Glycine max*	AMF	Enhanced leaf proline, photosynthesis, leaf area index, relative growth rate, fresh weight, and dry weight of seeds	Pavithra and Yapa (2018)
Drought	*Poncirus trifoliata*	*Funneliformis mosseae, Paraglomus occultum*	Increased hyphal length, hyphal water absorption rate, and leaf water potential	Zhang et al. (2018)
Drought	*Olea europaea*	AMF	Alleviated drought impact and increased turgor potential (Ψp) and mineral uptake	Sara et al. (2018)
Drought	*Triticum aestivum*	*Glomus mosseae, Glomus fasciculatum, Gigaspora decipiens*	Increased plant growth parameters, and total chlorophyll pigments	Pal and Pandey (2017)
Drought	*Digitaria eriantha*	*Rhizophagus irregularis*	Increased shoot dry matter, stomatal conductance, lipid peroxidation, H2O2 in shoot and root	Pedranzani et al. (2016)
Drought	*Triticum aestivum*	*Glomus mosseae*	Increased osmotic potential, chlorophyll content and fluorescence, activities of antioxidant enzymes, ascorbic acid, enzymes of N and P metabolism, and contents of N, P, and K	Rani (2016)
Drought	*Triticum durum*	*Rhizophagus intraradices*	Higher grain biomass, and higher contents of copper, iron, manganese, zinc, and gliadins in grains	Goicoechea et al. (2016)
Drought	*Ipomoea batatas*	*Glomus spp.*	Proline and soluble sugars adjust osmotic potential	Yooyongwech et al. (2016)
Drought	*Saccharum arundinaceum*	*Glomus spp.*	Increased leaf water uptake, and levels of metabolites, phenolics, ascorbic acid, glutathione, antioxidant enzymes, chlorophyll fluorescence, and plant biomass	Mirshad and Puthur (2016)
Drought	*Zea mays*	*Rhizophagus intraradices*	Increased plant dry weight, uptake of P, N, K, and Mg in shoot, and water use efficiency	Zhao et al. (2015)

(continued)

Table 3.1 (continued)

Stress	Host species	Fungus species	Observed responses	References
Drought	*Solanum lycopersicum*	*Rhizophagus irregularis, Glomus intraradices*	Increased biomass production, efficiency of photosystem II, ABA accumulation and synthesis, and strigolactone production	Ruiz-Lozano et al. (2016)
Drought	*Pelargonium graveolens*	*Rhizophagus intraradices, Funneliformis mosseae*	Improved nutrient concentration, plant biomass, and essential oil content, and glomalin related soil proteins (GRSP)	Amiri et al. (2015)
Drought	*Fragaria ananassa*	*F. mosseae BEG25, F. geosporus BEG11*	Increased shoot and root fresh weights, WUE, and plant survival	Boyer et al. (2015)
Drought	*Robinia pseudoacacia* L.	*Funneliformis mosseae and Rhizophagus intraradices*	Increased dry biomass, WUE, and net photosynthetic rate	Yang et al. (2015)
Drought	*Glycine max*	*Septoglomus constrictum, Glomus spp.* including *Glomus aggregatum*	Improved water content and P and N levels	Grümberg et al. (2015)
Drought	*Antirrhinum majus*	*Glomus deserticola*	Increased shoot and root diameter, shoot length, leaf area, leaf number per plant, water content, Chl content, and proline	Asrar et al. (2012)
Drought	*Vigna subterranea*	*Glomus intraradices, Gigaspora gregaria, Scutellospora gregaria*	Increased mineral content, soluble sugars, and acid phosphatase, but reduced proline content	Tsoata et al. (2015)
Drought	*Hordeum vulgare*	*Glomus intraradices*	Increased root volume, P content, and activity of phosphatase enzyme	Bayani et al. (2015)
Drought	*Cucumis melo*	*Glomus mosseae*	K/Na ratio has increased in several plant tissues	Turrini et al. (2005)
Drought	*Citrullus lanatus*	*Glomus mosseae*	Water use efficiency, leaf water content, and leaf osmotic potential has increased	Ortas et al. (2011)
Drought	*Lactuca sativa*	*Glomus mosseae*	Endogenous auxin and cytokinin levels are increased in the presence of *G. mosseae*	Huang et al. (2011); Varga et al. (1994)
Drought	*Brassica oleracea*	*Glomus occultum*	Yield and quality increased with mycorrhizae	Augé (2001)

(continued)

Table 3.1 (continued)

Stress	Host species	Fungus species	Observed responses	References
Drought	*Lactuca sativa*	*Glomus fasciculatum*	L-arabinose (L Ara), ribose (Rib); D-xylose (D Xyl), L-xylose (L Xyl), adonitol (Ado), betamethyl-D-xyloside (Mdx) levels increased	Cho et al. (2006)
Drought	*Solanum melongena*	*Glomus mosseae*	Water use efficiency, leaf water content, and leaf osmotic potential has increased	Berreck and Haselwandter 2001
Drought	*Piper nigrum*	*Glomus caledonium*	Activity of superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX) in leaves of plants treated with *Glomus* increased	Sannazzaro et al. 2006
Drought	*Cucumis melo*	*Glomus mosseae*	Water use efficiency, leaf water content, and leaf osmotic potential has increased	Seymen et al. 2015
Drought	*Eriobotrya japonica*	*Funneliformis mosseae*	Increased growth, leaf water, proline, osmotic adjustment in root	Zhang et al. (2015)
Drought	*Phoenix dactylifera*	*Funneliformis monosporum, Rhizophagus clarus,* and *Glomus deserticola*	Increase in growth, water potential, and relative water content	Meddich et al. (2015)
Drought	*Citrullus lanatus*	Mixed inoculum of *Rhizophagus irregularis* and *Funneliformis mosseae*	Increase in phosphorus and nitrogen content of roots, increase in water use efficiency of plants	Omirou et al. (2013)
Drought	*Helianthus annuus*	*Funneliformis mosseae*	Increase in phosphorus and nitrogen content of seeds, improvement in seed quality	Gholamhoseini et al. (2013)
Drought	*Knautia arvensis*	*Glomus* sp.	Increase in phosphorus content	Doubková et al. (2013)
Drought	*Trifolium repens*	*Glomus* sp.	Increase in relative water content	Benabdellah et al. (2011)
Drought	*Tagetes erecta*	*Septoglomus constrictum*	Increase in photosynthetic pigments, phosphorus content and improved flower quality	Asrar and Elhindi (2011)

(continued)

Table 3.1 (continued)

Stress	Host species	Fungus species	Observed responses	References
Drought	*Pistacia vera*	*Claroideoglomus etunicatum*	Growth in secondary metabolite content and peroxidase activity	Abbaspour et al. (2012)

the architecture and reproductive development of plants (Foo and Reid 2013), but the function for which they were initially recognized for is the intermediation capacity in the mycorrhizal symbiosis process, where they act as a molecular signal in unfavorable conditions for plants (López-Ráez et al. 2010). ABA and strigolactones are apocarotenoids (Auldridge et al. 2006) and their biosynthesis is similar to each other (Walter et al. 2010). It is found that ABA regulates synthesis and concentration of strigolactone. For example, tomato plants that were deficient in the synthesis of ABA or treated with ABA specific inhibitors demonstrated a reduced capacity for strigolactone biosynthesis (López-Ráez et al. 2010).

3.4.1.2 Jasmonic Acid and Abscisic Acid

Colonization of AMF in host plants also affects the activation of the JA signal pathway (Tejeda-Sartorius et al. 2008). Under drought stress, JA acts as stress signal and increases ABA concentration by mutualistic interaction between host plant and mycorrhizae (Asensio et al. 2012). JA also plays important roles in the development and functionality of arbuscules together with ABA (Isayenkov et al. 2005). The increase of JA could be related to the variation of the root osmotic potential, caused by an increase of carbohydrates from shoots (Ludwig-Müller 2010). It has been suggested that sugar could induce the expression of genes related to JA biosynthesis, which could elevate the JA level and produce an increase in the sink strength through the extracellular invertase, whose expression is induced in mycorrhizal roots (Schaarschmidt et al. 2006). The narrow relationship found between ABA and AMF colonization in water-deficit conditions, as well as the functionality of the arbuscules suggests that the association between AMF and some plants could be one strategy to deal with a water deficit, probably regulated by the interaction of ABA with other hormones (Table 3.1).

3.4.2 Improvement of Plant Water Status

It is clear through previous studies that AMF make facilitate uptake and transport of water in host plants (Augé 2004). Gholamhoseini et al. (2013) reported positive effect of independently colonizing AMF species (*Funneliformis mosseae* or *Glomus hoi*) in sunflowers (*Helianthus annuus* L.) and found improved water use efficiency as compared to non-inoculated host plant. This indicates AMF improves stomatal conductance, transpiration rate, hydraulic conductivity, and water potential of leaves under drought stress (Table 3.1) (Augé 2004). Mycorrhizal fungi improve photosynthesis of host plant by improving the plant water status and increasing stomatal conductance which allow greater diffusion of CO_2 within the mesophyll cells of leaves (Boldt et al. 2011).

3.4.2.1 Hydraulic Conductivity in Extraradical Hyphae and Roots

Mycorrhizal fungi improve abiotic stress tolerance to plants by increase in hydraulic conductivity of roots (Augé et al. 2008). This increased hydraulic conductivity results in larger root system and roots reach more deep into soil which has a positive effect on the relative water content (RWC) (Meddich et al. 2015) water potential, transpiration rate, and crop yield (Augé 2001). Mycorrhizal hyphae that are involved in water transport (Allen 2009) are characterized by a diameter between 2 μm and 5 μm and can penetrate smaller soil pores that are inaccessible to root hairs (10–20 μm diameter) and thereby absorb water that is not available to non-mycorrhizal plants (Marulanda et al. 2003). AMF produce a glycoprotein known as glomalin, which generates stable aggregates and beneficial effects on soil structures (Wu et al. 2008). Soil colonization by AMF is as important as root colonization by AMF and it affects water relationship in host plants (Augé et al. 2007). Difference in water improving capability by AMF is due to difference in their mycelium, hyphae length, and functional system (Table 3.1) (Cseresnyés et al. 2013).

3.4.2.2 Stomatal Conductance

In water-deficit conditions AM provide strength to plants by change in stomatal conductance such as rosemary, tangerine, and rice (Augé et al. 2015; Wu and Xia 2006; Ruíz-Sánchez et al. 2011). On the contrary white clover (*Trifolium repens* L.) represents a decrease in stomatal conductance and an increase in the relative water content and water use efficiency (Benabdellah et al. 2011). (Table 3.1). However, this drought tolerance also depends on symbiosis between plant and mycorrhizae, for an instance inoculation of *Rhizophagus irregularis* in rose plants is not found successful to mitigate the stress (Klingeman et al. 2005).

3.4.2.3 Membrane Conductivity

Symbiosis of AMF with host plant upregulates the expression of genes coding for aquaporins (Ruiz-Lozano 2003). Porcel et al. (2005) reported effect of inoculation of AMF in tobacco plants (*Nicotiana tabacum*) and found increased expression of genes coding for aquaporins, and increase in absorption of water by the plants (Porcel et al. 2005). On the other hand, Porcel et al. (2006) reported the effect of inoculation of *F. mosseae* and *R. irregularis* in lettuce (*Lactuca sativa*) and soy plants (*Glycine max*) and found downregulation in genes coding for aquaporins and high relative water content as compared with non-inoculated plants. It indicates differential mechanisms adopted by VAM to alleviate drought stress. Apart from difference in VAM host plant also affects the mechanisms to cope up with stress.

3.4.3 Osmotic Adjustment

Plants with mycorrhizae have a better osmotic adjustment than plants without mycorrhizae (Porcel and Ruiz-Lozano 2004). Abbaspour et al. (2012) reported AMF increased level of compounds for osmotic adjustment in pistachio (*Pistacia vera*) and protected it from drought stress. Yooyongwech et al. (2016) found inoculation of *Glomus* sp. and *Acaulospora* sp. in sweet potato (*Ipomoea batatas*) provided tolerance against drought stress by increasing accumulation of osmotic compounds (Table 3.1). Proline is one of the chief osmolytes for osmotic adjustment and its accumulation has been found in plants inoculated with AMF such as white clover (Medina et al. 2010), sweet potato (Yooyongwech et al. 2016), Loquat (*Eriobotrya japonica* Lindl.) (Zhang et al. 2015), rice (Ruíz-Sánchez et al. 2011), and pistachio (Abbaspour et al. 2012) in water deficit. On the other hand, some plants do not accumulate proline as a tolerance mechanism to water deficits. For example, mycorrhizal plants of the Indian coral tree (*Erythrina variegata* L.) displayed high tolerance to a water-deficit stress, associated with an accumulation of chlorophylls and carotenoids, but not proline (Manoharan et al. 2010). Inoculation of *Glomus versiforme in citrus* plant enhanced osmotic adjustment of plant by increasing level of macronutrients and micronutrients in plant (Jasper et al. 1991).

3.4.4 Antioxidant Activity

Plants inoculated with AMF face low oxidative damage under water deficits and this is explained with the help of two mechanisms. According to first one hyphae help in water absorption and transfer it to the host plant, increasing the water level and decreasing the generation of reactive oxygen species (ROS). Caravaca et al. (2005) reported that non-inoculated plants of *Myrtus communis* and *Phillyrea angustifolia* under drought stress increased their superoxide dismutase (SOD), catalase (CAT), and total peroxidase (POX) activity as compared to inoculated plants. According to second mechanism there is an increase in the production of enzymatic and non-enzymatic antioxidants in plants symbiosed with AMF especially in water-deficit conditions (Zou et al. 2015; Amiri et al. 2015; Abbaspour et al. 2012). AM fungi are found to reduce the content of malondialdehyde and soluble protein in host plant and improved the activity of SOD and CAT (Gaspar et al. 1991). Recently, maize plants under water-deficit conditions have been found to be benefited by the AMF symbiosis not only by a lower oxidative stress, but also by local restriction and non-systemic oxidative stress (Bárzana et al. 2015). However, the exact mechanism involved is not yet clear and requires further experiments to better understand the actual function of AMF in the changes of reactive oxygen metabolism and antioxidants production (Table 3.1).

3.4.5 Higher Nutrients Absorption

Under drought stress AM facilitate better nutrients supply to plants and increase pigments levels, stomatal conductance, transpiration rate, and CO_2 assimilation rate providing strength to cope up with stress (Table 3.1). It is found in corn plant inoculation of different species of mycorrhizal fungi improves contents of mineral nutrients such as nitrogen (N), phosphorus (P), and magnesium (Mg) in roots and shoots of plants as compared to non-inoculated plants (Zhao et al. 2015; Zhang et al. 2014; Boldt et al. 2011).

3.4.5.1 Phosphorus

Phosphorous (P) is a vital macronutrient for plants and is mandatory for all major metabolic processes such as photosynthesis, signal transduction, energy transfer, macromolecular biosynthesis, respiration, and nitrogen fixation in legumes (Rastegari et al. 2020a; Yadav et al. 2020e; Saber et al. 2005; Khan et al. 2010). Although phosphorous is abundant in soil, only 0.1% of the total phosphorous is available to plants (in the form of orthophosphates $H_2PO_4^-$ and HPO_4^{2-}), thus making it a major limiting factor for plant growth (Zhou et al. 1992; Illmer and Schinner 1995). Since it is less mobile in soil through ion transporters and aquaporins AM improve its transport in host plants (Augé 2004). Inoculation of AM increase P content in plants such as marigold, wheat, sorghum, and squash (Asrar and Elhindi 2011; Al-Karaki et al. 2004; Wu and Xia 2006; Augé et al. 2007). AM mediated P accumulation increases root growth in plants which uptake water from depth (Rastegari et al. 2020b; Yadav et al. 2018) (Table 3.1).

3.4.5.2 Nitrogen

AMF enhance the level of N in plants under drought stress, increasing the activity of the enzymes nitrate reductase (NR) and nitrite reductase (Table 3.1). Apart from increasing enzyme activity mycorrhizal fungi increase N transport through hyphae (Caravaca et al. 2005). Mycorrhizal fungi improve aquaporins activity which transports ammonium (Uehlein et al. 2007).

3.4.6 *Photosynthesis, Partitioning, and Production of Photoassimilates*

Drought stress leads to accumulation of reactive oxygen species in plants and damages photosynthetic apparatus (Abbaspour et al. 2012) due to this NADPH and ATP become limiting factor for Calvin cycle. AMF inoculation improves photosynthetic rate of plants by increasing stomatal conductance and, therefore, CO2 fixing (Boldt et al. 2011). Increased stomatal conductance enhances the rate of photosynthesis in corn, guava, and rosemary (Estrada et al. 2013; Estrada-Luna et al. 2000; Sánchez-Blanco et al. 2004). Some of the non-stomatal factors also enhance photosynthesis rate by increasing accumulation of photosynthetic pigments, and protecting photosynthetic apparatus from reactive oxygen species, avoiding photo inhibition (Asrar and Elhindi 2011). Inoculation of AM increases content of photosynthetic pigments in marigold (Asrar and Elhindi 2011), Indian coral tree (Manoharan et al. 2010), sweet potato (Yooyongwech et al. 2016), and tangerine (Wu and Xia 2006). AMF improves the efficiency of photosystem II (PSII) (Fv/Fm) in corn, tomato, olive and black hawthorn plants (Ruíz-Sánchez et al. 2010; Yooyongwech et al. 2016; Estrada et al. 2013; Boldt et al. 2011). As a consequence of increase in (Fv/Fm) plants use the excitation energy more efficiently for CO2 assimilation (Table 3.1). This increased CO_2 assimilation results in higher quantity of carbohydrates and plant biomass under drought stress (Boldt et al. 2011). *F. mosseae* (mycorrhizal fungi) establishes a symbiotic association with indian coral tree plants and increased contents of chlorophylls, carotenoids, and proteins and decreased the content of sugars, starches and proline (Manoharan et al. 2010). Wu and Xia (2006) reported symbiosis effect of *Glomus versiforme* with trifoliate orange (*Poncirus trifoliata*) and found increase in chlorophyll and carotenoids and decrease in sugars, starches, and proline. AMF are being used as an inoculum in sustainable production systems (Jeffries et al. 2003) because of the fact that their application can produce economic benefits, especially in crops of high commercial value (Borde et al. 2011).

3.5 Conclusion and Future Perspective

As already discussed drought is one of the most threatening problems and reduces or limits plant growth and productivity and AM are the symbiotic organisms which can cope with it. There are many reports in literature where AM fungi are reported as alleviator of drought stress. However, there are no more reports on synergistic effect of AMF with rhizobacteria and endophytes. Plant growth promoting rhizobacteria and endophytes also mitigate stress. Thus it will be an advancement of research to find out combining effect. AM provide drought tolerance by maintaining osmoregulation. Studies have been done on the concentration of osmolytes, research should be focused on the genes coding for osmolytes. This molecular investigation will deal with interaction studies of AM and roots of higher plants. AM symbiosis with plant also varies according to plant genotype and AM species. Thus research should be focused to find out which species can provide more drought tolerance. AM facillitate adjustment of hormonal balance in plants to provide tolerance but studies are done only for ABA and strigolactones wheresas Salicylic acid, brassinosteroids also involve during water deficit. Research should be planned to find out the synthesis and signaling mechanism of salicylic acid and brassinosteroids in AM under drought stress.

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Chapter 4
Soil Salinity and Its Alleviation Using Plant Growth–Promoting Fungi

Prem Chandra, Enespa, and Ranjan Singh

Contents

4.1 Introduction

Salinity stress inhibits the growth of crops, production of biomass, seed germination, and crop productivity. It is known as an abiotic environmental factor and is common globally (Wani et al. 2016). Salt stress also inhibits the growth of shoots and roots, and perturbs plant metabolism and physiological status as a result of ionic disparity in plant cells (Munns and Tester 2008). Salinity stress is caused by accumulation of compatible solutes and upregulation of antioxidants in cell signaling

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pathways and cellular responses (Wang et al. 2003). Additionally, observations have shown that ~6% of the total land area around the world and 50% of the irrigated land are acutely affected by salt stress (Shabala and Cuin 2008).

In all plants, calcium is an essential element, which maintains the integrity and structures of membranes and cell walls through formation of intermolecular linkages (Baluška et al. 2003). Toxic accumulation of Na^+ ions in the cytosol leads to increased ambient salt concentrations. Procurement and homeostasis of essential nutrients such as K^+ and Ca^{2+} are affected by inconsistent presence of Na^+ in both cellular and extracellular partitions (Banjara et al. 2012). A low K^+:Na^+ ratio is another specific symptom of salt toxicity. For activation of many enzymes, the presence of K^+ in the cytosol is essential (Maathuis and Amtmann 1999). Excess Na^+ tends to substitute K^+ with Na^+ at binding sites and hence impairs cellular biochemistry because of physicochemical similarities between Na^+ and K^+ (Benito et al. 2014).

Plants adapt by de novo synthesis of organic compatible solutes acting as osmolytes to cope with salt stress–induced osmotic problems (Paul 2013; Suman et al. 2016; Yadav et al. 2019a). The highly ordered states of membranes and quaternary protein structures are stabilized by glycine betaine, which acts as an osmoprotectant (Sakamoto and Murata 2001). Under salt stress, proline serves as a storage sink for carbon and nitrogen and also as a free-radical scavenger, stabilizes subcellular structures (membranes and proteins), and buffers cellular redox potential (Sotiropoulos 2007).

Accumulation of reactive oxygen species (ROS) such as superoxide radicals (O) hydrogen peroxide (HO) and hydroxyl radicals (OH) is induced by salt stress, with detrimental effects on plant growth and metabolism (Cakmak 2005). Therefore, soil amendment through exploitation of soil fungi is of considerable importance (Besharati et al. 2018). In saline conditions, various biological approaches such as use of arbuscular mycorrhizal fungi (AMF) to enhance plant growth and tolerance of abiotic environmental stress are receiving increasing recognition from scientists (Evelin et al. 2009).

AMF also improve nutrient access and physiological processes such as the water absorption capacity of plants by increasing root hydraulic conductivity and favorably adjusting the osmotic balance and composition of carbohydrates in saline soil (Abdelhamid et al. 2019; Yadav et al. 2019b). Therefore, excess salt accumulation in the root is also ameliorated, and various observations have demonstrated effects on osmotic adjustment (Arora and Sahni 2019). Pigeonpea (*Cajanus cajan* (L.)) is a major grain legume (pulse) annual crop in the tropics and subtropics. It can be used as a source of seed and forage for livestock and as a soil ameliorator in agroforestry and shifting cultivation systems (Dagar 2016). A number of cereals such as sorghum (*Sorghum bicolor* L.), pearl millet (*Pennisetum glaucum* L.), and maize (*Zea mays* L.) have traditionally been grown in intercropping or mixed cropping systems (Gemenet et al. 2016). AMF can play an important role in improvement of salt tolerance in various crops. The main objective of this chapter is to characterize salt resistance approaches by describing membrane peroxidation, electrolyte leakage, osmolyte accumulation, and enzymatic antioxidant defense systems under abiotic salinity stress (Laouane et al. 2019). To date, there is little information available on the effects of salinity on plant biomass and nitrogen fixation, antioxidant defense systems, and use of mycorrhizal inoculation for osmoprotection in legumes (Wang et al. 2016).

Observations have revealed a possible interrelationship between AMF inoculation and tolerance of ionic, osmotic, and oxidative stress in pigeonpea exposed to long-term salinity. *Trichoderma longibrachiatum* T6 (T6) has been shown to promote wheat growth and induce plant resistance to parasitic nematodes (Zhang et al. 2016a, b). *Aspergillus aculeatus* has an important effect on mitigation of salt stress by producing indole-3-acetic acid and siderophores, thereby conferring stress tolerance on plants, as shown in perennial ryegrass (Li et al. 2019). The possible effects of 24-epibrassinolide and the AMF *Glomus mosseae*, singularly and collectively, on salt stress in wheat (*Triticum aestivum* L.) plants have been studied (Tofighi et al. 2017). Important indicators of salt stress, such as the growth rate and nutritive values of perennial ryegrass, have been observed in order to explain mechanisms of protection against salt stress in ryegrass (Hu et al. 2012).

Antioxidant activities such as lipid peroxidation, photosynthetic routines, ionic homeostasis, and metabolic homeostasis have been scrutinized (Jackson et al. 2007). It has been estimated that associations between roots and AMF are present in over 80% of terrestrial plant species such as halophytes, hydrophytes, and xerophytes (Uhlmann et al. 2006). Mycorrhizal application represents a good option to alleviate salt stress through biological processes. Additionally, AMF can expand host physiological processes such as the water absorption capacity of plants by increasing root hydraulic conductivity and favorably adjusting the osmotic balance and composition of carbohydrates (Syvertsen and Garcia-Sanchez 2014). This may lead to increased plant growth and consequent dilution of toxic ion effects (Al-Karaki 2000; Yadav and Saxena 2018). These benefits of AMF have encouraged their use for mycoremediation of saline soils (Kumar et al. 2019a). Various plant growth–promoting fungi (PGPF) that reduce salinity stresses in various crops are listed in Table 4.1. These fungi—such as *Aspergillus*, *Fusarium*, *Trichoderma*, *Penicillium*, *Piriformospora*, *Phoma*, *Claroideoglomus*, *Glomus*, and *Rhizoctonia*—have a natural capability to stimulate various growth-related traits of plants and thereby benefit the plants (Contreras-Cornejo et al. 2009; Enespa and Chandra 2019).

Various observations in dicots and monocots have shown that PGPF mimic well-studied plant growth–promoting rhizobacteria (PGPR) in their interactions with host plants (Chandra and Singh 2016; Kour et al. 2019b; Kumar et al. 2019b; Singh et al. 2020; Yadav et al. 2018a). As an example, treatment of seeds with PGPF inoculum can improve germination and seedling vigor, and induces growth of longer and larger shoots in different plants. Some PGPF may exert effects on root development and performance (Enespa and Chandra 2017). The photosynthetic capability of plants can also be enhanced by PGPF inoculation, stimulating early and vigorous flowering of the plants. Various PGPF have the capability to stimulate the production of the host's secondary metabolites and increase crop productivity (Singh and Yadav 2020; Yadav et al. 2019c). PGPF show beneficial effects on growth and changes in biochemical, physiological, and molecular mechanisms used

Table 4.1 Effects of fungi in plants subjected to salinity stresses

Crops	Fungi	Effects	References
Triticum aestivum L.	*Glomus mosseae*	Stimulated leaf enzymatic antioxidant activities including those of catalase (2.24-fold) and ascorbate peroxidase (2.18-fold); increased malondialdehyde concentrations (36.17%) and H_2O_2 concentrations (49.74%)	Tofighi et al. (2017)
Solanum lycopersicum L.	*Piriformospora indica*	Increased content of phenolic compounds and nonenzymatic antioxidants; increased activity of antioxidant enzymes	Ghorbani et al. (2018)
Cucumis sativus L.	*Claroideoglomus etunicatum*, *Rhizophagus intraradices*	Enhanced growth, biomass, root activity, nutrient content, and gas exchange parameters in plants inoculated with arbuscular mycorrhizal fungi	Hashem et al. (2018)
Ricinus communis	*Funneliformis mosseae*, *Rhizophagus intraradices*	Increased chlorophyll content in leaves, increased P and Mg uptake, and increased proline content, protecting plant growth	Zhang et al. (2018a, b)
Lolium perenne	*Aspergillus aculeatus*	Lowered Na:K ratio; lowered concentrations of metabolites, amino acids (alanine, proline, gamma aminobutyric acid, and asparagine), and soluble sugars (glucose and fructose); improved plant photosynthetic efficiency; reduced activity of antioxidant enzymes (peroxidase and catalase); attenuated lipid peroxidation (decreased H_2O_2 and malondialdehyde accumulation)	Li et al. (2017)
Tomato cultivars (Sultana-7 and Super Strain-B)	*Glomus fasciculatum*	Increased chlorophyll content coupled with an increased chlorophyll a:b ratio	Ebrahim and Saleem (2017)
Rice	*Trichoderma harzianum*	Better photosynthetic performance; higher pigment concentrations and high proline content	
Triticum durum Desf.	*Rhizophagus irregularis*, *Funneliformis mosseae*	Increased root biomass, N uptake, and aboveground N concentrations; greater stability of plasma membranes	Fileccia et al. (2017)
Triticum aestivum	*Trichoderma longibrachiatum* T6	Promoted growth; induced plant resistance to parasitic nematodes	Zhang et al. (2016a, b)

(continued)

Table 4.1 (continued)

Crops	Fungi	Effects	References
Panicum turgidum	*Funneliformis mosseae*, *Rhizophagus intraradices*, *Claroideoglomus etunicatum*	Increased chlorophyll a, chlorophyll b, and carotenoid content; increased superoxide dismutase, peroxidase, catalase, and glutathione reductase activities	Hashem et al. (2015)

by host plants to alleviate salt stress (Zhang et al. 2016a, b; Rastegari et al. 2020a). This chapter discusses the effects of salinity on PGPF—such as colonization, hyphal length, and sporulation both in vivo and in vitro—and the presence of fungi in saline soils.

4.2 Causes of Soil Salinization and Associated Problems

The physicochemical processes resulting from the presence of various salts in soil and water are known as salinization. In irrigated agricultural systems, soil salinity is an enormous problem. There are two main types of soil salinity: primary and secondary (Qadir and Schubert 2002). Primary salinity refers to natural processes of salt formation in soil and water. Development of secondary salinity results from anthropogenic activities such as land development, agriculture, irrigation, and industrial development (Rengasamy 2006). Common causes of secondary salinity are rising groundwater tables due to excessive irrigation or use of poor-quality water, clearance of vegetation, and changes in land use. Soils in hot and dry regions of the world are frequently saline with low agricultural potential. Secondary salinization of land and water resources in arid and semiarid conditions results from major anthropogenic activities such as agricultural irrigation (Chandra and Enespa 2019a; Machado and Serralheiro 2017).

Anthropic salinization occurs in arid and semiarid areas because of waterlogging and mismanagement of irrigated water (Singh 2015). Worldwide, more than 45 million hectares of irrigated land, representing about 20% of all irrigated land and about 2% of all dryland agriculture, has already been damaged by salt (Carillo et al. 2011). Poor irrigation systems causing loss of once productive agricultural land represent the most serious salinity threat (Machado and Serralheiro 2017). Calcium (Ca^{2+}), magnesium (Mg^{2+}), and sodium (Na^{+}) salts are found in irrigation water. Evapotranspiration plays a very significant role in pedogenesis of saline soils in arid and semiarid regions. Ions of calcium (Ca^{2+}) and magnesium (Mg^{2+}) salts released after evaporation often precipitate into carbonates, leaving Na^{+} dominant in the soil (Acosta et al. 2011; Qadir et al. 2007). Therefore, high concentrations of Na^{+} in the soil solution may put a brake on nutrient ion activities and produce extreme $Na^{+}:Ca^{2+}$ or $Na^{+}:K^{+}$ ratios (Guan et al. 2017; Antoniadis et al. 2015). During the last century, physical, chemical, and/or biological land degradation processes have resulted in serious concerns about compaction, inorganic/organic contamination, and diminished microbial activity/diversity in natural soil resources worldwide (Mondal and Kaur 2017). As a result of introduction of irrigation, the areas of soils affected by these problems continue to increase each year. In India, saline soil mostly occurs in the Indo-Gangetic plain, which covers the states of Punjab, Haryana, Uttar Pradesh, and Bihar, and some parts of Rajasthan. Semiarid tracts in Gujarat, Madhya Pradesh, Maharashtra, Karnataka, and Andhra Pradesh are also largely affected by saline soils, as are arid tracts in Gujarat and Rajasthan (Chandra and Singh 2014; Shinde 2018; Silva et al. 2019).

4.3 Nature and Diversity of Plant Growth–Promoting Fungi

Plant growth–promoting fungi are a heterogeneous group of nonpathogenic fungi associated with plants and mediate improvements in plant growth and health (Hossain et al. 2017; Rana et al. 2019b; Yadav et al. 2020a; Yadav et al. 2018c). Individual PGPF may differ conspicuously from one another in terms of their taxonomy, habitats, physiology, and interactions with plants, as observed in various studies (Bhattacharyya et al. 2016; Venturi and Keel 2016). A fungus that stimulates the growth of a given plant may not have the same effect upon the growth of another plant, or the effect may vary under a different set of environmental conditions (Hardoim et al. 2015; Vejan et al. 2016; Yadav et al. 2019d). Not all fungi that promote plant growth are considered to be PGPF, in the same way that symbiotic mycorrhizal fungi are known to improve plant growth but are not considered to be PGPF (Baum et al. 2015; Hossain et al. 2017). Mycorrhizal fungi behave as obligate biotrophs and establish an intimate association with the roots of most host plants (Hiruma et al. 2018). On the other hand, PGPF are nonsymbiotic saprotrophic fungi, which live freely on the root surface, in the interior of the root itself, or in the rhizosphere (Kour et al. 2019a). Fungal microbial flora identified as PGPF have diverse taxonomy (Chagas et al. 2018). The majority of true fungi characterized as PGPF primarily belong to the phylum Ascomycota (*Aspergillus*, *Aureobasidium*, *Chaetomium*, *Cladosporium*, *Colletotrichum*, *Exophiala*, *Fusarium*, *Gliocladium*, *Penicillium*, *Phoma*, *Phomopsis*, *Purpureocillium*, *Talaromyce*s, and *Trichoderma*), and a few of them belong to Basidiomycota (*Limonomyces*, *Rhizoctonia*, *Rhodotorula*, and sterile fungi) and Zygomycota (*Mucor* and *Rhizopus*), according to the literature (Hossain et al. 2017; Rana et al. 2019a; Sharma et al. 2019; Yadav 2019; Zhang et al. 2018a, b). *Fusarium oxysporum*, *Colletotrichum*, and binucleate *Rhizoctonia* are phylogenetically related to plant pathogens but lack functional virulence determinants for many of the plant hosts from which they can be recovered (Lorenzo-Gutiérrez et al. 2019; Jiang et al. 2018). The members of the Oomycota are mostly virulent plant pathogens, while some are nonpathogenic (Hassani et al. 2018). *Pythium oligandrum* and *Phytophthora cryptogea*, which colonize root ecosystems and act as PGPF, are nonpathogenic oomycetes (Hossain et al. 2017). PGPF mostly have origins either in the soil or in the roots of a large range of hosts.

Commonly, 44% of rhizospheric fungal isolates are PGPF (Compant et al. 2010). The occurrence of PGPF in the rhizospheric region differs between different crop plants. Various fungi that live inside the root tissues or endophytes also have miscellaneous positive effects on plant growth and are PGPF (Cardoso Filho 2019). *Fusarium*, *Penicillium*, and *Alternaria* are the most dominant endophytes (Barsainya et al. 2016; Khalmuratova et al. 2015).

4.4 Effects of Salinity on Crops

The growth of various plant species, particularly glycophytes (which are salt-sensitive rather than salt-tolerant halophyte species), is greatly impacted by high soil salinity. Most agricultural crops come under the category of glycophytes, which exhibit a spectrum of responses under salt stress (Volkmar et al. 1998; Hester et al. 2001). Salinity affects the physicochemical properties and ecological balance of the land, leading to low economic returns, soil erosion, and decreased crop productivity (Karami et al. 2012).

The particular effects of salinity include the following:

- Excessive accumulation of sodium ions in cell walls results in osmotic stress and cell death (Flowers and Yeo 1986; Munns and Passioura 1984).
- Higher concentrations of salt in soil can interrupt nutrient stability in plants or interfere with uptake of some nutrients (Bernstein and Hayward 1958).
- Extensive decreases in leaf area, chlorophyll content, and stomatal conductance occur, leading to a less competent photosystem II (PS-II) (Hura et al. 2007).
- A substantial reduction in phosphorus uptake by plants occurs as a result of precipitation of phosphate ions in the form of calcium phosphate (Wendling et al. 2013).
- Salinity inhibits the development of fertilization by weakening microsporogenesis and stamen filament elongation, causing ovule abortion and senescence of fertilized embryos (Gómez et al. 2015).
- The supply of photosynthetic assimilates or hormones to growing tissues becomes impaired (Weber 2009).
- Salt stress is a result of ion toxicity in which the K^+:Na^+ ratio changes, leading to replacement of K^+ by Na^+ in biochemical reactions. Because of this, quite a few enzymatic activities, as well as binding of transfer RNA (tRNA) to ribosomes—and consequently protein synthesis, in which K^+ is a requisite—are inhibited (Almeida et al. 2017). Furthermore, high levels of Na^+ and Cl^- induce conformational changes in proteins. Recent reports have also shown that salinity adversely affects plant growth and development by hindering enzyme activity (Rani et al. 2019), DNA, RNA, protein synthesis, and mitosis (Atieno et al. 2017).
- Osmotic stress and ion toxicity can cause metabolic imbalance, which in turn leads to oxidative stress (Liang et al. 2018).

- Cyclin-dependent kinases and cyclin activities are reportedly hindered by soil salinity, resulting in fewer cells in the meristem and limited growth. The activity of cyclin-dependent kinase is also reduced by posttranslational inhibition during salinity stress (Chandra and Enespa 2019c; Raines et al. 2016).

4.5 Arbuscular Mycorrhizal Fungi

Endophytic and biotrophic fungi are known as mycorrhizal fungi and form mutualistic symbiosis with several plant species (Rana et al. 2019a; Verma et al. 2017). Various types of mycorrhizal fungi among the endomycorrhizal fungi (arbuscular mycorrhizal fungi) and ectomycorrhizal fungi are important in agriculture and forestry (Fesel and Zuccaro 2016). AMF are well known for their efficiency in plant growth promotion, especially in arid and semiarid regions. AMF may have appeared on earth more than 400 million years ago and are grouped into the phylum Glomeromycota (Berruti et al. 2016). For their growth and reproduction, AMF mainly depend on host plants. Various researchers have reported that AMF improve plant growth and productivity by increasing the supply of phosphorus to host plants (Baum et al. 2015).

4.5.1 Arbuscular Mycorrhizal Fungi in Saline Soils

AMF have been known to occur naturally in saline environments, in spite of the low mycorrhizal affinity of halophytes (Latef et al. 2016). In saline areas, the average density of spores has been reported to be low by some investigators but not others (Yang et al. 2018a, b). The most predominant species of AMF in the severely saline soils of the Tabriz plains (with an electrical conductivity (ECe) of 162 dS m^{-1}) were found to be *Glomus intraradices*, *Glomus versiform*, and *Glomus etunicatum* (Becerra et al. 2019; Sheng et al. 2019). Increases in AMF spore numbers in the presence of soil salinity (defined as a mean of 100 spores per 10 g of soil) have been observed by various investigators (Bencherif et al. 2019a, b). Sporulation is stimulated under salt stress in saline soil with a high fungal spore density (Kissoudis et al. 2015). It has also been revealed that in severely saline ecosystems with low root colonization levels, AMF may produce spores (Sheng et al. 2019). One study found that saline soils with ECe of approximately 45 dS m^{-1} had zero spore inhabitants, in contrast to other observations (Kong et al. 2017; Lee et al. 2015). A 150 mM NaCl concentration inhibited hyphal growth and spore germination of AMF. An abundance of AMF spores were found in highly alkaline soils with a pH of up to 11; the degree of colonization varied between individual AMF, independently of the soil type and salt type (NaCl, Na_2CO_3, Na_2SO_4, or $CaSO_4$) (Hage-Ahmed et al. 2019; Latef et al. 2016; Porcel et al. 2016). AMF spore distribution was evaluated in two salt marshes (Powell and Rillig 2018). Greater AMF biodiversity was observed in soil samples from both sites on the basis of morphological analysis of spores, but the overall biodiversity was lower in the roots at both sites, according to sequencing analysis (Faggioli et al. 2019; Berruti et al. 2017). AMF interactions were found to have valuable effects on water status, addition of osmolytes, and growth of *Phragmites australis* plants in a saline environment (Pereira et al. 2016).

In mycorrhizal *Aster tripolium* plants in saline soil, an amended water relationship was observed. It was reported that the most common AMF observed in salt-stressed soil were *Glomus* spp., and one species, *Glomus geosporum*, produced 80% of the spores detected by biological molecular techniques (Mahmood et al. 2019; Plouznikoff et al. 2016). In the primary stage of growth, *Glomus mosseae*, *Glomus intraradices*, and *Glomus claroideum* were found to ameliorate salt stress in olive trees (Yasmeen et al. 2019). In terms of olive tree performance, *Glomus mosseae* was the most proficient fungus in acting against unfavorable effects of salinity, particularly in terms of the protection it offered (Kour et al. 2019). The negative properties of salinity stress may be contingent on the behavior of each species of AMF and its capability in protecting the plants, as suggested by these observations (Igiehon and Babalol 2018). Various observations have revealed that AMF increase the growth and productivity of plants through ingredient uptake, but the exact apparatus used by AMF to alleviate the reduction of growth in saline conditions is not yet clear (Vangelisti et al. 2018).

In severely saline soil conditions, *Glomus intraradices*, *Glomus versiforme*, and *Glomus etunicatum* were found to be the most predominant species (Chun and Chandrasekaran 2018). Hyphal growth, spore germination, and colonization capability are adversely affected by extremely saline conditions, and salt can reduce formation of arbuscular mycorrhizae (Wang et al. 2017; Venneman et al. 2017). However, spore germination is not prevented or inhibited in severely saline ecosystems, although it may be delayed (Nagler et al. 2015). Multiple biochemical pathways such as ion homeostasis and retention and/or acquisition of water help to protect chloroplast functions in salt-tolerant plants (Suo et al. 2017).

4.5.1.1 Interactions Between Arbuscular Mycorrhizal Fungi and Plants

Approximately 80% of terrestrial plant species and 92% of terrestrial plant families form symbiotic or mutualistic associations through colonization of plant roots by AMF (Asmelash et al. 2016). Intraradical or extraradical hyphae are formed by AMF spores present in the soil. Plant roots are infected by intraradical hyphae penetrating their epidermal cells and colonizing their cortical cells (Yang et al. 2018a, b; Javeria et al. 2017). In the infected cortical cells, the formation of arbuscules is a unique property of AMF. This colonization benefits both the host and the AMF, which have no negative effects on each other (Chen et al. 2018). Intercellular and intracellular hyphae are formed by the AMF inside the root, and the intercellular hyphae between the cortical cells form vesicles, which store nutrients (Walker et al. 2018). *Glomus* spores are known to form these vesicles (Oehl and Körner 2014).

The arbuscules formed inside the cortical cells are used by the plant and fungi to exchange nutrients such as phosphorus and nitrogen (Cosme et al. 2018).

4.5.1.2 Importance of Arbuscular Mycorrhizal Fungi Under Stress Conditions

AMF are used in cultivars mainly for improvement of plant growth and crop productivity. Salinity stress decreases nutrient supply and uptake by roots (Ilangumaran and Smith 2017). In most soils, the ionic form of phosphate is poorly transferred. A phosphate-depleted soil zone forms around plant roots over time, as a result of continuous nutrient uptake by the roots (York et al. 2016; Hinsinger et al. 2018). The extraradical hyphae of AMF play a dynamic part in nutrient uptake from soil after colonization is successfully completed (Hodge et al. 2010). In the undepleted nutrient zone, extraradical hyphae infiltrate the soil and extend more widely (Bücking and Kafle 2015). From the undepleted nutrient zone, the hyphae absorb nutrients and supply them to the plant via the arbuscular membrane (Jakobsen and Hammer 2015). Under salinity stress, mycorrhizal plants absorb and accumulate more nutrients (such as phosphorus) from the soil than nonmycorrhizal plants do (Parihar and Bora 2019). Macromolecules such as lignin, chitin, protein, and nucleic acid are broken down into simple monomers, which are hydrolyzed by the hydrolytic enzymes produced by extraradical hyphae in the soil. Nutrients are absorbed as monomers more efficiently by AMF (Ma et al. 2015).

4.5.1.3 Genera of Arbuscular Mycorrhizal Fungae

Arbuscular mycorrhizal fungi have been found to occur naturally in saline ecosystems. *Glomus*, belonging to the family Glomeromycota, is the genus most commonly observed in saline soil, but the specificity of its ecology was not demonstrated until recently (Oehl et al. 2017). Only morphological characterization was used to identify AMF spores in earlier studies (Öpik et al. 2013; Wang et al. 2010). However, studies of fatty acid methyl ester (FAME), using polymerase chain reaction (PCR) and restriction fragment length polymorphism (RFLP) molecular techniques, have helped to provide better and more precise accounts of fungal diversity in NaCl-affected areas (Hinojosa et al. 2010). AMF genera with potential for salt stress amendment are *Glomus* (*Glomus intraradices*, *Glomus versiform*, *Glomus etunicatum* (Pagano et al. 2016; Vályi et al. 2016), *Glomus fasciculatum*, *Glomus macrocarpum*, *Glomus geosporum*, and *Glomus coronatum* (Bhattacharjya et al. 2018)), *Gigaspora* (*Gigaspora gigantean* and *Gigaspora margarita* (de Souza Moreira et al. 2015)), *Acaulospora*, *Archaeospora* (Muhammad and Setyaningrum 2017), *Funneliformis* (*Funneliformis mosseae*, *Funneliformis geosporum*, and *Funneliformis coronatum*), and *Rhizophagus* (*Rhizophagus fasciculatus*) (Bhattacharjya et al. 2018).

4.5.1.4 Nitrogen Fixation and Nodulation

Nitrogen-fixing bacteria, which form nodules through symbiosis, are a soft target for salt stress, and the density of these bacteria is reduced by salinity stress (Garg and Chandel 2015; Yadav et al. 2018b). This is due to early nodule senescence prompted by salinity stress (Matamoros et al. 2017), changes in formation of green pigments from leghemoglobin, damage to nitrogen fixation, and consequent acceleration of lytic activities (Savitha et al. 2016). The detrimental effects of salt on nodulation and nitrogen fixation in legumes is counteracted by application of AMF (Mia et al. 2014). It has been observed that AMF interaction can ameliorate drought stress–induced premature nodule senescence (Zahir et al. 2019). A resilience effect of a mycorrhizal booster on nodule development under salinity stress has been observed (Choudhary et al. 2016). The number of nodules and the colonization of legumes was observed to be increased by AMF (Mahdhi et al. 2017). A positive boost from AMF collaboration with nitrogen-fixing bacteria was observed in leguminous plants (Montaño et al. 2012). In mycorrhizal plants, higher leghemoglobin content was observed (Khatabi et al. 2019; Chandra and Singh 2016). In the synthesis of green pigments from leghemoglobin, a change of color in the nodule from pink to brownish pink was used to estimate the leghemoglobin content (Shahid et al. 2019). Higher nitrogenase activity occurs in mycorrhizal plants. Nodule interaction and mycorrhiza act synergistically to influence the infection rate, mineral nourishment, and plant growth (Muleta 2017; Zarea et al. 2011), which fulfill the requirement for both N and P, and improving plant tolerance of salt stress (Zhang et al. 2016a, b; Porcel et al. 2016).

4.5.1.5 Plant Growth and Biomass

Saline stress hinders the growth of plants and biomass. The toxic effects of NaCl in disbursement of energy and unavailability of nutrients are the main reasons (Pollastri et al. 2018; Hussein et al. 2017). The fitness of the host plant is increased by mycorrhization, augmenting its growth and biomass (Garcia et al. 2014). Various research studies have observed that AMF-inoculated plants grow better than noninoculated plants under salt stress (Lone et al. 2017; Talaat and Shawky 2017; Sellitto et al. 2019). Mycorrhizal *Acacia nilotica* seedlings had higher root and shoot dry weights than nonmycorrhizal seedlings (Porcel et al. 2016; Santander et al. 2017). Fruit weight, fruit number, shoot and root dry weights, and fresh fruit yield were higher in mycorrhizal tomato plants than in nonmycorrhizal plants (Shinde and Singh 2017). During exposure to salinity stress, *Glomus intraradices* colonization of *Cucurbita pepo* plants improved plant growth, fruit quality, water status, and nutrient content (Bowles et al. 2016; Latef et al. 2016; Bona et al. 2017).

4.5.2 Arbuscular Mycorrhizal Fungi and Salinity Stress Alleviation

Salt stress alleviation by host plants' interaction with AMF results from several mechanisms (Wang et al. 2015; Hashem et al. 2018). The protection against salt stress conferred by AMF has been attributed to increased uptake of nutrients as the result of interaction (Wu et al. 2010), osmoregulator accumulation, and increases in both water-use efficiency (WUE) and the rate of photosynthesis through a combination of nutritional effects (Waraich et al. 2011; Gattward et al. 2012), biochemical effects, and physiological effects, resulting in observations of salt stress alleviation in various studies (Katschnig et al. 2013).

During salinity stress, alterations at the cellular, anatomical, and morphological levels are initiated by the plant itself to increase its capability to tolerate or avoid stress (Fahad et al. 2015a, b; Julkowska and Testerink 2015). These adaptations are not common in plants and are a dynamic consequence in several species of plants (Lämke and Bäurle 2017). To combat these stresses, in addition to inherent adaptations that can alleviate the effects of stress, several rhizospheric soil microorganisms display interactions (Singh et al. 2011). Photosynthetic efficiency, membrane integrity, and water status are physiological mechanisms that are disrupted by salinity effects (Evelin et al. 2009; Van Oosten et al. 2017). Salinity stress can be alleviated by enrichment of the physiological processes of plants by AMF, in addition to the aforementioned mechanisms (Parray et al. 2016; Bhandari and Garg 2017). Colonization, spore germination, hyphal elongation, and growth of AMF (as well as that of host plants) have been shown to be hindered by salt stress (Lenoir et al. 2016; Mostofa et al. 2018). However, various studies have observed increased colonization and sporulation (Le Fevre et al. 2016). In saline and alkaline stress in soil, plant biomass, growth, elongation of roots and shoots, productivity, transformation of nutrients (Pii et al. 2015; Yadav et al. 2019d), production of phytohormones, water status, and various physiological and biochemical properties of plants can be increased by the interaction of mycorrhizal associations (Evelin et al. 2009; Chandra and Singh 2016). To protect plants from the adverse effects of salt stress, various approaches have been recommended (Fahad et al. 2015a, b; Jorge et al. 2016).

Nutrient enrichment in colonized plants is attributable not only to nutrient uptake via the mycorrhizal pathway but also to morphological and biophysical modifications that are indirectly due to root colonization (Delian et al. 2011; Chen et al. 2016). The rate of carbon dioxide exchange, transpiration, stomatal conductance, and WUE boost nutrient absorbency with truncated mobility of P, Zn, and Cu related to changes in physiological processes associated with upgraded halotolerance in mycorrhizal plants (Elhindi et al. 2017; Augé et al. 2016). Various studies have reported that plants that are not inoculated with AMF contain less water than those inoculated with AMF (Symanczik et al. 2018; Santander et al. 2017), in which low water potential is enhanced by the hydraulic conductivity of the root (Robbins and Dinneny 2015).

A change in the morphogenetic atmosphere of the roots is associated with upgraded root conductance (Forni et al. 2017; Yadav et al. 2020d). The meristem activity of the root apexes is decreased by AMF, leading to an increase in the formation of adventitious roots, and these AMF-facilitated amendments in the morphology of roots may contribute to sustaining nutrient absorbance and water stability in the host plant under salt stress (Bahadur et al. 2019). Alterations in root systems in response to AMF- predominantly augmentations in branching and root system volume- have been reviewed (Sánchez-Bel et al. 2018; Schmidt and Gaudin 2017). In a salt-stressed ecosystem, water absorbency was augmented per unit of root length in colonized plants (Metwally and Abdelhameed 2018). Mycorrhizal colonization helps host plants to use water more efficiently and also allows maintenance of lower concentrations of carbon dioxide intercellularly, as manifested by several parameters (Yooyongwech et al. 2016). Consequently, in mycorrhizal plants, the capability for gas exchange increases (Romero-Munar et al. 2017), and fungi are considered to be bioameliorators of saline soils (Al-Amri et al. 2016).

4.5.3 Ameliorative Mechanisms Involved in Abatement of Salt Stress in Crops

Salinity stress causes severe setbacks in plant growth, nutrient uptake behavior, physiological processes, and productivity (Beckles and Thitisaksakul 2014). Most observations have shown that the role of AMF in alleviating salt stress in plants has positive outcomes (Latef et al. 2016; Chandrasekaran et al. 2019). Different mechanisms used by AMF for reduction of salt stress in crops are summarized in Figure 4.1.

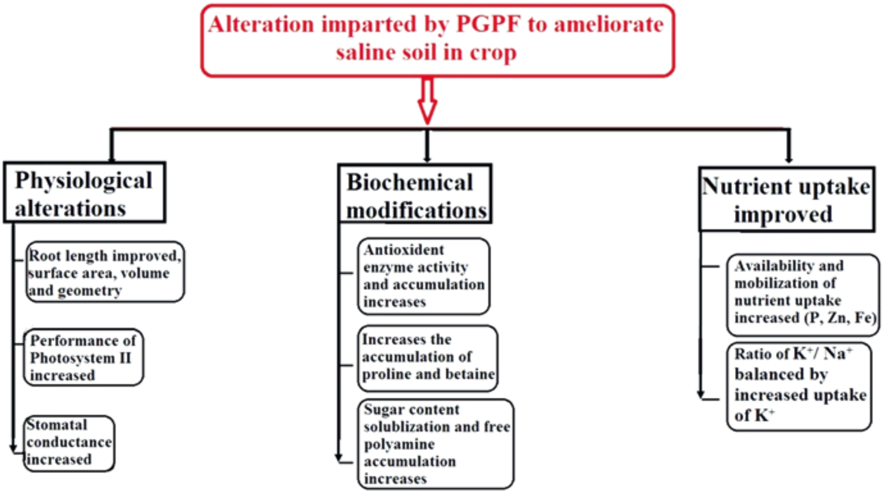

Fig. 4.1 Ameliorative mechanisms involved in alleviation of salt stress in crops

4.5.4 Improved Nutrient Uptake

In plants grown in salt-stressed ecosystems, AMF have shown positive effects on mineral nutrient composition by improving selective absorbance of mineral nutrients (Gosling et al. 2006; Pii et al. 2015). Increased transport (absorption and/or translocation) and supply of minerals and ions to the root system are regulated primarily by AMF (Jeffries et al. 2003). With increases in salt concentrations, the mycorrhizal dependency increases, and different fungal isolates have different effects in the same plant species (Tian et al. 2004). The impacts of mycorrhizal fungi on diverse mineral nutrients are described in the following subsections.

4.5.4.1 Phosphorus

Absorption of mineral nutrients, particularly phosphorus (P), is reduced significantly by soil salinity because phosphate ions are precipitated with Ca^{2+}, $Mg^{2},^{+}$ and Zn^{2+} ions and become unavailable to plants growing in saline soil (Grattan and Grieve 1999; Termaat and Munns 1986). Thus, solubilization of phosphorus to overcome the P-binding capacity of the soil is necessary for the growth of the plant and helps to alleviate salt stress (Kour et al. 2020; Reynolds and Davies 2001; Reef et al. 2010). Phosphate concentrations in plants are increased by mycorrhizal inoculation, which augments uptake. This is facilitated by the widespread hyphae of the fungus, giving mycorrhizal plants access to a greater soil volume than nonmycorrhizal plants (Casieri et al. 2013). It has been estimated that up to 80% of a plant's phosphorus requirement is fulfilled by external hyphae (Tarafdar and Marschner 1994). In saline soil with various levels of soil salinity (1.2, 4, 6.5, and 9.5 dS m^{-1}), higher P content was observed in mycorrhizal *Acacia nilotica* plants (1.2, 1.2, 0.9, and 0.6%, respectively) than in nonmycorrhizal plants (0.6, 0.5, 0.2, and 0.1%, respectively) (Giri et al. 2007; Soliman et al. 2012).

The concentration of phosphorus in *Trifolium alexandrium* plants was found to be reduced with increasing levels of salinity (Shokri and Maadi 2009). It was also determined that as soil salinity increased from 2.2 to 5 and 10 dS m^{-1}, P concentrations in shoots of nonmycorrhizal *Trifolium alexandrium* plants decreased from 0.41 to 0.36 and 0.28 mg L^{-1}, respectively, while the respective concentrations in mycorrhizal plants were 0.68, 0.62, and 0.47 mg L^{-1} (Navarro et al. 2014; Alqarawi et al. 2014). In mycorrhizal plants, higher P absorption at all salinity levels showed that AMF increased P uptake in plants under saline conditions (Frosi et al. 2017; Evelin et al. 2009). In legumes, AMF-inoculated plants increased their growth rate, antioxidant production, and nodulation when the supply of phosphate nutrition was increased (Ashrafi et al. 2014; Veselaj et al. 2018). In AMF-inoculated plants grown in saline ecosystems, phosphate uptake was increased and vacuolar membrane integrity was maintained, while compartmentalization within vacuoles and ion uptake were selectively enhanced and negative effects of Na^{+} and Cl_2 ions were reduced (Evelin et al. 2012; Zhang et al. 2014), thereby precluding those ions from interfering in growth via metabolic pathways.

4.5.4.2 Nitrogen

Uptake and reduction of NO^{3-} and protein synthesis influence the various stages of nitrogen acquisition and utilization after interference by salinity (Zahran 1999; Tischner 2000). AMF can enhance absorption of nitrogen in host plants (Verzeaux et al. 2017), as shown by greater N accumulation in shoots of mycorrhizal *Sesbania grandiflora* and *Sesbania aegyptiaca* plants than in nonmycorrhizal control plants (Giri and Mukerji 2004) (Yadav et al. 2020b, c). Inorganic nitrogen is absorbed from the soil in the form of nitrate by extraradical mycelia and assimilated by nitrate reductase sites on arbuscule cells (Toussaint et al. 2004), and arginine formation occurs via the glutamine synthetase–glutamine oxoglutarate aminotransferase (GS-GOGAT) cycle. In primary nitrogen fixation in extraradical mycelia, these processes are consistent with increased expression of enzymes involved in arginine catabolism (Bücking et al. 2012; Azcón-Aguilar and Barea 2015). Metabolism of nitrogen is changed by alterations in enzyme processes when absorption of nitrogen is increased in plants with AMF (Burns et al. 2013; Van Der Heijden et al. 2008). The toxic effects of Na^+ ions are decreased with upgraded nitrogen nutrition and this indirectly helps to maintain chlorophyll content (Friedman 2002). Plants absorb nitrogen in the form of nitrate (NO_3^{2-}) and ammonium (NH_4^+) ions, strongly affecting accumulation of Na^+ ions (Giri and Mukerji, 2004; Kaushal and Wani 2016). However, nitrogen uptake mechanisms in salt-stressed environments have not yet been clearly described (Dodd and Pérez-Alfocea 2012).

4.5.4.3 The K^+:Na^+ Ratio

Plants have a tendency to take up more Na^+ ions when the concentration of NaCl is increased in soil and the absorbency of K^+ ions is decreased. K^+ ions are essential for various cellular functions and compete with Na^+ ions (Rejili et al. 2007; Khan and Panda 2008). In plant metabolism, K^+ activates a range of enzymes and plays a dynamic role in protein synthesis and the movement of stomata (Martinoia et al. 2006). In protein synthesis, K^+ ions bind tRNA to ribosomes in high concentrations (Weinger et al. 2004). A high Na^+:K^+ ion ratio caused by salinity disrupts the ionic balance in the cytoplasm, disturbing various metabolic pathways (Tuteja 2007; Tester and Davenport 2003). The effect of salinity on K^+ and Na^+ nutrition in plants with AMF can be reversed through mycorrhizal colonization, improving the uptake of K^+ ions in saline ecosystems (Tester and Davenport 2003; Estrada et al. 2013a, b, c) while preventing Na^+ translocation to shoot tissues. Synthesis and storage of polyphosphate influence uptake of Na^+ ions and other cations (Giri and Mukerji 2004) by amending expression and movement of K^+ and Na^+ transporters and of H^+ pumps that produce the driving force for transportation of ions (Matsui and

Homareda 1982). The transfer of Na^+ out of the cytoplasm into either vacuoles or the apoplasm is catalyzed through Na^+/H^+ antiporters (Bassil et al. 2012; Ouziad et al. 2006). Interruption of various K-mediated enzymatic developments and protein synthesis is prevented by a higher K^+:Na^+ ion ratio. The ionic balance of the cytoplasm or Na^+ efflux from plants influences the high K^+:Na^+ ion ratio (Maathuis and Amtmann 1999; Wishnia et al. 1975). In mycorrhizal plants, in comparison with nonmycorrhizal plants, lower Na^+ ion concentrations are also attributable to the dilution effect due to growth enhancement (Garg and Manchanda 2009). In mycorrhizal plants, Na^+ concentrations are increased with increasing salinity up to a certain level but then successively diminish at higher concentrations of salinity (Chartzoulakis and Klapaki 2000). These observations suggest that AMF promote a buffering effect on uptake of Na^+ ions when the Na^+ content is within an acceptable limit (Onofre et al. 2015).

This also indicates an opportunity for a regulatory mechanism to function in the plant to contain Na^+ ions. However, the uptake of P by mycorrhizal plants is diminished when salt concentrations are too high (9.5 dS m^{-1}), because of the toxic effects of Na^+ ions on fungal growth (Wang et al. 2019), suggesting that mycorrhizal responses are only influential up to a certain level of salinity (4.7 dS m^{-1}) (Elhindi et al. 2017).

4.5.4.4 Chloride Ions

In saline ecosystems, root cells absorb Cl_2 from the soil solution through anion channels and also through H^+/Cl_2 symporters (White and Broadley 2001). Chloride ions pass through the root via a simplistic pathway and are released from cells within the stele through specific anion channels to reach the xylem and then the shoots (Clarkson 1993). Accumulation of chloride ions greatly increases at high salt concentrations but remains constant in the root (Schachtman et al. 1989; Chen et al. 2002). High chloride ion concentrations can be toxic to crop plants and may restrict agriculture in saline regions where concentrations are higher (Chartzoulakis 2005). AMF can tackle this problem by reducing uptake of Cl_2 ions (Evelin et al. 2009). In vacuolar membranes, Cl_2 ions can be clustered in a way that inhibits them from interfering with metabolic pathways in the plant. However, some reports have indicated that Cl_2 accumulation can actually be increased as a result of mycorrhizal colonization. This may be due to the carbon drain imposed by mycorrhizal hyphae on plants, which enhances translocation of highly mobile anions such as Cl_2 from the soil (Elhindi et al. 2017; Evelin et al. 2009).

4.5.4.5 Calcium

To transduce signals during salt stress, concentrations of Ca^{2+} are increased, and it acts as a second messenger (Kader and Lindberg 2010). Mycorrhization strongly affects Ca^{2+} in the plant, as shown in various studies. In mycorrhizal lettuce, Ca^{2+}

uptake was increased (Ruiz-Lozano and Azcón 1997; Hajiboland et al. 2010), and nonmycorrhizal banana plants were shown to have lower Ca^{2+} concentrations than mycorrhizal plants (Azcón et al. 2003). Furthermore, it was reported that colonization and sporulation of AMF were promoted by higher concentrations of Ca^{2+} (Doubková et al. 2013). However, in contrast to the above observations, the concentration of Ca^{2+} ions was found to remain unchanged in shoot tissues of mycorrhizal and nonmycorrhizal *Acacia auriculiformis* plants (Kaya et al. 2009). This suggests that AMF may not be as important to movement of nutrients to plant roots by mass flow as it is to nutrient movement by diffusion (Jakobsen et al. 2003).

4.5.4.6 Magnesium

Chlorophyll biosynthesis is reduced by saline stress, which also inhibits light harvesting and causes photosynthesis to diminish (Singh et al. 2018). Mycorrhizae can support higher chlorophyll concentrations by improving magnesium ion concentrations (Giri and Mukerji 2004). It has been reported that salt interferes with chlorophyll synthesis less in mycorrhizal plants than in nonmycorrhizal plants (Giri and Mukerji, 2004; Feng et al. 2002). The efficiency of photosynthesis and plant growth increase after sufficient absorption of Mg^{2+} ions, which also increases concentrations of chlorophyll (Gattward et al. 2012).

4.5.4.7 Other Micronutrients

Plants' access to micronutrients (Zn, Cu, and Fe) is profoundly affected by salinity (Viets Jr 1962). The solubility and mobility of micronutrients such as Cu and Fe is reduced in saline environments, where a depletion zone is created all around the root; therefore, the plant's absorption of micronutrients is reduced (Kaur et al. 2020; Rastegari et al. 2020b; Welch and Shuman 1995). However, higher concentrations of these micronutrients are found in plants inoculated with rhizospheric fungi than in noninoculated plants (Richardson et al. 2009; Wu et al. 2013). This may be attributable to (1) a widespread root–hyphal system that shortens the path of nutrients entry into the plant; (2) the mycelium of fungi acting as a substrate for nutrients to bind to; (3) changes in the rhizosphere after introduction of AMF, influencing the solubility of nutrients and their ability to be absorbed; (4) an increase in the sink size of Cu and Zn due to higher shoot P concentrations, successively instigating uptake of nutrients and their translocation to the shoots (Maathuis et al. 2011); or (5) upregulation of expression of transporter genes for these nutrients. As an example, a plasma membrane Zn transporter gene, *MtZIP2*, is upregulated upon colonization by AMF (Cavagnaro 2008). The ionic balance maintained by rhizospheric fungi is now being interpreted at the molecular level. However, much remains to be elucidated regarding AMF-influenced increases in Ca^{2+}:Na^{+} and Ca^{2+}:Mg^{2+} ratios, as well as uptake of micronutrients (Elhindi et al. 2017; Chandra and Enespa 2019b; Chandra and Enespa 2020).

4.5.5 Morphological and Physiological Alterations

The potential of soil and water becomes more negative in dry soil; to maintain a favorable gradient for water flow from the soil into the roots, the water potential must be decreased by the plants (Ruiz-Lozano 2003). A plethora of mechanisms have been developed by plants to achieve such an effect, the most essential being osmotic modification or osmoregulation, requiring a reduction in the plant osmotic potential, which is mitigated by active accumulation of organic ions or solutes (Yeo 1983). In plants exposed to saline stress, a number of nitrogen-containing compounds accumulate. Amino acids, amide, and proteins are the most common, along with quaternary ammonium compounds (betaines) and polyamines (Mansour 2000). When plants are not under salt stress, these compounds are generally present in low concentrations (Glick 2004). In saline ecosystems, the specific nitrogen-containing compounds that accumulate vary between plant species (Rare 1990).

4.5.5.1 Chlorophyll Content

The chlorophyll content is decreased by increasing salinity suppressing specific enzymes that are responsible for synthesis of photosynthetic pigments (Parida and Das 2005). Chlorophyll biosynthesis also reduces chlorophyll concentrations in leaves after a reduction in the uptake of minerals that are required for the process (Pal and Laloraya 1972). In the leaves of mycorrhizal plants in saline ecosystems, higher chlorophyll content has been observed by various authors (Beltrano et al. 2013). This suggests that salt interferes with synthesis of chlorophyll less in mycorrhizal plants than in nonmycorrhizal plants (Zhu et al. 2012). The antagonistic effect of Na^+ on Mg^{2+} uptake is well controlled and suppressed in mycorrhizal plants (Allen and Shachar-Hill 2009). Under salt stress, inoculated plants reach levels of photosynthetic capacity (estimated by chlorophyll content) that are even superior to those seen with relative permeability (Shabala et al. 2012).

4.5.5.2 Water Status

In the rhizospheric region, high concentrations of salt cause physiological drought for plants. Salts put water out of action and make it unobtainable by plants (Carillo et al. 2011). In *Malus hupehensis*, mycorrhizal inoculation resulted in relatively higher leaf turgidity being maintained by seedlings, with lower leaf osmotic potential, in comparison with nonmycorrhizal plants in salt stress conditions (Yang et al. 2014a, b). Higher relative water content was observed in mycorrhizal *Robinia pseudoacacia* plants than in nonmycorrhizal plants under salt stress (Stratu et al. 2016). The improved hydraulic conductivity in mycorrhizal plants was attributed to AMF-induced transformation of root morphology and the capability of mycorrhizal plants to source macroelements well beyond the depletion zone, facilitated by the extensive extrametrical mycelium of AMF (Bitterlich et al. 2018). Additionally, more compatible solutes were accumulated by mycorrhizal plants to adjust the osmotic potential and enable efficient water usage by the host plants (Juniper and Abbott 1993). In salt-stressed mycorrhizal plants, improved water status may be due to AMF-regulated expression of aquaporin genes present in the leaves and roots (Rapparini and Peñuelas 2014).

However, each aquaporin gene in the roots of mycorrhizal plants may react differently to salt stress (Bárzana et al. 2014). For instance, the *LePIP1* gene was downregulated with AMF colonization in *Lycopersicon esculentum*, while the same gene was upregulated in *Lactuca sativa* (Ouziad et al. 2006; Jahromi et al. 2008). The expression profiles of aquaporin genes (*RpPIP1;1*, *RpPIP1;3*, *RpPIP2;1*, *RpTIP1;1*, *RpTIP1;3*, and *RpTIP2;1*) were described in the leaves and roots of mycorrhizal and nonmycorrhizal *Robinia pseudoacacia* plants exposed to saline stress (Chen et al. 2017; Li et al. 2014). The AMF symbiosis effect on transcription of aquaporin genes varies between different plant species, the type of plant tissue in which they are expressed, and the level of salinity (Ruiz-Lozano et al. 2012). In addition, the potential of various aquaporin genes to influence transport of water and other solutes may fluctuate and may be contingent on their location in the cell (Tyerman et al. 2002).

4.5.5.3 Osmoregulation

Lowering the turgor pressure in plant cells under salinity stress causes cellular dehydration. Plants use osmoregulation as a mechanism to tolerate salt stress to counteract this effect (Shabala and Lew 2002). The water potential of the soil decreases after formation of Na^+ and Cl^- in the soil (Chao-Yin et al. 2011). The plants must respond to the lower water potential to sustain a favorable gradient for water flow from the soil into the roots and to prevent dehydration of cells in this situation (Ruiz-Lozano et al. 2006, 2012). Proline, betaine, polyamines, sugars, organic acids, amino acids, and osmolytes such as trehalose start to accumulate in the plants (Mansour 2000). Small organic solutes are osmolytes (i.e., nontoxic and water soluble) at high concentrations and are known as compatible solutes (Gibon et al. 1997; Low 1985). These osmolytes contribute to osmotic adjustment (Augé et al. 2014). Furthermore, they are involved in ROS quenching and in maintaining membrane integrity, the enzyme balance, and the protein balance; thus, they are also known as osmoprotectants (Xiao et al. 2008).

4.5.5.4 Relative Permeability

Mycorrhizal fungal inoculation of host plants empowers the plants to maintain higher concentrations of electrolytes than nonmycorrhizal plants through enhanced membrane integrity and immovability (Franken and Bui 2018). Consequently, the electrical conductivity of mycorrhizal roots has been shown to be greater than that of nonmycorrhizal roots (Sands et al. 1982). The roots of *Cajanus cajan* with fungi displayed higher relative permeability than those of nonmycorrhizal plants at various levels of soil salinity (ECe 4, 6, and 8 dS m^{-1}). The leakage of electrolyte in leaves of *Capsicum annum* treated with 50 mM and 100 mM concentrations of NaCl were 31.66 and 42.45 mM. respectively, while AMF-inoculated plants had relatively lower electrolyte leakage values of 26.87 and 30.98 mM respectively (Parihar and Rakshit 2016). This suggests that the mycorrhizal plants had considerably lower root plasma membrane electrolyte permeability than the nonmycorrhizal plants. The membrane stability increase has been attributed to mycorrhiza-mediated increased uptake of phosphorus and increased antioxidant production (Chang et al. 2018; Evelin and Kapoor 2014).

4.5.6 Biochemical Alterations

Plants must decrease their water potential to maintain a favorable gradient for water flow from the soil into the roots when the soil dries and the water potential reduces (Cook and Papendick 1972; Sharp and Davies 1985). Osmotic adjustment is promoted by the plants through active accumulations of organic ions or solutes, which mitigate the osmotic potential and counteract adverse effects (Eisa et al. 2012; Blum 2017). In plants grown in saline ecosystems, compatible osmolytes are commonly found—for example, nitrogen-holding complexes such as amino acids, amides, imino acids, ectoine (1,4,5,6-tetrahydro-2-methyl-4-carboxylpyrimidine), proteins, quaternary ammonium complexes, low molecular weight sugars, organic acids, and polyols (Ciulla et al. 1997; Slama et al. 2015). Various biochemical changes are discussed briefly here. In plants' reactions to salt stress, several compounds that accumulate are nitrogen-containing ones such as quaternary ammonium compounds (betaines) and polyamines, and also amino acids, amides, and proteins (Rhodes and Hanson 1993). These compounds are generally present in low concentrations when the plant is not under salt stress (Edreva et al. 2008; Sudha and Ravishankar 2002). The compounds that accumulate in saline ecosystems vary from species to species (Al Hassan et al. 2016) and are present in very low concentrations in the absence of salt stress (Wu et al. 1988). To maintain turgor and turgor-dependent processes such as photosynthesis and stomatal opening, growth and cellular expansion occur in cells by osmoregulation (Daie and Patrick 1988; Hsiao 1973).

4.5.6.1 Proline

Accumulation of the amino acid proline, induced by abiotic salinity stress, is the most frequently reported alteration in plants (de Carvalho et al. 2013). Proline is a nontoxic and defensive osmolyte, which maintains an osmotic balance under a lower water potential in saline ecosystems and is accumulated by various plants under saline conditions (Hayat et al. 2012; Hare et al. 1998). During salt stress, it acts as a pool of energy and nitrogen for utilization (Mansour 2000). When a plant is inoculated with AMF, proline accumulation has been found to increase. *Vigna radiata* and *Glycine max* (L.) mycorrhizal plants were shown to have higher proline content than nonmycorrhizal plants (Nadeem et al. 2014; Kim et al. 2012), and higher concentrations of proline were found in the roots and shoots of the plants. The osmotic balance between water-absorbing root cells and external media is maintained by the roots, which are the primary sites of water absorption (Bernstein and Hayward 1958; Sharifi et al. 2007). In contrast, more proline was found to accumulate in nonmycorrhizal *Vicia faba* plants than in mycorrhizal plants at various salinity levels (0–6 dS m^{-1}). In less-salinity-tolerant plant species, proline accumulation may be a symptom of stress and its involvement in the adjustment of osmotic may be insignificant and associated with potassium ions (Chun and Chandrasekaran 2018). Accumulation of proline in response to salinity may not necessarily be due to mycorrhizal colonization (Porcel et al. 2012). In response to salinity, high levels of proline were shown to accumulate in *Lotus glaber* (Sanchez et al. 2005), and AMF influenced this proline accumulation. To determine the salt tolerance mechanisms operating in different plant systems, better explanations are needed (Andrade et al. 2009).

4.5.6.2 Betaines

Under salinity stress, betaine accumulation is a common occurrence (Hossain and Fujita 2010). Betaines are N-methylated derivatives of amino acids, and quaternary ammonium compounds are metabolized infrequently after their formation (D’Agostino and Mabury 2013; Annunziata et al. 2019). They are also used as an indicator of salt stress (Juan et al. 2005; Tramontano and Jouve 1997). Betaines are simple nontoxic cellular osmolytes, improve the construction and actions of enzymes and complexes of proteins, and also maintain membrane integrity against the destructive effects of excess salt (Burg and Ferraris 2008; Papageorgiou and Murata 1995). When a plant is colonized by fungi, the accumulation of betaines is found to increase under salinity stress (Hameed et al. 2014). At higher salinity levels, the glycine betaine content of fungi-associated plants was found to be about twice that of plants not associated with fungi (Papageorgiou and Murata 1995; Kumar et al. 2014).

4.5.6.3 Polyamines

Free polyamines are small organic cations, which are essential for growth of eukaryotic cells. Putrescine (Put), spermidine (Spd), and spermine (Spm) are the three main polyamines in plants (Galston and Sawhney 1990). As a result of sequential accumulation of amino propyl groups, spermidine and spermine are synthesized from putrescine (Pál et al. 2018; Moschou et al. 2008). Putrescine is manufactured indirectly via decarboxylation of arginine and directly from ornithine decarboxylase

(Panagiotidis et al. 1987). A significant role is played by these cations in plant responses to a wide collection of ecological stressors such as salt stress (Urano et al. 2004), high osmolarity (Rajam et al. 1998), and antioxidative stress. Under salt stress conditions, they have been suggested to regulate root development (Sannazzaro et al. 2007) and pools of free polyamine have been observed to be reduced (Talaat and Shawky 2013). However, host plant inoculation with rhizofungi increases concentrations of free polyamines (Barea et al. 2005). In *Lotus glaber* plants colonized by *Glomus intraradices*, the total free polyamine pools were increased, as observed by Sannazzaro et al. (2007). Individual polyamines determine variations in response to salinity and mycorrhization, contingent on the genotype of the plant and the organ (root/shoot) being considered. Salt-tolerant genotypes of mycorrhizal *Lotus glaber* plants displayed higher levels of root spermine than nonmycorrhizal plants (Abdel-Fattah et al. 2016). Under salt stress, salt-sensitive *Lotus glaber* mycorrhizal plants exhibited higher root spermine, lower shoot and root putrescine, and lower spermidine levels than nonmycorrhizal plants (Talaat and Shawky 2015). Polyamine pool modulations may be one of the apparatuses used by AMF to increase plants' adaptation to saline soils (Acosta-Motos et al. 2017; Augé et al. 2014).

4.5.6.4 Carbohydrates

A significant plant protection mechanism formed against the salt stress using to addition of soluble sugars counter to that stress by the osmotic potential of plants. Using the addition of soluble sugars a significant plant protection mechanism formed by the osmotic potential of plants against salt stress (Ashraf and Harris 2004). With increased concentrations of NaCl, the soluble sugar content in *Phragmites australis* was found to be expressively increased (Li et al. 2019; Vilela and Barbosa 2019). *Phragmites australis* plants inoculated with *Glomus fasciculatum* had higher levels of soluble sugars than nonmycorrhizal plants (Nasim 2010). Sugar concentrations were increased in soybean roots inhabited by *Glomus intraradices* (St-Arnaud et al. 1995). The presence of mycorrhizae and sugar content were positively correlated as a result of the sink effect of the fungus obtaining sugars from the shoot tissues (Abbaspour et al. 2012; Ruiz-Lozano et al. 2012). The presence of carbon compounds in the root system of mycorrhizal host plants habitually leads to increased rates of photosynthesis involvement in the development process (Fitter 2002). As a result of hydrolysis of starch to sugars in seedlings immunized with mycorrhizae, sugar accumulation was found to be increased (Conrath 2009). Correlations between sugar accumulation and P concentration were observed in host plants grown in saline conditions (Hammer et al. 2011; Flowers et al. 2010).

Soluble sugar concentrations were found to be higher in the roots of mycorrhizal maize plants than in those of nonmycorrhizal plants in spite of similar P concentrations (Feng et al. 2002). It was suggested that the higher soluble sugar concentrations in mycorrhizal roots were due to AMF settlement and not to an enhancement in the P status of the plants (Délano-Frier and Tejeda-Sartorius 2008; Mohammadi et al. 2011). Trehalose carbohydrate is a nonreducing disaccharide stored in AMF and plays a significant role as an abiotic stress protectant, stabilizing dehydrated enzymes and membranes, and protecting biological structures from drying damage (Redillas et al. 2012; Moussaid et al. 2015). It is also present in spores and in the extraradical mycelium of AMF (Hajiboland 2013). Trehalose is a rare sugar involved in AMF settlement and helps to defend plant roots against saline stress in higher vascular plants (Iordachescu and Imai 2011; Kosar et al. 2019). It is believed to possibly play a role in defending plants against abiotic stresses, as shown by the effect of salinity stress on trehalose content and metabolism in the extraradical hyphae of *Glomus intraradices* (Kaushal 2019). After treatment with 0.5 M NaCl in *Glomus intraradices*, no alteration in trehalose content was observed (Bencherif et al. 2019a, b; Liu et al. 2014). Trehalose-6-phosphate phosphatase activations of moderate transient and neutral trehalase actions not associated with any transcriptional changes have been detected (Zhou et al. 2014).

In extraradical hyphae and mycorrhizal roots, trehalose accumulation is of interest and may influence the response of AMF to stress environments, with trehalose being used as a stress defense agent (Kravić et al. 2013; Maralian et al. 2010). A substantial role in alteration of hyperosmotic conditions in symbiotic bacteria is played by trehalose metabolism (Reina-Bueno et al. 2012). This molecule plays a part in initiating tolerance of salt stress (Ghosh et al. 2011). Consequently, the potential of trehalose in protecting cells from salt stress needs to be determined (Mostofa et al. 2015). A reduction in carbohydrate concentrations with proliferation in the percentage of root colonization has been determined (Zangaro et al. 2012). In the responses to salinity of soybean plants colonized by *Glomus etunicatum*, no role of soluble carbohydrates was detected (Dodd and Pérez-Alfocea 2012).

4.5.6.5 Antioxidants

Singlet oxygen, superoxide anions, hydrogen peroxide, and hydroxyl radicals are activated oxygen species and expected by-products of the interface between oxygen and electrons trickling from electron transport chains during normal aerobic metabolism in chloroplasts and mitochondria (Phaniendra et al. 2015). Proteins, lipids, and DNA react with all activated oxygen species and when defensive mechanisms are deficient, cell structure and function can be damaged (Birben et al. 2012). Plants released antioxidants and enzymes from oxidative destruction which used as defense mechanisms. Thus, defensive mechanisms are found in plants outflow from oxidative destruction connecting antioxidant fragments and enzymes (Grassi et al. 2010). Correlations between antioxidant capability and NaCl tolerance have been established in various plant species (Arbona et al. 2013; Ashraf et al. 2012). Maximum antioxidant concentrations providing plants with more resistance to oxidative impairment have been determined (de Bernonville et al. 2010). Superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APOX), glutathione reductase (Wang 2011), dehydroascorbate, monodehydroascorbate reductase (Yin et al. 2010; Eltelib et al. 2011), guaiacol peroxidase, oxidized glutathione (Bela et al.

2015), glutathione peroxidase, and enzymes involved in the ascorbate–glutathione cycle are considered to be antioxidants (Caverzan et al. 2012; Joseph et al. 2011).

Activated oxygen species such as carotenoids, glutathione, tocopherols, and ascorbic acid are scavenged by nonenzymatic compounds (Carocho and Ferreira 2013). AMF symbiosis helps plants to alleviate salt stress by enhancing the activities of antioxidant enzymes, as shown by various observations (Estrada et al. 2013a, b, c; Ruiz-Lozano et al. 2012). In mycorrhizal plants, these advanced antioxidant enzymes indomitable comparison to the non-mycorrhizal plants observed in various studies (Zhu et al. 2010). Higher antioxidant activities of SOD, peroxidase, and APOX have been observed in mycorrhizal soybean plants than in nonmycorrhizal plants (Gong et al. 2015). SOD helps to detoxify superoxide into hydrogen peroxide (Rodrigues and Gomes 2010). CAT and peroxidase detoxify hydrogen peroxide (Ramos et al. 2014). Detoxification of hydrogen peroxide produced in the chloroplasts of stressed host plants by APOX has also been reported (Liang et al. 2013). Increased glutathione reductase activity may assist nicotinamide adenine dinucleotide phosphate ($NADP^+$) to receive electrons resulting from photosynthetic electron transport, thereby attracting electrons away from oxygen and reducing the production of O_2 (Jing et al. 2011; Yamamori et al. 2012).

4.5.6.6 Hormonal Regulation

Phytohormones (also known as growth regulators) are known to regulate plant growth under both ambient and stress conditions (Fahad et al. 2015a, b). They are derived via biosynthetic pathways in plants and can act at the site of production or away from it. Abscisic acid (ABA), auxins, brassinosteroids (BRs), cytokinins (CKs), gibberellins (GAs), jasmonic acid (JA), salicylic acid (SA), strigolactones (SLs), nitric oxide (NO), and triazoles are phytohormones known to play substantial roles in communicating salt stress tolerance in plants (Hilbert et al. 2012). Hormonal interactions between them modify biological and physiological processes, translating into mediation of growth, development, nutrient allocation, and source/sink transitions in response to environmental stimuli (Lüttge 2013). Furthermore, ABA, auxins, JA, and SA are known to act as signaling molecules in AMF symbiosis (Miransari et al. 2014; Martínez-Medina et al. 2011). Consequently, it is assumed that these hormones reduce soil salinity and play significant roles in improving plant growth (Paul and Lade 2014; Yaish et al. 2015). A newly recognized class of phytohormones is strigolactones, which are involved in various characteristics of plant development such as root growth coordination and shape, access to soil nutrients, secondary branch suppression in shoots, influence on internode length in cross talk with auxin, leaf senescence regulation, and induction of AMF symbiosis (Koltai and Kapulnik 2011).

H_2O_2 accumulation depends on reduced $NADP^+$ (NADPH) oxidase activities, which play an important role in ABA signaling (Ishibashi et al. 2010). In *Solanum lycopersicum* and *Cicer arietinum*, exogenous applications of GA and SA, respectively, have been shown to boost salinity tolerance (Hasanuzzaman et al. 2013).

Greater nutrient access and manifold increases in GA concentrations in mycorrhizal *Solanum lycopersicum* indicated that GA can stimulate salinity tolerance as a result of foliar spraying of gibberellic acid (GA3) (Maggio et al. 2010; Peleg and Blumwald 2011). AMF colonization was shown to have a positive influence on endogenous concentrations of GA (Kiers et al. 2010; Jung et al. 2012). The phytohormone JA, which belongs to the octadecanoid family, is involved in plant responses to both biotic and abiotic stresses (Santino et al. 2013; Avanci et al. 2010).

4.5.7 Molecular and Ultrastructural Changes

In the root cells of *Sorghum* plants, salinity stress cause increases in membrane surfaces and vesicle quantities (Beltrano et al. 2013; Grover et al. 2011). In response to salt stress in the shoot apical meristems of canola, increases in plasmodesmata numbers, cytoplasm vacuolization, and thickening of cell walls have been observed (Rewald et al. 2013). In *Arabidopsis thaliana*, as a result of dissipation of mitochondrial membranes, potential disruptions in thylakoid and thylakoid membranes and induction of ovule abortion have been observed (Waraich et al. 2012; Cossani and Reynolds 2012). Consequently, ROS accumulate in the cells of gametophytes, gradually leading to programmed cell death (Xie et al. 2014; Wang et al. 2013). Aborting gametophytes are produced from the concentric rings of endoplasmic reticulum, surrounding chloroplasts, mitochondria, microbodies, and cytoplasm due to the accumulation of ROS (Perry et al. 2011). The cytoplasmic content and organelles were invaginated into the vacuole. Antioxidant activities are increased in plants by inoculation with AMF (Yang et al. 2014a, b; Hoeksema et al. 2010), and AMF can be applied to neutralize the actions of ROS and alleviate salt stress (Estrada et al. 2013a, b, c; Filippou et al. 2013).

Expression of a few proteins such as Na^+/H^+ antiporters, D1-pyrroline-5-carboxylate synthetase (LsP5CS), late embryogenesis abundant protein (LsLea), and ABA (Lsnced) has been the focus of various molecular inventions (Vaseva et al. 2010; Shu et al. 2013). Aquaporins are major intrinsic proteins (MIPs), belonging to the family of transmembrane channels, which permit the passage of water and a few other compounds (but not H^+ and other ions) via selective membranes (Hachez et al. 2014) controlled by tonoplast aquaporins (TIPs) and plasmalemma aquaporins (PIPs) (Obroucheva 2013). Abiotic factors such as salt stress influence the expression of aquaporins, most probably via the phytohormones ABA and GA (Popko et al. 2010; Skirycz and Inzé 2010). In salt-stressed AMF plants, analysis of the expression of aquaporin genes revealed antagonistic consequences. AMF expressively reduced messenger RNA (mRNA) transcription of *LePIP1* and *LeTIP* but not *LePIP2* in salt-stressed roots of untreated control plants (Li et al. 2013; Gu et al. 2010).

4.6 Conclusion and Future Prospects

Salinity stress in soil causes adverse effects on growth and physiology at the molecular level. However, plant growth–promoting fungi (PGPF) and arbuscular mycorrhizal fungi associated with the rhizospheric region of the plant effectively improve plant growth and crop productivity through accumulation of different solutes and greater uptake of water and nutrients in saline ecosystems. Ongoing improvements in molecular tools are improving our comprehension of cellular procedures and signaling mechanisms associated with development and resistance due to PGPF–plant interactions. The benefits of high-performing PGPF can be obtained by application of innovative biotechnological procedures to form genetically modified strains with amended features, such as functional articulation of PGPF genes in plants to yield beneficial results. Diverse rhizofungi such as *Trichoderma viride*, *Trichoderma harzianum*, *Trichoderma longibrachiatum* T6, *Claroideoglomus etunicatum*, *Rhizophagus intraradices*, *Aspergillus aculeatus*, *Glomus fasciculatum*, *Glomus mosseae*, *Piriformospora indica*, *Claroideoglomus etunicatum*, *Rhizophagus intraradices*, *Funneliformis mosseae*, and *Rhizophagus intraradices* increase the activity of soil enzymes, which helps to enhance plant growth hormones. These activities improve plant growth and productivity with the help of osmoregulation in saline soil.

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Chapter 5
Fungal Secondary Metabolites and Bioactive Compounds for Plant Defense

Shomaila Sikandar, Asfand Yar Saqib, and Imran Afzal

Contents

5.1 Introduction

The relation between the variety of plants, ecosystem, ecological stability, and overall productivity is of utmost importance to nature organization. Pathogens causing disease in plants affect such a relationship by influencing plant defense, fitness, hindering plant growth, and sustainability greatly impacting plant ecosystem and population (Creissen et al. 2016). Over 100 different diseases affect crop plants. While, only a single pathogen under given circumstances multiplies enough to become a disease causing agent. These crop plant diseases falls among the biggest hurdles limiting the production of large and adequate quantities of food (Savary et al. 2012). It is estimated that various plant diseases at different planting stages and plant pests are responsible for half of the total agricultural production loss in the world (Khan 2008).

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Plant disease can be defined as “a physiological disorder or structural abnormality that is harmful to the plant or to any of its parts or products that reduces the economic value” (Stalkman and Harrar 1957). Phytopathogenic agents are responsible for significant loss of crops resulting from plant diseases. In order to sustain the standard and diversity of feed, food and fiber all over the globe, plant diseases need to be eradicated and controlled. For this purpose, various approaches for plant disease control have been proposed. Apart from efficient horticulture and agronomical applications, often producers are heavily reliant upon chemically synthesized pesticides and fertilizers, while, the environmental pollution and fluctuations resulting from these synthetic pesticides, fertilizers, and agrochemicals have caused significant changes over their use in agriculture, plant disease control and prevention (Kaur et al. 2020; Kour et al. 2020; Singh and Yadav 2020). Biological control of fungal plant pathogens is of great interest and in recent times, more emphasis is provided as potential alternatives to the chemical use (Rastegari et al. 2020b; Yadav et al. 2020b, e; Vinale et al. 2014). Synthetically produced pesticides are expensive, pollutants of environment and hazardous to humans and animals as well. Moreover, repeated exposure of such chemicals enhances the stride of resistant pathogenic strains. Pest management mediated by microbes is among the most efficient and inexpensive biological control applications in agriculture (Rana et al. 2019; Verma et al. 2017; Yadav 2019).

Outcome of such an approach is largely based upon the choice of microbial strain. The benefits for the plant associated involve: (1) plant growth promotion; (2) establishment of microbial community within the rhizosphere involving antagonistic activity; (3) pathogen elimination; (4) plant health benefits; (5) greater uptake and availability of nutrients, and (6) improved biotic and abiotic stress resistance to host (Harman et al. 2004; Vinale et al. 2008; Yadav et al. 2017). Advantageous microbes have been known to have various mode of action such as: pathogen inhibition or parasitism using antibiotics sometimes in conjugation with cell wall decomposing extracellular enzymes; contention for nutrients (i.e., carbon, iron or nitrogen) in sites of colonization; onset of plant developmental and resistance phenomenon (Kour et al. 2020; Howell 2003; Whipps 2001). Microbial species, particularly of fungi, secrete diverse range of secondary metabolites involving a variety of industrially and economically important compounds (Herbert 1989; Yadav et al. 2019b). Chemically, secondary metabolites are naturally different compounds characterized by low molecular weight usually, less than 3 kDa.

Secondary metabolites are assigned to each specific genera, strain or species being mainly synthesized by plants and microorganisms (Rastegari et al. 2019b; Yadav et al. 2019a). Their biosynthesis involves primary metabolites in specific pathways such as mevalonate or polyketide pathways driven through amino acids or Acetyl Coenzyme A along with a few clustered genes. Some global regulators appear to be the gene expression inducers of such genes (Herbert 1989; Rastegari et al. 2019a). Secondary metabolites exhibit several biological functions in relevance to survival of organisms (Yadav et al. 2020a). For instance, metal transportation, symbiotic association, and contention with both micro and macroorganisms. Secondary metabolite synthesis in fungi is often held parallel to distinct phases of structural differentiation along with active growth phase (Keller et al. 2005). Their range of distribution varies from among a few related species to individual strains emphasizing diverse activities of each metabolite in contrast to a universal activity (Keller et al. 2005).

Secondary metabolites of fungal origin display various biological features while offering essential regulatory interactions among organisms (Hanson 2003; Yadav et al. 2019b). For example, mycotoxins (toxic secondary metabolite produced by fungi colonizing crops causing disease and death in animals and humans), phytotoxins (secondary metabolite that invades the plant defense), antibiotics (compounds possessing inhibitory and antimicrobial activities), and pigments (colored compounds involving antioxidant features) (Chiang et al. 2009; Vinale et al. 2014; Yadav et al. 2019c) (Fig. 5.1). However, interestingly, a few secondary metabolites of fungal origin possess the ability to alter plant growth and metabolism while others act on specialized fungal phenomenon including hyphal elongation, growth, and sporulation (Keller et al. 2005). Soil borne fungal species thrive in extremely competent environments. Virtually every fungal community is known to have antagonistic relationship among natural competing fungal species (Ghisalberti 2002). Fungi known to be invasive function indirectly or directly towards fungal phytopathogens. Indirectly by facing contention for physical space and nutrient availability, altering

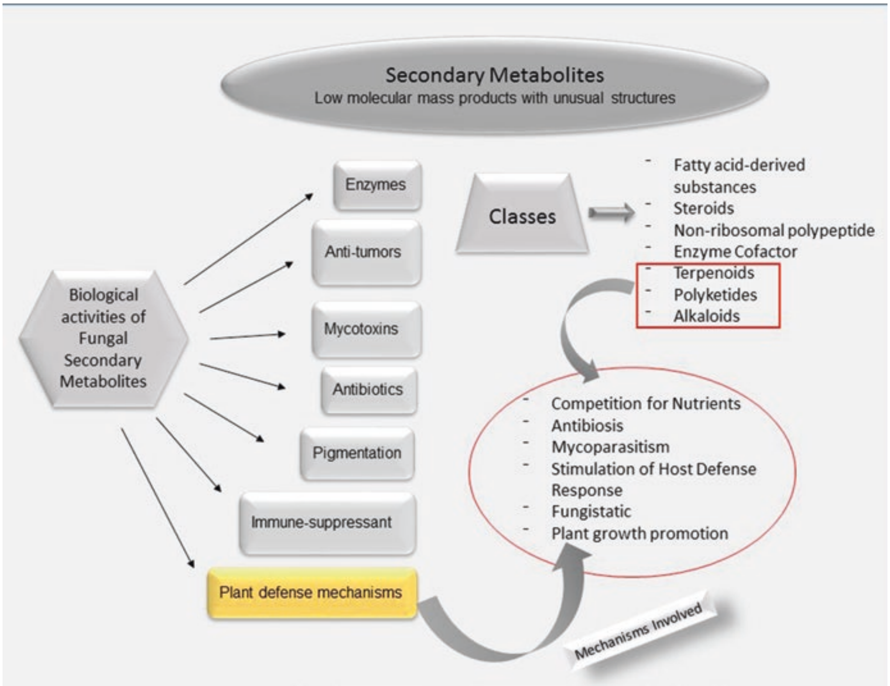


Fig. 5.1 Schematic diagram of biologically active secondary metabolites and their major classes involved in the plant defense mechanisms

environmental circumstances or by enhancing plant growth. Fungi are also known by its defense and antibiosis mechanisms and by the processes like mycoparasitism against phytopathogens (Yadav et al. 2019d, 2020d). This influence is attained by production of a great variety of secondary metabolites, evolving a wide array of natural and xenobiotics, developing altered degradative enzymes like chitinase (Gloer 1997; Kumar et al. 2019a). Biological activities having integral impact on crop regulation and production are greatly influenced by fungal metabolites.

5.2 Fungi as Biological Control Agent

Biocontrol agents are the microorganisms that suppress the effects of pests or pathogens by a variety of mechanisms or induce stimulatory effects on the plants growth. Currently, various microbial biocontrol agents are present. Bacterial biocontrol agents include *Pseudomonas* spp., *Bacillus* spp., and *Agrobacterium* sp., while, biocontrol agents of fungal origin are *Aspergillus* spp., *Candida* sp., *Ampelomyces* sp., *Coniothyrium* sp., *Trichoderma* spp., and *Gliocladium* sp. (Atehnkeng et al. 2008; Gilardi et al. 2008; Koumoutsi et al. 2004; Mavrodi et al. 2002; Papavizas 1985). Among these, *Trichoderma* sp. stands out as the most versatile and diverse fungal biocontrol agent mainly towards pathogenic fungi. Various studies claimed *Trichoderma* spp. as an effective biocontrol weapon against pant diseases (Sharma et al. 2019; Yadav et al. 2020c). Commercially available *Trichoderma* products as biopesticides are in use presently that alter the soil properties enhancing plant growth promotion (Chet 1987; Harman et al. 2004; Papavizas 1985; Vinale et al. 2008). In 1934, *Trichoderma lignorum* was utilized as biocontrol agent against the fungal plant pathogen *Rhizoctonia solani* by Weindling (1934). Similarly, *Trichoderma lignorum* displayed mycoparasitic features towards *Rhizopus*, *Phytophthora*, *Sclerotium rolfsii,* and *Pythium* (Wells 1988). Many diverse secondary metabolites are also reported from *Trichoderma* spp., which has therefore drawn great interest in fungus being designated as a biocontrol model (Chet 1993; Chet et al. 1981; Rastegari et al. 2020a) (Table 5.1).

Presently, mankind faces huge challenges in the form of environmental degradation, deterioration of land, water and loss of biological diversity (Kour et al. 2019; Kumar et al. 2019b). Secondary metabolites, therefore, hold great potential in rectifying these challenges of nature. Fungi secrete a great number of diverse bioactive secondary metabolites with broad range of functions (Fig. 5.2). Major categories of natural products from fungal origin include antioxidants, antidiabetics, antibiotics, insecticides, and immunosuppressant of various chemical characters (Rana et al. 2020; Singh et al. 2020). The present chapter focuses on the three major and most abundant classes of secondary metabolites synthesized by fungi along with their functions and complex interactions in response with phytopathogens.

Table 5.1 Plant crop diseases controlled by fungal biocontrol agents

Crop disease	Pathogen	Biocontrol agents
Blight of *Sesamum*	*Phytophthora* sp.	*T. harzianum*
		T. viride
Root rot of *Sesamum*	*M. phaseolina*	*Trichoderma* sp.
		Gliocladium sp.
Root rot chilli	*S. rolfsii*	*T. harzianum*
Dieback of chilli	*Colletotrichum capsici*	*T. viride*
		T. harzianum
Wilt of eggplant	*F. solani*	*T. viride*
		T. koningii
Damping-off of eggplant	*P. aphanidermatum*	*T. viride*
		T. koningii
Wilt of tomato	*F. oxysporum*	*T. harzianum*
Root knot of tomato	*Meloidogyne incognita*	*T. harzianum*
	M. javanica	
Wilt of okra	*Pythium* spp.	*A. niger*
Leaf blight of sunflower	*Alternaria helianthi*	*T. virens*
Wilt of pigeon pea	*Fusarium udum*	*T. viride*
		T. hamatum
		T. harzianum
		T. koningii
Wilt of chickpea	*F. oxysporum*	*T. viride*
	*f.*sp. *ciceri*	*T. harzianum*
		T. virens
Dry root rot of soybean	*M. phaseolina*	*T. viride*
		T. harzianum
Stem rot of groundnut	*Sclerotium rolfsii*	*T. harzianum*
Damping-off of mustard	*Pythium aphanidermatum*	*T. harzianum*
		T. viride
Root rot of mung bean	*M. phaseolina*	*T. harzianum*
		T. viride

Source: Gawai (2018)

5.3 Sesquiterpenes

Sesquiterpenes are the most abundant sub-class of terpenoids group of fungal secondary metabolites that involves an arrangement of three isoprene units with a molecular formula of $C_{15}H_{24}$. Their classification is based upon the presence or absence of carbon rings acyclic in nature or monocyclic, bicyclic, tri-cyclic and onwards. Sesquiterpenes are known to be anti-inflammatory with characteristic bactericidal properties involving strong odors (Waterman 1993).

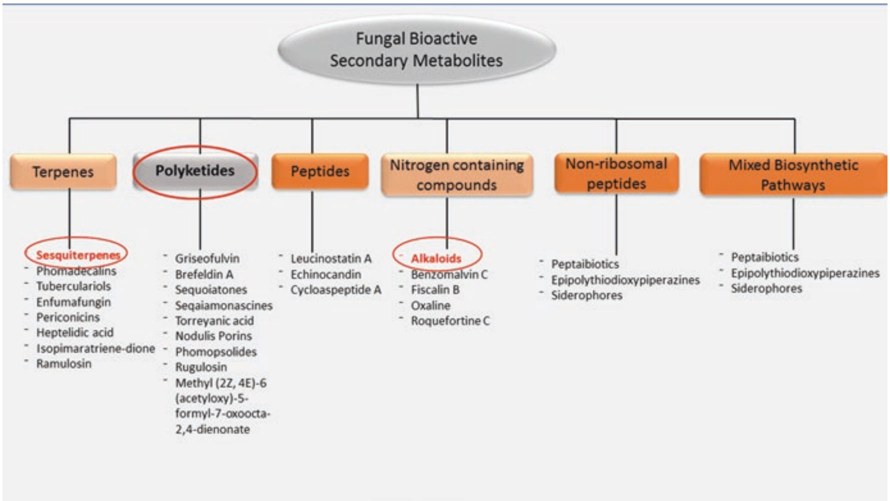


Fig. 5.2 Broad classification of fungal bioactive secondary metabolites

5.3.1 Sources and Their Function

Daucane, a class of sesquiterpenes which is also referred as carotanes are rarely known fungal metabolites. A novel daucane (carotene) metabolite (**1**) (Fig. 5.3) from one of the strains of *T. virens* showed antifungal properties against a number of dermatophytes and yeast with significant effect recorded on *C. albicans* (Watanabe et al. 1990). *T. virens* was also reported as a source of four novel metabolites with carotene backbone, trichocaranes A, B, C, and D (**2–5**) (Fig. 5.3). The structure of each trichocarane was confirmed by mass spectroscopy and NMR emphasizing each compound remarkably inhibited the growth rate of etiolated wheat coleoptiles (Macias et al. 2000).

Numerous sesquiterpenes from endophytic fungi have also been identified. Two caryophyllene (pestalotiopsin A and B) along with a novel 2α-hydroxydimeninol (**6–8**) (Fig. 5.4) sesquiterpenes from *Pestalotiopsis* spp. that forms an endophytic relationship with *Taxus brevifolia* evaluated by spectral and X-ray diffraction analysis (Pulici et al. 1996a, b). Sesquiterpenes are also known to exhibit insecticidal properties. For instance, toxicity against the larvae of spruce budworm (*Choristoneura fumiferana*) of *Phyllosticta* sp., that involves an endophytic association with *Abies balsamea* from the family *Pinaceae* by the action of heptelidic and hydroheptelidic acid (**9–10**) (Fig. 5.5) (Calhoun et al. 1992).

Epichloë typhina, a species of fungus of cool season grass that is endophytic in nature on plant *Phleum pretense*. It has been reported to elicit sesquiterpenes chokols A–G (Fig. 5.6) involving antifungal activity against the pathogen of leaf spot disease *Cladosporium phlei* (Koshino et al. 1989). *Trichoderma* sp. PR-35 exhibiting endophytic association with *Paeonia delavayi* provided three compounds cyclonerodiol, cyclonerodiol oxide, and sorbicillin (**11–13**) with two new

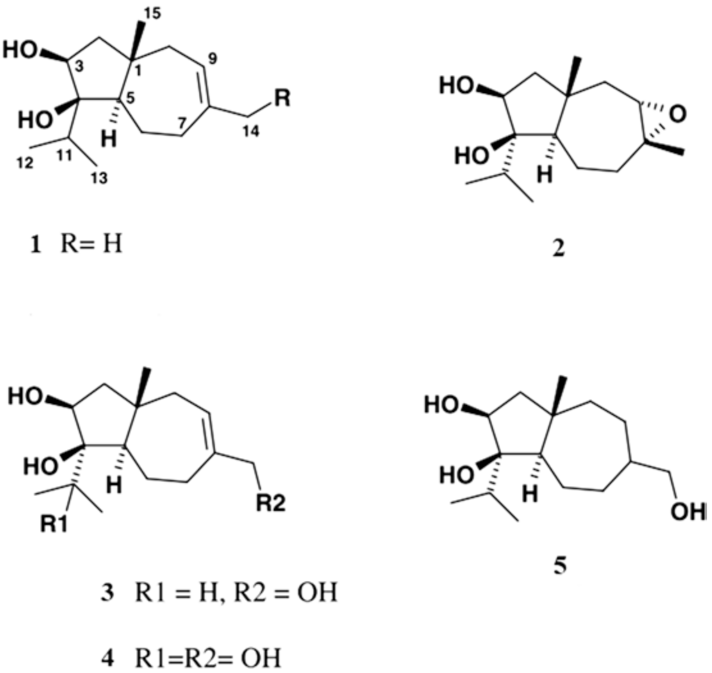


Fig. 5.3 Chemical structure of: 1 carotane-type metabolite; 2, 3, 4, 5 trichocaranes A, B, C, and D

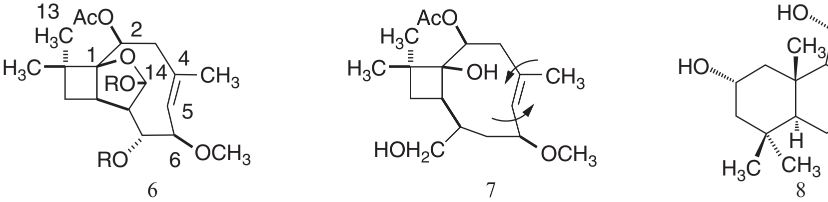


Fig. 5.4 Chemical structure of: 6 pestalotiopsin A; 7 pestalotiopsin B; 8 2α-hydroxydimeninol

sesquiterpene: trichoderic acid and 2β-hydroxytrichoacorenol (**14–15**), a bisabolane type and acorane type sesquiterpene (Fig. 5.7), respectively. Most of these compounds displayed varying levels of both antibacterial and antifungal characteristics against different types of pathogens (Wu et al. 2011). The medicinal plant *Costus speciosus* is host to fungal endophyte *Bipolaris sorokiniana* identified to yield helminthosporal acid (**16**) and helminthosporol (**17**)**,** two quite rare sesquiterpenes (Fig. 5.8). Compound **16** exhibited antifungal activity (Qader et al. 2017). Helminthosporol (**17**) has also been reported from *Drechslera dematioidea* obtained from *Liagora viscida*, red algae of marine origin (Osterhage et al. 2002). Helminthosporol (**17**) is also experimented to show elongation effect upon the shoots of rice seedlings (Tamura et al. 1965).

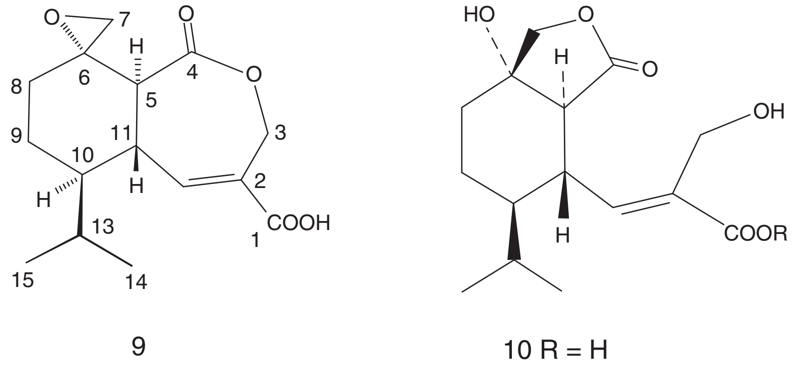


Fig. 5.5 Chemical structure of: 9 heptelidic and 10 hydroheptelidic acid

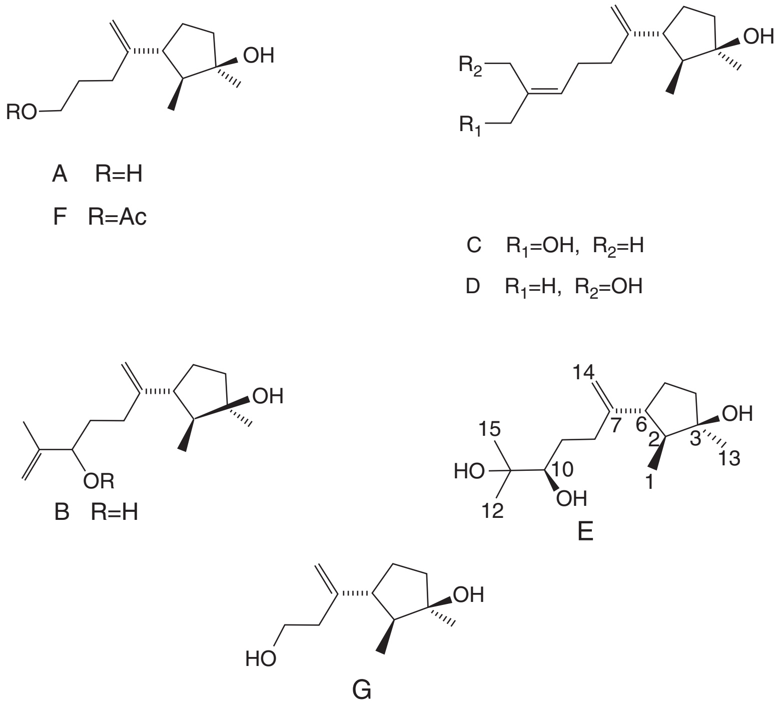


Fig. 5.6 Chemical structure of: chokols A–G

5.3.2 Synthesis

Biosynthesis of metabolites belonging to the class of terpenoids are synthesized via the CoA derived C-5-isopentenyl-diphosphate intermediate products isopentenyl and dimethylallyl-diphosphate. The isoprene units are processed through prenyl

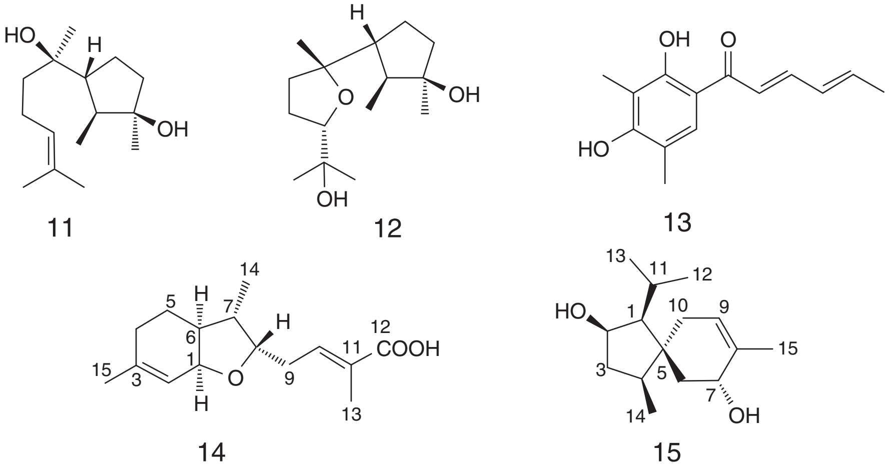
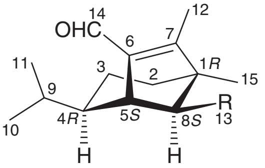


Fig. 5.7 Chemical structure of: 11 cyclonerodiol; 12 cyclonerodiol oxide; 13 sorbicillin; 14 trichoderic acid; 15 2β-hydroxytrichoacorenol

Fig. 5.8 Chemical structure of: 16 helminthosporal acid and helminthosporol 17



16 R=COOH

17 R=CH_2OH

synthases with post synthetic modifications by the action of numerous enzymes, producing different classes of terpenoids from lesser isoprene units (Schmidt-Dannert 2015). The genome of *C. rosea* comprises eight of the terpene synthase genes (Karlsson et al. 2015). While *E. weberi* involves six terpene synthase genes and three of these genes are known to exist at the biosynthetic clusters of secondary metabolite (de Man et al. 2016). In comparison to *T. reesei* and *T. atroviride*, the genome of *T. virens* contains enriched region of terpene cyclase genes (Bansal and Mukherjee 2016). The terpene class of cyclase gene vir4 was determined to be involved in greater than 20 sesquiterpene biosynthesis volatile in nature (Crutcher et al. 2013).

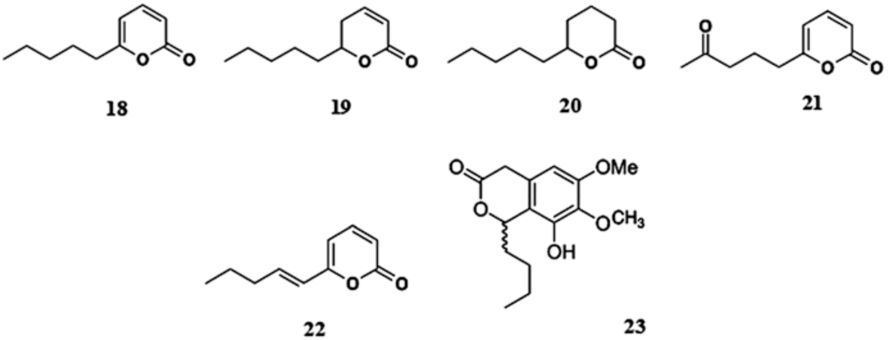
5.4 Polyketides

Polyketides are generated from coenzyme A esters such as acetyl CoA or malonyl CoA by polyketide synthases decarboxylation condensation and post-synthetic modification (Pfeifer et al. 2001). Polyketide synthases of fungal origin are complex interchangeable enzymes with characteristic inclusion of ketoacyl CoA synthase, involved in the generation of long chain fatty acids belonging to the enzyme family, acyltransferase (Keller et al. 2005). Polyketides are diverse in nature while being the core class of secondary metabolites produced from the kingdom of fungi including antibiotics, toxins, antiparasitics to antifungals, insecticides (Karlsson et al. 2017).

5.4.1 Source and Function

6-pentyl-a-pyrone (18) (Fig. 5.9) is among the characteristic metabolite of the genus *Trichoderma* first discovered in 1972 (Collins and Halim 1972) from *T. viride* growth culture broth. In the same way, *T. koningii* and *T. harzianum* have also been reported as the metabolite producer (Claydon et al. 1987; Simon et al. 1988). Plate tests evaluation effects against *Fusarium oxysporum f.* sp. *Lycopersici* and *Rhizoctonia solani* have also been investigated. An addition of this compound in agar medium resulted in growth reduction of *F. oxysporum* and *R. solani* within 48 h by 69.6% and 31.7%, respectively, to an amount of 0.3 mg/ml. Complete spore germination was halted at 0.45 mg/ml when spore germination tests were performed against the spores of *Fusarium*. Similarly, Poole et al. identified the control against *Botrytis cinerea* causing rots of stored kiwi fruits (Poole et al. 1998).

Massoilactone and delta-decanolactone (19–20) (Fig. 5.9) have been patented (Hill et al. 1995) due to their broad range of controlling plant disorders caused by *Phytophthora* and *Botrytis* species as they involve the ability to halt the growth at 62–250 µg/ml of *S. aureus* and at 31–125 µg/ml of *A. niger* and *C. albicans*. This is



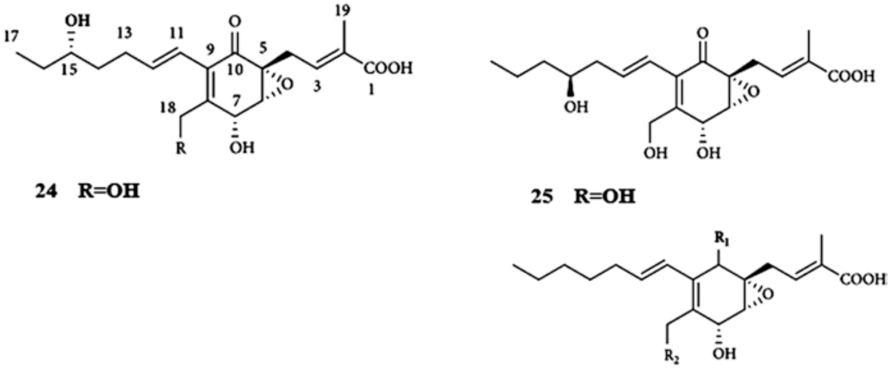
18 19 20 21

22 23

Fig. 5.9 Chemical structure of: 18 6-pentyl-a-pyrone; 19 massoilactone; 20 delta-decanolactone; 21 viridepyronone; 22 6-(1′-pentenyl)-2H-pyran-2-one; 23 cytosporone S achieved by adopting 96 well equipped microbioassay and agar dilution method (Kishimoto et al. 2005). *T. viridae* has been identified as a source of viridepyronone (21) (Fig. 5.9) showing in vitro inhibitory effects of over 90% against *Sclerotium rolfsii* (Evidente et al. 2003). Studies conducted on 6-(1′-pentenyl)-2H-pyran-2-one (22) (Fig. 5.9) displayed inhibitory effects to *Cryptococcus neoformans, Candida albicans, Penicillium spp.,* and *Aspergillus fumigatus* isolated from two strains of *T. harzianum* (Claydon et al. 1987; Parker et al. 1997). In vitro antibiotic response from cytosporone S (pyrone) (23) (Fig. 5.9) has been reported against numerous fungi and bacteria as well from a *Trichoderma* sp. strain as the source (Ishii et al. 2013). Similarly, novel polyketide terpene metabolites (24–26) (Fig. 5.10) from endolichenic fungus belonging to *Pestalotiopsis* sp. showed potential as antifungal agents capable of being employed in crop and agricultural protection practices. Compounds 24 and 25 inhibited the plant pathogen fungus *F. oxysporum,* while compounds 25 and 26 inhibited the growth of *F. gramineum* at an MIC of 8 ug/ml (Yuan et al. 2017).

Hormonema dematioides endophytic to balsam fir, produces a quinone compound rugulosin (**27**) (Fig. 5.11) exhibiting insecticidal activity (Calhoun et al. 1992). A quinone 1′,5′-trihydroxy-3′,4′dihydro-1′H-[2,4′]binaphthalenyl-1,4,2′-trione (**28**) (Fig. 5.11) elicited from an endophytic fungi of *Larix laricin*a needle displays toxicity towards the larvae of spruce budworm (Findlay et al. 1997). Similarly, *Alternaria spp.* and *Phoma sp.* in conjugation with plants secrete hydroxyl quinone altersolanol A (29) (Fig. 5.11) with antibacterial characteristics (Yang et al. 1994).

Anthraquinones pachybasin, chrysophanol, and emodin (30–32) (Fig. 5.11) have been reported from wild *T. viridae* strain sampled from soil (Slater et al. 1967). The mixture of these compounds along with their *O*-acetyl and *O*-methyl derivatives towards two *F. annosus* strains resulted in a linear reduction of fungal growth in particular when *O*-acetyl derivatives were employed (Donnelly and Sheridan 1986).

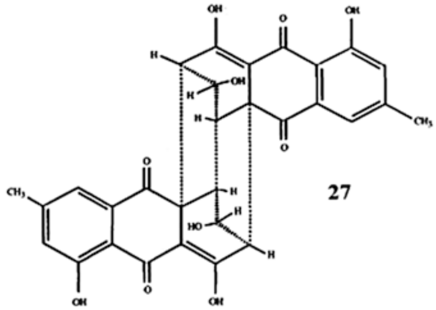


24 **R=OH**

25 **R=OH**

26 **R$_1$= ?OH, R$_2$=OH**

Fig. 5.10 Chemical structures of novel polyketide terepene metabolites **24**, **25,** and **26**



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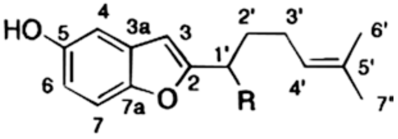
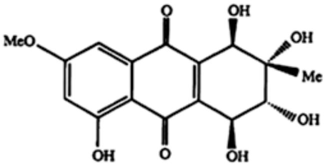


28 R=O



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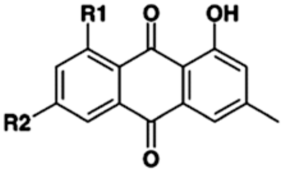
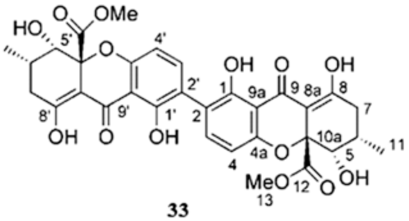


30 $R_1=R_2=H$

31 $R_1=OH, R_2=H$

32 $R_1=R_2=OH$

Fig. 5.11 Chemical structure of: 27 rugulosin; anthraquinones 30 pachybasin; 31 chrysophanol; 32 emodin



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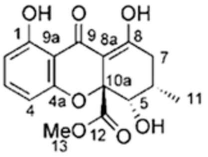

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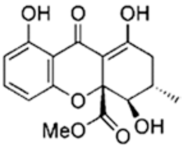

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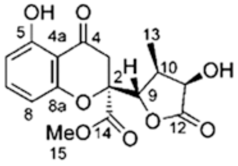

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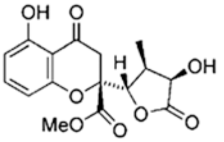


37

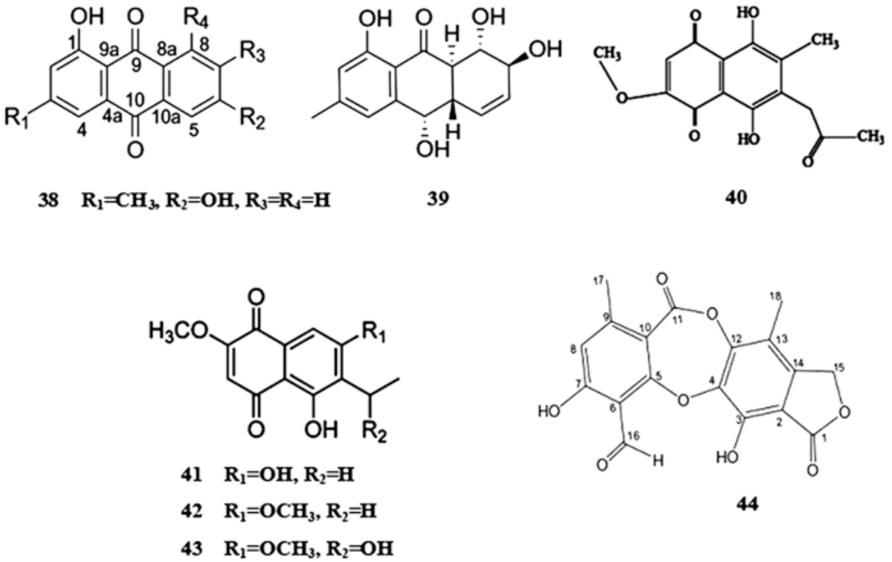
Fig. 5.12 Chemical structure of: **33** secalonic acid B; 34, 35, 36, 37 blennolides A, B, D, and E

Emodin (**32**) is known to have the activities of tyrosine kinase (Jayasuriya et al. 1992; Kumar et al. 1998) and monoamine oxidase (Fujimoto et al. 1998).

Blennoria sp. exhibiting endophytic relation to *Carpobrotus edulis* has been reported as a source of secalonic acid B (33) (Fig. 5.12), blennolides A, B, D, and E

(34–37) (Fig. 5.12). Compounds 33–35 show antialgal, antibacterial, and antifungal properties, while compound **33** was antagonistic against *Bacillus megaterium* and *M. violaceum*. Compounds **36** and **37** showed appreciable antialgal and antifungal properties (Zhang et al. 2008).

Compounds 38 and 39 (Fig. 5.13) obtained from fungal culture of *Coniothyrium* sp., an endophyte of *Salsola oppostifolia* is known to have notable effects against *Botrytis cinerea* and *M. violaceum* (Sun et al. 2013). Javanicin (40), a naphthoquinone counterpart (Fig. 5.13), was identified from *Fusarium* sp. (Kornsakulkarn et al. 2011) and as well as *Chloridium* sp. It is known to inhibit the fungal growth of *Verticillium dahliae*, *Fusarium oxysporum*, *Rhizoctonia solani*, and *Cercospora arachidicola* (Kharwar et al. 2009). Similarly, *Delitschia corticola* secretes a series of naphthoquinone 6-ethyl-7-hydroxyl-2-methoxyjuglone (**41**), 6-ethyl-2,7-dimethoxyjuglone (**42**), and 6-(1-hydroxyethyl)-2,7-dimethoxyjuglone (**43**) (Fig. 5.13) displaying antifungal activity against *Fusarium* sp., *Alternaria* sp., and *Sclerotium* sp. (Sun et al. 2011). The depsidones called cordycepsidone A (**44**) (Fig. 5.13) was reported to exhibit strong antifungal characteristics against fungus known to be plant pathogens viz., *Gibberella fujikuroi* with intermediate effects towards *Pythium ultimum* with the fungus *Cordyceps dipterigena* as a source (Varughese et al. 2012). Pyrenocine analogs called phomopsinones A and D (**45–46**) (Fig. 5.14) are reported from *Phomopsis* sp. that resides as an endophytic fungus on *Santolina chamaecyparissus* (Hussain et al. 2012b). Phomopsinone A (**45**) showed strong antifungal properties against plant and crop pathogens *Pyricularia oryzae*, *Septoria tritici*, and



38 R_1=CH_3, R_2=OH, R_3=R_4=H

39

40

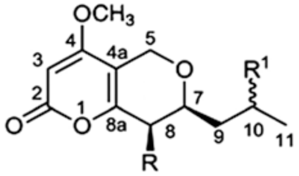
41 R_1=OH, R_2=H

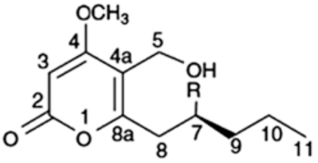
42 R_1=OCH_3, R_2=H

43 R_1=OCH_3, R_2=OH

44

Fig. 5.13 Chemical structure of: 38 1,6-dihydroxy-3-methyl-9,10-anthraquinone (phomarin); 39 coniothyrinone A; 40 javanicin; 41 6-ethyl-7-hydroxyl-2-methoxyjuglone; 42 6-ethyl-2,7-dimethoxyjuglone; 43 6-(1-hydroxyethyl)-2,7-dimethoxyjuglone; **44** cordycepsidones A





45 R=R_1=H

46 R=OH, R_1=H

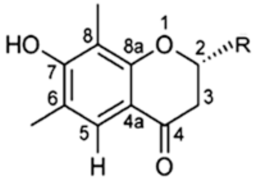
47 R=H, R_1=R_2=H

48 R=H, R_1="=O" (keto), R_2=CH_3

49 R=H

Fig. 5.14 Chemical structure of: **45**, **46** phomopsinones A and D; pyrenocines 47, 48, 49 J, K, and M

Fig. 5.15 Chemical structure of: 50, 51 phomochromone A and B



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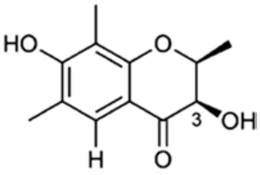


51

B. cinerea. Phomopsinone D (**46**) is reported to only inhibit the growth of *B. cinerea* and *S. tritici*. In the same way, four pyrocine counterparts were isolated from the fungus belonging to *Phomopsis* sp., endophyte of *Cistus salvifolius* (Hussain et al. 2012a). Out of these four, pyrenocines K (**48**) and M (**49**) (Fig. 5.14) displayed antifungal effects against *M. violaceum* and *S. tritici,* whereas, pyrenocine J (**47**) (Fig. 5.14) was antifungal only against *S. tritici*. Phomochromone A (**50**) and B (**51**) (Fig. 5.15), two novel chromones were reported from *Phomopsis* sp. displaying appreciable antifungal, antibacterial, and antialgal properties when tested against *S. tritici*, *B. cinerea*, *B. megaterium*, *M. violaceum* and also against *E. coli* and *C. fusca* (Ahmed et al. 2011).

Mellein (**52**) (Fig. 5.14), an isocoumarin analog isolated from *Pezicula* sp., inhibits *B. cinerea* and *Fulvia fulva* with EC_{50} values of less than 50 μg/ml (Wang et al. 2014). Palmarumycin C_8 (**53**) (Fig. 5.14) obtained from the fungal species *Berkleasmium* inhibits and antifungal in spore germination with 9.1 μg/ml IC_{50} value against *Magnaporthe oryzae* (Shan et al. 2014). Seimatoporic acid A and B (**54–55**) (Fig. 5.16) obtained from fungus *Seimatosporium* sp., endophytic in association exhibits strong antifungal effects towards *S. tritici*, *P. oryzae,* and *B. cinerea* (Hussain et al. 2012c).

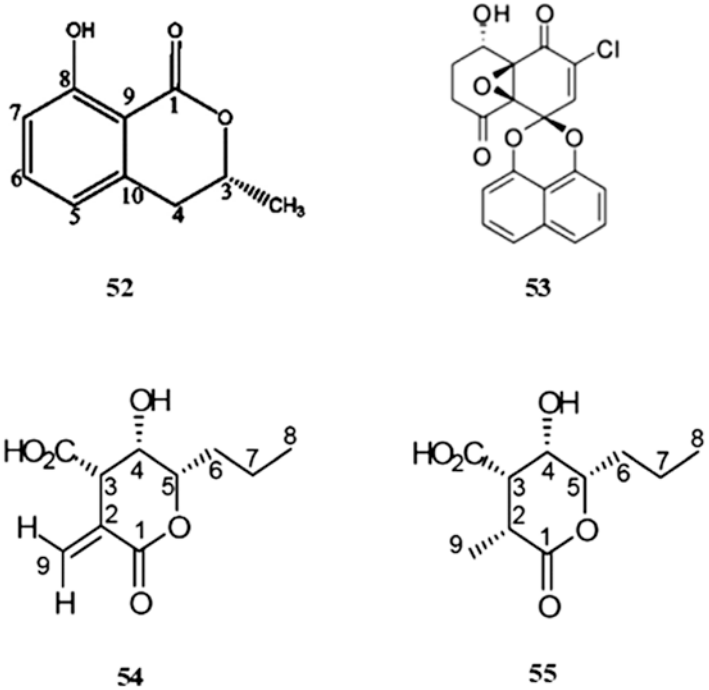


Fig. 5.16 Chemical structure of: **52** mellein; 53 palmarumycin C_8; **54**, **55** seimatoporic acid A and B

5.4.2 Synthesis

In comparison to *T. reesei*, the genomes of *T. virens* and *T. atroviridae* contain 60% polyketide synthase genes (Kubicek et al. 2011). *T. ophioglossoides* involves 15 polyketide synthases in its genome (Quandt et al. 2016), while *C. rosea* contains 31 polyketide synthase genes (Karlsson et al. 2015). *C. rosea* imparts antibacterial activity due to the action of TMC-151 type polyketides (Zhai et al. 2016). On the other hand, *T. ophioglossoides* is responsible for eliciting two antibacterial and antifungal compounds: the NRPS/PKS enzyme hybrid driven ophiosetin and polyketide ophiocordin (Kneifel et al. 1977; Putri et al. 2010; Quandt et al. 2016). The *pks4* deletion in *Fusarium* spp. which codes for aurofusarin and bikaverin orthologue for polyketides synthases, resulted in considerable alterations of metabolism, morphology, and physiology in *T. reesei*. Inhibition of teleomorph structures and conidia pigmentation were evaluated along with reduced stability of cell wall in conidia in delta-*pks4* mutants. Deletion of the of the mutant *Pks4* caused a decrease in hostile characteristics in confrontation estimation assays of *T. reesei*, decreased the antifungal properties induced by polar soluble and resilient metabolites along with altered gene expression of other polyketide synthases (Atanasova et al. 2013).

5.5 Alkaloids

Alkaloids consists of a diverse molecular class pertaining nitrogen and amino acid containing molecular entities representing wide functions in nature, while occurring in animals, plants, and microorganisms (Pelletier 1983).

5.5.1 *Source and Function*

Pyrrolizidines are organic compounds heterocyclic in nature biosynthesized by plants as a defense mechanism against herbivores (Macel 2011). 1-aminopyrrolizidine, also known as lolines (56) (Fig. 5.17), have been reportedly secreted by endophytic fungi residing on grasses. Neither endophytic fungal cultures nor the infected grasses separately produced lolines in vitro (Schardl and Phillips 1997). Emphasizing, secretion only took place during plant-endophyte interaction. Lolines are diverse insecticides playing the role of metabolic toxicants and feeding repellents. The allelopathic phenomenon when grasses reside as host is credited to certain endophyte secreted loline counterparts (Bush et al. 1997). For instance, *F. pratensis* when infected by *N. uncinatum* and *N. coenophialum* infecting *Festuca arundinacea* distinctively produces lolines (**56**). These are also

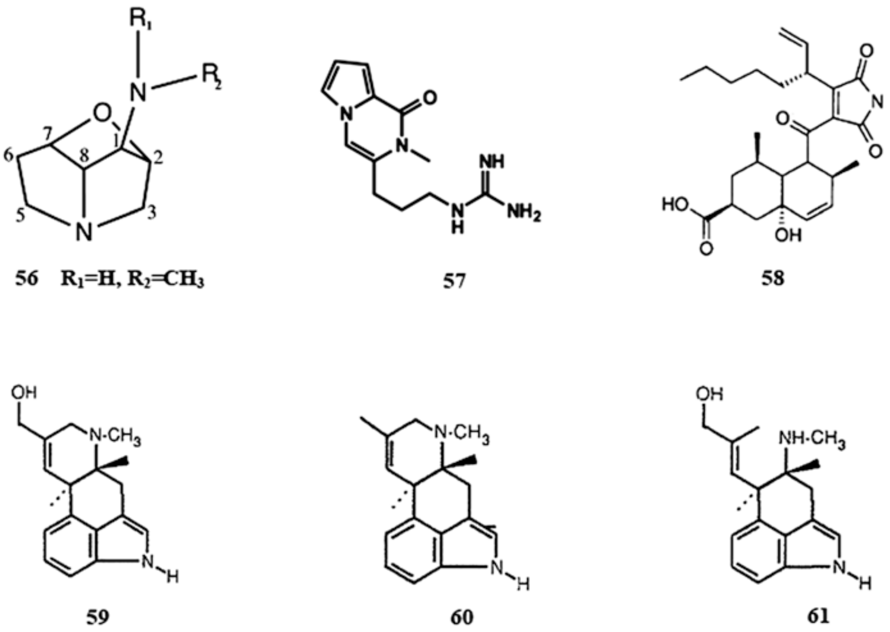


Fig. 5.17 Chemical structure of: 56 lolines; 57 peramine; 58 1-*N*-methylalbonoursin; indole alkaloids 59 elymoclavine; 60 agroclavine; 61 chanoclavine

relatively lesser toxicants when made a comparison with indole diterpene alkaloids and ergot alkaloids.

Secondary metabolites classified under amine and amides have been identified from *Neotyphodium*, also referred as *Epichloë* and the grass endophytes from the genus *Acremonium* (Glenn et al. 1996; Schardl and Phillips 1997). Peramine (**57**), a pyrrolopyrazine (Fig. 5.15) classified alkaloid is reportedly secreted by *E. typhina*, *Neotyphodium coenophialum*, *N. lolli,* and *Epichloë festucae* within the culture, in leaves of taller fescue, ryegrass and as well as in plants having association with the stem while being a toxicant against insects such as Argentine stem weevil having no hazardous influence on mammals (Dew et al. 1990; Rowan and Latch 1994). Ras farnesyl transferase is known to be inhibited due to the production of 1-*N*-methylalbonoursin (**58**) (Fig. 5.17) from *Phoma* sp. (Ishii et al. 2000). Secretion of Indole alkaloids like elymoclavine, agroclavine, and chanoclavine (**59–61**) (Fig. 5.17) providing toxicity against some insects and mammals are reported from *Neotyphodium* (Powell and Petroski 1992; Schardl and Phillips 1997). *Neotyphodium* endophytes provides plant hosts with numerous advantages like enhanced growth rate, increased reproduction, and herbivores resistance using endophyte alkaloids (Clay and Schardl 2002; Faeth 2009; Müller and Krauss 2005).

Cavendishia pubescens tree bark isolated *Phomopsis* sp. and indole byproducts like tremorgenic aspalitrems A (62) and C (63) (Fig. 5.18) of *Aspergillus flavus* are produced by the endophyte (Bills et al. 1992). Similarly, 3-IAA (64) (Fig. 5.18) of auxin class is produced by *Artemisia annua* residing *Epicoccum purpurascens*, *Aureobasidium pullulans*, *Colletotrichum* sp., and *Acremonium coenophialum* endophytes. Tobacco isolated strains of *Hypoxylon serpens* elicites IAA, cytokinins with 3-indoleacetonitrile (65) (Fig. 5.18) (Petrini 1991).

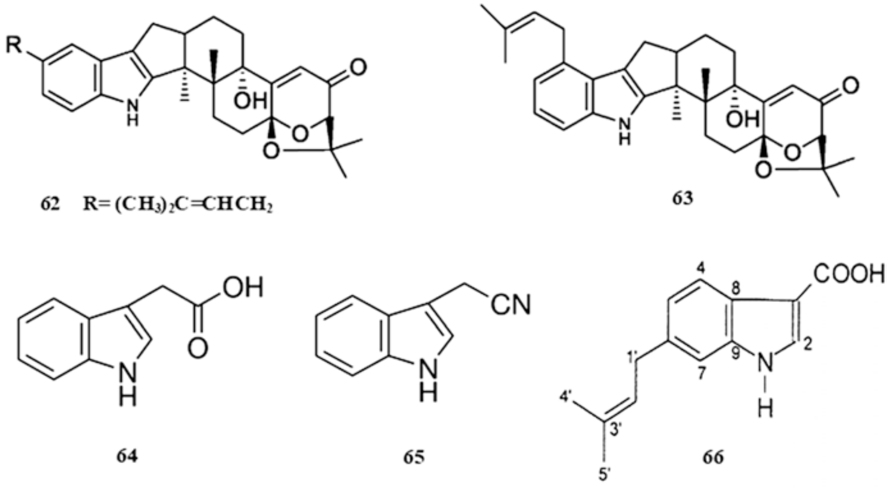
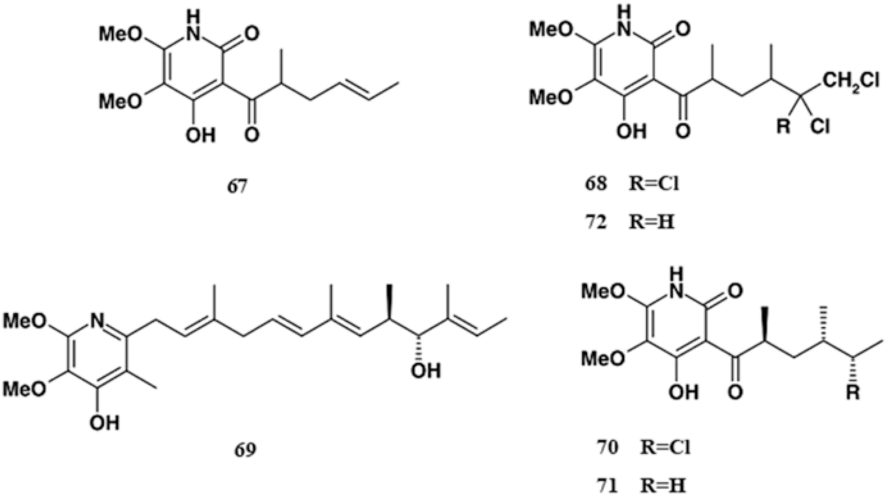


Fig. 5.18 Chemical structure of: 62, 63 aspalitrems A and C; 64 indole-3-acetic acid; 65 3-indoleacetonitrile; 66 6-isoprenylindole-3-carboxylic acid

6-isoprenylindole-3-carboxylic acid (66), an indole byproduct (Fig. 5.18), has been identified from *Colletotrichum* sp. endophyte to *Artemisia. annua*. This derivative is hostile towards pathogenic bacteria and as well as phytopathogenic fungi such as *Rhizoctonia cerealis*, *Gaeumannomyces graminis var. tritici,* and *Phytophthora capsici* (Lu et al. 2000). A 4-year long field experiment examined alkaloids associated infection on *Achnatherum robustum*, the sleepygrass. Results emphasized the potential of alkaloidal infection in protection from extreme winter circumstances and underground herbivore antagonism (Faeth et al. 2010).

Pyridine ring containing metabolites of fungal origin exist with 2,3-dimethoxy-4-pyridinol structure (Fig. 5.19). For example, harzianopyridone (67) (Fig. 5.19) obtained from *T. harzianum* whose racemic structure display huge antifungal potential towards *Pythium ultimum, Gaeumannomyces graminis var. tritici, Botrytis cinerea,* and *Rhizoctonia solani* (Dickinson et al. 1989; Vinale et al. 2006). On the other hand, remarkable phytotoxic effects were observed in etiolated wheat coleoptile bioassay with marginal antibacterial and antifungal characteristics from the laevorotatory form Cutler and Jacyno (1991). This form of compound 67 was also shown to elicit necrosis among corn, tobacco, and bean in accordance to the concentration. Thus, signifying the potential of harzianopyridone (67) enantiomers to exhibit altering characteristics (Sivasithamparam and Ghisalberti 1998). Penta-substituted ring structure of pyridine is reportedly involved in WF-16775 A2 (68) (Fig. 5.19) obtained by *Chaetasbolisia erysiophoides* (Otsuka et al. 1992), piericidin A (69) (Fig. 5.19) isolated from *Streptomyces mobaraensis* and *S. pactum* (Jansen and Höfle 1983; Takahashi et al. 1965) and atpenin compounds (70–72) (Fig. 5.19) secreted from *Penicillium* sp. (Kumagai et al. 1990; Omura et al. 1988; Oshino et al. 1990).



67

68 R=Cl

72 R=H

69

70 R=Cl

71 R=H

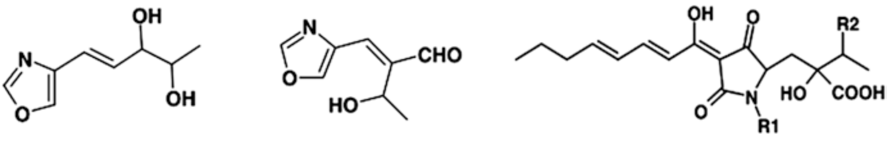
Fig. 5.19 Chemical structure of: 67 harzianopyridone; 68 WF-16775 A2; 69 piericidin A; 70–72 atpenin compounds

Oxazole derivatives and pirrolidindione ring structures of fungal origin have been reported. ATF-451 strain of *Trichoderma* was reported to produce melanoxadin (73) and melanoxazal (74), oxazole byproducts (Fig. 5.20) from the post fermentation cultural broth. Significant inhibition potential has been reported towards mushroom tyrosinase from melanoxazal (74) while the silkworm *Bombyx mori* had inhibited melanin production within the hemolymph larval fluid from both compounds (73–74) (Hashimoto et al. 1995; Takahashi et al. 1965). Harzianic acid (75) (Fig. 5.20) consisting of a pirrolidindione ring structure is identified from a strain of *T. harzianum* subjected to fermentation (Sawa et al. 1994). Harzianic acid have also been found from F-1531 fungal strain along with dimethyl harzianic (76) and homoharzianic (77) acids (Fig. 5.20) (Kawada et al. 2004). Compounds (75–77) showed similar function of inhibiting PP2A (protein phosphatase type 2A) (Sivasithamparam and Ghisalberti 1998).

Fungal bioactive secondary metabolites and their role in plant defense along with their activities have been enlisted in Table 5.2.

5.6 Conclusion and Future Prospects

Secondary metabolites are the microbial products play a major role in the controlling of pest and phytopathogens harmful for agricultural crops. Different secondary metabolites produced by beneficial fungi have been commercially used for the plant defense mechanisms. The fungal secondary metabolites involved in the interactions with phytopathogenic agents used various mechanisms due to their complex nature of chemical composition and their synthesis based on their source of isolation. The quality of the synthesized secondary metabolites depends on the species and the strains, their growth conditions, the occurrence of the other organisms, and the absence and presence of the pathogenic agents. Therefore, the applications of fungal secondary metabolites to induce resistance against phytopathogens may be an interesting alternative to the chemical pesticides.



73

74

75 $R_1 = CH_3, R_2 = CH_3$

76 $R_1 = H, R_2 = CH_3$

77 $R_1 = CH_3, R_2 = C_2H_5$

Fig. 5.20 Chemical structure of: 73 melanoxadin; 74 melanoxazal; 75 harzianic acid; 76 demethylharzianic; 77 homoharzianic acid

Table 5.2 Secondary metabolites; sesquiterpenes, polyketides and alkaloids from fungal species

Source	Secondary metabolites	Activity	Class	References
T. virens	Carotane-type metabolite	Antifungal	Sesquiterpenes	Watanabe et al. (1990)
T. virens	Trichocaranes A, B, C and D	Inhibition of etiolated wheat coleoptiles	Sesquiterpenes	Macias et al. (2000)
Phyllosticta sp. (endophyte of *Abies balsamea*)	Heptelidic and hydroheptelidic acid	Toxic to spruce budworm larvae	Sesquiterpenes	Calhoun et al. (1992)
Epichloë typhina (endophyte of *Phleum pretense*)	Chokols A–G	Antifungal to pathogen of leaf spot disease	Sesquiterpenes	Koshino et al. (1989)
Trichoderma sp. PR-35 (endophyte of *Paeonia delavayi*)	Cyclonerodiol, cyclonerodiol oxide and sorbicillin	Antibacterial and antifungal	Sesquiterpenes	Wu et al. (2011)
Trichoderma sp. PR-35	2β-hydroxytrichoacorenol and trichoderic acid	Antibacterial and antifungal	Sesquiterpenes	Wu et al. (2011)
Bipolaris sorokiniana (endophyte of *Costus speciosus*)	Helminthosporal acid	Antifungal	Sesquiterpenes	Qader et al. (2017)
Bipolaris sorokiniana, Drechslera dematioidea	Helminthosporol	Shoot elongation of rice seedlings	Sesquiterpenes	Osterhage et al. (2002), Tamura et al. (1965)
T. harzianum, T. koningii	Cyclonerodiol	Inhibits growth of etiolated wheat coleoptiles	Sesquiterpenes	Vinale et al. (2014)
T. harzianum, T. brevicompactum, Trichoderma sp.YMF1.02647	Trichodermin	Antifungal Nematicidal	Sesquiterpenes	Shentu et al. (2014), Shi et al. (2009), Yang et al. (2010)
T. viride, T. koningii, T. harzianum	6-pentyl-a-pyrone	Antifungal to *F. oxysporum* and *R. solani*	Polyketides	Collins and Halim (1972)
T. viride, T. koningii, T. harzianum	6-pentyl-a-pyrone	Antifungal to *Botrytis cinerea*	Polyketides	Poole et al. (1998)
Trichoderma spp.	Massoilactone and delta-decanolactone	Antifungal	Polyketides	Kishimoto et al. (2005)

(continued)

Table 5.2 (continued)

Source	Secondary metabolites	Activity	Class	References
T. viridae	Viridepyronone	Antifungal to *Sclerotium rolfsii*	Polyketides	Evidente et al. (2003)
T. harzianum	6-(1′-pentenyl)-2H-pyran-2-one	Antifungal	Polyketides	Claydon et al. (1987), Parker et al. (1997)
Trichoderma sp.	Cytosporone S	Antibacterial and antifungal	Polyketides	Ishii et al. (2013)
T. viride, T. atroviride, T. koningii, T. harzianum	6-pentyl-2H-pyran-2-one	Antifungal, anti-nematode and enhances growth in tomato and *Arabidopsis thaliana*	Polyketides	Garnica-Vergara et al. (2016)
Pestalotiopsis sp.	Polyketide terpene metabolites	Antifungal to *F. oxysporum* and *F. gramineum*	Polyketides	Yuan et al. (2017)
Hormonema dematioides endophyte of balsam fir	Rugulosin	Insecticidal	Polyketides	Calhoun et al. (1992)
Endophytic fungus of *Larix laricin*a needle	1′,5′-trihydroxy-3′,4′dihydro-1′H-[2,4′] binaphthalenyl-1,4,2′-trione	Toxic to spruce budworm larvae	Polyketides	Findlay et al. (1997)
Alternaria spp., *Phoma sp.*	Altersolanol A	Antibacterial	Polyketides	Yang et al. (1994)
T. viridae	Pachybasin, chrysophanol and emodin	Growth reduction of *F. annosus*	Polyketides	Donnelly and Sheridan (1986)
Blennoria sp. endophyte of *Carpobrotus edulis*	Secalonic acid B	Antimicrobial to *Bacillus megaterium* and *M. violaceum*	Polyketides	Zhang et al. (2008)
Blennoria sp. endophyte of *Carpobrotus edulis*	Blennolides A, B, D and E	Antimicrobial	Polyketides	Zhang et al. (2008)
Coniothyrium sp., endophyte of *Salsola oppostifolia*	Phomarin and coniothyrinone A	Antifungal to *Botrytis cinerea* and *M. violaceum*	Polyketides	Sun et al. (2013)

(continued)

Table 5.2 (continued)

Source	Secondary metabolites	Activity	Class	References
Fusarium sp., Chloridium sp.	Javanicin	Antifungal to *V. dahliae*, *F. oxysporum*, *R. solani*, and *C. arachidicola*	Polyketides	Kornsakulkarn et al. (2011)
Delitschia corticola	6-ethyl-7-hydroxyl-2-methoxyjuglone, 6-ethyl-2,7-dimethoxyjuglone and 6-(1-hydroxyethyl)-2,7-dimethoxyjuglone	Antifungal to *Fusarium* sp., *Alternaria* sp. and *Sclerotium* sp.	Polyketides	Sun et al. (2011)
Cordyceps dipterigena	Cordycepsidone A	Antifungal to *G. fujikuroi* and *P. ultimum*	Polyketides	Varughese et al. (2012)
Phomopsis sp. endophyte of *Santolina chamaecyparissus*	Phomopsinone A	Antifungal to *P. oryzae*, *S. tritici*, and *B. cinerea*	Polyketides	Hussain et al. (2012b)
Phomopsis sp. endophyte of *Santolina chamaecyparissus*	Phomopsinone D	Antifungal to *B. cinerea* and *S. tritici*	Polyketides	Hussain et al. (2012c)
Phomopsis sp., endophyte of *Cistus salvifolius*	Pyrenocines K and M	Antifungal to *M. violaceum* and *S. tritici*	Polyketides	Hussain et al. (2012a)
Phomopsis sp., endophyte of *Cistus salvifolius*	Pyrenocine J	Antifungal to *S. tritici*.	Polyketides	Hussain et al. (2012a)
Phomopsis sp.	Phomochromone A and B	Antifungal to *S. tritici*, *B. cinerea*, *B. megaterium*, *M. violaceum*	Polyketides	Ahmed et al. (2011)
Pezicula sp.	Mellein	Antifungal to *B. cinerea* and *Fulvia fulva*	Polyketides	Wang et al. (2014)
Berkleasmium sp.	Palmarumycin C_8	Antifungal to *Magnaporthe oryzae*	Polyketides	Shan et al. (2014)
Seimatosporium sp.	Seimatoporic acid A and B	Antifungal to *S. tritici*, *P. oryzae* and *B. cinerea*	Polyketides	Hussain et al. (2012b)

(continued)

Table 5.2 (continued)

Source	Secondary metabolites	Activity	Class	References
N. uncinatum and *N. coenophialum* endophyte of *F. pratensis* *F. arundinacea*	Lolines	Insecticides and feeding deterrents	Alkaloids	Schardl and Phillips (1997)
E. typhina, *N. coenophialum*, *N. lolli*, *E. festucae*	Peramine	Insecticidal to Argentine stem weevil	Alkaloids	Dew et al. (1990), Rowan and Latch (1994)
Neotyphodium	Indole alkaloids: elymoclavine, agroclavine and chanoclavine	Insecticide	Alkaloids	Powell and Petroski (1992), Schardl and Phillips (1997)
Neotyphodium endophytes	Endophyte alkaloids	Enhanced growth rate, reproduction and herbivores resistance	Alkaloids	Clay and Schardl (2002), Faeth (2009), Müller and Krauss (2005)
Phomopsis sp. from *Cavendishia pubescens* tree bark, *Aspergillus flavus*	Aspalitrems A and C	Toxic to insects and vertebrates	Alkaloids	Bills et al. (1992)
E. purpurascens, *A. pullulans*, *Colletotrichum* sp., *A. coenophialum* endophytes of *Artemisia annua*	Indole-3-acetic acid	Major plant growth promoting hormone	Alkaloids	Petrini (1991)
Hypoxylon serpens	IAA and 3-indoleacetonitrile	Major plant growth promoting hormones	Alkaloids	Petrini (1991)
T. atroviride, T. virens	Indole-3-carboxaldehyde	Stimulates adventitious root formation in *Arabidopsis thaliana*	Alkaloids	Contreras-Cornejo et al. (2011)
T. atroviride, T. virens	Indole-3-acetaldehyde	Influences root growth in *Arabidopsis thaliana*	Alkaloids	Contreras-Cornejo et al. (2009)

(continued)

Table 5.2 (continued)

Source	Secondary metabolites	Activity	Class	References
Colletotrichum sp. endophyte to *Artemisia. annua*	6-isoprenylindole-3-carboxylic acid	Antifungal to *R. cerealis*, *G. graminis var. tritici* and *P. capsici*	Alkaloids	Lu et al. (2000)
T. harzianum	Racemic harzianopyridone	Antifungal to *P. ultimum, G. graminis var. tritici, B. cinerea* and *R. solani*	Alkaloids	Dickinson et al. (1989), Vinale et al. (2006)
T. harzianum	Laevorotatory form of harzianopyridone	Phytotoxic to etiolated wheat coleoptile	Alkaloids	Cutler and Jacyno (1991)
S. mobaraensis, *S. pactum*	Piericidin A	Insecticide	Alkaloids	Jansen and Höfle (1983), Takahashi et al. (1965)
Penicillium sp.	Atpein compounds	Antifungal	Alkaloids	Kumagai et al. (1990), Omura et al. (1988)
Trichoderma sp. ATF-451	Melanoxadin and melanoxazal	Inhibition of melanin in larval hemolymph of *Bombyx mori*	Alkaloids	Hashimoto et al. (1995), Takahashi et al. (1965)
T. harzianum, *T. arundinaceum,*	Harzianic acid	Antimicrobial and plant growth regulation	Alkaloids	Malmierca et al. (2013), Sawa et al. (1994)

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Chapter 6
Fungal Endophytes: A Source for Biological Control Agents

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Contents

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6.1 Introduction

Endophytes are the hidden microflora that live inside the plant for a part or lifetime within the plant tissue and promote the plant to fight against odd conditions like physiological stress, microorganism attacks, thus produce a wide range of bioactive compounds with deep industrial or agricultural application (Yadav et al. 2020a, d). Endophytes have been exploited for their novel bioactive compound production for a long time but in recent past emphasis has been given by the endophyte biologist regarding their use in agricultural sectors for minimizing the crop loss caused by fungal pathogenic attack as well as insect, burrowing nematode, flies, and moth infections (Rana et al. 2019). It has been evidenced by scientists from all over the world that endophyte has been proved to be an appropriate agent in this respect and due to its organic origin the products are found to be biodegradable and does not hamper the natural sustainability at all (Yadav et al. 2019a, b). So nowaday the trend has been shifted to endophytes with mycofumigating or biocontrol ability for minimizing the use of chemical insecticides or fungicides. Some endophytic genus like *Muscodor albus* is reported to be the storehouse of a wide and diverse range of volatile bioactive product with anti-pathogenic activity and this volatile antimicrobial producing endophyte is widely used in agricultural lands for minimizing fungal pathogen mediated crop loss or for reducing the economic loss caused by the fungal toxins during food transport or storage.

The isolation of novel endophyte is dependent on the screening of plant as plants with particular odor or inhabiting in tropical rain forest are known to harbor greater diversity of endophytic genus as those environments are supportive for endophytes survival. As they share necessary characters with their host plants they are easy to exploit for bioactive compound production (Rastegari et al. 2020a, b; Yadav et al. 2020b, c). The crying need of this modern era of science is the maintenance of sustainability on the one hand and development of biological tools with no negative impact on environment for solving the fungal pathogenesis issues on the other hand. Fungal pathogens are known to be the prime agent for agricultural crop loss. This chapter summarizes the remarkable scientific works related to the endophytic fungi with their biocontrol ability on common and severe dreadful agricultural pathogens in vitro and in vivo conditions.

6.2 Detection of Antifungal Activity

Plants of medicinal importance or with special characters are selected for endophytic fungi isolation and plant parts are washed in tap water thoroughly for the avoidance of surface microbes. Plant parts are cut into small pieces and surface sterilized using sodium hypochlorite or 80% ethanol and immediately flamed in spirit lamp for 5–10 s. Then they are plated on water agar medium supplemented with 2% of agar (Fig. 6.1). After proper incubation at 28 °C for 24–72 h when the first hyphae comes out from the plant segments they are immediately transferred to a medium containing selective media supplemented with antibacterial streptomycin

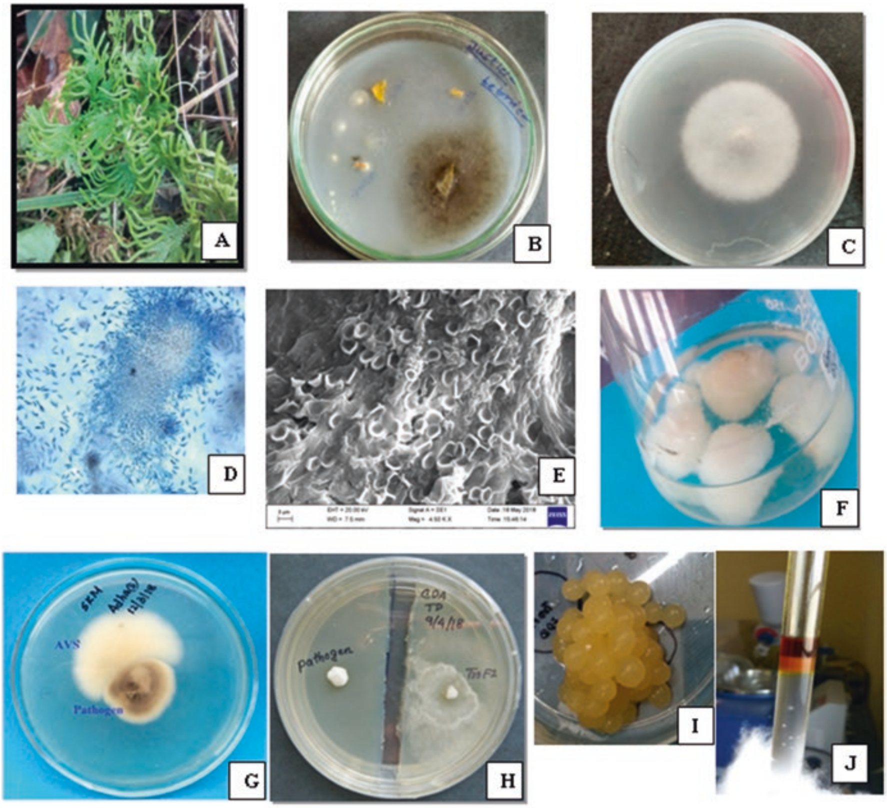

Fig. 6.1 (**a**) *Selaginella* sp., a pteridophytic genus; a source of endophytic fungus. (**b**) Water agar plate with the explants; an endophytic fungus emerges out from that explant. (**c**) Plate morphology of the pure culture of the endophytic isolate. (**d**) Light microscopic view of the endophytic isolate showing the spores. (**e**) Scanning electron microscopic view of the fungal spores. (**f**) Round fungal colony in culture broth. (**g**) Antagonistic activity of the endophytic isolate against the pathogen in dual culture assay. (**h**) Split plate showing the inhibition of the pathogen by endophytic volatiles. (**i**) Fungal morphology in liquid culture. (**j**) Crude extract put into column for purification of active compounds

and potato dextrose agar as growth substance. After successful isolation they are identified by their microscopic morphology (scanning electron micrographs are also taken), colony characters, and using molecular biology methods (Fig. 6.1). The endophytic isolates are then tested for their antagonistic ability by dual culture plate assay and the diameters of the both the pathogen and the fungal growth are recorded and the clear zone of inhibition is recorded, this is called as antagonistic activity of the endophytic fungal isolates (Fig. 6.1). Next the potent isolates are screened for their culture broth assay.

The fungal blocks are transferred to the culture broth provided with potato dextrose medium and agitated in 120 rotations per minute (rpm) in shaker incubator. The culture broth are filtrated and mixed with ethyl acetate and bioactive compounds are extracted. The extracted liquid is tested for their antifungal activity in agar well diffusion technique and the clear zone of inhibition is measured immediately after 12 h of incubation. The antifungal compounds are isolated using purification techniques based on column chromatographic procedures and further identification is done by IR spectral analysis and using HPLC technique (Fig. 6.1). For the detection of volatile antifungal emissions of the endophytic isolates split plate assay is performed where at one side endophytes is placed and on the other side the targeted pathogen is inoculated and on successful volatile emission the pathogen growth would be inhibited (Fig. 6.1). The volatile organic compounds (VOCs) are recorded using the GC-MS instrument. The volatiles are detected by growing the fungal mycelium on specialized GC vials and then finally comparing the chromatographic spectra with the NIST library (Fig. 6.2). The chemical compounds are checked in vitro or in vivo using standards and they are noted as the bioactive chemicals of endophytic origin (Fig. 6.3).

6.3 Biocontrol of Nematodes

Endophytic microorganism especially fungus not only inhibits the growth of the pathogenic fungus in vitro but also in in vivo conditions. Reports include the inhibition of mycelial growth of the *Fusarium oxysporum* F.sp. Cubense, the causal agent of panama disease by the endophytes (Pocasangre 2000). The endophytes are also reported to inhibit the growth of the burrowing nematode *Radopholus similis* that causes potential damage in banana plant crop production. So use of endophyte for the control of nematode and pathogenic fungus is a new approach.

Pederson and his co-workers in the year of 1988 worked on the effect of endophytic fungus (*Acremonium coenophialum* Morgan-Jones and Gams) of tall fescue on the behavior of the nematodes associated with the host plant's infection. They reported that the removal of endophyte from the plant *Festuca arundinacea* Schreb. (Tall fescue) is increasing the susceptibility of the nematodal (lower spiral [*Helicotylenchus dihystera* (Cobb) Sher.] and stubby root [*Paratrichodorus minor* (Colbran) Siddiqi]) infection. They performed experiments taking soybean plants and tall fescue plants with rye grass cultivars (annual and perennial). Finally there

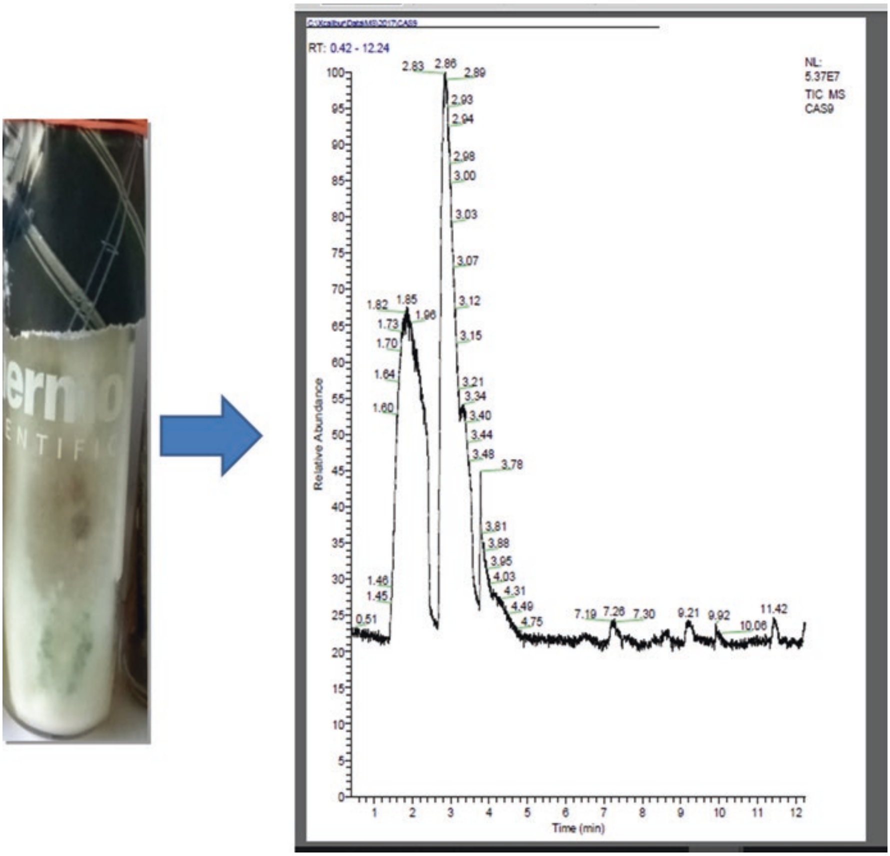

Fig. 6.2 Endophytic isolates is grown on specialized GC vials and the volatile compounds emitted are detected in GC-MS resulting in the development of complete chromatogram of 12 min run

motto was to check the ability of the double cropping system (nematode susceptible soybean cultivars and annual rye grass) to eliminate the nematodal infection. They experimented with 13 annual rye grass cultivars, nematode susceptible soybean, and tall fescue plants with or without *Acremonium coenophialum* infection. After 7 weeks of continuous growth in pots of green house with a soil of sandy or fine loam infected with huge numbers of phytonematodes they ended up with the conclusion that nematode infection sensitive soybean plants are not affected and their growth or annual production is not affected but tall fescue stand decline has occurred.

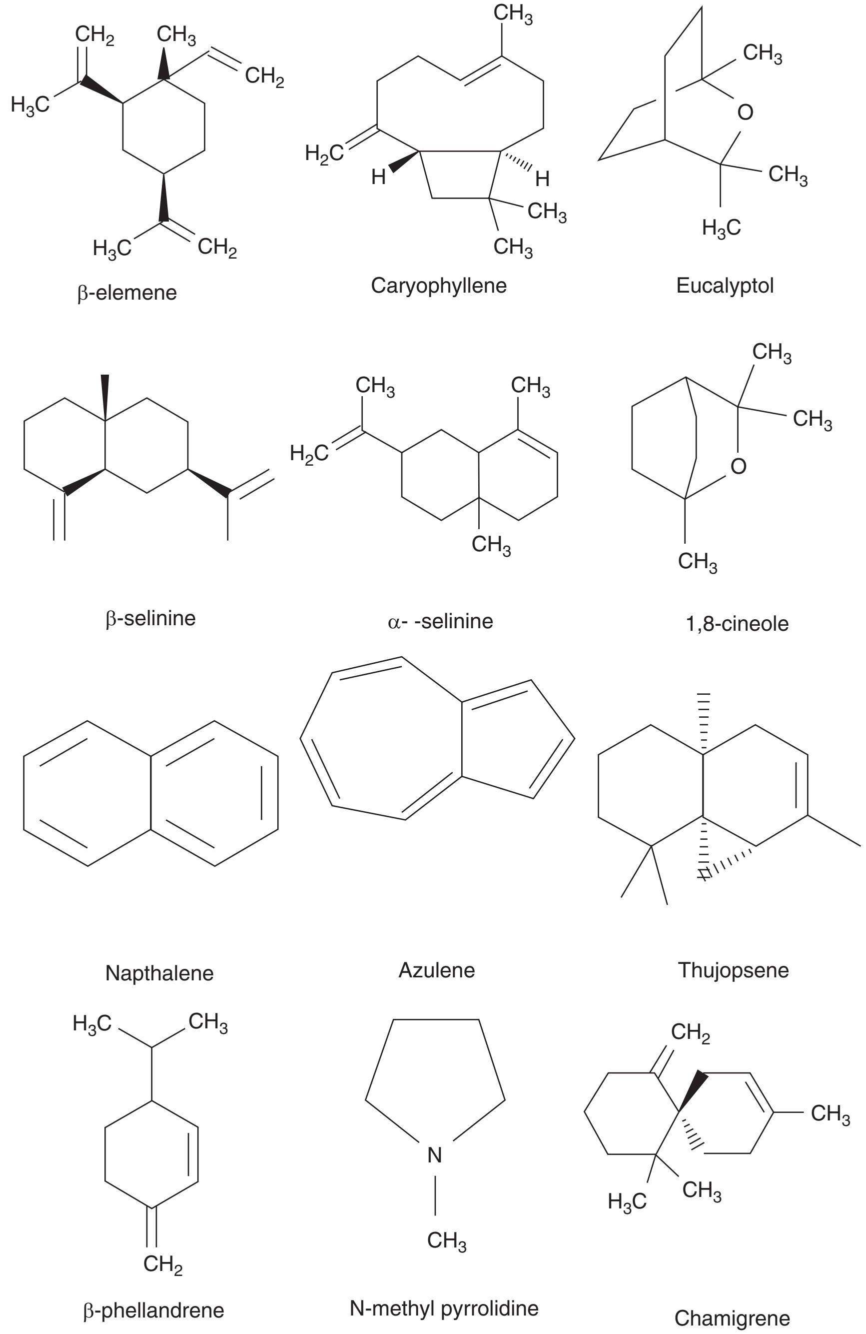

Fig. 6.3 Chemical structures of the volatiles emitted by the endophytic volatiles

6.4 Reduction in Number of Gall Formation of *Meloidogyne* Incognita by *Lolium perenne* Endophytes

Stewart and his scientific partners in the year of 1993 worked on the infection of *Meloidogyne naasi* Franklin on endophyte infected as well as non-endophyte infected perennial rye grass and evaluated the gall formation (in quantitative measurement) and proliferation of this gall forming nematode. Lolium perenne L. is globally called as the Perennial rye grass and has been a major plant of New Zealand. Earlier reports include that this plant is susceptible to the infection of gall forming nematode (Sheridan and Grbavac 1979). Acremonium spp. has been reported to protect rye grass from Argentine stem weevil pathogen but there had been no previous report on the effect of this endophytic species on gall formation mediated by *M. naasi* (Popay and Mainland 1991). Seeds of the experimental grass were sown in 5 cm pots filled with 50:50 mixtures of silt-loam soil and sand (pasteurized) and thinned to individual pots after germination. Occurrence of endophyte was confirmed microscopically by staining of leaf sheath with lacto-phenol cotton blue. Infection procedure includes the application of 3 mL water to all the plants by syringe into a pencil hole made on the plant body after 21 days of complete emergence. Ten endophyte infected and ten free pots were provided with nematode inoculum and the other set got only water. Final observation was made after the proper supply of nutrients and maintenance of the plants in glass house at 18–24 °C and separation of root from soil followed by the counting of number of galls per root sample. Not only the number of gall decreased but also the number of females present in each root sample of the endophyte treated plants was lesser in number in comparison to the endophyte treated one. Absence of juvenile ones was also a remarkable observation. This type of observation supports the results of experiments on similar area performed by Pederson et al. (1988), Kimmons et al. (1990), and Kirkpatrick et al. (1990).

The results are of complete conclusion with Cook et al. (1991). The probable explanation of the deviation of the result could be drawn from observations of Kirkpatrick et al. (1990) that differences among endophytes isolates or in interactions between host genotype and fungal isolate are important. The occurrence of lower number of galls and females support the fact that endophytes resistance occurred early in the plant and nematode interaction. The probable explanation of this type of enhanced resistance like reduced invasion and increased emigration of juveniles or death of nematodes in the roots is due to the toxins produced by the endophytic fungus produced in the roots that repel or kill nematodes. This concept is also supported by the investigations of Siegel et al. (1989) that emphasized the production of toxins by the endophytic fungus and also the presence of endophytic fungus increased resistance.

6.5 Control of European Pepper Moth by Endophytes of Strawberry

Fragaria ananassa (Sc, name of the strawberry plant) is an economically important fruit plant worldwide and is affected by a large number of bacterial, fungal, viral, and nematodal pathogens. Such an example is the occurrence of nematodal pest *Duponchelia fovealis* Zeller, 1847, a member of Lepidoptera: Crambidae (the European pepper moth). Being native to marshy habitats of Southern Europe and eastern part of Mediterranean region this nematode is a green-house pest of flowers, fruits, and vegetables of aquatic and terrestrial plants found abundantly in Europe and Canada (CABI 2016) and recent reports include its invasion on strawberry plants (Bonsignore and Vacante 2009; Franco and Baptista 2010; Efil et al. 2014; Zawadneak et al. 2016). The popular control measures include chemical and physical controls with huge amount of side effects and natural enemies are also not effective against this nematode as this is considered to be an exotic species (Zawadneak et al. 2015). So focus is on endophytic fungus being the best suitable method in this respect. Endophyte isolated from strawberry plant is used as a biological control agent against the strawberry nematode pathogen (Amatuzzia et al. 2018).

In total 400 leaves of the strawberry cultivar “Albion” collected from four different commercial farms were placed into potato dextrose agar Petri-dishes after proper disinfection of the explants and maintained in incubation for 30 days with tetracycline supplemented media. Out of 517 fungal colonies some of them are identified as *Alternaria* sp., *Aspergillus* sp., *Bipolaris* sp., *Cladosporium* sp., *Chaetomium* sp., *Diaporthe* sp., *Fusarium* sp., *Nigrospora* sp., *Paecilomyces* sp., *Penicillium* sp., *Phoma* sp., *Trichoderma* sp., and *Ulocladium* sp. Eight isolates (belonging to genera *Aspergillus*, *Cladosporium*, *Diaporthe*, and *Paecilomyces*) were found to be effective against third instar larvae of *Duponchelia fovealis*. Isolates *Paecilomyces* sp. exhibited highest effectivity against the nematodal larvae.

6.6 Biocontrol of Sirex Wood-Wasp by Endophytic Isolates

Sirex noctilio also called as Sirex wood-wasp is a horntail species generally found as a native one to Asia, Europe, and northern parts of Africa. This wasp species is involved in a symbiotic relationship with a fungus *Amylostereum areolatum* that promotes the invasion of the wasp into the tree trunk by boring the trunk and the larvae are generally feed on the fungal hypha. Fungus also helps the invasion by secreting mucus like materials. Wang et al. in the year of 2019 selected nine species of Pinus in China; *Pinus tabuliformis*, *Pinus sylvestris*, var. *mongolica*, *Pinus koraiensis*, *Picea koraiensis*, *Larix gmelinii*, *Pinus yunnanensis*, *Pinus massoniana*, *Pinus taeda*, *Pinus elliottii* and evaluated the effect of endophyte diversity on the *Sirex noctilio* infection in terms of their oviposition behavior. They isolated a total number of 1626 endophytic fungi from 2025 explants (wooden blocks) of nine selected coniferous tree species and identified them by ITS (internal transcribed spacer) sequencing system. Each host plant is characterized by a unique structure of endophytic community and that varies from one host plant to another and from one region to another. The isolates belong to 61 species under 34 genera. Fifty-one out species (83.40%) were confirmed through molecular identification and ten species (16.60%) were identified by microscopic morphological characters. The isolates belong to the genera of *Alternaria* sp., *Arthrinium* sp., *Ascocoryne* sp., *Aspergillus* sp., *Capronia* sp., *Chaetomium* sp., *Coprinopsis* sp., *Cylindrobasidium* sp., *Cytospora* sp., *Diaporthe* sp., *Fusarium* sp., *Gliocladium* sp., *Gliomastix* sp., *Lasiodiplodia* sp., M*ucor* sp., *Ophiostoma* sp., *Paecilomyces* sp., *Paraconiothyrium* sp., *Penicillium* sp., *Pestalotiopsis* sp., *Peyronellaea* sp., *Phaeomollisia* sp., *Phoma* sp., *Phomopsis* sp., *Pythium* sp., *Schizophyllum* sp., *Seiridium* sp., *Sphaeropsis* sp., *Sydowia* sp., *Trichoderma* sp., and *Umbelopsis* sp. CR (colonization rate) and IR (isolation rate) of endophytes from *Pinus tabuliformis* were the lowest and were the highest for *Pinus elliottii*. CR and IR values for other species were of no such significant deviation. The endophytic community also varied from different portions of the same species like base portion, central part, and also upper portions of the trunk of the Pine tree. The chances of getting infected by this wasp is negatively proportionate to the diversity of the endophytic fungus in Pinus plant as the higher occurrence of infection is due to the poor diversity of endophytic fungus in the host plant. Results are indicative that out of the nine tested coniferous plant the highest chances of getting infected by wasp is in case of *Pinus tabuliformis* and lowest in case of *Pinus elliottii* and intermediate in case of others due to the lower occurrence of endophytic species in case of *P. tabuliformis*.

6.7 Endophytic Fungal Isolates Against Cotton Leaf Worm (*Spodoptera littoralis* (Boisd.)

Saad et al. (2019) isolated ten endophytic fungus from four angiospermic plants (two were medicinal plants and two were weeds); *Pelargonium graveolens* (Geraniaceae), *Melia azedarach* (Meliaceae), *Chenopodium album* (Chenopodiaceae), and *Malva parviflora* (Malvaceae). The isolates of *C. album* were identified as *Fusarium chlamydosporum* saad3 MG786540, *Alternaria alternata* saad5 MG786542, *Alternaria alternata* saad8 MG786545, *Fusarium oxysporum* saad4 MG786541, *Phoma* sp. Two endophytes were identified from each of the plants (*Melia azedarach* and *Malva parviflora*) as *Curvularia lunata* and *Nigrospora sphaerica* saad1 MF113055 and *F. equiseti* saad7 MG786544 and *Stemphylium* sp., respectively. And only one is isolated from aromatic plant species of *P. graveolens* identified as *Alternaria solani* saad6 MG786543. They tested the spore suspension of *A. alternata*, *A. solani*, *C. lunata*, *N. sphaerica*, and *Stemphylium* sp. against the third instar larvae of cotton leaf worm scientifically named as *Spodoptera littoralis* (Boisd.) belonging to order Lepidoptera and family Noctuidae. Two popular techniques were used for this assay that includes either dipping in spore suspension or residual film technique.

The endophytes were screened having their insecticidal capacity by calculating the mortality rates of the larvae. In residual film technique no such endophytic fungus yielded positive results. Secondary metabolites were subjected to isolation from the endophytic isolates in order to evaluate their insecticidal property using ethyl acetate as a standard organic solvent for the effective extraction. Dipping assay revealed the insecticidal property of the isolates named *C. lunata*, followed by *A. solani* and *A. alternata*, respectively, with a mortality percentage of 60% as highest among all the tested ones, 40% and 33.3%. This type of study strongly evidences the fact that endophytic secondary metabolites are effective in vivo against the larval infection.

6.8 Endophyte Mediated Plant Volatiles Restrict *Planococcus ficus* Infection

A unique study had been performed in recent past by Moloinyane and Nchu (2019) on the effect of endophytic fungus on insect (*Planococcus ficus*) infection. They actually tested the efficiency of the fungus to modify the host plant in terms of volatile compounds production with insecticidal activity. *Beauveria bassiana* (Hypocreales), an entomopathogenic fungus is a common parasite of insects and is distributed worldwide. They isolated *B. bassiana* from soil sample of grape vineyard and inoculated the fungus (1×10^8 conidia mL^{-1}) on grape vine (*Vitis vinifera*) and again re-isolated the fungal species from the grape plant leaves after 25 days from the first inoculation. The effect of inoculation has led to production of unique volatile compounds with insecticidal compounds like benzaldehyde (Paulraj et al. 2011), limonene (Hebeish et al. 2008), geraniol (Chen and Viljoen 2010), geranylacetone (Maia and Moore 2011), gamma-terpinene (Wang et al. 2006), beta-Pinene (Dambolena et al. 2016), napthelene (Daisy et al. 2002), M-Cymene (Chang et al. 2002), Citral, naphthalene, 2-hexanoic acid, terpinolene, benzene, benzofuranone, heptadecane, nerolidol, pentanoic acid. The occurrences of these insecticidal compounds increase the plants' resistance by reducing the number of female nematodes and their infestation activity. The re-isolation confirms the endophytic nature of the phytophagous fungus and inoculation is done before the artificial inoculation of *Planococcus ficus* on *Vitis vinifera*. Though plant growth parameters were not (N, P, K, Na, Mn, Fe, Cu, Zn, B contents of leaf) sharply deviating from the fungus treated and untreated Vitis plant but there was a change in (calcium) Ca and (magnesium) Mg content of the plant leaf tissues. This type of study elaborates the fact that endophytic fungi are effective against insects of economically important plants also, thus, enhancing the plants' protection.

6.9 Biocontrol of *Radopholus similis* (Root Burrowing Nematode) by Banana Endophytes

Radopholus similis also known as the burrowing nematode is a devastating pathogen of banana (*Musa paradisiaca*) and has led to qualitative and quantitative decrease of the yield. It is an agent of root rot causing reddish brown lesions in the cortical portions of the root and hampering the water conduction, nutrient uptake leading to the lengthy vegetative cycle and finally to the death of the plant (Gowen and Quénéhérvé 1990). Chemical control measures being too much expensive and non-eco-friendly lead to hazardous problems of human health. Till date a very few reports include development of complete resistant banana species against the banana plant (Gowen 1995). Scientist has moved to biological methods for this reason (Kerry 1990 and Sikora 1992). Endophytes could be an alternative solution in this respect (Hallmann and Sikora 1994; Schuster et al. 1995). Some fungal species are reported to be anti-endoparasitic (Sikora 1992; Schuster et al. 1995). Previously endophytic fungus isolated from banana root tissue has been checked for the anti-nematodal activity in vitro by culture filtrate assay (Schuster et al. 1995).

Niere et al. (1999) investigated the in vivo and in vitro effectivity of the *Fusarium oxysporum* isolates (from banana root) against burrowing nematode and also their influence on plant growth. They prepared PDB (potato dextrose broth) culture extracts with spore suspensions (1.4–3.2 × 106 spores/ml) of 4 selected isolates V4w5, III3w3, III4w1, and V5w2 and inoculated them on the previously tested (in vitro) banana seedling (Musa AAA, cv. Gros Michel) raised through tissue culture techniques (Vuylsteke 1989). The plantlets were potted in 100 ml cups with sterilized soil filled in it and after 4 weeks transferred to carry bags containing 2 l of sterilized soil. Two set of experiments were carried out just having the difference between the time (one setup of 13 weeks aged and another of 32 weeks aged). Plants were removed from the polythene bags and after gentle wash of the roots they were inoculated with 10 *Radopholus similis* females singly collected from soil populations and kept directly on the root surface. Then they are infected with fungal endophytes for the observation of their morphological changes at 4 weeks constant interval. Beginning 6 weeks after nematode inoculation (plant age 19 and 38 weeks, respectively), the root segments inoculated with the nematode in the cup were cut free from the intact root and the nematodes extracted overnight by the extraction dish method (Oostenbrink 1960). All nematodes extracted were concentrated on a 20 μm sieve and counted.

Endophyte treated plants are reported to be enhanced in their growth parameters by 11–25%. After the complete removal of soil, transplantation of the plant and nematodal infection Fo1 is known to be promoting plant height by 29% in relation to the control plant. The nematode multiplication rate is reduced in plants treated with endophytic isolates. The reduction rate varied but Fo4 is proved to be the potent one regarding the reduction in number (26% than the control, i.e., untreated plant) of nematode population in a 19-weeks-old root segment whereas the nematode population increased up to 33% (in comparison to the initial number of nematode) in a

38-week-old control (without any endophyte inoculation) plant. The nematode populations were reduced from 51% to 99% after the endophytic treatment.

6.10 Muscodor Albus Volatiles Control Codling Moth in Storage Conditions

Codling moth (Sc. Name—*Cydia pomonella* (L)) belongs to the group Lepidoptera and class Torticidae is known to be a harmful pest pathogen of apple fruit (*Malus* spp.). It is one of the giant causes of worldwide severe economic loss in pome fruit marketing. Chemical fumigants like methyl bromide are restricted due to quarantine issues in case of international import and export. So there is an urgent need for the discovery of effective moth inhibiting agents with minimum amount of side effects. In this regard endophytic fungus from medicinal plant has been an effective alternative. Such a remarkable work had been done by Lacey and his co-workers in the year of 2009. They collected the endophytic *Muscodor albus* Worapong, Strobel, and Hess (A member of Ascomycota; family—Xylariaceae) and evaluated the bioactivity of the volatile compounds emitted by the endophytic isolates against the growth and development of the different stages (codling moth adults, diapausing cocooned larvae, larvae in infested apple, neonate larvae) of codling moth.

The fumigation of the adult moths with *M. albus* VOCs for a continuous exposure of 72 h and immediate incubation in fresh open air for 24 h time at a temperature of 25 °C leads to 81% mortality of the total larvae. When the time of treatment or exposure is enhanced to 48 h or 120 h the mortality increased from 84% to 100%. The control apple fruits were also found to be with dead moths due to their short life span. Treatment of neonate larvae for 72 h on apple fruits and then immediate incubation for 7 days resulted in 86% of mortality. The larvae were mostly of third instars stage and when apples infested (for 5 days) with moth larvae exposed to volatiles for 3 continuous days 71% mortality occurred. Not only that the diapausing cocooned moth larvae when exposed to volatile organic compounds for one or 2 weeks resulted in 31% to 100% of mortality. So this type of biocontrol ability of endophytic *M. albus* opens up new popular angles of environment friendly techniques for the broad spectrum protection of economically important plants like apple from pest devastation.

6.11 Biological Control of PTM-Potato Tuber Moth (Sc. Name: *Phthorimaea operculella*)

Potato tubers are one of the major vegetable products of the world with several uses in the food and junk food industry. *Solanum tuberosum* (potato) is a plant of Solanaceae family and has been subjected to a large number of fungal, bacterial, and viral pathogens leading to mass destruction of potato farms. One such pathogen is PTM (potato tuber moth) scientifically named as *Phthorimaea operculella* (Lepidoptera: Gelechiidae) found all over the world as a serious pest of potato tubers on field and in storage conditions in the countries especially where potato tubers are grown. Biological control of this serious pest has been performed by the unique volatiles of the novel endophytic fungus *Muscodor albus* (Lacey and Neven 2006). The volatile antimicrobial includes alcohols, esters, ketones, acids, and lipids and shows insecticidal activity. They exposed adult and neonate larvae to the VOCs generated by *M. albus* sterile mycelium (15 g or 30 g) for 72 h at 24 °C in a sealed 28.3 L chambers. When the mycelial weight of *M. albus* is increased from 0 to 15 g and finally to 30 g as a source of volatile exposure the mortality increased from 84.6% to 90.6%, respectively. When the pupal stages were exposed to 15 g and 30 g of *M. albus* culture their growth reduced by 61.8% and 72.8% in relation to control conditions.

The time of exposure is also a valuable parameter for the control of PTM. Though the higher exposure leads to the accumulation of excess CO_2 generated by the respiration of the endophytic fungus *M. albus* which is harmful for tuber storage but still exposure for 3 days, 7 days, and 14 days and incubation at 27 °C leads to the increased mortality of 84.2%, 95.5%, and 99.6%, respectively. Increased exposure significantly affected on mortality of larvae; determined in terms of percentage as larvae fail to survive to the adult stage. Temperature for incubation has a direct effect on larval death and studies are indicative that lower temperature leads to reduced mortality, so this type of biological control measure is effective in warm and humid countries where potato tubers grow generally at 25–35 °C. When the temperature are fluctuated from 10 °C to 15 °C and finally to 24 °C with an exposure of 7 days followed by clean air incubation at 27 °C the mortality rates are 50.8%, 76.8%, and 95.4%, respectively (Lacey et al. 2008). Storage conditions and degree of cooling are also valuable factors for using this biocontrol method. So this study clearly states the fact that if some correction could be made like the excess CO_2 production *M. albus* volatiles could be an effective tool in this respect. Proper detection of volatiles in GC-MS and preparation of artificial mixtures of those chemicals could replace the harmful side effects of other measures of pest control.

6.12 Entomopathogenic Fungi Affecting *Aphis gossypii* Infections on Melon Plants (*Cucumis melo* var. *cantalupensis*)

Aphid control has been a grave problem for the farmers and agriculturalists as they not only involve direct damage of crops but also are effective agents of transmission of economically important plant virus (Van Emden and Harrington 2007). Aphids are characterized with high fecundity rates and short lifetimes as a result they grow rapidly (Dixon 1998). Chemical control leads to development of resistance.

Entopathogenic fungi here play a vital role for biological control measure (Brodeur et al. 2018). A high percentage of fungus that infects aphids belongs to Entomopthoromycota and Ascomycota (Order Hypocreales) and the Ascomycota members are highly commercialized due to their fast mass production in vitro and easy spray formulation (Burges 1998). The myco-insecticides are environmentally safe and meet the guidelines of legislation requirements (Lacey et al. 2005). They are not only used in spraying, drenching, and seed dressing but also as endophyte for protecting the plant (Quesada-Moraga et al. 2009; Sánchez-Rodríguez et al. 2018). Using entomopathogenic fungi as a tool for the biological control of aphids is one of the possible measures of plant protection especially in green house conditions.

González-Mas et al. (2019) study on the behavior of entomopathogenic fungi as an endophyte of those treated plant and evaluated the enhancement of resistance against the aphid attack. Generally *Beauveria bassiana* and *Metarhizium brunneum* acts as common entomopathogens of serious pest like aphid; *Aphis gossypii* and protect the economically important vegetable crops that are largely affected worldwide regarding their quality and quantity of production due to this type of pathogenic aphid attack. They studied that when the entomopathogen is sprayed on the leaves of the host melon plant (*Cucumis melo* var. *cantalupensis*; Family-Cucurbitaceae) they acted as endophyte and infected the host plants leaf tissues. This statement was confirmed by the successful isolation (100% for infected leaves and 20–40% for non-sprayed leaves) of that fungus again from leaf tissues as an endophytic one. These herbivores' life table parameters and behavior are drastically affected by the endophytic nature of this fungus. Investigations were made on lethal and pre-mortality rates of those two entomopathogens on the cotton aphid (*Aphis gossypii*). The effect of endophyte on the mortality rates were determined either by feeding the aphid population on endophyte colonized leaves or on endophytic fungus sprayed leaves. The comparison were made by feeding the larvae on un-colonized leaves. Mortality rates of this Hemiptera aphid were found to be between the values of 37.70–50.00% in case of endophyte colonized leaves and in comparison to fungus sprayed leaves where the values ranged between 48.2% and 56.9%.

The nymph productions were also affected by endophytic colonization. Though endophytic colonization had no drastic effect on aphid control but plants are benefitted by indirect methods like defense enhancement, resistance development to plant pathogens, and also abiotic stress tolerance. Endophytic colonization on plants largely affects the volatile emissions of those plant tissues in contrast to the controlled or untreated plants. The VOCs were recorded using GC-MS and by comparing with standards. The volatiles emitted by the crushed homogenized melon plant tissues fall under several chemical classes like aldehyde, alcohols, ketones. The major aldehydes are 2-pentenal, 2-heptenal, 2-octenal, 2-nonenal, 2-hexenal, 2,4-hexadienal, 2,4-heptadienal, 2,6-nonadienal, 3-methyl-hexanal, 3-methyl-butanal, 4-heptenal, 4-oxohex-2-enal, 5-methyl-hexanal, 6-nonenal, butanal, hexanal, heptanal, nonanal, octanal, pentanal. The predominant alcohols include ethanol, 1-octen-3-ol, 1-penten-3-ol, 2-hexen-1-ol, 2-propyl-1-pentanol, 2-ethyl-1-hexanol, 3-hexen-1-ol, 4-methyl-1-pentanol. The keton bodies are 6-methyl-2-heptanone, 3-octanone, 6-methyl-5-hepten-2-one, 3,5-octadien-2-one. Chemical compounds like 2,2,6-trimethyl-cyclohexanone, β-cyclocitral, β-citral, β-ionone, eucarvone, geranial, isomethyl-α-ionone were also recorded.

Phenolic derivatives include 2-phenyl-isopranol, acetophenone, benzaldehyde, benzophenone, benzyl alcohol, phenol, toluene. In spite of such huge production of different types of volatiles by the endophyte infected leaf tissues the host selection of aphid population (confirmed by choice based assays) has not been affected by the blend of volatiles emitted. This type of biological control is environment friendly and does not develop resistance, so should be adopted in large scale and is one of the unique applications of endophyte as biological control agent.

6.13 Biological Control of Agricultural Fungal Pathogens by Endophytic Isolates

6.13.1 Citrus Endophytes Protect the Host from Citrus Black Spot Pathogen

Citrus fruit is a common economically plant species found all over the World. Tran et al. (2019) isolated 33 endophytic fungus from different citrus plants (*Citrus reticulata*, *C. maxima*, *C. aurantium*, *C. australasica*, *C. wintersii*, *C. japonica*, *C. hystrix*, *C. limon*) found in Queensland of Australia and studied their diversity on citrus plants and also their bioactivity in terms of antifungal activity. The endophytes were identified as species of *Phyllosticta capitalensis* and *Phyllosticta paracapitalensis*. These endophytes are tested for their in vitro antifungal activity against citrus black spot pathogen *Phyllosticta citricarpa*. For the first time these species are reported from Australia (Queensland) and proved through the principles of Koch's postulate that these endophytic isolates are non-pathogenic to the host citrus species, thus could be confirmed as a true endophyte of citrus and providing protection against one of the dreadful diseases of these economically important plants. In vivo test also shows reduction of *P. citricarpa* pathogen on citrus fruits after inoculation of endophytic isolate *P. capitalensis* 14 days before the pathogen inoculation. So it is a classic example of biological control by endophytic fungus.

6.13.2 Biocontrol of **Verticillium** *Wilts by Cotton Root Endophytes*

Verticillium wilt is caused by the fungus *Verticillium dahliae* and hugely impacts on the growth of the cotton plant (*Gossypium herbaceum*) as it is generally pathogenic to cotton plant species and leads to qualitative and quantitative deterioration of the cotton yield. Yuan et al. (2017) isolated four endophytic fungi (CEF-818 (*Penicillium simplicissimum*), CEF-714 (*Leptosphaeria* sp.), CEF-642 (*Talaromyces flavus*.), and CEF-193 (*Acremonium* sp.) from different portions of the cotton plant collected from Anyang region of Henan province of China. The phytopathogen was isolated from infected soils of Xinji of Hebei province of China. They used two upland cotton cultivars named *Gossypium hirsutum* Jimian 11 and Lumianyan 21 which were susceptible and tolerant to the disease, respectively.

The isolates were tested for their disease control activity in vivo in green house condition where the tested plants were maintained and results indicated the control efficacy of the isolates ranged from 26% (*Talaromyces flavus*) to 67% (*Penicillium simplicissimum*) after a treatment of 25 days from the time of inoculation. In comparison to the controls of the disease nursery the isolates showed a better level of protection efficiency of 69.5%, 69.2%, 54.6%, and 45.7% by *Penicillium simplicissimum*, *Acremonium* sp., and *Leptosphaeria* sp., *Talaromyces flavus*, respectively. Reports include that endophytic isolates CEF-818 and CEF-714 offer protection to the host plant even in the heavily infected cases (during the time of early July; the first peak of the disease). These types of result are indicative that endophytic isolates not only delayed the wilt symptoms but they reduced the symptoms on the host plants.

The treatment with endophyte causes the enhancement of harvest up to 13.1 and 12.2% increase from the untreated ones. When the seeds are treated with the isolates the production increased (7.3%) from 3207.51 kg/ha to 3442.04 kg/ha. Study up to molecular details included that treatment of endophytes increased the transcript level of PAL (phenylalanine ammonia lyase), PPO (polyphenol oxidase), and POD (peroxidase) that results in the increase of defense reactions in the cotton plant. So the summary of the performed experiment is that the endophytic treatment in vitro conditions improved the yield of cotton seed in cotton fields and also results in the enhancement of the disease resistance ability of this plant. So it will be a great chance of biological control against the verticillium wilt of cotton.

6.13.3 Biocontrol of **Moniliophthora** *spp. by Endophytes of* **Theobroma cacao** *(Malvaceae)*

Theobroma cacao, a plant of Malvaceae family is commonly known as the cocoa tree and the seeds are commercially exploited in chocolate industry for making of chocolate liquor, cocoa solids, and cocoa butter. The economically important taxon is affected largely by frosty pod rot and witches' broom diseases caused by the aggressive fungal pathogens *Moniliophthora roreri* and *Moniliophthora perniciosa,* respectively. *M. roreri* affects the development of fruits leading to severe yield loss up to 30–100% (Bowers et al. 2001; Sánchez et al. 2015) and *M. perniciosa* affects the leaves, branches, shoots, flowers (Parra and Sánchez 2005). Villavicencio-vásquez and his co-workers in the year of 2018 tried the biological control methods for the reduction of these dreadful fungal pathogenic attacks using endophytic fungal flora of the host plant (*T. cacao*) itself as a tool. They isolated 17 fungal strains from leaves of *T. cacao* collected from two different parts of Ecuador; Balao and Naranjal of Guayas province and Molleturo of Azuay province. Out of 17 endophytic fungal isolates seven were identified as *Lasiodiplodia theobromae*, three isolates are known as *Pestalotiopsis microspora*, two proved to be *Colletotrichum gloeosporioides*, others are identified as *Phanerochaete chrysosporium*, *Xylaria feejeensis*, *Daldinia eschscholtzii*, *Xylaria* sp., *Hypoxylon investiens*, and *Nigrospora sphaerica*. The biocontrol ability of these isolates were determined by two ways; by detecting the mycoparasitism of foliar endophytic fungus against *Moniliophthora* spp., antifungal activity by the crude extracts containing secondary metabolites. The true endophytic nature was confirmed by the re-inoculation test.

Three strains of *L. theobromae* (Ec098, Ec151, Ec157) were found to effective antifungal agent in both the cases of direct antagonism and crude extract tests. They were successfully recolonized onto the host plant for almost 80–100%. The strains of *L. theobromae* were all square in all the three formats whereas other isolates were magnificent in only one parameter each like Ec035 (identified as *L. theobromae*) is an effective agent for mycoparasitism against both of the indicator organism when both the colonies were brought into contact but is the second best in antifungal activity shown by the crude extracts and moreover they were unable to re-infect host plant. Another strain of endophytic fungus Ec059 identified as *Xylaria feejeensis* has the 100% of re-inoculation but is negative in antagonistic tests. *Colletotrichum gloeosporioides* (Ec107) inhibited *Moniliophthora roreri* but also stimulated the growth of another phytopathogen *Moniliophthora perniciosa*. So the fungal endophytes of *T. cacao* could be largely exploited as biological control agent. Alternative biological control of the above said two pathogens were already done by antagonistic native microorganisms such as bacteria and fungi (Hebbar 2007; Bailey et al., 2008; Hernández-Rodríguez et al. 2014). This study focuses on the ability of the endophyte on the above said purpose as they help the plant to defend against pathogenic attack (Arnold et al. 2003). Previously scientists have tried integrated management system with the use of biological agent like *Trichoderma* spp., chemicals like azoxystrobin, chlorothalonil, cupric oxide, copper sulfate and also physical techniques like pruning and removal of diseased fruits. But endophytes were not explored widely for this purpose.

6.13.4 Biocontrol of Potato Tuber Pathogen **Rhizoctonia solani**

Rhizoctonia solani, a pathogenic fungus of Basidiomycota is a serious tuber and stem colonizer of potato plant (Scientifically known as *Solanum tuberosum* under the family Solanaceae) that causes stem canker and tuber blemishes. This soil borne pathogen is one of the prime causes of qualitative and quantitative damage of potato crop production worldwide (Woodhall et al. 2007). Previous techniques include the control through chemical fungicide or by physical separation of affected individuals. But nowaday focus has been totally shifted to the alternative mode of biological control measures maintaining the sustainability of the environment. The use of mycoparasites or antagonists leading to interhyphal physical interference using the volatile or non-volatile secondary metabolites has already been studied in large scale (Benítez et al. 2004). *Verticillium biguttatum* (an obligate mycoparasite) and *Trichoderma* sp. have been used as biological control agent of *R. solani* (Van Den Boogert & Jager). Earlier researchers have confirmed the anti-Rhizoctonia activity of *Ampelomyces, Coniothyrium*, and *Trichoderma* (Berg 2009). Lahlali and Hijri (2010) isolated six fungal endophytes from *Acer platanoides* (Family Sapindaceae), commonly called as Norway maple and identified them (by microscopic morphology and ITS rDNA sequences) as *Trichoderma atroviride*, *Epicoccum nigrum* (E1, E8, E18), *Alternaria longipes* (E13), and *Phomopsis* sp. (R24).

They evaluated the antifungal activity of the isolates against the potato tuber pathogen *Rhizoctonia solani* in vitro and in green house conditions by direct confrontation methods. It has been found that endophytic fungal isolate *T. atroviride* and *E. nigrum* inhibited the pathogenic fungus in vitro in dual culture assays having the highest zone of inhibition of mycelial growth among the tested individuals. Evaluation of antifungal ability includes the screening by secondary metabolites production. The highest inhibition zone was displayed by the culture filtrates of *T. atroviride*. The inhibitory effect of the fungal isolates was further studied in detail using confocal microscopy that confirmed that *Trichoderma atroviride* acts as mycoparasite and competitor. *Epicoccum nigrum* covers the mycelium of *R. solani* and causes the lysis of cell wall leading to loss of turgidity of the cells of the pathogen. The fungal hyphae of *Trichoderma atroviride* rolls up and penetrates into the mycelium of tuber pathogen leading to the formation of dense coils tightly encircling the fungal hyphae.

Phomopsis sp. invades the pathogen colony and competes for nutrients finally limiting its growth and the fungal hyphal densities are found to be higher than *R. solani*. Though hyphae of *A. longipes* were of more density than *R. solani* and hyphae of the pathogen were of abnormal morphology in comparison to the control or untreated one but endophytic Alternaria shows no hyphal penetration or inhibition of the pathogen. So it could be drawn that *Phomopsis* sp. causes loss of turgor. The fungal isolates were recorded for the antifungal volatile emissions in split plate method and the remarkable antagonistic properties are shown by *T. atrovirde*, *Phomopsis* sp., *A. longipes*, *E. nigrum* E18, E1, and E8 with an inhibition percentage of 81.81, 38.63, 21.02, 20.73, 11.36, and 10.22, respectively. In vivo tests performed in green house conditions confirmed the endophytic fungal isolates *T. atroviride* and *E. nigrum* enhanced the yield of potato tuber and significantly reduced the stem disease caused by the pathogens. So this endophytic genus could be used in large-scale as a biocontrol agent of stem and tuber pathogens.

6.13.5 Endophytic Fungi Mediated Control of Rice Blast Disease

Magnaporthe grisea is known as the causative agent of blast disease of rice (*Oryza sativa*) leading to irreparable crop loss worldwide. Chemical fungicides are found to be ineffective due to development of resistance. In this occasion biological control is the best effective way. Atugala and Deshappriya (2015) for the first time isolated 41 fungal endophytes from 160 explants of leaves, stems, seeds, roots of two rice plant varieties Suwandel (35 endophytic fungal isolates from 80 explants) and Kaluheenati (31 endophytic fungal isolates from 80 explants) grown in Sri Lanka. The isolates were identified as *Cylindrocladium* sp., *Absidia* sp., *Aspergillus* sp.1, *Cladosporium* sp., *Penicillium* sp., *Paecilomyces* sp., *Phoma* sp., *Gliocladium* sp., *Acremonium* sp., *Aspergillus* sp. 2, *Rhizoctonia* sp., *Aspergillus* sp. 3, *Varicosporium* sp., *Rhizopus* sp., *Arthroderma* sp., *Aureobasidium* sp. Most of the fungal endophytes belonged to Ascomycetes group and only one genus fall under Basidiomycetes and two under Zygomycetes. *Absidia* sp. and *Cylindrospermum* sp. were the dominant fungi found in Suwandel and Kaluheenati, respectively.

They selected the two most commonly occurring endophyte and tested their effect on crop plants' growth and also antagonistic or antifungal ability against the pathogen. Results include that the treated plants show remarkable enhancement of plant height and plant weight (dry weight and fresh weight). They screened 22 endophytic isolates with antifungal activity checked in dual culture assay. The potent isolates inhibited the pathogenic fungal growth (*M. grisea*) by coiling their hyphae around pathogenic fungal hyphae and forming loops and clamps. *Absidia* sp. and *Acremonium* sp. were the best agents for growth inhibition of the pathogenic one by their inhibitory structures. Thirteen endophytic fungi were cultured in broth medium and were checked for the presence of antifungal secondary metabolites by diffusion plate method. In vivo studies were performed with three endophytic fungi (*Acremonium* sp., *Absidia* sp., *Penicillium* sp.) against *M. grisea*. A set of plant was kept separate and designated as control and other three sets were inoculated by the endophytic fungus first then by pathogenic fungus. The control plant only received the spore suspension as inoculum of the pathogen in an amount of 1×10^7 spores/mL. Plants pre-inoculated with endophytic fungi and next infected with pathogen show no disease symptoms. Only endophytic *Penicillium* sp. treated plants showed the occurrence of disease symptoms. So, endophytic *Absidia* sp., *Acremonium* sp. could be used commercially in field trials for the protection of rice plants from pathogenic fungal attack.

6.13.6 Biocontrol of Vascular Streak Disease

Indonesia represents the third highest producers of Cacao (ICCO Annual Report 2014/2015). Sulawesi Island of this Southeast Asian country is the prime producer and is reported to be largely affected by the systemic VSD (vascular streak disease). This vascular streak disease leads to the loss of almost 774 million US dollar (Abdurrahman (2017)). The causal agent is named as *Ceratobasidium theobromae* (earlier known as *Oncobasidium theobromae*), belongs to the basidiomycete (Guest and Keane 2007; Samuels et al. 2012). It not only hampers the cacao production but also questions its existence in the affected areas especially in small-scale farms. Wind-borne spores matures during midnight to early morning time, penetrate the unhardened leaves at terminal portions of the branch, and grow through the cuticular portions just above the veins of the leaves finally infecting the xylem and stem tissues after 3 or 5 months of first penetration through ramification of the hypha (Prior 1979). Being a systemic disease the control measures are tough including the application of fungitoxic triadimefon, triazole, triadimenol, and propiconazole that protect the leaves from the germination of the basidiospores on it.

Chemical methods are avoided due to their high cost and cultural or biological control measures are focused in this respect. Asman et al. (2018) isolated ten fungal endophytes from the healthy branch of vascular streak disease resistance cacao plants. The fungal identification was done by comparing the colony characters with standard literature and identified as Aspergillus-like colony, Curvularia-like colony, Colletotrichum-like colony, Fusarium-like colony, Gliocladium-like colony, Geotrichum-like colony, another four isolates due to the absence of their reproductive structures are known as mycelia sterilia 1–4. The fungal isolates were infected to a 2.5-months-old cacao seedling and after 30 days the fungal pathogen was inoculated and the seedlings were placed in a region surrounded by the cacao infected plants for the facilitation of the secondary infection. They started recording the disease incidence after 30 days, 60 days, 90 days, and 120 days of disease incidence. The results proved that endophytic fungi when pre-inoculated to the cacao plants can reduce infection occurrence but vary from days (60, 90, 120 days) after detection.

The incidence occurrence were reduced after 60 days when the treatment was done by *Curvularia*-like colony, followed by *Geotrichum*-like colony, *Fusarium*-like colony, mycelia sterilia isolate 4 and the results were better than the standard antifungal antibiotic copper fungicide. After 90 days still *Curvularia*-like colony was found to be best effective followed by mycelia sterilia isolate 1 which was equal or better than the copper fungicide treatment. Final tests were again done using the 120-days-old plants and the results include *Curvularia*-like colony showed higher degree of resistance even higher than the standard copper fungicide followed by sterile mycelia (isolate no. 1), colony resembling *Gliocladium*, colony similar with *Fusarium*-, *Geotrichum*-like colony, sterile mycelia 3, *Colletotrichum*-like colony, *Aspergillus*-like colony and lastly control (no application), sterile mycelia 2, sterile mycelia 4 with percentage of 3.0, 8.3, 9.5, 11.3, 15.8, 18.0, 19.0, 19.3, 21.3, 26.5, 30.5, respectively. So the disease incidence will increase as the days goes by. The re-isolation of the endophytes from the infected plants was made and it was found that after 150 days no endophyte was potentially re-isolated from root, stem, or leaf but after 30 days all the endophytic isolates were found to be reappeared from leaf tissues but not from the root or stem tissues except *Colletotrichum*-like colony morphology showing endophyte. This type of experimental result can conclude that endophytes could be used for biological control of dreadful fungal diseases.

6.13.7 Wheat Endophytes in the Control of **Fusarium** *Head Blight*

Comby et al. (2017) isolated 86 endophytic fungi from the inner tissues of *Triticum aestivum* (wheat plant). They were screened for their ability to inhibit the growth of pathogenic fungus *Fusarium graminearum* and *Fusarium culmorum* in vitro in dual culture assays. A group consisting of 22 fungal isolates was found to very effective in the control (30–51% inhibition) of *F. graminearum* and these strains were known to be effective controller (15–53% inhibition) of *F. culmorum* also globally. New findings of this study include the identification of three previously unknown species with anti-Fusarium head blight activity. They confirmed *Phoma glomerata*, *Aureobasidium proteae,* and *Sarocladium kiliense* to be antifungal by screening on a detached spikelet inflorescence of the wheat plant. This was the first report from wheat endophyte that these three species are effective biocontrol agent of the dreadful pathogen *Fusarium culmorum* and *F. graminearum*. Authors pointed out a significant difference among the antifungal ability of the endophytic fungal isolates in the two different types of in vitro screening approaches applied in this study. Findings emphasizes on the procedure that includes the use of detached wheat spikelet which potentially points out the pathogenicity of the endophyte and also growth ability of the endophytic isolate on the targeted host plant. So, proper screening procedure is needed in search of biocontrol agent before trying them on the whole plant.

6.13.8 Reduction of Gibberella Ear Rot (GER) by **Epicoccum nigrum** *and* **Sordaria fimicola**

Fusarium graminearum is known as a serious pathogen of wheat causing Gibberella ear rot and blight disease of seedlings. Not only that the huge production of mycotoxins but also accumulation of those toxins like zearalenone, trichothecenes, and deoxynivalenol (its acetylated forms also) causes destructive loss of global wheat production and transport or consumption. Abdallah et al. (2018) isolated five endophytic fungi; four from soil sample and one from maize stubble. They were identified as *Clonostachys rosea*, *Sordaria fimicola,* and *Epicoccum nigrum* (three species) according to their macroscopic and microscopic morphology along with their nucleotide sequencing. *Sordaria fimicola* is found to be a potent inhibitor of the pathogenic fungal growth in vitro tested by dual culture assay for 4 days in a sharp comparison with other well-known biocontrol agent like *Trichoderma harzianum*. Other isolates *Clonostachys rosea* and *Epicoccum nigrum* showed similar antifungal activity whereas the control *Piriformospora* sp. was not efficient in this respect. The absolute mycotoxin levels were variable in PDA plates of different endophytic genus and between different strains of the same endophytic species especially for reduction in deoxynivalenol (DON) and 15-acetyldeoxynivalenol (15-ADON) production. *Sordaria fimicola* and one isolate of *E. nigrum* could decrease the DON levels in comparison to the reference strains of biological control agents. Though the results were of high variation after repeated replication *Clonostachys rosea* was average in mycotoxin reduction. Endophytic *Sordaria fimicola* UG 106, *Epicoccum nigrum* UG 1703 reduced completely the ZEN (Zearalenone) production. These isolates were consistent in their reduction ability against ZEN production. It is concluded from the above mycotoxin reduction studies that DON and 15-ADON levels are related to reduction of fungal hyphal growth. The more the fungal growth is reduced more the mycotoxin levels are reduced. In case of ZEN synthesis the hyphal growth in one way and in another way the mycotoxins are inhibited by the endophytes directly. The volatiles of *Sordaria fimicola* reduced the fungal growth up to 60–70% in comparison to the control. In vivo tests revealed the reduction of DON levels in maize plant after endophytic treatment. Except *E. nigrum* UG 11703 the other endophytic isolates *Sordaria fimicola*, *E. nigrum* UG 11701, *E. nigrum* 11702, and *Clonostachys rosea* cause significant reduction in 15-ADON levels. These type of results highlight the unique potential of some selected endophytic fungal strains as new and novel biocontrol agents in agricultural science and technology.

6.13.9 Biocontrol of Tan Spot Disease

Larran et al. (2016) isolated endophytes from cultivars of wheat found in Buenos Aires province of Argentina. The endophytes were tested for their antifungal activity against *Pyrenophora tritici-repentis* (Died.) Drechsler (anamorph *Drechslera tritici-repentis)* (Died.) Shoem (*Dtr*), the causal agent of tan spot disease of wheat using dual culture assay. The endophytes were identified as *Alternaria alternata*, *Chaetomium globosum*, *Cladosporium herbarum*, *Epicoccum nigrum*, F*usarium* sp., *Penicillium* sp., *Paecilomyces lilacinus*, *Rhodotorula rubra,* and *Trichoderma hamatum*. They were evaluated for their pathogenicity on 30-day-old wheat plant (susceptible cultivar Buck Poncho) in green house conditions. Except *Rhodotorula rubra* all the other endophytic fungal isolates reduced the pathogenic fungal growth. *Penicillium* sp., *Trichoderma hamatum* and *Paecilomyces lilacinus* reduced the diameter of the colony of the pathogenic fungus. The endophytes showed sharp morphological changes in the conidia or the vegetative mycelium of *Drechslera tritici-repentis*. Endophytic *Fusarium* sp. reduced the spore germination percentage (6.82–52%). In in vivo green-house tests using *Trichoderma hamatum*, *Chaetomium globosum* and *Fusarium* sp. significantly reduce the disease severity on all the three leaves treated with endophytic isolate and infected with the fungal pathogen. *Trichoderma hamatum* is reported to be the best effective in in vitro plate assay as well as in vivo green-house experiments. So from this experiment it could be drawn that endophytic *T. hamatum* is a potent biological control agent of tan spot pathogen of wheat.

6.13.10 Biocontrol of Ginseng Pathogens by Ginseng Endophytes

Park et al. (2015) isolated 1300 endophytic fungus from root, stem, and leaf tissues from mountain cultivated ginseng tree (*Panax ginseng* Meyer) collected from 24 different geographical locations in Korea. One hundred and twenty-nine fungal endophytes were identified using internal transcribed spacer sequences. Phyllogenetic analysis revealed that endophytic isolates belonged to group of Ascomycota, Basidiomycota, Zygomycota with a percentage of 81.7%, 7.08%, 10%, respectively. Fifty-nine genera were found to be unknown. The endophytes are tested for their biocontrol or antifungal ability against destructive pathogen of gingseng known as *Alternaria panax*, *Botrytis cinerea*, *Cylindrospermum destructans*, *Pythium* sp., *Rhizoctonia solani*. The endophytic diversity was determined using Shannon diversity index that revealed that root tissues are colonized by endophytic fungal isolates more than stem or leaf tissues. The cause might be due to the rhizospheric nature of the soil. Diversity of the endophytic fungus are totally dependent on geographical locations and the environmental factors of that particular area in reference to its temperature, rainfall, humidity, and soil type or other physical or abiotic factors. Some fungal isolates are found to be tissue specific extremely. The fungal isolates were grown in culture broth and extraction of the bioactive compounds is made by using ethyl acetate organic solvent. The ethyl acetate extracts were tested for their antifungal ability and results revealed that only one endophytic fungal isolates identified as *Trichoderma polysporum* shows broad spectrum antifungal activity against all the 5 fungal pathogens of ginseng. Other isolates *Tricharina ochroleuca*, *Lachnum virgineum*, *Phoma* sp., *Alternaria longissima*, unknown fungal endophyte, *Penicillium chrysogenum* inhibited the growth of at least one pathogenic fungi but not all. So from this study it could be concluded that endophytic *Trichoderma polysporum* could be used as an alternative approach for the biocontrol of ginseng pathogens reducing the worldwide huge economic loss.

6.13.11 Biocontrol of Root Rot of Pepper

Fungal root rot pathogens causing severe disease symptoms are the main reason of destruction of bell pepper production in United States even when the environmental factors are favorable (Kelley et al. 2009; Kelly et al. 2010). The prime destructive fungal pathogens are *Phytophthora capsici*, *Phytophthora nicotianae* var *parasitica*, *Fusarium solani*, *Fusarium oxysporum*, *Verticillium* spp., *Rhizoctonia solani*, *Pythium aphanidermatum*, *Macrophomina phaseolina*. In spite of chemical and biological control measures still it is a grave problem for economic earning based on pepper production but endophytes are being introduced in these respects nowadays with a high degree of success rates. Mmbaga et al. (2018) isolated 16 endophytic fungi from stem tissues of *Cornus florida* (flowering dogwood). Endophytes were identified as *Dothideomycetes* sp., *Cornus florida*, *Hypoxylon howeanum*, *Hypoxylon* sp., *Nigrospora sphaerica*, *Entonaema* sp., *Whalleya microplaca*, *Hypoxylon submonticulosum*, *Hypoxylon rubiginosum*, *Hypoxylon* sp., *Dothideales* sp, *Hypoxylon submonticulosum*, *Botryosphaeria dothidea*. These endophytes were screened for their antifungal activity against fungal pathogen *Fusarium solani*, *Fusarium oxysporum*, *Macrophomina phaseolina*, *Phytophthora nicotianae*, *Phytophthora irrigate*, *Phytophthora cryptogea*, *Phytophthora capsici* (Lt6745, OP97, and Lt263), *Cercospora nicotianae* causing root rot of *Capsicum annum* L. Most of the endophytes exhibited antifungal potency in dual culture assay and one isolate A22F1 (*Nigrospora sphaerica*) was tested in green house conditions for their disease inhibiting ability in vivo in three separate cultivars of pepper (California Wonder, *Pepper Cayenne* and *Numex Primavera*). So this endophytic A22F1 could be exploited commercially for root rot pathogen control of Bell pepper.

6.13.12 Mycofumigation by **M. albus** *Reduces Verticillium Wilt of Egg-Plant*

Volatiles from endophytic fungus are a promising source of new and novel bioactive compounds for agricultural exploitation in terms of their antifungal activity and biocontrol ability. A very potent genus Muscodor plays an important role in this respect and is commercially exploited worldwide for their broad spectrum anti-pathogenic activity that has open up new areas of agricultural research on microbial volatiles. Muscodor species has been isolated as a true endophyte worldwide by several workers from different type of plants residing in diverse environments and they have checked for their biocontrol (mycofumigating) ability in vitro (Table 6.1). Usually the identity of the genus is confirmed by molecular means, also supporting evidences are collected from their channel tests and specialized microscopic structure unique for this genus. One such application is documented here. Mycofumigation with the two agents; *Muscodor albus* and *M. roseus* has effectively enhanced the Sugar beet (*Beta vulgaris L.*) stand establishment and reduced the disease severity

Table 6.1 Biocontrol ability of volatile organic compounds of different types of Muscodor species

Muscodor species	Volatile compounds	Biocontrol ability	References
Muscodor albus	1-butanol, 3-methyl-acetate, naphthalene, tetrohydrofuran, 2-methyl furan, 2-butanone, aciphyllene, azulene, germacrene B, acetic acid, methyl ester, 1-Butanol, benzeneethanol, acetate, Pyrrolidine, 2-Heptanoic acid, 4-cyclopropyl-, Bicyclo[3.1.1] heptane, 6-methyl-2- propanoic acid	Mycofumigating agent for the control of storage insects like potato tuber moth and coddling moth. A biological control agent of *Aphanomyces cochliodides*, *Aspergillus fumigatus*, *Fusarium culmorum*, and *Glomerella cingulata*	Worapong et al. (2001) Ezra and Strobel (2003) Ezra et al. (2004) Strobel et al. (2007) Banerjee et al. (2010a, b)
Muscodor roseus	2-butenoic acid, ethyl ester, 1,2,4-trimethylbenzene, 2,3-nonadiene	Antifungal activity	Worapong et al. (2002)
Muscodor vitigenus	Naphthalene, azulene, 3-methylbutan-1-ol, 3-methylbutyl acetate	Insect repellent of a crop pest *C. cinctus*	Daisy et al. (2002) Siri-udom et al. (2016)
Muscodor fengyangensis	Naphthalene derivatives; α-phellandrene; β-phellandrene; 2-cyclohexen; propionic acid, its 2-methyl-, and methyl ester	Antifungal against *Botrytis cinerea*, *Aspergillus clavatus*, *Colletotrichum fragariae*, *Didymella bryoniae*, *Magnaporthe oryzae*, *Pythium ultimum*, *Rhizoctonia solani*, *Sclerotium rolfsii*, *Verticillium dahlia*, *Penicillium digitatum*	Zhang et al. (2010)
Muscodor sutura (Xylariaceae)	Thujopsene, chamigrene, isocaryophyllene, butanoic acid, 2-methyl	Antifungal activity against pathogenic fungus *A. fumigatus*, *Botrytis cinerea*, *Colletotrichum lagenarium*, *Ceratocystis ulmi*, *Cercospora beticola*, *Geotrichum candidum*, *Mycosphaerella fijiensis*, *Phytophthora cinnamomi*, *Phytophthora palmivora*, *Pythium ultimum*, *Rhizoctonia solani*, *Sclerotinia sclerotiorum*, *Verticillium dahlia*	Kudalkar et al. (2012)

(continued)

Table 6.1 (continued)

Muscodor species	Volatile compounds	Biocontrol ability	References
Muscodor cinnamomi	Azulene; butanoic acid, 2-methyl, methyl ester, propanoic acid, 2-methyl, methyl ester	Biocontrol agent for *Rhizoctonia solani*	Suwannarach et al. (2010, 2012)
Muscodor equiseti *Muscodor musae*	Isobutyric acid, $C_4H_8O_2$ 2-methylpropanoic acid, 3,7-dimethyl-1,6-octadiene, 6-nitro-2-picoline, Ethyl 2-methylpropanoate, Methyl 2-methylbutanoate, 2-Methylpropyl acetate, Methyl 3-methylbutanoate, 2-Methylpropyl propanoate, 2-Methylpropan-1-ol, 3-Methylbutanoyl acetate, 2-Methylbutyl 2-methylpropanoate, 3-Methylbutan-1-ol, Ethyl 2-hydroxy-2-methylpropanoate	Antifungal activity against pathogenic fungus like *Alternaria porri*, *Alternaria solani*, *Aspergillus flavus* *Botrytis cinerea*, *Colletotrichum capsici*, *Colletotrichum gloeosporioides*, *Colletotrichum musae*, *Fusarium oxysporum*, *Fusarium solani*, *Nigrospora oryzae*, *Penicillium digitatum*, *Penicillium expansum*, *Rhizoctonia solani*, *Sclerotium rolfsii*	Suwannarach et al. (2013) Siri-udom et al. (2016)
Muscodor kashayum	3-cyclohexen-1-ol,1-(1,5-dimethyl-4-hexenyl)-4-methyl; 1,6-dioxacyclododecane-7,12-dione; 2,6-bis(1,1-dimethylethyl)-4-(1-oxopropyl) phenol; 2,4-di-tert-butylthiophenol and 4-octadecylmorpholine	Antifungal against a wide range of fungus *Alternaria alternate*, *Aspergillus flavus*, *Aspergillus japonicas*, *Bionectria ochroleuca*, *Botrytis cinerea*, *Cercospora beticola*, *Chaetomium heterosporum*, *Colletotrichum gloeosporioides*, *Curvularia lunata*, *Fusarium equiseti*, *Fusarium oxysporum*, *Lasiodiplodia theobromae*, *Mycosphaerella fijiensis* *Penicillium citreonigrum*, *Penicillium marneffei*, *Rhizoctonia solani*, *Trichderma viridae*, *Agaricus bisporus*, *Pleurotus flabellatus*	Meshram et al. (2013)

(continued)

Table 6.1 (continued)

Muscodor species	Volatile compounds	Biocontrol ability	References
Muscodor strobelii	Viridiflorol, tetraoxapropellan, terpinolene, octadec-9-enoic acid, aspidofractinine-3-methanol	Antifungal against *Penicillium citreonigrum*, *Botrytis cinerea*, *Aspergillus japonicas*, *Mycosphaerella fijiensis*, *Cercospora beticola*, *Rhizoctonia solani*, *Colletotrichum gloeosporioides*, *Fusarium oxysporum*, *Lasiodiplodia theobromae*	Meshram et al. (2014)
Muscodor darjeelingensis	2, 6-Bis (1,1-dimethylethyl)-4-(1-oxopropyl) phenol, 1, 6-Dioxacyclododecane-7, 12-dione and 4-octadecylmorpholine	Inhibits the growth of fungal pathogen *Candida* species	Saxena et al. (2014)
Muscodor tigerii	4-octadecylmorpholine, 1-tetradecanamine, N,N-dimethyl and 1,2-Benzenedicarboxylic acid, mono(2-ethylhexyl) ester	Inhibits the growth of fungal pathogens *Cercospora beticola*, *Penicillium marneffei*, *Rhizoctonia solani*, *Candida albicans*	Saxena et al. (2015)
M. suthepensis	2-methylpropanoic acid, by 3-methylbutan-1-ol	Myco-fumigant agent to control tangerine fruit rot caused by *Penicillium digitatum*	Suwannarach et al. (2015)
Muscodor heveae	3-methylbutan-1-ol, 3-methylbutyl acetate, 2 methyl propanoic acid and azulene derivatives	Antifungal to pathogenic fungi *Phellinus noxius* and *Rigidoporus microporus*	Siri-udom et al. (2016)
Muscodor ghoomensis, *M. indica*, *M. camphora*	Tetracontane, 4-octadecylmorpholine, N,N-dimethyl-1-pentadecanamine and cis-9-hexadecena, 4-octadecylmorpholine; 1,6-dioxacyclododecane-7,12-dione, 1,4-dimethyl-7-prop-1-en-2-yl-2,3,3a,5,6,7,8,8a-octahydro-1H-azulen-4-ol	Mycofumigating agent against *Cercospora beticola*, *Penicillium marneffei,* and *Colletotrichum gloeosporioides*	Meshram et al. (2015, 2017)

when these two mycofumigating agents are applied in autoclaved sterilized soil prior infested with severe pathogens like *Rhizoctonia solani*, *Pythium ultimum*, *Aphanomyces cochlioides* (Stinson et al. 2003). Experiment with egg-plant seedlings include the mycofumigation of the autoclaved soil previously inoculated with pathogens that significantly reduces the disease incidence on *Solanum melongena* after 4–5 weeks when compared with non-fumigated but *Verticillium* pathogen infested soil. Damping off disease (caused by *Pythium ultimum*) is controlled effectively by *Muscodor roseus* volatiles but in case of sugar beet pathogen *Fusarium* sp. (Causal agent of Fusarium wilt of sugar beet) mycofumigation was not effective. The common formulations include potato dextrose agar strips with fungal mycelium, alginate capsules having hyphae, barley grains infected with *M. roseus* or *M. albus*, stabilize or Pesta granules with fungal inoculum. The best control of *Aphanomyces cochliodes* (causal agent of damping off) was obtained by Stabileze formulation and *Rhizoctonia solani* damping off was minimized by agar strip method coupled with barley grain inoculation technique. None of the fungal volatiles affected the plant growth or external morphological appearance. So it could be said that mycofumigation using *M. albus* and *M. roseus* is a new way for control of soil-borne pathogens *P. ultimum*, *A. cochlioides*, *R. solani*, and *V. dahliae*.

6.13.13 **M. albus** *Controlling the Post-Harvest Decay*

Mercier and Jiménez (2004) worked on the ability of the fungal volatiles of *M. albus* for the control of decay on economically important fruits apple and peach. They assessed the mycofumigating property of the *Muscodor albus* in vitro and in vivo. In vitro tests resulted in death of a wide range of storage pathogens like *Botrytis cinerea*, *Colletotrichum acutatum*, *Geotrichum candidum*, *Monilinia fructicola*, *Penicillium digitatum,* and *Rhizopus* sp. In vivo tests include the treatment of apples for 7 days with the culture of *M. albus* and resulted in complete inhibition of blue and gray mold growth (*P. expansum* and *B. cinerea,* respectively). The fruits were inoculated with pathogen and *M. albus* culture is not in direct contact with the fruit but exposed to its volatiles. In case of wound inoculated peach fruits 24–72 h of fumigation controlled the brown rot disease (*Monilinia fructicola*). Shorter fumigation time also resulted in complete control of mold and gray mold. Headspace GC-FID detection showed the maximum occurrence of 2-methyl-1-butanol, isobutyric acid.

6.13.14 *Volatiles of Endophytic* **Daldinia cf concentrica** *Control* **Aspergillus niger**

Other than Muscodor species a lots of endophytes have been isolated those are efficient producers of volatile bioactive compounds with antifungal activity (Table 6.2). One of such example includes the biocontrol of *Aspergillus niger* and other food pathogens or agricultural pathogens (*Alternaria alternata* pathotype tangelo, *Alternaria alternate*, *Aspergillus niger*, *Botrytis cinerea*, *Colletotrichum* sp., *Coniella* sp., *Fusarium euwallaceae*, *Fusarium mangiferae*, *Fusarium oxysporum*,

Table 6.2 Biocontrol activity of endophytic isolates by their volatile organic compounds

Endophytic isolates	Prime VOCs emitted	Biocontrol ability	References
Gliocladium sp.	Butanol, 3-methyl-octene, 1-propanol, 2-methyl-1-butanol, 2-methyl-propanoic acid, octanone, 1,3,5,7-cyclooctatetraene (azulene), acetic acid, 2-phenylethyl ester, phenylethyl alcohol	*Pythium ultimum*, *Verticillium dahliae*	Stinson et al. (2003)
Colletotrichum gloeosporioides, *Clonostachys rosea*, *Botryosphaeria ribis*	None	Controls the frosty pod rot, black pod rot, and witches broom pathogen *Moniliophthora roreri*, *Phytophthora palmivora*, *Moniliophthora perniciosa,* respectively	Mejıa et al. (2008)
Nodulisporium sp.2 *Nodulisporium* sp.3	1,3,8-p-menthatriene; caryophyllene; eucalyptol	*Rhizoctonia fragariae*, *Fuasrium oxysporum*, *Sclerotium rolfsii* *Verticillium dahlia*, *Colletotrichum acutatum*	Mann et al. (2008)
Oidium sp.	Butanoic acid, 3-methyl-,methyl ester; butanoic acid, 3-methyl-ethyl ester	*Pythium ultimum.*	Strobel et al. (2008)
Oxyporus latemarginatus	5-pentyl-2-furaldehyde	Controls post-harvest apple decay and *Rhizoctonia* sp. root rot on moth orchid	Lee et al. (2009)
Botrytis sp. BTF 21	Butane-2-methyl; β-butyrolactone, 2-butenedinitrile	*Fusarium oxysporum*	Ting et al. (2010)
Cladosporium sp. MIF01	Butane-2-methyl, 1-propanol 2-methyl	Biocontrol potential against phytopathogen *Fusarium oxysporum*	Ting et al. (2010)
Myrothecium inundatum	3-octanone, 3-octanol, 7-octen-4-ol, cyclo hexane, 1,4-cyclo hexadiene,	Biocontrol of *Pythium ultimum* and *Sclerotinia sclerotiorum*	Banerjee et al. (2010a, b)
Nodulisporium sp.	β-elemene, β-selinene, α-selinene; 1-methyl-1,4-cyclohexadiene	Post-harvest biocontrol agent of apple and a potent bio-fumigant agent	Park et al. (2010)
Penicillium sp. BTF08	1-butanol, 3-methyl; β-butyrolactone; 2-butenedinitrile	Biocontrol potential against phytopathogen *Fusarium oxysporum*	Ting et al. (2010)
Candida intermedia	1,3,5,7-cyclooctatetraene; 3-methyl-1-butanol	Post-harvest control agent for strawberry against Botrytis fruit rot	Huang et al. (2011)

(continued)

Table 6.2 (continued)

Endophytic isolates	Prime VOCs emitted	Biocontrol ability	References
Phomopsis sp.	Sabinene (monoterpene), 1-butanol, 3-methyl, benzeneethanol, 1-propanol, 2-methyl, 2-propanone	Biocontrol of *Sclerotinia* sp., *Botrytis* sp.	Singh et al. (2011)
Phoma sp.	Alpha-humulene (sesquiterpene); alcohols, reduced naphthalene derivatives, trans-caryophyllene	Minimize the growth of *Verticillium* sp., *Ceratocystis* sp., *Cercospora* sp., *Sclerotinia* sp.	Strobel et al. (2011)
Nodulisporium sp., *Daldina* sp., *Hypoxylon* spp.	Series of ketones, including acetone; 2-pentanone, 3-hexanone, 4-methyl, 3-hexanone, 2,4-dimethyl, 2-hexanone, 4-methyl and 5-hepten, 2-one, 1,8-cineole, 1-butanol, 2-methyl and phenylethanol alcohol, cyclohexane, propyl	Biological control of plant pathogen *Phytophthora cinnamomi*	UL-Hassan et al. (2013)
Nodulisporium sp. GS4d2llla	Mono and sesquiterpenes, especially eucalyptol and limonene	Antifungal agent against *Pythium aphanidermatum*	Fernández et al. (2016)
Xylaria sp.	3-methyl-1-butanol, thujopsene, 2-methyl-1-butanol, 2-methyl-1-propanol	Inhibits the growth of pathogenic *Pythium aphanidermatum*, *Phytophthora capsici*, *Alternaria solani*, *Fusarium oxysporum*	Sánchez-Ortiz et al. (2016)
Fusarium oxysporum	Caryophyllene, 4-methyl-2,6-di-tert-butylphenol	a potent post-harvest biocontrol agent for tomato plant from pathogenic *Fusarium oxysporum*	Romero et al. (2017)

Lasiodiplodia theobromae, *Neoscytalidium dimidiatum*, *Penicillium digitatum*, *Phoma tracheiphila*, *Pythium aphanidermatum*, *Pythium ultimum*, *Rhizoctonia solani*, *Sclerotinia sclerotiorum*) by *D. concentrica* endophyte isolated from olive tree (*Olea europaea*) (Liarzi et al. 2016). In total 27 volatiles (3-methyl-1-butanol, 2-methyl-1-butanol, 1-methyl-1,3-cyclohexadiene, 1-methyl-1,4-cyclohexadiene, 4-heptanone, isoamyl acetate, 4-heptyn-2-ol, 2-octenal, octanal, 4,4-dimethyl-1,3-cyclopentanedione, 2, 2, 5-trimethylcyclopentanone, phenyl ethyl alcohol, β-elemene,-α-funebrene, α-guaiene, 2-(4-hydroxyphenyl)ethanol, terpenes, β-selinene, α-selinene, α-bulnesene, germacrene,α-selinene, veratryl acetone, 3-methoxy-2-naphthol, pogostol) have been identified from its unique mixture of volatiles that have immense importance in food processing and storage industry as they are proved to be inhibiting the growth of the one of the common food pathogen or contaminant *Aspergillus niger*.

6.14 Conclusion and Future Prospects

The vast nature of the Science could be interpreted by its definition "to know the unknown and to see the unseen" and it is a quite obvious fact that a lots of knowledge are still to be explored even in the high tech time of the twenty-first century. Sustainability maintenance in one hand and assuring the optimum pace of development finding fast solution to the leading problems is the crying need of this era. In this respect dependence on endophytic microorganism solely as a tool for biological control of agricultural pest or pathogens not only assures the nature's longevity but also a step ahead towards our secured future. This is just a try to sum up all the recent or past remarkable discoveries on endophytic bioactivity but it is quite obvious that it is of very little percentage of the huge arena of endophyte biology. After going through all the popular discoveries it could be sum up that still we use endophytic biocontrol as the last step or alternative step for the survival of crops or protection from pests but in true sense the sustainability of our agricultural policies along with our environment would be maintained when endophytes would be used as a common and frequently used most dominant mode of protection against agricultural disease related issues.

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Chapter 7
Aspergillus Mycotoxins: Potential as Biocontrol Agents

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Contents

7.1 Introductions

Aspergillus species are widespread in nature; they are regarded as soil fungi, frequently colonizing plant debris and decaying agricultural crops, and are among the commonest airborne fungi. They occur with high frequency as saprophytes on a wide range of substrates, including foods and feeds, and several species are among

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the typical pathogens of harvested fruits and vegetables (Barkai-Golan 2008). Mycotoxins are a group of secondary metabolites characterized by both a diversity of chemical structures and biological activities. Mycotoxigenic species can be found in all major taxonomic groups of fungi, but the genus *Aspergillus* is undoubtedly one of the most important (Abarca et al. 2001; Rana et al. 2019b; Yadav et al. 2017). The *Aspergillus* species that produce mycotoxins are more common in the warmer, subtropical, and tropical areas than in the temperate areas of the world (Wilson et al. 2002). Some of the *Aspergillus* species and teleomorphs that potentially produce mycotoxins include *A. candidus*, *A. clavatus*, *A. flavus*, *A. fumigatus*, *A. niger*, *A. nomius*, *A. ochraceus*, *A. parasiticus*, *A. restrictus*, *A. tamarii*, *A. terreus*, *A. versicolor*, *Emericella nidulans*, and *Eurotium amstelodami* (Wilson et al. 2002; Rana et al. 2019a; Yadav et al. 2020a).

The term mycotoxin was first used in the 1960s to describe the toxin associated with contaminated peanuts in animal feed and the loss of turkeys in England (Turkey X disease). This mycotoxin was later identified as the *Aspergillus flavus* toxin (aflatoxin B1) (Ismaiel and Papenbrock 2015). Mycotoxins are defined as natural products produced by fungi that evoke a toxic response when introduced in low concentration to higher vertebrates and other animals by natural route (Alshannaq and Yu 2017(. Mycotoxins produced by *Aspergillus* have a serious impact on the health of humans and animals. The main mycotoxins produced by species belonging to *Aspergillus* genus are aflatoxins (B_1, B_2, G_1, G_2); ochratoxin A (OTA); fumonisins (B_2 and B_4); patulin (PAT); cyclopiazonic acid (CPA); gliotoxin (GT) (Abarca et al. 2001; Wilson et al. 2002; Varga et al. 2015; Perrone and Gallo 2017). Although OTA and aflatoxins are the most important *Aspergillus* mycotoxins in fruits, other mycotoxins synthesized by *Aspergillus*, such as cyclopiazonic acid, fumonisins, patulin, gliotoxin, and other secondary metabolites, may also elicit toxicological effects (Barkai-Golan 2008).

7.2 Aflatoxin

7.2.1 *Historical Perspective and Producing* Aspergillus *Species*

The toxin of aflatoxin was first discovered in 1960 when there were increase deaths from liver disease of turkeys in England followed by deaths of other farm animals; more than 100,000 turkeys died within a few months. Scientists first called the new disease “Turkey X Disease” because they did not know its reason. It was finally founded that all birds affected had been fed with fodder prepared with contaminated groundnut meal; examination of the incriminated groundnut meal revealed the presence of mold (Liu et al. 2004). They were first identified from peanut samples in 1961 as responsible for Turkey X disease. The main causative agent was *A. flavus*. Since then, aflatoxin is considered as one of the most harmful mycotoxins in the world (Varga et al. 2015).

Aflatoxin term is derived from three source words, “a” from *Aspergillus*, “fla” from *flavus*, with toxin added (Obioha 1979). The aflatoxins are a group of mycotoxins structurally have related to many secondary metabolites of fungi produced by certain *Aspergillus species* (Gourama and Bullerman 1995), especially *Aspergillus flavus*, *A. parasiticus*, and *A. nominus* (Garber and Cotty 1997; Fente et al. 2001). Recently, *A. ochraceoroseus and A. pseudotamari* are also aflatoxin-producing species in nature, but they are less encountered with them (Li et al. 2011). The aflatoxins are extremely potent carcinogenic, teratogenic, mutogenic, hepatotoxin, with hepatocarcinogenic effects and immunosuppressive agents that cause significant damage to human and animal health (Brown et al. 1991; Razzaghi-Abyaneh et al. 2005). Aflatoxins are decaketide-derived secondary metabolites produced by a complex biosynthetic pathway which could lead to different metabolites: aflatoxin M1, M2 (Murphy et al. 2006; Amalaradjou 2008), B1, B2, G1, and G2 (Perrone and Gallo 2017). The most potent and frequently occurring of these compounds is aflatoxin B1 (Richard et al. 1993; Amalaradjou 2008). Mainly AFB1 is the most toxic and carcinogenic naturally occurring mycotoxins, and exhibits hepatocarcinogenic and hepatotoxic properties, and epidemiological data implicating AFB1 as a component of liver cancer in humans in certain parts of the world (Kocsubé et al. 2013). The International Agency for Research on Cancer (IARC) assigned all aflatoxins to group 1 (carcinogenic to humans) (Varga et al. 2015).

Aflatoxins are produced in nature only by *A. flavus*, *A. parasiticus*, and a recently described species *A. nomius*. *A. flavus* is ubiquitous. *A. parasiticus* is apparently less widely distributed, but the extent of its occurrence may be obscured by the tendency for *A. flavus* and *A. parasiticus* to be reported only as *A. flavus*. *A. nomius* is not of practical importance (Pitt 2000). Among 18 different types of aflatoxins produced by *A. flavus* strains (Ismaiel and Papenbrock 2015) these toxins are produced by at least 14 species assigned to three sections of the genus *Aspergillus*: section Flavi (*A. flavus*, *A. pseudotamarii*, *A. parasiticus*, *A. nomius*, *A. bombycis*, *A. parvisclerotigenus*, *A. minisclerotigenes*, *A. arachidicola*, *A. togoensis*) (Kocsubé et al. 2013), and several other species whose importance and ecology; less importance has some aflatoxin-producing species belonging to section Nidulantes (Emericella *astellata*, *E. venezuelensis*, *E. olivicola*) and section Ochraceorosei (*A. ochraceoroseus*, *A. rambellii*) (Perrone and Gallo 2017). Recent data indicate that aflatoxins are produced by at least 20 species assigned to three sections of the genus *Aspergillus*: sections Flavi, Nidulantes, and Ochraceorosei including the newly described *A. pseudonomius*, *A. pseudocaelatus*, *A. togoensis*, *A. mottae*, *A. sergii*, *A. transmontanensis*, and *A. novoparasiticus* (Varga et al. 2015).

7.2.2 Occurrence and Common Food Products Involved

Aflatoxins many times occur naturally on crops in the field before to harvest. Postharvest contamination of foods and crops can occur if crop drying is delayed and the moisture content is allowed to exceed critical values supporting mold growth during storage (Amalaradjou 2008; Yadav et al. 2019a). Aflatoxins have been found in milk, cheese, corn, peanuts, cottonseed, nuts, almonds, figs, spices, and a variety of other foods and feeds. Milk, eggs, and meat products are contaminated due to the ingestion of aflatoxin-contaminated feed by animals and birds (Amalaradjou 2008). Natural contamination of cereals (maize, wheat, and rice principally), oilseeds (cotton, peanut, rapeseed, coconut, sunflowers, and others), cassava, tobacco, and a long list of other commodities is a common occurrence (Detroy et al. 1971; Diener et al. 1987; Bennett and Klich 2003; Rizzi et al. 2003; Azziz-Baumgartner et al. 2005; Saleemullah et al. 2006; Strosnider et al. 2006; Masoero et al. 2007; Wild and Gong 2010). However, the commodities with the highest risk of aflatoxin contamination are corn, peanuts, and cottonseed. Corn attracted the attention as a commodity of greatest concern worldwide, because it is grown in climates that are likely to contaminate with aflatoxin (Heathcote and Hibbert 1978). Feeding of aflatoxin-contaminated corn and cottonseed meal to dairy cattle can result in aflatoxin M1 contaminated-milk and milk products, including non-fat dry milk, cheese, and yogurt (Amalaradjou 2008). Due to climatic factors, aflatoxins are mainly detected in products imported (e.g., Brazil nuts, pistachio nuts, peanuts, and figs) into Central Europe (Kocsubé et al. 2013).

A. flavus and *A. parasiticus* have a particular affinity for nuts and oilseeds. Peanuts, maize, and cottonseed are the three most important crops affected (Pitt 2000). *A. flavus*, which is primarily known as a producer of the aflatoxins, is a frequent contaminant of corn, peanuts (Domer 2002), stored wheat, onions, grapes, rice, cattle feed, sunflower flour, and spices (Kocsubé et al. 2013).

7.3 Ochratoxin A

7.3.1 Historical Perspective and Producing Aspergillus *Species*

OTA was originally isolated as a secondary metabolite from a strain of *Aspergillus ochraceus* in a corn meal in South Africa in 1965 (Abarca et al. 1994; Zinedine 2010; Malir et al. 2016). Its isolation was part of a large-scale screening for aflatoxins, during the "mycotoxin gold rush" that followed the discovery of aflatoxins (Bayman and Baker 2006). In the following years, the OTA production of six other species from section Circumdati (*A. melleus*, *A. sulphureus* (Lai et al. 1970), *A. ostianus*, *A. petrakii*, *A. sclerotiorum*, and *A. alliaceus*) was reported (Hesseltine et al. 1972; Tsubouchi et al. 1995), but *A. alliaceus* is now placed in section Flavi (Bayman and Baker 2006).

The economically most important OTA producers belong to *Aspergillus* sections Circumdati and Nigri, with only two minor OTA-producing species in section Flavi (ochratoxins are produced by a range of *Aspergillus* species assigned to sections Circumdati, Nigri, and Flavi (Kocsubé et al. 2013; Perrone and Gallo 2017). Section

Circumdati, named also *Aspergillus* ochraceus group responsible for production of several mycotoxins harmful for animals and humans. The most important mycotoxin is OTA, named after the producer *A. ochraceus*. Some species of the section are utilized for the biochemical transformation of steroids and alkaloids, or as sources of proteolytic enzymes; while other produces several promising anticancer compounds (Frisvad et al. 2004; Perrone and Gallo 2017). Many species produce large amounts of OTA: *A. pseudoelegans*, *A. sulphureus* (Kocsubé et al. 2013); *A. steynii*, *A. westerdijkiae* (Ismaiel and Papenbrock 2015); *A. cretensis*, *A. fresenii*, *A. flocculosus (syn: A. ochraceopetaliformis)*, *A. muricatus*, *A. ochraceus*, *A. pseudoelegans*, *A. pulvericola*, *A. roseoglobulosus*, *A. sclerotiorum* (Perrone and Gallo 2017). In section, section Nigri OTA is produced by *A. niger* (Abarca et al. 1994); *A. awamori*, *A. carbonarius* (Teren et al. 1996); *A. lacticoffeatus*, *and A. sclerotioniger* (Kocsubé et al. 2013). Members of *Aspergillus* section Nigri are widely distributed throughout the world. Some are used in the food industry because they are good producers of organic acids and hydrolytic enzymes (Abarca et al. 2001). OTA production in *A. niger* is alarming because this species is used in fermentations for food and enzyme production; industrial strains should be tested for OTA production (Bayman and Baker 2006). While in Flavi, *A. lanosus* (Bayman and Baker 2006); *A. alliaceus and A. albertensis* produce OTA (Kocsubé et al. 2013; Majeed et al. 2013). The ochratoxin family consists of three members A, B, and C which differ slightly from each other in chemical structures (Ciconova et al. 2010). OTA is the most toxic mycotoxin in the group of ochratoxins (Anjorin et al. 2013). OTA may also exhibit teratogenic, genotoxic, mutagenic (Barkai-Golan 2008); carcinogenic and nephrotoxic effects, and also has been regarded as an immunosuppressive agent (Kocsubé et al. 2013).

7.3.2 Occurrence and Common Food Products Involved

OTA is a mycotoxin that is a common contaminant of a wide variety of food products (plant products and animal products). The molecular structure comprises a chlorinated polyketide dihydroisocoumarin ring linked to phenylalanine and, as shown in different producing fungal species, a polyketide synthase (PKS) is a major part of the biosynthetic pathway (Wang et al. 2016). Because of its widespread occurrence on a large variety of agricultural commodities and the potential health risks, mainly toward humans, OTA has been classified as a possible human carcinogen (group 2B) by the International Agency for Research on Cancer (Ismaiel and Papenbrock 2015; Frisvad et al. 2018). OTA have been detected in several agricultural products from temperate and tropical zones (Adegoke and Letuma 2013).

OTA is found mainly in cereal and cereal products starting in the 1960s (Abarca et al. 2001; Barkai-Golan 2008; Kocsubé et al. 2013; Perrone and Gallo 2017). Higher amounts of OTA were produced on wheat than on other substrates (Zinedine

2010; Wang et al. 2016). OTA is found in wheat, barley, rye corn, oats (Abarca et al. 2001; Wilson et al. 2002; Stoev 2013; Adegoke and Letuma 2013), maize (Abarca et al. 2001), rice (Abarca et al. 2001; Stoev 2013; Alshannaq and Yu 2017), and cassava flour (Zain 2011; Adegoke and Letuma 2013). More recently, besides cereals and cereal products OTA is found in a range of other food commodities, including legumes (Abarca et al. 2001; Bayman et al. 2002; Bayman and Baker 2006; Barkai-Golan 2008; Perrone and Gallo 2017), coffee beans (Nakajima et al. 1997; Bucheli et al. 2000), cocoa beans, dried fruits (Pitt 2000; Bayman et al. 2002; Aish et al. 2004; Barkai-Golan 2008), peanuts (Pitt 2000; Zain 2011; Adegoke and Letuma 2013; Kocsubé et al. 2013; Stoev 2013; Perrone and Gallo 2017). Grapes, wine (Abarca et al. 2001; Wilson et al. 2002; Battilani and Pietri 2002; Adegoke and Letuma 2013; Stoev 2013; Ostry et al. 2017; Perrone and Gallo 2017), beers, spices (Aziz et al. 1998; Bayman and Baker 2006; Aish et al. 2004), baby foods, crackers, raisins, pecans, figs (Wilson et al. 2002); raisins (Abarca et al. 2001); pulses (Kocsubé et al. 2013; Perrone and Gallo 2017), and oilseeds (Wang et al. 2016). OTA can also contaminate animal-derived products, such as meat (Pitt 2000; Bayman et al. 2002; Wilson et al. 2002; Perrone and Gallo 2017), pork, poultry meat (Nakajima et al. 1997; Bucheli et al. 2000), milk (Barkai-Golan 2008; Stoev 2013), fish and eggs (Adegoke and Letuma 2013).

The fungi responsible for OTA contamination vary from crop to crop and from place to place. OTA found in cereals in storage is primarily produced by growth of *Penicillium verrucosum*, and perhaps the associated *Aspergillus* species, *A. ochraceus* and *A. ostianus* (Wilson et al. 2002). *A. ochraceus* is likely the most important *Aspergillus* species involved with OTA contamination in storage (Wilson et al. 2002). In contrast, *A. ochraceus* is most commonly found in dried and stored foods, such as smoked and salted dried fish, soya beans, chick peas, nuts, pepper, and dried fruit. It has been reported infrequently in cereals and green coffee beans. *A. ochraceus* is generally present at low levels and rarely causes spoilage (Aish et al. 2004). The most important toxin of the group is OTA; generally *A. ochraceus* prefers to grow in hot-tropical regions (Alshannaq and Yu 2017). OTA is produced by *A. carbonarius* in grapes, wines, and vine fruits, and by *A. ochraceus* sometimes in coffee beans (Pitt 2000; Bayman and Baker 2006). *A. carbonarius* its major habitat is dried vine fruit. It is therefore the main source of OTA in grapes and grape products, such as raisins and wine. *A. niger* is often found in association with *A. carbonarius* and is commonly isolated from nuts, fresh fruit, and some vegetables in warm climates (Aish et al. 2004). The most important species regarding potential OTA production in coffee, rice, beverages, and other foodstuffs are *A. ochraceus*, *A. westerdijkiae*, and *A. steynii* (Frisvad et al. 2004); and recently, in two newly described species from coffee *A. lacticoffeatus* and *A. sclerotioniger* (Samson et al. 2004; Bayman and Baker 2006). *Aspergillus* species producing OTA in fruits include: *A. ochraceus*, *A. carbonarius*, *A. niger*, *A. tubingensis*, *A. sclerotiorum*, *A. sulphureus*, *A. aculeatus*, *A. japonicus* var. aculeatus, *A. alliaceus*, *A. melleus* (Barkai-Golan 2008).

7.4 Fumonisins

7.4.1 Historical Perspective and Producing Aspergillus *Species*

Fumonisins were discovered only recently as the result of many years of study of the disease known as leukoencephalomalacia (LEM) (Pitt 2000). Fumonisins were first isolated in 1988 from cultures of *F. verticillioides* strain MRC 826 at the Programme on Mycotoxins and Experimental Carcinogenesis (PROMEC) of the Medical Research Council (MRC) in South Africa (Jackson and Jablonski 2004). Fumonisins are mycotoxins produced by group of Fusarium fungi commonly found on crops, produced mainly by *Fusarium verticillioides* and *F. proliferatum*, and producing by group of *Aspergillus* fungi. The most common species are *A. flavus* and *A. niger*, *A. welwitschiae*, *A. parasiticus*, *A. ochraceus*, *A. carbonarius*, *A. tubingensis*, *A. nomius*, *A. alliaceus*, and recently also *A. westerdijkiae* and *A. steynii* (Perrone and Gallo 2017). Most of these reports claimed that *A. niger* produced only fumonisins B2 and B4 (Kocsubé et al. 2013).

Fumonisin B (FB) analogs are the most common among which FB1 predominates on FB2 and FB3, while FB4 is detected in insignificant amounts (Gelderblom et al. 1988; Munkvold and Desjardins 1997; Pagliuca et al. 2005; Afolabi et al. 2007; Dall'Asta et al. 2009; Gazzotti et al. 2011; Bryła et al. 2013). FB1 can cause two diseases to animals: leucoencephalomalacia in horses and porcine pulmonary edema. It is also carcinogenic, hepatotoxic, and embryotoxic in laboratory animals. In humans fumonisins can cause esophageal cancer and neural tube defects (Marasas 2001; Missmer et al. 2006; Scott 2012). The IARC evaluated FB1 as a Group 2B carcinogen. However FB2 was reported as more cytotoxic than FB1 (Perrone and Gallo 2017).

7.4.2 Occurrence and Common Food Products Involved

Fumonisins are natural contaminants of cereal grains worldwide and are mostly found in corn and products derived from corn (Jackson and Jablonski 2004). Fumonisins are mycotoxins which frequently contaminate maize and maize products worldwide. Limits for total fumonisins B_1 and B_2 have been set for cereals and cereal-based products (Perrone and Gallo 2017). Findings of fumonisins in grains (other than maize and sorghum) and grain-based products and found in a wide variety of other foods such as garlic bulbs (Seefelder et al. 2002; Scott 2012), black tea (Martins et al. 2001; Omurtag and Yazicioglu 2004; Scott 2012), garlic (powder), onion powder (Boonzaaijer et al. 2008; Scott 2012), fig (Senyuva and Gilbert 2008; Scott 2012), peanuts (Sangare-Tigori et al. 2006; Liu et al. 2008; Njobeh et al. 2010; Scott 2012), and soybeans (Scott 2012). While FB_1 has been detected in cow's milk (Gazzotti et al. 2009; Scott 2012). Fumonisins have been found in medicinal wild plants in South Africa (Sewram et al. 2006; Scott 2012). Found also in mint and stinging nettle in Turkey (Omurtag and Yazicioglu 2004; Scott 2012) and sage leaves, valerian root (Santos et al. 2009; Scott 2012). Of particular note and interest is that for some foods, FB_1 is not the major fumonisin as it is for maize and other grains. Of current concern is the occurrence of FB_2 in wine (Logrieco et al. 2010), in beer (Romero-González et al. 2009) and, together with FB_4, in coffee (Noonim et al. 2009; Scott 2012). In recent years, FB_2 produced by *Aspergilli* was detected in coffee beans, beer, other grain-based products, barley, and wheat (Perrone and Gallo 2017). Black *Aspergilli* were suspected to be responsible for fumonisin contamination of grape-derived products, figs, and onions (Kocsubé et al. 2013). Among *Aspergilli*, *A. niger* and *A. welwitschiae* are fumonisin producers. *A. niger* is frequently detected on grape-derived products, while *A. welwitschiae* infects onions and *Welwitschiae mirabilis* (Varga et al. 2015).

7.5 Patulin

7.5.1 Historical Perspective and Producing Aspergillus *Species*

Patulin (PAT) was originally isolated and named as claviformin due to its isolation from *Penicillium claviforme*, later it was renamed PAT according to the PAT-producing mold, *P. patulum* (now *P. griseofulvum*) (Ismaiel and Papenbrock 2015). PAT is a water-soluble lactone first isolated as an antibiotic during the 1940s. Owing to co-discovery of the compound by various groups, it has historically been known by names such as clavicin, clavitin, expansin, gigantic acid, leucopin, mycoin, penicidin, and tercinin. Initially isolated as a broadspectrum antifungal antibiotic, it was later found to inhibit more than 75 different bacterial species including both Gram-positive and Gram-negative bacteria (Moake et al. 2005). The early findings that PAT had antibiotic activity led to its testing against the common cold in humans. PAT was soon found almost useless in curing the common cold and was too toxic for use as an antimicrobial agent (Ismaiel and Papenbrock 2015). During the 1960s it was found to be toxic to biological systems comprising of bacteria, mammalian cell cultures, higher plants, and animals. The adverse effects of patulin in biological systems are genotoxicity, carcinogenicity, embryotoxicity, and teratogenicity, immunotoxicity, and genotoxicity (Erdoğan et al. 2014).

PAT is a fungal secondary metabolite that produced by some *Penicillium*, *Aspergillus*, and *Byssochlamys* mold species (Kadakal and Nas 2002). PAT has been isolated from *Aspergillus terreus* (Jiménez et al. 1991), *A. clavatus*, *A. giganteus*, *A. longivesica* (Varga et al. 2007). Several *Aspergillus* species are also able to produce patulin, including species assigned to *Aspergillus* sections Clavati and Terrei (Kocsubé et al. 2013). Among the *Aspergillus* species, the number of patulin producing species is limited to three of the Clavati group: *A. clavatus*, *A. giganteus*, and *A. longivesica* (Puel et al. 2010).

7.5.2 Occurrence and Common Food Products Involved

Patulin is first of all found in pomaceous foods like apples and pears, but also in other fruits (Frisvad 2018). In nature, PAT is found commonly in different products and especially in apples and apple products in which these molds can grow. The results of experiments on animals have shown that patulin is mutagenic, carcinogenic, and teratogenic (Kadakal and Nas 2002). While it predominantly contaminates apples, apple juice, and apple products, other fruit including pears, peach, and grapes may also be vulnerable to patulin contamination (Moake et al. 2005). Several studies have shown that patulin is stable in dry cereals, and in apple and grape juice (Speijers 2004), apricots, grapes, grape fruit, peaches, pears, apples, olives and cereals (Laidou et al. 2001; Kadakal and Nas 2002; Adegoke and Letuma 2013), dried fig (Senyuva and Gilbert 2008). PAT has been detected in apples and apple products, and occasionally in other fruits such as pears, apricots, peaches, and grapes. It has also become a quality indicator of fruit used for the production of apple juice concentrates. It is mainly produced in rotten parts of the fruits after infestation with PAT-producing fungus that can occur at 0 °C during storage or develops rapidly when fruits are returned to room temperature. PAT also appears to increase after storage when fruits remain at room temperature (20 °C) for short periods of time, a common procedure in fruit processing industries (Ismaiel and Papenbrock 2015). The contamination of PAT in fruit and fruit-derived products, especially in apple and derived products is very common worldwide (Alshannaq and Yu 2017). *A. clavatus* have been found to produce patulin in varieties of fruits, also *A. sydowii*, *and A. oryzae* in grapes (Erdoğan et al. 2014).

7.6 Gliotoxin

7.6.1 Historical Perspective and Producing **Aspergillus** *Species*

Gliotoxin (GT) is a first epipolythiodioxopiperazine (ETP's) reported and is the best characterized. Its name was derived from its identification as a metabolite of *Gliocladium fimbriatum* first isolated from cultures of the fungus *Gliocladium fimbriatum* (Nouri et al. 2015). GT is a sulfur-containing mycotoxin produced by several fungal species belonging to genera including *Penicillium*, *Gliocladium*, *Thermoascus*, and *Aspergillus* (Sugui et al. 2007). Regarding *Aspergillus*, GT is produced by *A. fumigatus* and related species in section Fumigati including *A. denticulatus*, *A. cejpii*, and *A. pseudofischeri*. Even though pathogenic *Aspergillus* including *A. niger*, *A. flavus*, and *A. terreus*, and *A. chevalieri* (Varga et al. 2015), the most abundantly produced gliotoxins *A. fumigatus*, which exhibits a diverse array of biologic effects on the immune system (Lewis et al. 2005).

A. fumigatus produces a variety of secondary metabolites, including gliotoxin, and this mycotoxin has received considerable attention for over two decades as a putative virulence factor based on the following observations: (1) up to 93% of *A. fumigatus* strains recovered from cancer patients with IA produced gliotoxin compared to less than 20% of the environmental isolates (2) *A. fumigatus* is the most prolific producer of gliotoxin among the pathogenic *Aspergillus* species tested (Sugui et al. 2007). Production of gliotoxin from clinical isolates of various *Aspergillus* species indicated that most of the *A. fumigatus* isolates produced gliotoxin (95%) in comparison with other *Aspergillus* species (Kupfahl et al. 2008). The amount of toxin produced by *A. fumigatus* was substantially higher than the amount produced by other less frequent species of pathogenic *Aspergillus* including *A. terreus* and *A. flavus*.

The most common species of *Aspergillus* that cause invasive aspergillosis worldwide are *A. fumigatus*, *A. terreus*, *A. flavus*, and *A. niger*. Although all the species produce gliotoxin, not every strain is a gliotoxin producer (Kwon-Chung and Sugui 2009). GT is an alkaloid with a low molecular size which has been known to possess a number of immunosuppressive activities, such as inhibition of superoxide release, migration, microbicidal activity cytokine release by leukoyctes, and T-lymphocyte-mediated cytotoxicity (Kamei and Watanabe 2005), also have genotoxic, cytotoxic, and apoptotic effects. A recent study demonstrated the presence of gliotoxin in cattle feedstuff. However, information is scarce about the presence of *A. fumigatus* and its mycotoxins in other feedstuffs (Pena et al. 2010). This mycotoxin has been suspected as one of the most likely virulence determinants among various secondary metabolites produced by the species (Nouri et al. 2015).

7.6.2 Occurrence and Common Food Products Involved

There are reports of gliotoxin being confirmed in silage, hay, and straw and a number of studies of the metabolites formed by strains of *A. fumigatus* isolated from these feeding stuffs have been shown to produce gliotoxin in culture (Kurbatskaya and Trotstanetskii 1987). Previous studies claimed that environmental isolates of *A. fumigatus* rarely produce gliotoxin, in contrast to clinical isolates (Lewis et al. 2005). Kosalec et al. (2005) studied the in vitro production of gliotoxin in clinical strains of *A. fumigatus* and demonstrated that incubation at 37 °C resulted in higher gliotoxin production than at 25 °C. They found that gliotoxin was produced during mycelial growth (Keller et al. 2012). Other studies showed the isolation of *A. fumigatus* from cereal grains and other animal feed silages with ability to produce gliotoxin (Garon et al. 2006; Kupfahl et al. 2008; Richard et al. 2009).

The *A. fumigatus* strains isolated from mixed cattle feed had higher gliotoxin levels than those isolated from corn silage (Pereyra et al. 2008). Keller et al. (2012) reported that high percentage of strains among *A. fumigatus* and related species isolated from pre- and post-fermented samples such as corn, sorghum, and wet brewer's grains silage were able to produce gliotoxin. The *A. fumigatus* could be grown on all culture media used to produce gliotoxin, but the substrates varied in their ability to induce gliotoxin production. Researchers recorded gliotoxin in agricultural substrates e.g. oats and hay (Scudamore and Livesey 1998) and corn (Alonso et al. 2013). Recently according to Nouri et al. (2015) in rice and barley media the growth of the isolate was better than in corn and wheat media. A rice medium is the best culture medium for gliotoxin production from *A. fumigatus* isolates. And also has the advantage of being quick, easy, cheap, and available.

7.7 Cyclopiazonic Acid

7.7.1 Historical Perspective and Producing Aspergillus *Species*

Cyclopiazonic acid (CPA) is a mycotoxin that producing by strain of *Aspergillus* and *Penicillium*, which is an indole-derived compound and is a stable compound that tolerates a broad range of temperature, was first detected in 1968 as a metabolite of *Penicillium cyclopium* in groundnuts (Holzapfel 1968). The original isolate (*P. cyclopium*) was later referred to as *P. griseofulvum* and *P. verrucosum var. cyclopium*) Domer 2002). However, some strains of *Aspergillus* are also producers of CPA mycotoxin such as *A. flavus* (Luk et al. 1977; Trucksess et al. 1987). At the outbreak of Turkey X disease in Britain in the early 1960s may well have been a combination of aflatoxin and CPA, which are often produced concurrently (Trucksess et al. 1987; Gallagher et al. 1978).

Further, empirical evidence indicates that commercial samples of CPA may be contaminated with, among other things, aflatoxin, yielding sometimes variable and confusing experimental data (Voss et al. 1990). Similarly to aflatoxins, CPA also been detected in both the mycelium and the sclerotia of *A. flavus* (Wicklow and Cole 1982: Barkai-Golan 2008). Other *Aspergillus*, including *A. versicolor*, *A. oryzae*, and *A. tamarii* have also been recorded as CPA producers (Dorner 1983; Dorner et al. 1984). CPA is consider as serious mycotoxins that cause degenerative disease and necrosis in the liver, spleen, pancreas, kidney, salivary glands, myocardium, heart, digestive tract, and skeletal muscles (Cole 1984; Barkai-Golan 2008). CPA was found to be sub-acutely toxic to rats, swine, guinea pigs, dogs, and poultry, involving several vital organs (Voss et al. 1990). Recently, the main producers of Claiming Aspergilli, several species in section Flavi including *A. flavus*, *A. minisclerotigenes*, *A. oryzae*, *A. parvisclerotigenus*, *A. pseudocaelatus*, *A. pseudotamarii*, *A. tamarii*, *A. bertholletius*, in section Versicolores including *A. versicolor*, and in section Fumigati including *A. lentulus* and *A. fumisynnematus* (Varga et al. 2015).

7.7.2 Occurrence and Common Food Products Involved

Molds may be divided into two main groups, namely the field fungi and the storage fungi. The former group CPA contains those species that proliferate in and under field conditions and that do not multiply once the grain is in storage. Thus, for instance, the CPA producing spp., commonly found on crops, is seldom found after about 6 weeks storage (Burdock and Flamm 2000).

Natural occurrence of CPA has been reported in a variety of commodities including: millet (Lalitha Rao and Husain 1985; Amalaradjou 2008), Pinto beans (Trucksess et al. 1987), walnuts, Penguin, Brazil “Macuco” bird (Gallagher et al. 1978), rice, brown sausage (Norred et al. 1987), corn (Urano et al. 1992; Aresta et al. 2003; Amalaradjou 2008), peanuts (Urano et al. 1992), maize (Urano et al. 1992; Amalaradjou 2008), cheese (Le Bars 1990), sunflower (Ross et al. 1991), tomato products (Motta and Soares 2001; Amalaradjou 2008). The toxin has also been accumulating in meat and eggs of chickens (Norred et al. 1988; Domer et al. 1994) and the milk of sheep (Domer et al. 1994) dosed with CPA)Domer 2002). Several *A. flavus* strains isolated from vine fruits produced cyclopiazonic acid, while all the *A. tamarii* strains isolated from fig orchards were cyclopiazonic acid producers (Barkai-Golan 2008).

7.8 *Aspergillus* Mycotoxins as Biocontrol Agents

Mycotoxins are defined as the chemicals synthesized by fungi and released as toxic secondary metabolites. Mycotoxins might play a role in terms of economic and safe farming procedure (Yadav et al. 2019b, 2020c; Rastegari et al. 2020a). The effects of mycotoxins on insects have already been addressed by several research groups 50 years ago (Schrögel and Wätjen 2019). Insects encounter mycotoxins when they consume fungus-infected mummy fruits from their host plants. Mycotoxins can cause toxicity to insects, including insecticidal effects and developmental delay (Zeng et al. 2006). There are many reports concerning the toxicity of mycotoxins towards insects (Rastegari et al. 2020b; Yadav et al. 2020b). AFB_1 proved to be harmful to *Drosophila melanogaster*, *Aedes aegypti*, *Heterotermes indicola*, *Heliothis virescens*, *Corcyra cephalonica*, *mycophagous mites*, *Musca domestica*, *Locusta migratoria*, *Schistocerca gregoria,* and *Tenebrio molitor* (Reiss 1975).

There is variable sensitivity of insects to aflatoxin toxicity, initially examined in the fruit fly *D. melanogaster* (Alderman and Marth 1976), drosophila with larval growth in media contaminated with AFB1 leading to decreased viability, and small pupal case (Bettinger and Chinnici 1991). PAT had insecticidal activity towards *D. melanogaster* and *Lucilia sericata*. In concentrations of 20, 10, and 1 pg/cma PAT had strong insecticidal activities (Reiss 1975). *D. melanogaster* larvae, which feed naturally on fermenting fruits, exhibit significantly altered development on diets containing low AFB_1 concentrations (i.e., less than 1 ppm); larvae feeding on higher concentrations will die (Niu et al. 2009). Toll-deficient *D. melanogaster* was significantly less susceptible to GT of the *A. fumigatus* (Kwon-Chung and Sugui 2009)

Zeng et al. (2006) described toxicity of AFB_1 to the corn earworm (CEW) (*Helicoverpa zea*) (Lepidoptera: Nuctuidae) larvae at different larval stages. For newly hatched first instar larvae 20 ng/g AFB_1 caused 50% mortality while a higher concentration 200 ng/g AFB_1 caused 100% mortality. Pupal weight of the larvae fed with 1 ng/g AFB_1 in diet was significantly decreased compared with control insects. Low concentrations of AFB_1 in the diet of first instars (less than 100 ng/g) can affect development, causing delayed pupation and reduced pupal weight; higher concentrations of AFB_1 (200 ng/g) are lethal (Zeng et al. 2006).

Spores of *Aspergillus flavus* have been observed to be highly pathogenic to freshly emerged house flies (Musca domestica (Diptera: Muscidae) by ingestion or even by contact (Amonkar and Nair 1965). *A. flavus* showed developmental toxicity also to rice moth larvae (Hedge et al. 1967). Feeding aflatoxin to larvae of mosquitos and house flies as well as to young *Heliothis virescens* (Lepidoptera: Nuctuidae) led to high mortality rates (Schrögel and Wätjen 2019).

Abado-Becognee et al. (1998) investigated the effect of fumonisin B_1 on the growth and metabolism of yellow mealworm *molitor*. The presence of fumonisin B_1 at a concentration of 450 μg/g diet reduced larval growth and metabolism for several weeks, but did not increase mortality (Broekhoven et al. 2014). Guo et al. (2014) observed the parameters of food choice, weight gain, and mortality for larvae *T. molitor* when reared on wheat grains colonized by various *Fusarium* species. Compared to the control grain several grains were avoided by the larvae while others were preferred by the larvae, which correlated with larval feeding behavior and weight gain. However, larvae were not always able to sense threats derived from infested grain, as among the preferred grains one grain which was colonized by *Fusarium culmorum* led to increased mortality (Schrögel and Wätjen 2019). The growth rate of yellow mealworm larvae is decreased also by AFB_1 and OTA (Schrögel and Wätjen 2019).

The *A. flavus* isolates were obtained from coconut insect pests naturally colonized cadavers of *Stephanitis typica* (lace bug) (nymphs and adults), *Opisina arenosella* (leaf-eating caterpillar) (larval stages), and *Proutista moesta* (plant hopper) (adults). The laboratory bioassay conducted with these fungi on the respective hosts yielded 80% mortality of *S. typica* nymphs within 3 days; 80–90% *O. arenosella* larvae were mycosed within 3–4 days (Gopal et al. 2000a) and 62.5% *P. moesta* insects died within 4 days (Ponnamma et al. 2000) under laboratory conditions. The mortality was 100% when the experiment was continued for 2–3 days more. The ideal spore concentration for achieving 100% mortality in short period (5–6 days) was 10^6 spores ml^{-1} (Gopal et al. 2000b). In response to *A. flavus* infection, within 24 h, the insects became lethargic, refused food indicating loss of appetite, and did not respond to external stimuli. After death due to fungal parasitism, their body became mummified and brittle (Gupta and Gopal 2002). In this background, the toxigenic nature of A. flavus isolates (AF_1 and AF_2) pathogenic to *S. typica*, *O.*

arenosella, and *P. moesta* tested for their possible use as biological control agents against some of the insect pests of coconut(Gupta and Gopal 2002).

The navel orange worm (NOW) (*Amyelois transitella*) (Lepidoptera: Pyralidae) is a serious crop pest that attacks almonds, pistachio, walnuts, and figs, causing millions of dollars of agricultural damage in the United States (Connell 2001; Campbell et al. 2003; Burks and Brandl 2004). Niu et al. (2009) demonstrated the extremely high tolerance of *A. transitella* to concentrations of AFB_1 and OTA and showed that this tolerance exceeds that of other mycotoxin-associated species such as *H. zea*. The concentrations analyzed did not kill *A. transitella* when administered at early developmental stages and caused only marginal sub lethal effects. Comparisons of the toxicological effects in *A. transitella* and *H. zea* demonstrated that *A. transitella* larvae are 100 times more tolerant of AFB_1 than *H. zea* and also are significantly more resistant to OTA.

GT has been demonstrated to inhibit the growth of an array of different fungal species including *A. nidulans*, *A. terreus*, *A. niger* and has been utilized as an antifungal, antibiotic, most notably in the treatment of soilborne fungi (Howell & Stipanovic 1995; Aliaa 2008; Losada et al. 2009). Similarly, GT has been demonstrated to possess antibacterial properties inhibiting proteasomal activity in certain bacterial strains (*Toxoplasma gondii* and *Plasmodium falciparum* and ultimately growth (Paugam et al. 2002; Hatabu et al. 2006). Patulin has also been evaluated for control of several plant pathogens, including downy mildew of cucumbers, damping off of safflower, crown gall, and loose smut of wheat (Stott and Bullerman 1975). Strong fungistatic activity by PAT against *Rhizopus nigricans*, *Monilia albicans*, and *Sporotrichum schenckii* but no effect upon *Aspergillus clavatus* a PAT producer (Stott and Bullerman 1975). PAT was initially suggested for treatment of common cold, as it is anti-viral in addition to being antibacterial, but the trials on humans were quickly dropped because of the toxicity of PAT (Frisvad 2018).

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Chapter 8
Trichoderma: Biocontrol Agents for Promoting Plant Growth and Soil Health

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8.1 Introduction

Trichoderma is a saprotrophic fungus which largely can be found in environments such as forest soil, roots and leaves. This fungus has been declared as soil fungi due to its significant for their fast growth. They exhibited high capacity to utilize different types of complex substrates and can act as a strong resistances towards different kind of toxic chemicals. Therefore, *Trichoderma* species is very abundance on decaying wood. This is mainly because of the heterotropic interactions such as decomposition and opportunistic endophytism. It can be found in all type of soils which includes from forest, salt marsh, agricultural even in desert soils. In addition to that, *Trichoderma* has been used as an efficient biocontrol agent against the phytopathogens (Sharma et al. 2019). The main mechanisms for the biocontrol process in this type of fungi have been assumed due to antibiosis, mycoparasitism and competition for space and resources (Bissett et al. 2015).

This fungus evolved many mechanisms which contribute for the improvement of the plant resistance towards diseases, the plant's growth as well as its productivity (Rastegari et al. 2020; Yadav et al. 2020d, 2019b). According to Bissett et al. (2015), out of 260 species, around 35 established species was mainly discovered for its economic importance mainly due to its capability of various enzyme productions or to be used as biocontrol agents. Global interest was given to researches related to *Trichoderma* fungus thanks to its applications in the field of agricultural and biotechnology (Verma et al. 2017a).

Trichoderma has been thought to be associated with plants as epiphytes and endophytes. Epiphytes are beneficial microflora that can be found at the aerial parts of the plants that can be either harmful or beneficial towards the plant (Yadav et al. 2020b, c). The word endo derived from the Greek words which carry the meaning of within and "phyte" stands for plant. In another word, endophytes are the colonization which takes place inside the plants by any fungus or bacteria (Suman et al. 2016; Verma et al. 2017a; Yadav et al. 2020a). There are few reports supporting the fact that *Trichoderma* species found as endophytes of the plants. One of the well-known examples is the presence of *Trichoderma* in banana tissues (Wang et al. 2000). According to the Pocasangre et al. (2000) study on the distribution of endophytic fungi from banana was conducted which is mainly about isolating the fungus from the central cylinder. Besides that, Sikora et al. (2008) did survey on isolating endorhiza of banana and use it for biocontrol of nematodes.

8.2 Methodology of Studying *Trichoderma* Biodiversity

Most of the species identification for *Trichoderma* species has been performed according to their morphological characteristics. In order to carry out this, solid media with different components which are targeted for conidium production and its branching observation were used for the culture characteristics as well as for the morphological studies (Hermosa et al. 2000). Most of the times, the morphological studies which aimed for conidiosphores structure identification can be done by referring to the taxonomic keys and the information provided by the literature studies. However, without having any professional expertise this practice may lead to incorrect conclusion. In order to overcome this issue for better species identification, biochemical and molecular methods are highly recommended (Photita et al. 2001).

One of the useful tools which used for better species identification and give data for the ecological purpose of the species is metabolic profiling technique which also provides the possibilities of the quantitative measurement of the growth and consumption of different carbon and nitrogen sources. According to Kredics et al. (2011), the cellulose-acetate electrophoresis based isoenyzme analysis with using glucose-6-phosphate dehydrogenase, glucose-6-phosphate isomerase, 6-phosphogluconate dehydrogenase, peptidases A, B and D and phoshoglucomutase enzymes was used for isolation and identification of *Trichoderma* strains which derived from some clinical samples and wheat fields. On the other hand, another alternative for the biochemical technique was suggested by Neuhof et al. (2007), where the identification process was mainly based on intact-cell mass spectrometry. This method will help to identify hydrophobins in the mycelia as well as spores of the strains. The patterns of the hydrophobin reflect the characteristic of the species that being isolate and this method can also give a rapid and direct identification of class II hydrophobins (Hanada et al. 2008).

When it comes to the molecular methods, methods like the DNA-fingerprinting, the sequence analysis of ribosomal internal transcribed spacer (ITS) region and the segments from genes encoding for the translation elongation factor 1-alpha (*tef1*), endochitinase (*chi18-5*, formerly known as *ech42*), RNA polymerase II subunit (*rpb2*) and calmodulin (*cal1*) is the suitable method for giving the accurate species identification for *Trichoderma* strains (Druzhinina et al. 2008). The *Trich*OKEY which is also known as ITS-based online barcoding program becomes another useful tool for the species identification. For the analysis of *tef1*, ITS and *rpb2* sequences the online programme known as *Tricho*BLAST and its updated version named *Tricho*MARK can be used. As an example, according to Nagy et al. (2007), by using the online barcoding programme name *Tricho*CHIT, any potential chitinase producing strain such as *Trichoderma harzianum* was used. Moreover, species-specific primers in polymerase chain reaction can be used for a quick and precise diagnosis. According to Kredics et al. (2011), this method allows for a fast and specific identification of *Trichoderma pleurotum* and *Trichoderma pleuroticola.* Both the strain is known as agent that causes the formation of green mould in the global production of *Pleurotus ostreatus* within the growing substrate and without any requirement of cultivation time (Xia et al. 2011a, b).

The studies related to *Trichoderma* biodiversity mainly based on the standard culture approach which contains the collection of samples, the isolation of *Trichoderma* strains on selective media, however when this method is being applied, some strains can be easily identified and there are some which is even harder to do the isolation procedure. The diversity that had been detected by using this method does not reflect the accurate diversity of the genus from the tested habitat. The metagenomic method provides the best solution to overcome this problem as it examining the habitat without doing any isolation or culturing of the strains. When the first attempt is done on biodiversity detection using this metagenomic approach by Hagn et al. (2007) the primers for *Trichoderma* specific were created for the ITSI fragment of the rRNA gene cluster. However, using this approach, only around 12 species have been identified as this ITSI alone is could not identify all the species because certain strains share the same allele (Samuels et al. 2006).

To overcome these issues, Meincke et al. (2010) created the primer pair which is specific for *Trichoderma* for diversity analysis purpose. This specific primer help to amplify around 650 bp fragment of the ITS region which is suitable for identification by *TrichO*KEY and *Tricho*BLAST. The very first PCR-amplification was performed by having fungal specific forward primer and *Trichoderma*-specific reverse primer. For the second reaction, the *Trichoderma*-specific forward and reverse primers are used together. The ITS amplicons help to denature the gradient gel electrophoresis or help to clone to the pGEM-T easy vector. The currently developed primer system was applied on *Trichoderma* communities in the rhizosphere of potatoes. But this method could not detect the several species because reverse primer is located 30 bp upstream of the last genus-specific *Trich*OKEY hallmark (Nawaz et al. 2018).

However, in a recent study conducted by Nawaz et al. (2018), six reverse primers were designed and their specificity and selectivity were tested. Along with the forward primer ITS5 this reverse primer can help to amplify the whole diagnostic region of ITS1. The six separated PCR amplifications from the tested soil that contain same forward and one reverse primers were combined, purified and subcloned to pGEM-T. The sequences of the individual clones were determined and analysed with *Trich*OKEY 2.0 and *Tricho*BLAST. Atanasova et al. (2010) applied this strategy to determine the diversity of the strain in samples.

8.3 *Trichoderma* Diversity in Different Habitats

8.3.1 Natural Soils, Decaying Wood and Plant Material

Danielson and Davey (1973) found out that at the south part of the USA and at the state of Washington, *Trichoderma* can be found at variety of forest soil. Some of the strains like *Trichoderma polysporum* and *Trichoderma viride* were located near the strictly cool temperature regions. *Trichoderma harzianum* was isolated from warm climate area, while *Trichoderma hamatum* and *Trichoderma pseudokoningii* were dominantly growing at area with excessive moisture. Besides that, the isolation, morphological characterization as well as full identification of strains like *Trichoderma aureoviride*, *T. harzianum*, *T. koningii*, *T. longibrachiatum* and *T. viride* from area like the wood of the oak, cork wood and dead wood of the apple twigs have been studied (Vasanthakumari and Shivanna 2011).

The broad studies on the biodiversity of *Trichoderma* were conducted in North America and at some region in Europe. The isolated *Trichoderma* strains were analysed for their function to degrade the organochlorine xenobiotics but as mentioned earlier, the results from this method are difficult to be evaluated. This is mainly due to the fact that there is no available of molecular tools for the identification (Vasanthakumari and Shivanna 2011). According to Zhang et al. (2005), around 135 isolates of *Trichoderma* were obtained from four regions of China which are from Hebei, the northmost side, followed by Zheji-ang, the south-east side, Yunnan, west part and from the Himalayan part as well. The result from this study indicates from among the North to South part, the Northern China finalized as potential centre for origin of the haplotype of *Trichoderma harzianum* (Vasanthakumari and Shivanna 2011).

One the other hand, Abd-Elsalam et al. (2010) isolated the fungi strain from the soil of protected area in Saudi Arabia and the identification process were carried out by suing M13-microsatelite PCR and ITS barcoding. Results from the investigation reveal that *Trichoderma harzianum* and *Trichoderma longibrachiatum* are present. The biodiversity study of *Trichoderma* from the European river floodplain habitat near the Danube national park, which was originally known for its riparian forest area in Vienna, Austria was carried out mainly based on the morphological examinations, sequence analysis of the ITS region and fragment of the tef1 gene as RAPD analysis (Zhang et al. 2005). Plant litter associated fungi was examined from the spring of the sheep herd in the western of Norway and isolated wide variety of fungi which includes two *Trichoderma* strains. However, the authors failed to determine the species by NCBI BLAST for its ITS sequences. But by using *Trich*OKEY the isolated named as *Trichoderma hamatum* while other were identified as *Trichoderma koningiopsis* (Sun et al. 2012).

A wide-scale survey was done over 14 European countries which have temperate climate in order to learn about the biodiversity of *Trichoderma* by testing their morphology, ITS and tef1 sequences. Around 75 species were detected from European countries. By doing ITS barcoding-based study, some of the strains are found from soil and decaying wood. Then taxon-specific metagenomic method was used by Friedl and Druzhinina (2012), in order to determine the *Trichoderma* biodiversity in situ in soil samples from aspen and beech forests along the Danube floodplain. The obtained result shows that not only small number of *Trichoderma* species were capable of forming teleomorph but suggested that the biodiversity of the genus is higher on and above the small layer than inside the soil. Some of the strains associated with the host fungi or trees were found but the major of the species suggested to be necrotrophic on diverse fungi on wood and tree bark (Samuels et al. 2012b).

8.3.2 Endophytes

Living plants or endophytes can be defined as organisms which live within the plant cells. They established a relationship with the plant that varies from symbiotic to pathogenic (Bailey et al. 2006). There are certain types of *Trichoderma* strains which are capable of colonizing the root part of the plant and continue to have a symbiotic relationship with that particular plant. There has been a lot of investigation being carried out in order to prove that *Trichoderma* strains can develop endophytic relationship within the inner tissue part of the plant (Samuels et al. 2012a).

Theobroma cacao which commonly known as cocoa plant was become the first target to carry out the study as this plant can grow easily at any country which have tropical climates. In South America the most common diseases that cause by this cocoa plant are black pod, witches broom and frosty pod rot. To overcome this major issue, extensive study was carried out on the endophytic microbial community of the cocoa plant (Samuels et al. 2012a). From this study, it was concluded that several fungus strains such as *Trichoderma koningii*, *T. ovalisporum*, and *T. koningiopsis* can play its role as endophytes in the cocoa plant (Degenkolb et al. 2008).

According to the study done by Rubini et al. (2005), diversity study about endophytic fungi in the cocoa plant give rise for variety of fungal strains but low prevalence was given to the isolated strains. Posada et al. (2007) reported that there are few endophytic microbiota can be found in the coffee seedlings which contain some of the *Trichoderma* strains such as *Trichoderma harzianum* and *Trichoderma hamatum.*

Besides the cocoa plant, similar studies were also conducted on other plants. One of the good example for this scenario is the *Hevea* spp. which also known as rubber tree. According to Chaverri et al. (2011), a new species named *Trichoderma amazonicum* was isolated from this rubber tree. In Mexico, two other *Trichoderma* fungus functioned as endophyte in two different plants. Zhang et al. (2007) *Trichoderma* strain was identified from *Taxus mairei,* while Samuels et al. (2012b) identified *Trichoderma solani* from the tubers of *Solanum hintonii*. Six types of *Trichoderma* species were identified from the banana root where four of them were from the inside the root, while the rest two were isolated from the surface of the root. Among the species *Trichoderma asperllum* and *Trichoderma virens* showed the highest frequencies in the samples (Xia et al. 2011a, b).

According to Dang et al. (2010), *Trichoderma ovalisporum* was isolated from the traditional Chinese medicinal plant where the strain shows effective antibacterial activity against several pathogenic microorganisms such as *Staphylococcus aureus* and *Escherichia coli. Trichoderma* strains were also isolated from other important medicinal plants such as *Huperzia serrata and Salvia miltiorrhiza.* Strains also were detected from some of the carnivorous plants. Some studies were done on *Drosera rotundifolia* which is also known as common sundew during the season of autumn and spring by Quilliam and Jones (2010). *Trichoderma viride* was isolated from all the samples. Other carnivorous plant which is *Pinguicula vulgaris* was also studied for the potential endophytic fungi. The root and seed from *Dendrobium nobile* and

Dendrobium chrysanthum also studied for the presence of endophytic and mycorrhizal fungi (Ming et al. 2012). Numerous studies and efforts were taken to overcome the growth of the harmful pathogenic fungi, *Rhizoctonia solani.* This fungus has the ability to cause serious quality as well as quantity damages on the potato tuber. However, the endophytic fungi that isolated from the potato plants were tested and based on the obtained result, isolates of *Trichoderma atroviride* show the highest inhibition against *R. solani* due to the mycoparasitic phenomena (Chen et al. 2011).

8.3.3 Air and Settled Dust

Air plays pivotal role when it comes to the dispersal of spores and conidia of fungus. According to the study done by Madsen et al. (2007), *Trichoderma* species can be isolated from air of different environment which varies from outdoor to indoor air. Some good example of indoor air samples are those from heated wooden chips inside the buildings, from air filters that being used in hospitals, air ducts of the households, air conditioners, and achieve storage facilities. *Trichoderma* can be isolated from the outdoor air samples as well which normally from the rooftop of hospitals and houses. The air samples from agricultural area can be potential for this fungus isolation as well. According to Madsen et al. (2007) the dust blown from hay in England can be used for the isolation purpose. However, no species level identification was done for the samples that has been isolated from the air samples and settles dust. From the clinical wise, presence of conidia in the air plays a significant role for the occurrence of allergic diseases and can cause the infections like sinusitis or pneumonia. On the other hand, Hansen et al. (2010) concluded that *Trichoderma harzianum* which used as biocontrol agent can be detected in the air only during the treatment period.

8.4 Agricultural Habitats

Abiotic and biotic stress plays a significant role towards the population and diversity of any microbial communities in the agricultural ecosystems (Rana et al. 2019a, b; Yadav et al. 2018a). This includes the species of the plant and its growth stage, soil physical and properties of the chemical that being used, usage of pesticides, the geographical region and most importantly the total microbial competition (Druzhinina et al. 2011). *Trichoderma* spp can be isolated from any type of agricultural fields as it exhinited significant positive impacts on plant cultivation. Those impacts include its role as efficient biocontrol agent, induction of systemic resistance, increase the uptake of nutrient, promote the plant growth and degradation of any pesticides that can bring negative impact to the soil. The rhizosphere attracts this fungus by having the presence of different soil borne fungi which function as its prey and rich derived nutrient. The members of *Trichoderma* are preferred to be isolated from rhizosphere and non-rhizosphere soil rather than phyllosphere. Some of the species are ubiquitous where some are limited to certain geographical areas (Kour et al. 2019c).

As mentioned earlier, the isolation of this fungus from various agricultural crop fields was carried out to conduct studies on its biological control ability against phytopathogens, so only limited number of studies that deal with the population, abundance and diversity of the genus of *Trichoderma* from specific crop fields were carried out. *Trichoderma* spp can be highly found in cereal crop fields and is one of the dominating fungi and prevalent taxa among other fungal communities. When it comes to the cereal crop field, the weather, the type of soil and farming management bring big influence to the distribution of the *Trichoderma* spp. Six different species of the fungus were discovered by the ITS barcoding and restriction fragment length polymorphism (RFLP) from the rhizosphere, rhizoplane and the soil bulk of potato (Liang et al. 2004).

From the rhizosphere of coffee, *Trichoderma* isolates also have been discovered particularly from the soil of the coffee plants in the forest and semi-distributed forest area. The identification was done by ITS barcoding. Either its cultivated or uncultivated coffee regions, both of the different area show higher diversity of this isolates but the indices and the evenness for this isolates were the same at the both the habitats. Some chemical properties and the altitude of the samples concluded that the growth of the isolates was not preferred by the ecological perspective. It was also concluded that the host plant influence the genetic diversity of *Trichoderma* strains. Around 135 isolates of *Trichoderma* were collected from the rhizospheres of cocoa plant of different locations (Pavone and Domenico 2012).

From the rhizosphere of sugar beet, sixteen isolates were collected and the identification process was done based on the morphology, ITS and *tef1* analysis. When it comes to the oilseed rape rhizosphere, *Trichoderma* spp. were the most prevalent fungi and most importantly it showed high biodiversity and specificity in the bulk soil of oilseed rape. Another most important plant that acts as a rhizosphere for *Trichoderma* isolates is the oil palm. Among the isolates strains, *Trichoderma harzianum* and *Trichoderma virens* were the most prevalent species that had been recovered from the soils of oil palm in Malaysia. Population wise, it shows the high in both the cultivated and semi-cultivated oil palm ecosystems. However, the population increased when empty fruit bunches were added to the fields and the moisture content and the pH of the soil did not bring any effect towards the distribution of the strains. In conclusion the diversity and the abundance of the *Trichoderma* were higher in bulk soil than in rhizosphere soil (Naeimi et al. 2011).

8.5 *Trichoderma*: Promoting Healthy Plant Growth

In the recent time, *Trichoderma* spp. has been widely suggested to be used for efficient plant growth as a good plant growth promoting fungi (PGPF). These have capability of producing some of the secondary metabolites in particularly siderophores, phosphate-solubilizing enzymes and phytohormones for plant growth and soil health (Doni et al. 2013; Kour et al. 2019b; Yadav 2019). This plant growth promoting traits is considered one of their beneficial trait and this traits can be seen through different type of mechanisms such as antibiosis, degradation of toxins, mycoparasitism, inactivation of pathogenic enzymatic pathway and also but not least the enhanced nutrient uptake which leads to the overall development (Lorito et al. 2010; Kaur et al. 2020; Kumar et al. 2019; Singh et al. 2020). This fungus is known as hemibiotrophic fungus which is effective towards reducing the severity of the plant diseases by several mechanisms which have been mentioned above (Fontanelle et al. 2011). Most of the secondary metabolites produced by *Trichoderma* are strain dependent, can contain both volatile and nonvolatile antifungal substances and it is rhizosphere-competent strains which mainly involve in colonizing the surface root which have been shown for causing direct impact on the plants. It helps to increase the nutrient uptakes which eventually leads to better physical growth of the plant (Gal-Hemed et al. 2011).

According to Doni et al. (2014), the usage of *Trichoderma* as plant growth promoter shows significant positive impact towards the height of the plant, number of leaf and the length of the root. The possibilities for this to occur are mainly because of mechanisms which involve nutrient usage and the tolerance to abiotic and biotic stress. In addition to that, phytohormones produced by this fungus play a pivotal role for the enhanced growth of the plant. Some of the reports include phytohormones such as cytokinin like molecules and gibberellins related molecules can make biological enhancement on the crop fertility. On the other hand, Kashyap et al. (2017) also mentioned that the rice which inoculated with the *Trichoderma* shows higher photosynthetic rate. Other good impact shown by rice with the presence of *Trichoderma* is better uptake of the nutrients and increased resistance towards drought. On the other hand, maize plant, this fungus increased the plant's biomass production as well as developed better root hair. *Trichoderma* also helped to increase the seed germination process, increase the osmotic, salinity and chilling by initiate the physiological protection against any form of cellular damage (Mastouri et al. 2010).

The interaction in between *Trichoderma harzianum* strain and tomato-root system was also studied at the beginning stage of the root colonization. The presences of the fungus inoculation in the production medium cause the profuse adhesion of the hyphae to the roots and the colonization of the root epidermis and cortex. The green fluorescent protein (GFP) shows the hyphal growth and the formation of the papilla like hyphal tips which induced by the plant.

Trichoderma harzianum in particular is able to control and inhibit the growth of *B. cinerea* on grapes by colonize the blossom tissue and exclude the pathogen from the infected side. According to Kashyap et al. (2017), *Trichoderma* species used the competition for nutrient as their major mechanisms to inhibit the soil *microorganisms*. In addition to that, *Trichoderma* has the advantage of mobilizing and take up all the nutrients which makes much more efficient and more competitive than many other soil microbes. However, the biotic components of the soil have several impacts on the bio control activity of *Trichoderma* against other plant pathogens. According to Kashyap et al. (2017), when the *Gfp* contained mutant strain used, it shows higher level of microbial soil biomass that induce the shift from the hyphal growth to sporulate in *Trichoderma* (Table 8.1).

8.6 *Trichoderma*: Biological Control Agent

Fungi have been used for biocontrol purpose in much modern agricultural system. This is mainly because most of the fungi have the ability to reduce the negative impact of plant pathogen (Rana et al. 2020; Yadav et al. 2018b). *Trichoderma* sp. have gained much more interest than any other fungi due to their surviving ability under any form of unfavourable condition, high capacity for reproductive purpose,

Table 8.1 The effect of *Trichoderma* inoculum on the agronomical and physiological aspects of the crops

Trichoderma strain	Crop	Application mode	Effects	References
Trichoderma sp.	Chickpea	Agar plates were inoculated with a fungal mycelial disc of 5 mm diameter	Increased solubilization of inorganic phosphate	Rawat et al. (2011)
Trichoderma harzianum	Cucumber	5 × 106 conidia per g of soil or sprayed on roots at a concentration of 1 × 108 conidia/ml	Promoted seed germination, vegetative growth, and flowering	Chang et al. (1986)
Trichoderma harzianum	Chrysanthemum	5 × 106 conidia per g of soil or sprayed on roots at a concentration of 1 × 108 conidia/ml	Promoted seed germination, vegetative growth and flowering	Chang et al. (1986)
Trichoderma asperelloides T203	Arabidopsis	Root system was inoculated with a solution containing 1 × 10^5 spores/ml	Improved seed germination	Brotman et al. (2013)
Trichoderma hamatum	Arabidopsis	Trichoderma bran inoculum added to soil before sowing	Promoted root and shoot growth	Studholme et al. (2013)
Trichoderma atroviride	Lettuce	The substrate was supplied with prepared tablets containing 4.5 × 10^5 conidia	Enhanced shoot and root dry weight, and chlorophyll content	Colla et al. 2015

capability to resist against other plant pathogenic fungi and can able to produce secondary metabolites (Contreras-Comejo et al. 2016; Benítez et al. 2004). Besides that, this fungus has been also used in various biotechnological applications and used in agriculture field mainly to enhance the growth and the yield of the plants (Lorito et al. 2010; Hermosa et al. 2012).

Any form of penetration or interaction in plant roots normally will activate its immune system but in case of *Trichoderma* sp. it will remodel the immune system of the plant and help it to be recognized as non-pathogenic plant. The strains of the fungus can able to eliminate the synthesis of JA and ET which mainly involved in inducing systematic resistance (Hermosa et al. 2012). The systematic resistance induced by *T. asperellum* or *T. harzianum* T39 against *B. cinerea* in *A. thaliana* was determined as well. *Trichoderma* sp. plays an important role when it comes to suppressing the formation of any plant disease and plant pathogen in both the field condition and greenhouse condition. The fungus can produce wide range of elicitors which will interact with the receptors and recognition of *Trichoderma* and this will lead to the induction of resistance in the plant (Salas-Marina et al. 2011). In addition, different types of *Trichoderma* strains are able to produce little amount of secondary metabolites and these metabolites seem to induce the pathogenesis-related protein and eventually reduce the symptoms of any disease (Vinale et al. 2006). Through the mycoparasistm process, *Trichoderma* can parasitize the plant pathogen during different stages of development. This is done by producing several enzymes such as chitinase, proteases and glucanases which will help to flow the nutrient into the mycoparasite and finally degrade the host of the pathogen (Inch and Gilbert 2011). Table 8.2 shows the different *Trichoderma* strains against different bacterial pathogens.

Both the mono and dicotyledonous species show strong resistance towards attack of various pathogens when the plant is well pre-treated with *Trichoderma*. The plant colonization caused by this fungus inhibits the growth of different pathogens at the side of inoculation and also when the biocontrol fungus inoculated at different times or sites than that of the pathogen. In addition to that, the resistance of the plant shown by the colonization of some of the *Trichoderma* sp. is pretty much similar to that elicited by the rhizobacteria where it enhance the defense system of the plant but do not directly involve with the production of the pathogenesis-related proteins known as PR proteins. Recent studies have been done at the molecular level by using the high-density oligonucleotide microarray approach and it was found out that the gene induced by *Trichoderma* was associated with the biotic and abiotic stresses and also RNA, DNA and protein metabolism. The genes that codify for the extensin and also extensin look like proteins were mainly induced by the biological agents.

The plant starts to interact with *Trichoderma*, different types of metabolites which belong to different classes will start to be produced as elicitors or as resistance inducers (Woo and Lorito 2007). Proteins with enzymatic activity such as xylanase, avirulence are able to induce the plant defence mechanisms and induce the production of low molecular weight compound as a result of fungus–plant interaction. Some of these low molecular weight compounds which have the ability to

Table 8.2 Different *Trichoderma* strains against different bacterial pathogens

Trichoderma Strains	Plant	Pathogen	Mechanisms/activity	References
Trichoderma harzianum	Tomato	*Clavibacter michiganensis subsp. michiganensis*	Lysosime and prevent activity	Utkhede and Koch (2004)
Trichoderma spp.	Rice	*Xanthomonas oryzae* pv. *Oryzae*	Biocontrol activity	Gokil-Prasad and Sinha (2012)
Trichoderma asperellum	Tomato	*Xanthomonas campestris pv. vesicatoria*	Biocontrol activity, antagonism dosage	Suárez-Estrella et al. (2014)
Trichoderma harzianum T23	Activity in vitro	*Clavibacter michiganensis* and *Erwinia Amylovora*	Production of viridiofungin A (VFA)	El-Hasan et al. (2009)
Trichoderma reesei	Arabidopsis and tomato	*Clavibacter michiganensis*	Production of extracellular enzyme, swollenin	Saloheimo et al. (2002)
Trichoderma asperelloides T203	Tomato	*Pseudomonas syringe* pv.	Increase level of WRKY 40 transcription factor	Brotman et al. (2012)
Trichoderma atroviride	Tomato	*Alternaria solani*	Secrete Sm1 and Ep11 protein	Salas-Marina et al. (2011)

degrade fungal cell wall have been purified and further characterized. These compounds have been mainly composed of oligosaccharides with or without amino acids moiety. In these interaction mechanisms *Trichoderma* activates the mycoparasitic gene expression cascade. Besides the activated antimicrobial effect, their action might stimulate the biological activity of the resident antagonistic microbial populations or the introduced *Trichoderma* strains and this will induce the effect of induced systematic resistance on the plant.

8.7 Biotechnological Applications

8.7.1 Production of Antibiotics and Other Secondary Metabolites

There are several compounds which are not involved for the normal growth and the reproduction of any organisms. These compounds are called as secondary metabolites. However, they play pivotal role when it comes to the development, signaling and the interaction between one organism and other (Rastegari et al. 2019; Yadav et al. 2019a; Saxena et al. 2016). The absence of these metabolites will result in the long term impairment on the survival of the organism rather than causing a direct and immediate death. According to Mukherjee et al. (2012), certain environmental factors will cause the organism to be dependent on the secondary metabolites such as in case of iron deficiency as siderophores act as replacement to support growth. Plants use these secondary metabolites as a defence system against herbivores and other inters species. According to Vipul et al. (2014), humans use it for medicine, flavourings and drug creation purposes. On the other hand, it also can be used as efficient weapon against other pathogenic bacteria, amoeba, fungi, insects and even large animals. Secondary metabolites can be used as agent for symbiosis purpose between plants and other organisms (Kour et al. 2019a).

Commonly known as filamentous fungi, *Trichoderma* spp., can be found nearly in most of the soils and other habitats. They have the capability of adapting to different ecological conditions and lifestyles. *Trichoderma* fungus has economical important mainly due to the fact that it can be used as a good biocontrol agent which help to inhibit the growth of phytopathogenic fungi. It can be functioned as biocontrol agent because of the presence of extracellular enzymes and secondary metabolites. Particularly the secondary metabolites produced by the fungus can be used in biotechnological and pharmaceutical purposes. This includes secondary metabolites such as peptaibols, non-ribosomal peptides, terpenes, steroid and many more. Although there have been 373 different molecules that have been identified so far, their specific activity is still cannot be determined.

According to Verma et al. (2017b), these fungal biocontrol agents have been mainly used against any soil related diseases. In order for them to perform as an efficient biocontrol agent they must show different mechanisms of action when it comes to their antagonistic interaction with any fungal pathogens. Some good examples are the mycoparasitism, antibiotic activity, basic competitions for nutrients, induction of systematic resistance and cell wall lytic enzyme activity. Trichodermin, gliovirin and harzianic acid are the best known metabolites that being produced by *Trichoderma* species (Singh 2010). Strains such as *T. viride*, *T. harzianum* and *T. atroviride* are capable of producing pyrone (6-pentyl-2H-pyran-2-one). These metabolites are the main reason behind the release of coconut aroma. Pyrone is also known for its antifungal activity against plant pathogenic fungi. The fungus also produces cytosporone which show strong in vitro antibiotic activity against some pathogenic bacteria and fungi.

Koninginis metabolites are also capable of inhibiting the growth of fungus such as *Gaeumannomyces graminis* var. It also can kill some of the soil-borne plant pathogens such as *Fusarium oxysporum*, *Pythium middletonii*, *Rhizoctonia solani* and many more (Vinale et al. 2006). These secondary metabolites in particular can prevent the spore germination by the fungal pathogens. According to Vinale et al. (2006), a secondary metabolite called T22 azaphilone from the liquid culture of *T. harzianum* was isolated. These metabolites inhibit several plant pathogens such as *R. solani* and *G. graminis* var. *Trichoderma hamatum* produces viridiol which reduces and at certain circumstances inhibits mycotoxin like aflatoxin which produced during the fungal interaction. So the usage of this secondary metabolites produced by *Trichoderma* strains can induce the resistance level of the host and also promote the yield of the crop which can be the most suitable replacement for the chemical usages. Due to the presence of the secondary metabolites, *Trichoderma* strains can also be used as biofertilizers where there are two strains, namely *Trichoderma harzianum* T22 and T39 used as active agents for various commercial biopesticides and biofertilizers.

Most of the fungus around the world has the ability to produce potential toxins in the form of antibiotics which can kill other pathogenic microbes regardless its concentration level. The differences in between these antibiotics somehow show different activities against both prokaryotes and eukaryotes. Paracelsin is the first antibiotic discovered that produced by the species *Trichoderma.* Most of the time it produces large compounds that have the antibiotic activity and this production is mainly dependent on the factors such as pH, temperature and quantity of microorganisms. A single *Trichoderma* species can produce different type of antibiotic compounds and likewise the given antibiotic has the potential of being produced by different strains. However, according to the study done by Sivasithamparam and Ghisalberti (2014), it revealed that different isolates of same species can produce different compounds as well.

Trichoderma harzianum often leads to the production of antibiotic where the methanolic extract from the dual culture of this fungus showed strong antimicrobial activity against *Staphylococcus aureus*. Moreover, general *Trichoderma* species that can be found in marine habitat also known to produce bioactive metabolites such as antimycobacterial. According to the study conducted by Wu et al. (2014), from the culture of marine *Trichoderma* strain tentatively named as MF106, the particular strain shows antimicrobial effects towards human pathogenic strains such as *Staphylococcus aureus.* The strains also known to be used for the protection purpose of grapevine wounds from the infected trunk pathogens. In a nutshell, *Trichoderma* spp. can be used on a wide spectrum for both in vitro and in vivo (Kotze et al. 2011).

8.7.2 Production of Hydrolytic Enzymes

Currently, most of important crops which have economic purposes largely are being destroyed by the pathogens fungi in particular which the most aggressive is soilborne pathogen. There is some investigation being carried out in order to overcome this problem. One of the well-known steps is the usage of chemical pesticides to control the growth of these pathogenic microorganisms (Yadav et al. 2018a, b). However, using chemical pesticides can cause long term effect towards the human health as well as the environment. Thus, eco-friendly alternatives have been approached to replace the usage of the chemical pesticides.

*Trichoderm*a fungus can be an eco-friendly replacement for the chemical pesticides due to its ability of producing hydrolytic enzymes. The cell wall of the fungus can able to produce hydrolytic enzymes such as cellulase, chitinase and more. This enzyme plays a pivotal role when it comes to the degradation of biomass (Schuster and Schmoll 2010). The cell wall of *Trichoderma* is mainly made up of β-1,3-glucans and chitin and sometimes cellulose in some of the oomycetes. There are some demonstrations that have been done to give a clear picture on how some of the *Trichoderma* strains produce hydrolytic enzymes to inhibit the growth of pathogenic microorganisms such as in case of *Trichoderm harzianum*.

In most cases, the production of this enzymes mainly depends on factors such as availability of type of carbon source, presence of light, growth rate and secretion stress (Tisch and Schmoll 2013). Besides than the strain that have been mentioned above, *Trichoderma reesei* is another widely used strain which produces cellulose and the hemicellulose degrading enzyme. Both of these enzymes are highly used for industrial purposes. Häkkinen et al. (2012) mentioned that a complex system will be formed by the large number of carbohydrate active enzymes that being produced by the fungus which will be regulated by the series of environmental and physical factors. *Trichoderma hamatum* on the other hand possesses high antimicrobial activity mainly because it consists of specific β-glucanase and chitinase. Both of these enzymes play significant role when it comes to the cell wall degradation. According to Ahmed et al. (2009) three type of glucanases: exoglucanase (EXG), endoglucanase (EG), and β-glucosidase (BGL) have been isolated from *Trichoderma harzianum*. These enzymes also being used for malting, baking, alcohol production, paper and textile industries (Galante et al. 2014).

8.8 Conclusion and Future Prospect

For many years, based on its GRAS status according to FDA, Trichoderma has been applied in agriculture to promote cell growth and control of plant diseases without any potential risk to the environment. However, the non-agriculture applications of this microbe are still very limited even it consider as one of the safest microbes without any potential pathogenicity to human and animal. Based on the high capacity of *Trichoderma* for the production of hydrolysis enzymes, primary and secondary metabolites, it is strongly believed that this microbe has very high potential in biotechnology industries. In addition, this microbe has high capacity to grow on wide range of cheap substrates as a result of the high capacity to produce wide range of hydrolases enzymes to breakdown the complex carbon and nitrogen sources. The high capacity for enzyme excretion makes it also a very attractive biofactory for native and recombinant enzyme production. These all together giving us the strong confident of the high potential future application of *Trichoderma* not only in green biotechnology (agriculture) but also in white biotechnology (industry) for the production of their own native and recombinant products.

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Chapter 9
Piriformospora indica: Endophytic Fungus for Salt Stress Tolerance and Disease Resistance

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Contents

9.1 Introduction

Increased incidences of abiotic and biotic stresses impacting productivity in important crops are being witnessed all over the world. The problem of soil drought and salinity presents one of the greatest problems in agriculture. Many keys to agricultural success in arid and semiarid areas are to use adequate plant species and to use the soil biology potential to maintain soil fertility, to guard against abiotic stress (Kour et al. 2020a; Zarea et al. 2013) and biotic stress (Dresselhaus and Hückelhoven 2018). The fungal endophytes provide immune system to host plant to defend

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against phytopathogenic organisms (Jain and Pundir 2017; Rana et al. 2019a) and help plants to adapt to new habitats and against abiotic stress by making genetical, physiological, and ecological modification to its host plants (Lugtenberg et al. 2016; Ali et al. 2018; Yadav et al. 2019c). Focusing on fungal microbe's endophytes *P. indica* were defined as organisms that colonize in living plant tissue during their entire life cycle (Kusari and Spiteller 2012; Anitha et al. 2013; Lugtenberg et al. 2016; Arora and Ramawat 2017; Jain and Pundir 2017; Khare et al. 2018; Lata et al. 2018; Abo Nouh 2019; Chhipa and Deshmukh 2019); and live in a broad variety of host plant species (e.g., barley, maize, parsley, poplar, tobacco, and wheat) without causing disease symptoms (Desisa 2017).

The symbiotic fungus *P. indica* displays an endophytic lifestyle and has the ability to colonize the root cortex cells of a wide range of mono- and dicotyledonous plants, displaying a broad range of beneficial effects to the host (Baltruschat et al. 2008; Sherameti et al. 2005, 2008; Waller et al. 2005; Yadav et al. 2010; Lahrmann and Zuccaro 2012). The root endophyte fungus *P. indica* enhances the tolerance of colonized plants against drought, acidity, heavy metals, and various other abiotic stresses as well as biotic stresses (microbial pathogens/insects), promotes nutrient uptake, and stimulates growth and seed production (Verma et al. 1998; Varma et al. 1999; Sahay and Varma. 1999; Peškan-Berghöfer et al. 2004; Waller et al. 2005, 2008; Oelmüller et al. 2009; Krishnaveni et al. 2014; Basu et al. 2016; Justice et al. 2018; Xu et al. 2018).

9.2 History of *P. indica* and Systemic Position

During a routine isolation of AM fungi in the desert Thar (Rajasthan, India), Verma and his collaborators were isolated *P. indica* for the first time from the soil of two xerophytic plants, namely *Prosopis juliflora* and *Ziziphus nummularia* as a contaminant (Verma et al. 1998; Varma et al. 2013). At the first superficial view it seems that the isolated spore is a vesicle of an AM fungus and belongs to a fungus of the Glomeromycota. But this spore was well growing on artificial complex media (*P. indica* can be easily cultivated in axenic culture). Therefore, this species could not be a member of the Glomeromycota because Glomeromycota are growing in biotrophic interaction with plants only (Verma et al. 1998). The isolated fungus was described as a new species of family Sebacinaceae, order Sebacinales, phylum Hymenomycetes, Basidiomycota. The fungus was named *P. indica* based on its characteristic pear-shaped chlamydospores (Verma et al. 1998; Varma et al. 1999; Kost and Rexer 2013; Varma et al. 2013; Krishnaveni et al. 2014; Pan et al. 2017). *P. indica*, an axenically cultivable phytopromotional, is a biotrophic mutualistic root endosymbiont and has been reported to mimic capabilities of typical arbuscular mycorrhizal (AM) fungi (Gill et al. 2016). They also lack cystidia and structures formed during cytokinesis on some basidiomycetous hyphae, the so-called clamp connections. Like other cultivable species of the Sebacinales, *P. indica* forms moniliod hyphae, which look like pearls in a chain (Selosse et al. 2007). The first experiments with *P. indica* revealed that the co-cultivation of the fungus together with young maize seedlings causes a strong support for the growth of their shoots (Kost and Rexer 2013).

9.3 The Diversity of *P. indica* and Plant Habitat

P. indica is a cultivable fungus and can grow on synthetic media without a host (Verma et al. 1998; Peškan-Berghöfer et al. 2004). The host range includes trees, agricultural, horticultural, monocots, dicots, and mosses (Glen et al. 2002; Peškan-Berghöfer et al. 2004; Barazani et al. 2005; Sherameti et al. 2005; Waller et al. 2005), suggesting that the interaction is based on general recognition and signaling processes (Camehl et al. 2013). Inoculation of a broad variety of plants with *P. indica* had a positive effect on their general biomass production (Varma et al. 1999), and subsequent analyses showed that *P. indica* exerts a variety of physiological effects. It promotes the establishment of micro-propagated plants (Sahay and Varma 1999), adventitious root formation in cuttings, and lignan production of hairy root cultures; enhances flowering; increases yield; and induces higher tolerance of and resistance to abiotic and biotic stresses (Waller et al. 2005).

P. indica has been termed as plant probiotic because of its plant growth-promoting activity and its role in enhancement of the tolerance of the host plants against abiotic and biotic stresses (Basu et al. 2016). The fungus possesses unique properties to act as biofertilizer, bioprotector, and immunoregulator. It also plays a key role in protecting roots from insects by increasing the tolerance of the host roots (Varma et al. 1999; Waller et al. 2005; Serfling et al. 2007; Prasad et al. 2008; Bagde et al. 2010). The underlying mechanism of the fungus beneficial activity is not yet understood, but it is observed that the plant antioxidant system is activated and thus implicated in the improvement of abiotic and biotic stress tolerance (Waller et al. 2005; Varma et al. 2013). *P. indica* is capable to colonize with the root of both gymnosperm and angiosperm and the colonization is restricted to the rhizodermis (Deshmukh et al. 2006). *P. indica* tremendously improves the growth and overall biomass of diverse hosts including legumes (Verma et al. 1998; Varma et al. 1999); industrial crops (Singh et al. 2011); important plants such as *Oryza sativa*, *Zea mays*, *Tridax procumbens*, *Nicotiana tabacum*, *Arabidopsis thaliana,* and *Brassica oleracea var. capitata* (Varma et al. 2012a); tobacco (Tanha et al. 2014); the agriculturally important barley, the model plants (Lugtenberg et al. 2016); and medicinal plants such as *Artemisia annua*, *Abrus precatorius*, *Azadirachta indica*, *Bacopa monnieri*, *Curcuma longa*, *Linum album*, *Stevia rebaudiana*, *Trigonella foenum-graecum* (Oelmüller et al. 2009, Kumar et al. 2017). It colonizes the root cortex, grows inter- and intracellularly, forms pear-shaped spores within the cortex and extramatrically, and does not invade the endodermis and the aerial parts of the plants (Oelmüller et al. 2009; Abo Nouh 2019).

This fungus can colonize roots of a wide range of higher plants and provide plants with multifaceted amenities such as nutrient uptake, disease resistance, stress tolerance, and growth promotion involving value addition (Unnikumar et al. 2013). Interaction between *P. indica* and Chinese cabbage (*Brassica campestris* cv. Chinensis) results in growth and biomass promotion of the host plant and in particular in root hair development (Dong et al. 2013). *P. indica* can be cultivated easily on synthetic media and colonized with cabbage and spinach of Brassicaceae family, in contrast to Arbuscular mycorrhizal fungi (AMF) (Bagheri et al. 2014). Unlike AM fungi, *P. indica* can grow without a plant host. This characteristic is advantageous for mass production and potential commercialization because production does not require the additional complexity of growing plants to rear the fungus. *P. indica* also colonizes plants that AM fungi cannot, such as members of the Brassicaceae family (Deshmukh et al. 2006) and members of Cruciferae family (Gosal et al. 2013).

P. indica has been reported to perform multifarious functions e.g. biological hardening during transplantation of micro-propagated plantlets (Singh et al. 2003), and increased endogenous content of spilanthol after realization of its mutual interaction with medicinal plants such as *Spilanthes calva* (Rai et al. 2004). *P. indica* colonizes the epidermal and rhizodermal parts of the Arabidopsis roots and root hairs, and forms pear-shaped spores. The hyphae never invade the endodermis or central meristematic tissue of the root and never proceed to aerial systems, stem, or foliage. Propagation of the fungus does not only exclusively occur within the cells, but also at the root surface and in its environment (soil system). Interaction between the two partners leads to growth promotion of the seedlings (Oelmüller et al. 2009). *P. indica* infestation in *Helianthus annuus* and *Aristolochia elegans* has resulted into the stimulated synthesis of valuable compounds (Bagde et al. 2010; Gill et al. 2016). Mutualistic fungi *P. indica*, added to propagation media, have been shown to increase root weight and root initiation in a range of plant species, including dwarf umbrella tree (*Schefflera arboricola*), anglojap yew (*Taxus media*), bearberry (*Arctostaphylos uva-ursi*), geranium (*Pelargonium* sp.), rose (*Rosa 'Scarlet Cupido'*), malabar nut (*Adhatoda vasica*), and poinsettia (Justice et al. 2018).

9.4 *P. indica* Strategies for Root Colonization and Interaction Structures

One of the specific features of *P. indica* is the ability to interact with the roots of many plant species of different taxa. The morphology of the interacting structures depends on the involved partners. These interacting partners could be mosses, ferns, gymnosperms, and angiosperms (Kost and Rexer 2013). Some facts related with the lifestyle and the mechanisms underlying root colonization of *P. indica* from its interaction with many plants (such as *Hordeum vulgare* and *Arabidopsis thaliana*) have been unraveled (Deshmukh et al. 2006; Schäfer and Kogel 2009). Within the host plant root tissues, structures similar to arbuscules and vesicles occur in the intercellular spaces as well as may be packed intracellularly which enhances the interaction interface among the microsymbiont and the host plant tissues or may act as storage organ of the microsymbiont (Gosal et al. 2013). All plant species, which are able to form one of the different mycorrhizal types, can be used by *Piriformospora* as a host (Kost and Rexer 2013). Generally, symbionts colonize rhizodermal and cortical cell layers of roots. The sites of *P. indica* infection include the root tip, root hairs, and the root differentiation zone from where the fungus reaches the cortical tissue and starts producing spores in epidermis and cortex within a week.

The intracellular existence of this fungus indicates its potential to exist inside root cells as hyphae and spores, without provoking tissue necrotization (Deshmukh et al. 2006; Gosal et al. 2013). Root colonization by *P. indica* is also known to start within interacellular chlamydospore germination and forming extracellular hyphal mats, and simultaneously penetrating rhizodermal and cortical cells (Deshmukh et al. 2006; Jacobs et al. 2011). The fungus either colonizes roots intracellularly via rhizodermal cells or penetrates cortical cells after an initial intercellular growth phase. Root colonization gradiently increases with tissue age as the maturation zone is predominantly colonized, while the fungus is almost absent at the meristematic zone. Accordingly, sporulation is mainly found at extracellular regions of the maturation zone in addition to intracellular sporulation at rhizodermal and cortical cells of the same tissue (Jacobs et al. 2013). *P. indica* forms typical pyriform chlamydospores which act as perennation bodies similar to the AM spores and forms extended hyphal structures that ramify the soil in vicinity of the host roots hunting and accumulating nutrients like phosphorus, iron, manganese, zinc, and many more from a diameter of several square meters of the soil (Gosal et al. 2013).

The colonization patterns of the various root regions harbor some quantitative as well as qualitative differences, which distinguish *P. indica* on *H. vulgare* and *A. thaliana* from endomycorrhizal fungi. The fungal root colonization increases with root maturation and the highest fungal biomass has been found in the differentiation, particularly in the root hair zones (Deshmukh et al. 2006). Importantly, the physiological activity of host cells has been considered as a prerequisite for efficient nutrient exchange between the symbiotic partners (Schäfer and Kogel 2009). Thus, root colonization pattern of *P. indica* differs from than that of AM fungi, which are known to prefer entially colonize younger root parts (Gill et al. 2016). *P. indica* with plants, especially emphasizing its life strategies in host plants, has shown that root colonization by *P. indica* and its lifestyle in plant may vary depending on the environmental factors, the genetic predisposition, and the developmental stage of host plants and plant organs, respectively (Desisa 2017).

Interaction structures occur in *P. indica* by two ways according to Kost and Rexer (2013): Endophytic and Necrotrophic Mode of Life and Biotrophic Interaction with Living Plant Cells.

9.4.1 *Endophytic and Necrotrophic Mode of Life*

The fungal colonization of roots begins with a biotrophic growth phase, in which living cells are colonized, and followed by a cell death dependent phase, in which root cells are actively killed by the fungus (Qiang et al. 2011; Yadav et al. 2020c, d). *P. indica* is able to destroy the cells at the beginning of the interaction and behaves itself like a necrotrophic parasite in some cases (Deshmukh et al. 2006; Kogel et al. 2006; Schäfer et al. 2007). If hyphae of *P. indica* invade into a plant cell, the hyphal tip forms a small inconspicuous appressorium on the surface of the outer wall of the rhizoids or root cells. After the plant cell wall is locally dissoluted by fungal enzymes, the hyphal tip intrudes into the plant cell. Mostly the invaded root cells of plant species are killed before infection, or they die off during the contact phase of the hyphae. The fungal hyphae cross the cell wall with thin penetration peg. The cell content will be saprophytically decomposed by the fungus. Very often *P. indica* develops its chlamydospores inside these dead root cells (Kost and Rexer 2013). The established fungus is located within the root's cortical cells but does not colonize or damage meristematic cells (Harman and Uphoff 2019).

9.4.2 *Biotrophic Interaction with Living Plant Cells*

It possesses genes for a biotrophic lifestyle, and lacks genes for nitrogen metabolism, but also shares characteristics with symbiotic fungi and obligates biotrophic pathogens (Zuccaro et al. 2011). In contrast to the widely distributed necrotrophic type of interaction between the hyphae of *P. indica* and the root cells of plants, a small group of plants have developed an equilibrated biotrophic interaction between the hyphae of *P. indica* and the living cells of the plant. In case of this interaction, the invading hyphae of *P. indica* do not destroy the invaded cells of host plant. This interaction could be interpreted as biotrophic and mutualistic (Kost and Rexer 2013).

9.5 Effects of Biotic and Abiotic Stresses on Plants

Due to global warming, and potential climate abnormalities associated with it, plants have evolved to live in environments where they are often exposed to number of abiotic and biotic stress combinations (Rastegari et al. 2020a, b; Yadav et al. 2020e). Being sessile, they have developed specific mechanisms that allow them to detect precise environmental changes and respond to complex stress conditions, minimizing damage while conserving valuable resources for growth and reproduction (Fig. 9.1). Plants activate a specific and unique stress response when subjected to a combination of multiple stresses (Atkinson and Urwin 2012). Based on the number of interacting factors, stresses can be grouped into three categories: single,

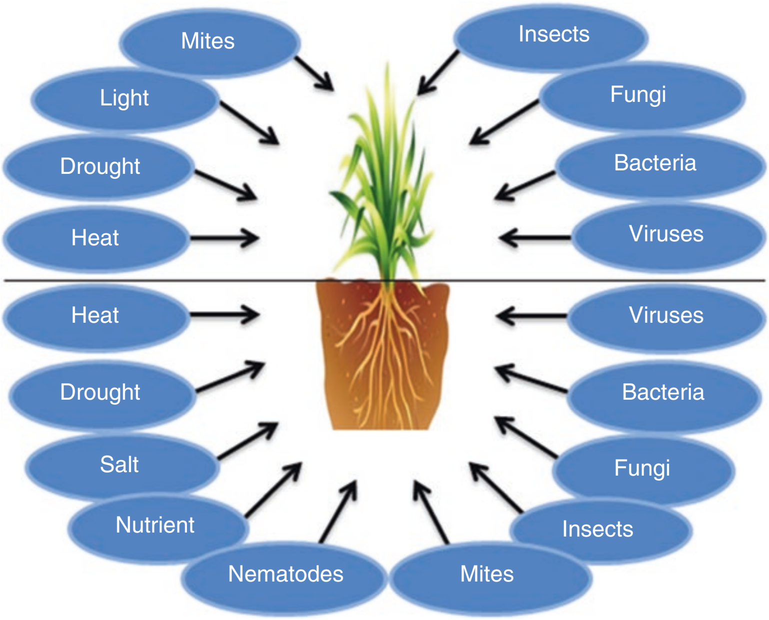

Fig. 9.1 Abiotic and biotic stress factors on plant

multiple individual, and combined stresses. A single stress represents only one stress factor affecting plant growth and development, whereas multiple stresses represent the impact of two or more stresses occurring at different time periods without any overlap (multiple individual) or occurring concurrently with at least some degree of overlap between them (combined) (Singh and Yadav 2020; Yadav et al. 2020a, b). The co-occurrence of drought and heat stresses during summer is an example of a combined abiotic stress, whereas a bacterial and fungal pathogen attacking a plant at the same time represents a case of combined biotic stress (Kour et al. 2020a, b; Pandey et al. 2017). Plants are faced with numerous biotic stresses and adverse environmental conditions. They respond to these stresses through several morphological, biochemical, and molecular mechanisms and evidence suggests that there are interactions among their respective signaling pathways (Gimenez et al. 2018; Kour et al. 2020c; Yadav et al. 2017).

Abiotic stress factors such as heat, cold, drought, salinity, and nutrient stress have a huge impact on world agriculture, and it has been suggested that they reduce average yields by >50% for most major crop plants (Yadav and Yadav 2018; Wang et al. 2003; Atkinson and Urwin 2012). Abiotic stresses have become an integral part of crop production. In general, plants suffer from dehydration or osmotic stress under drought, salinity, and low temperature condition which causes reduced availability of water (dehydration) for cellular function and maintenance of cellular turgor pressure (Kumar et al. 2019a; Varma et al. 2013; Yadav et al. 2019e). Plants become nutrient deficient and lose their normal physiological pattern of growth and development due to varying levels of acidic conditions; early exposure to salinity results in ion toxicity; drought decreases germination rates, causes inhibition of photosynthesis, loss of membrane integrity, and increased generation of reactive oxygen species (Lata et al. 2018; Yadav et al. 2019a).

Drought, heat, and salt stress affect plant–water relations triggering complex plant responses, which include increased production of osmolytes (Bohnert et al. 1995; Wang et al. 2003; Verma et al. 2017). Osmotic potential is determined primarily by two components: solute potential and matrix potential, and it is likely that symbiotic fungi contribute to the matrix potential, which is particularly important in helping plants retain water and thereby enhance plant drought tolerance (Rodriguez et al. 2008). Plant growth is greatly affected by drought stress and plants must adapt to this stress to survive (Xiong et al. 2002; Bartels and Sunkar 2005; Yamaguchi-Shinozaki and Shinozaki 2006, Shinozaki and Yamaguchi-Shinozaki 2007). Drought and salinity are two major environmental factors determining plant productivity and plant distribution (Rana et al. 2019b; Yadav et al. 2018a, b). Drought and salinity affect more than 10% of arable land, and desertification and salinization are rapidly increasing on a global scale declining average yields for most major crop plants by more than 50% (Bartels and Sunkar 2005; Kour et al. 2019a, c). Salt stress affects plants in numerous ways such as ion toxicity, nutritional disorders, physiological drought, oxidative stress, modification of metabolic processes, membrane incompetence, and reduction of cell division. When plant is exposed to high salt at germination it causes physiological drought and reduction in leaf expansion (Kumar et al. 2019b, c). The osmotic effects of salinity stress can be observed immediately after salt application and are believed to continue for the duration of exposure, resulting in inhibited cell expansion and cell division, as well as stomatal closure (Munns 2002). Exposure to drought or salt stress triggers many common reactions in plants. Both stresses lead to cellular dehydration, which causes osmotic stress and removal of water from the cytoplasm into the extracellular space resulting in a reduction of the cytosolic and vacuolar volumes. Another consequence is the production of reactive oxygen species which then in turn affects cellular structures and metabolism negatively (Bartels and Sunkar 2005).

One of the severe factors is salt accumulation in soil, limiting the productivity of plants, that causes adverse effects on germination, plant growth, and crop yield (Munns and Tester 2008). Salt stress causes loss of water use efficacy, increases ions, induces heat stress, and reduces stem extension. Biological macromolecules are damaged due to production of free ions. It was found that salinity stress resulted in decrease of water content, accumulation of hydrogen peroxide, and electrolyte release in plants (Batool et al. 2014). High salt concentration in soil is a main factor that limits the yield of agricultural crops (Munns and Tester 2008). High salinity affects plants in two main ways: high concentrations of salts in the soil disturb the capacity of roots to extract water and high concentrations of salts within the plant itself can be toxic, resulting in an inhibition of many physiological and biochemical processes such as nutrient uptake and assimilation (Carillo et al. 2011).

At low salt concentrations, yields are mildly affected or not affected at all. As the concentrations increase, the yields move towards zero, since most plants, glycophytes, including most crop plants, will not grow in high concentrations of salt and are severely inhibited or even killed by 100–200 mM NaCl. The reason is that they have evolved under conditions of low soil salinity and do not display salt tolerance (Carillo et al. 2011). Salt stress has been shown to affect carbohydrate partitioning and metabolism, leading to the synthesis of new compounds. In plants exposed to salinity, the total nonstructural carbohydrate content in the leaves was reduced significantly compared with plants that are not exposed to salinity. The decrease in total soluble carbohydrates due to salinity could also be related to limited carbohydrate availability as a consequence of a decline in photosynthesis (Zarea et al. 2013).

Drought stress induces a range of physiological and biochemical responses in plants such as stomatal closure, repression of growth and photosynthesis, and activation of respiration (Kour et al. 2019b; Yadav et al. 2019b; Singh et al. 2011). Heat and drought stress in particular can cause disproportionate damage to crops compared with either stress individually. However, when examining the effects of an abiotic stress with simultaneous impact of a pathogen or herbivore, both positive and negative interactions have been observed depending on the timing, nature, and severity of each stress. An increase in temperature can create a negative interactive effect by lowering resistance to bacterial, viral, fungal, and nematode pathogens: in wheat (Atkinson and Urwin 2012; Verma et al. 2016, 2019). Drought stress can cause detrimental effects to plant pathogen resistance. In both sorghum and the common bean, drought-treated plants had a higher susceptibility to the charcoal rot fungus *Macrophomina phaseolina*. Similarly, drought stress increased the spread of fungal and bacterial leaf scorch symptoms on date. Exposure of Arabidopsis to drought stress allowed greater infection levels of an avirulent isolate of *P. syringae* (Atkinson and Urwin 2012).

Drought is one of the major abiotic stress limiting plants growth and productivity in many areas of the world. Expansion of drought leads to osmotic stress, specific ions toxicity, and ionic imbalances (Tanha et al. 2014). Drought stress induces a range of physiological and biochemical responses in plants such as stomatal closure (Schroeder et al. 2001). Prolonged water stress causes decline in leaf water potential and stomatal opening, reduces leaf size, suppresses root growth, reduces seed number, size, and viability, delays flowering and fruiting, and limits plant growth and productivity, while high salinity and drought have been the major causes of osmotic stress to plants (Lata et al. 2018).

Upon exposure to heat stress, non-symbiotic panic grass and tomato plants significantly increased osmolyte concentrations as predicted. Increased osmolyte concentrations correlated with the development of subsequent wilting and desiccation symptoms prior to plant death (Rodriguez et al. 2008). Higher temperature results in extensive denaturation and aggregation of cellular proteins, which, if unchecked, lead to cell death. Low temperature impairs metabolic processes, through alterations in membrane properties, changes in structure of proteins and interactions between macromolecules as well as inhibition of enzymatic reactions (Lata et al. 2018). Heavy metals interfere with numerous biochemical and physiological processes including photosynthesis, respiration, nitrogen and protein metabolism, and nutrient uptake (Lata et al. 2018).

The plant has to bear several biotic stresses like the infection by a variety of phytopathogens belonging to diverse groups of viruses, bacteria, fungi, nematodes, insects, and higher animals particular concern for the herbivores (Gosal et al. 2013). Biotic stresses mainly result in disease in plants. Microorganisms can cause plant wilt, leaf spots, root rot, seed damage, and many more problems. Insects can cause severe physical damage to plants, including to the leaves, stem, bark, and flowers. Insects' canals act as a vector of viruses and bacteria from infected plants to healthy plants. Invasive plants through allelopathy cause severe damage to native plants (Lata et al. 2018). There are two types of fungi parasites: nectrotrophs, which kill host cells using toxins, and biotrophs. Together with bacteria, they cause vascular wilts, leaf spots, and cankers among other symptoms, and can infect different parts of the plant. Nematodes withdraw the contents of plant cells and can feed on all parts of the plant, but plant parasitic nematodes primarily cause soil-borne diseases and attack plants' root system. They produce symptoms related to nutrient deficiency, such as wilting or stunting. Viruses produce not only local lesions but also systemic damage that causes stunting, chlorosis, and malformations affecting different parts of the plant, although they rarely kill their hosts. On the other hand, insects and mites are the pest to be highlighted. They damage plants through feeding or egg laying (Gimenez et al. 2018).

In contrast, abiotic stress may also interact positively with pathogen stress. In barley, increase in salt-induced osmotic stress was directly correlated with resistance to powdery mildew, while drought stress can enhance resistance to the fungus *Botrytis cinerea* in tomato. Pathogens may also actively interfere with plant–water relations in order to increase pathogenesis. For example, they may cause stomatal closure to reduce water loss from infected tissues, thus having a positive effect on plant tolerance against abiotic stress (Atkinson and Urwin 2012). Infection with viruses can actually provide protection from drought stress. In virus-infected tobacco, beet, and rice drought symptoms appeared later and leaves maintained water longer than their uninfected counterparts (Atkinson and Urwin 2012). Abiotic stress conditions also directly affect plant–pest interactions by altering plant physiology and defense responses. Additionally, abiotic stress conditions such as drought enhance competitive interactions of weeds on crops as several weeds exhibit enhanced water use efficiency than crops, and also known to influence the occurrence and spread of pathogens, insects, and weeds (Pandey et al. 2017). On the other hand, drought stress is reported to provide endurance to tomato, *Medicago sativa,* and *Arabidopsis thaliana* against *Botrytis cinerea* (causal agent of gray mold), *Oidium neolycopersici* (causal agent of powdery mildew), *Verticillium albo-atrum* (causal agent of verticillium wilt), and *Pseudomonas syringae* (causal agent of bacterial speck disease), respectively (Pandey et al. 2017).

9.6 *P. indica* Fungal Endophytes for Conferring Salt Stress Tolerance

Salinity is the concentration of dissolved mineral salts present in the soils (soil solution) and waters. The dissolved mineral salts consist of the electrolytes of cations and anions. The major cations in saline soil solutions consist of Na^+, Ca^{2+}, Mg^{2+}, and K^+, and the major anions are Cl^-, SO_4^{2-}, HCO^{3-}, CO_3^{2-}, and NO^{3-} (Zarea et al. 2013). The composition and concentration of soluble salts in root zone medium solution are known to influence plant growth, both by creating osmotic imbalance and via specific physiological toxicity of ions. Osmotic stress lowers the potential energy of the solution and causes reduced growth, due to the additional energy required by plants to take up water (Zarea et al. 2013). *P. indica* is known to impart tolerance towards many abiotic stress factors like extreme cold temperature, drought, and saline soil conditions (Gosal et al. 2013).

The main mechanisms thought to be involved in salt stress alleviation by *P. indica* fungus may be summarized as follows: (1) improvement of mineral nutrition leading to plant growth promotion and (2) modification of some physiological processes and enzymatic activities involved in plant antioxidative reactions (Zarea et al. 2013). During salt and drought stress, *P. indica* maintains a high antioxidative environment by primarily inducing the defense system. Also, it has shown to induce several antioxidative enzymes during salt and drought stress that are involved in detoxification of reactive oxygen species such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), peroxidase (POD), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR). P. indica also increased the level of osmolytes (polyamines, proline, etc.), in response to salinity and drought stress (Varma et al. 2013). Salinity affects all important processes, such as growth, photosynthesis, protein synthesis, and lipid and energy metabolism, resulting in all phases of plant life from germination to seed production (Bagheri et al. 2014).

P. indica has been shown to increase resistance against tolerance to abiotic stress in plants. Fungal colonization has shown to promote plant growth which is a characteristic effect and can also be observed under stress conditions. *P. indica* modulates the defense system and alters the metabolism to compensate the loss in photosynthesis and prevent oxidative damage caused by stress (Varma et al. 2013). Waller et al. (2005) investigated salt stress tolerance in barley leaves which were exposed to moderate and high salt concentrations in hydroponic culture. The plants show leaf chlorosis and reduced growth. The detrimental effect of moderate salt stress is completely abolished by *P. indica*, as shown by the fact that infested plants produce higher biomass than non-stressed control plants under these conditions.

P. indica can with stand alkaline pH up to 11.0. The fungus found to have optimum growth at pH 6.0–10.0. Increase in cell dry biomass and radial growth along with presence of significant amount of chlamydospores at a wide range of pH 4.0–11.0 has been recorded for *P. indica*. The fungus can tolerate and shows prominent growth and metabolism at low acidic pH 4.0 to high alkaline pH 11.0 (Basu et al. 2016). *P. indica* a root endophytic fungus has already been proved to have beneficial influence on plant growth especially under water scarcity and salt stress (Basu et al. 2016). *P. indica* also increased plant tolerance to abiotic stresses including salt stress in barley (Baltruschat et al. 2008; Alikhani et al. 2013), tomato (Cruz et al. 2010), and wheat (Rabiey et al. 2015). The fungus conferred drought tolerance in Chinese cabbage and enhanced seed production and grain yield (Sun et al. 2010). Interaction between barley and *P. indica* has been studied with respect to salt tolerance, and findings have suggested that barley was able to tolerate moderate salt stress (100 mM) in hydroponic culture (Waller et al. 2005). They investigated salt stress tolerance in barley leaves which were exposed to moderate (100 mM NaCl) and high (300 mM NaCl) salt concentrations in hydroponic culture. They found that detrimental effect of moderate salt stress was completely abolished by *P. indica*, with a higher biomass gain. However, under high salt stress conditions, both noninfested and infested plants exhibited a severe biomass reduction. Also*, P. indica* has shown to induce elevated amount of ascorbic acid and increase activities of antioxidant enzymes in barley roots during its symbiotic association under salt stress conditions suggesting that antioxidants might play a role in both inherited and endophyte-mediated plant tolerance to salinity (Baltruschat et al. 2008; Varma et al. 2013). Waller et al. (2005) observed that the root endophytic fungus P. indica had increased *Hordeum vulgare* L. tolerance to salt stress. Similarly, they showed that *P*. *indica* protects *H. vulgare* from high salt stress (300 mM NaCl) (Terhonen et al. 2019).

Tolerance of plants to salt stress is associated with the alleviation of antioxidant enzymes as suggested by earlier studies (Rodriguez et al. 2008). Considerable research has been carried out on the mechanism of salt stress tolerance conferred to plants colonized with *P. indica* and this trait has been demonstrated for barley as well as wheat, rice, and tobacco and involves the induction of a high antioxidant environment for the detoxification of reactive oxygen species and an enhanced photosynthetic efficiency (Johnson et al. 2014). According to Basu et al. (2016) *P. indica* showed a tendency to grow under calcareous condition with at high alkaline pH in vitro.

The study explores the possibilities of *P. indica* as an excellent bio-inoculant for nutrient management in calcareous soil. Present study was conducted to understand *P. indica* capacity to withstand high alkaline pH. *P indica* was also subjected to stress of different concentration of calcium carbonate with respect to calcareous soil. This study has great significance as the fungus is being exploited and tested for bioremediation of calcareous soil. The pre-colonization of roots with *P. indica* resulted in decreased disease severity in tomato caused by early blight. They concluded that P. indica treatments led to priming of defense-related gene expression in tomato. Recent studies have shown that root fungal endophytes of agricultural crops can help host plants to live in harsh environments, thereby increasing their stress tolerance against abiotic factors (Terhonen et al. 2019).

9.7 *P. indica* Fungal Endophytes for Conferring Disease Resistance

Biotic stress results due to damage done to plants by other living microorganisms, such as bacteria, viruses, fungi, parasites, and organisms such as beneficial and harmful insects, weeds, and cultivated or native plants (Lata et al. 2018; Yadav 2017a, b). Fungal endophytes are capable of protecting the plant against pathogens through various strategies, such as competition with pathogens for colonization and nutrients, the production of antibiotics, and the induction of resistance in the host plant (Kumar et al. 2019; Suman et al. 2016; Yadav et al. 2018c, 2019d). *P. indica* is an interesting endophytic fungus capable of colonizing roots and forming symbiotic relationship with every possible plant on earth (Desisa 2017). Biotic stress protection by *P. indica* was first shown in barley roots. *P. indica* enhanced barley grain yield, tolerance to mild salt stress, and resistance against root and leaf pathogens, including the necrotrophic fungus *F. culmorum* (root rot) and the biotrophic fungus *Blumeria graminis*. Beneficial effects are also observed for the crops like wheat, maize, and rice (Waller et al. 2005; Oelmüller et al. 2009). *P. indica* colonizes the cortex of roots of a wide variety of plant species, promotes their growth, and induces resistance against soil-borne fungal pathogens in a manner similar to arbuscular mycorrhizal fungi.

The inoculation of *P. indica* followed by colonization of the internal tissues of the plant may impart systemic resistance to various fungal and bacterial pathogens (Gosal et al. 2013). On inoculation, *P. indica* vigorously infects host root tissue and blocks the receptors for the attachment and adsorption of the phytopathogens which could be considered as the nonspecific physical way of this beneficial fungus to safeguard the inoculated plant (Gosal et al. 2013). *P. indica*-infested plants are more resistant to biotic stress. When barley plants are exposed to the necrotrophic fungal pathogen *F. culmorum*, *P. indica*-infested plants are more resistant to root diseases. Root infection of wild-type plants causes a severe reduction in the root fresh weight and this devastating effect is strongly diminished in the presence of *P. indica* (Waller et al. 2005; Oelmüller et al. 2009).

In barley, the root endophyte *P. indica* confers disease resistance by a different mechanism. Symbiotic plants are thought to resist necrotrophic root pathogens due to increased activity of glutathione–ascorbate antioxidant systems (Waller et al. 2005; Rodriguez and Redman 2008). *P. indica* has been shown to increase resistance to biotic stresses including a wheat leaf disease (caused by *B. graminis*), a wheat stem base disease (caused by *Oculimacula spp.*), wheat and barley root rot diseases (caused by *F. culmorum*, *Gaeumannomyces graminis*) (Serfling et al. 2007; Harrach et al. 2013), a maize root disease (caused by *F. verticillioides)* (Kumar et al. 2009), a lentil vascular wilt disease (caused by *F. oxysporum*) (Dolatabadi et al. 2012), crown rot disease (caused by *F. culmorum* and *F. graminearum*) (Rabiey et al. 2015). In tomato infected with *Verticillium dahliae, P. indica* increased leaf and fruit biomass and decreased disease severity. Also in tomato, *P. indica* reduced the concentration of Pepino mosaic virus in shoots (Fakhro et al. 2010).

The inoculated wheat with *P. indica* may subsequently reduce the symptoms caused by several fungal pathogens on leaves, stems, and roots that were addressed under greenhouse and field conditions and also indicated by increased hydrogen peroxide formation in leaves challenged with powdery mildew (Desisa 2017). Root colonization by *P. indica* protects plants against various diseases. These include the root rot pathogens *Verticillium*, Fusarium foot rot, *Rhizoctonia* and *Thielavopsis,* and several fungal diseases of roots and stems, including *Alternaria brassicae*, *Botrytis cinerea*, and powdery mildew (Harman and Uphoff 2019). 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).

P. indica has bio protection performance against the root parasite *F. verticillioides* in maize and observed stimulated increase in biomass, root length, and root number compared to the plants grown with *F. verticillioides* alone. The decrease of antioxidant enzyme activities due to the presence of *P. indica* helped the plant to overcome the disease load of *F. verticillioides* (Kumar et al. 2009; Varma et al. 2013). The effect of *P. indica* as bio protector on barley was assessed under semi-natural conditions using Mitscherlich pots (Waller et al. 2005), under these conditions *P. indica* acted as both a biofertilizer and a biocontrol agent (Waller et al. 2005; Varma et al. 2013). *P. indica* exerts beneficial activity against two major cereal pathogens (*F. culmorum* and *Cochliobolus sativus*) that cause enormous worldwide economic losses (Waller et al. 2005). The effect of *P. indica* against pathogen is based on inhibitory activity by dual bixenic culture technique, volatile metabolites against pathogen, *P. indica* culture filtrate, and role of lytic enzymes in pathogen inhibition (Varma et al. 2013). Major mechanisms of biological plant disease protection by P. indica are: Competition for occupying niches or nutrients, Production of antibiotics, Induced resistance and mycoparasitism (Desisa 2017). *P. indica* has also been shown to increase both crop yield and plant defense of a variety of crops (barley, tomato, maize) against root pathogens (Desisa 2017).

9.8 Applications and Recent Researches in *P. indica*

Notably, compared to many other endophytes, *P. indica* can be cultured very easily in a bioreactor in order to prepare effective biofertilizer formulations (Singh et al. 2003; Oelmüller et al. 2009; Bagde et al. 2010; Qiang et al. 2011). *P. indica* reduces the harmful impact of stress on photosynthetic concert of the host plants and stabilizes growth and nutrition under salinity, drought, and heat (Baltruschat et al. 2008; Sherameti et al. 2008; Varma et al. 2012b). *P. indica* induces antioxidant system, the expression of abiotic stress-responsive genes, and protein to confer tolerance in different plant species such as Chinese cabbage (Sun et al. 2010), *Arabidopsis thaliana* (Sherameti et al. 2008), and *Hordeum vulgare* (Baltruschat et al. 2008; Ansari et al.

2014). However, despite all of these described benefits, Franken (2012) states that it may be difficult to place *P. indica* on the market because (1) the fungus was first isolated in India and is protected by patent in many countries (international publication number—WO 99/29177) making any commercial prospect reliant on the patent owner to manufacturing it or licensing it for manufacture and (2) it sometimes has unexplained negative effects on plant growth.

The fungus possesses positive phytopromotional effects due to production/modulation of phytohormone levels (plant bioregulation ability), apart from its role in mobilization and transportation of the plant unavailable phosphorous reserves in soil beyond the depletion zone (P-mobilizer ability) (Gosal et al. 2013). Endophyte-enhanced plant growth promotion is another conferred beneficial trait that, at least for the root-colonizing endophyte *P. indica*, is likely achieved through enhanced nutrient uptake and translocation, and by the modulation of phytohormones involved in growth and development (Johnson et al. 2014; Lugtenberg et al. 2016). *P. indica* is already reported to be involved in high salt tolerance, disease resistance, and strong growth-promoting activities leading to enhancement of host plant yield (Basu et al. 2016). *P. indica* inocula are very effective for their commercial applications to various crops within the defined parameters, viz. inocula quantity, inoculation time point, as well as soils election for plant cultivation. Moreover, *P. indica* root endophyte has been credibly evidenced to minimize the use of chemical fertilizers, control crop yield, and also to provide increased resistance and tolerance in plants against biotic and abiotic stresses (Unnikumar et al. 2013; Gill et al. 2016). The axenic cultivability of *P. indica* on economically viable synthetic media makes it suitable for mass scale inoculum production for application in agro-forestry and horticulture (Desisa 2017).

P. indica confers drought stress tolerance to Arabidopsis, and this is associated with the priming of the expression of a quite diverse set of stress-related genes in the leaves. When seedlings are first exposed to drought stress and then transferred to soil, many colonized seedlings reach the flowering stage and produce seeds, while the percentage for uncolonized seedlings is much lower (Desisa 2017). *P. indica's* wide host benefits as well as its amenability for fundamental biological studies are attractive properties for research and its potential to transform the productivity of agricultural crops sustainably is exciting. With respect to barley, *P. indica* interactions have shown enhanced grain yield (Murphy et al. 2014) and at low temperatures with higher nutrient input, *P. indica* also appeared to trigger flowering earlier and still increase grain yield. These results indicate that *P. indica* could be developed as an effective crop treatment in low temperature-stressed barley and may have the potential to increase crop yield under colder growing environments on the proviso that adequate nutrients are supplied (Lugtenberg et al. 2016).

P. indica as a mycofertilizer has produced a greater keenness among mycorrhizologists, due to being easily culturable, plant growth enhancer and inducer. In the present work, the recently discovered root endophytic-fungi *P. indica* has been optimized and tested for its growth enhancement (Krishnaveni et al. 2014). Considering the recent researches, *P. indica* is a promising agent for use in organic agriculture to manage nutrient deficiency in calcareous soil (Basu et al. 2016). *P. indica* is one of the most studied fungi for its plant growth promotion activity and stress resistance (Varma et al. 1999; Franken 2012; Kumar et al. 2017). *P. indica*, a wide host root-colonizing, has been used as a model to study the mechanisms and evolution of mutualistic symbiosis (Dong et al. 2013). Nonetheless, a powder formulation of *P. indica* has been developed under the trade name “ROOTONIC” and is currently deployed in field trials in India (Shrivastava and Varma 2014; Lugtenberg et al. 2016). Presently, these fungi can be grown with host plants in pot culture containing soil, sand, or expanded clay. They have also been grown by using hydroponics, aeroponics, and root organ culture; all of which are not a cost-effective proposition. *P. indica* can be propagated on several economically viable synthetic media, potato dextrose media. Fermentation technique should be optimized to device a simple, cheap, and commercially viable technique for the mass scale inoculums production for application in agro-forestry and horticulture (Desisa 2017).

General characteristics of *P. indica* according to Krishnaveni et al. (2014); Gill et al. (2016); Desisa (2017).

- Increase the potential of plants and their essential ingredients.
- Applicable in agriculture, floriculture, viticulture, and reclamation of degraded and heavily mined soils.
- Used in form of culture filtrate for development and formulation into biofertilizer.
- Acts as biofertilizer, bioprotector, immune regulator, and agent for biological hardening of tissue cultured plants.
- Mediates nutrient uptake, pathogenic inhibitor, stimulates growth and seed production.
- Confers resistance to toxins, resistance to heavy metal ions, promotes salt stress and other abiotic stress.

9.9 Conclusion and Future Prospects

Many plant growth-promoting fungi and bacteria have been identified in the last decades and the basis for their molecular interaction with plants has been studied. It is conceivable that the primary interest of the heterotrophic fungus is to gain access to photoassimilates. This is also obvious for *P. indica*, which was originally identified in a desert, where survival is dependent on an efficient association with roots due to the limitations of C compounds in the soil. The beneficial effects for the plant are at least in part caused by a better nutrient supply by the fungal hyphae. Many studies show that symbiosis of plants with endophytic-fungi could be a good solution for reducing the effects of salinity. *P. indica* possesses the phytopromotional to biocontrol properties, imparts stress tolerance to abiotic as well as biotic factors, and also exhibits enhanced nutritional availability to the inoculated plant. It has enormous application potentials for the biotization of the micro-propagated plants and thus has a pivotal role to play in the new age phenomena of sustainable agriculture for enhanced productivity.

Finally, several studies have demonstrated that *P. indica* may be used for phytoremediation, because it accumulates heavy metals and prevents their uptake into the plants. Taken together, the increasing interest in this fungus worldwide will lead to novel information that will disclose potential agronomical and biotechnological applications.

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Chapter 10
Fungi: A Bio-resource for the Control of Plant Parasitic Nematodes

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Contents

10.1 Introduction

Plant parasitic nematodes are considered to be the major constraint on plant productivity, and they have been found to attack almost every part of the plant including roots, stems, leaves, fruits, and seeds. They are also responsible for invasion of secondary pests and pathogens by causing wounds in the host roots (Caboni et al. 2016). Global annual yield losses from plant parasitic nematodes have been estimated at 12.6% ($215.77 billion) for top 20 life sustaining crops (Abd-Elgawad and Askary 2015). Among different groups of plant parasitic nematodes, root knot (*Meloidogyne* spp.) and cyst nematodes (*Heterodera* and *Globodera* spp.) are economically important by forming complex feeding structures like giant cells and

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syncytia in the roots of their hosts which act as a nutrient sink to the nematode. Apart from these, root-lesion nematodes (*Pratylenchus* spp.), burrowing nematode (*Radopholus similis*), stem nematode (*Ditylenchus dipsaci*), reniform nematode (*Rotylenchulus reniformis*), and several other plant parasitic nematodes causing economic damage to the crops (Jones et al. 2013).

Many traditional chemical pesticides such as fumigants, organophosphates, and carbamates have been used for the management of plant parasitic nematodes (Kour et al. 2020). However, the usage of harmful chemical pesticides cause environmental toxicity, health effects and further withdrawal of some pesticides has led to the development and adoption of non-chemical alternatives for the management of plant parasitic nematodes (Davies and Curtis 2011; Kumar et al. 2018). In addition, these chemicals do not affect the development of nematode eggs in soil, since the egg shell of nematode acts as a barrier which makes them resistant to chemical pesticides (Baron et al. 2019). Crop rotation and use of resistant cultivars have been used as the management strategies for plant parasitic nematodes. However, these practices are limited by the size of growing area, wide host range of nematode species, and high genetic diversity among or within nematode populations (Berlitz et al. 2014; Li et al. 2015).

Biological control, an alternative for the management of plant parasitic nematodes. The usage of biocontrol agents is increasing these days, due to their reduced environmental toxicity, target specificity, and safety to non-target organisms (Kumar and Singh 2015; Jiang et al. 2017). These biocontrol agents include fungi, bacteria, viruses, nematodes, and other invertebrates which have an antagonistic activity against plant parasitic nematodes. The market for biological nematicides has risen by nearly 20% from 2009 to the present, according to the Markets and Markets report, with most of the development in field crops. Nematicide sales amounted to just over $1 billion in 2014 and are anticipated to expand at a compound annual growth rate (CAGR) of 2.7% over the next 10 years to $1.3 billion over 20 years (Jiang et al. 2017).

Currently several biocontrol agents such as fungi and bacteria have been widely used as commercial products for the management of plant parasitic nematodes. Fungal antagonists have been considered as the most promising biocontrol agents and attention is being paid to the exploitation of fungi to control plant parasitic nematodes (Stirling 2011; Moosavi and Zare 2012; Lamovsek et al. 2013). Among different fungal biocontrol agents, the most widely studied species for nematode management include *Pochonia chlamydosporia*, *Purpureocillium lilacinum*, *Arthrobotrys oligospora*, *Trichoderma* spp. and *Verticillium* spp. (Rastegari et al. 2020a, b; Yadav et al. 2020a, b). This chapter reviews different categories of nematophagous fungi, mode of action, and knowledge of the interactions between nematodes and nematode trapping fungi and commercialization of different fungal products for the management of plant parasitic nematodes.

10.2 Nematophagous Fungi

This group of fungi has been widely used as biocontrol agents of plant parasitic nematodes due to their antagonistic, parasitic, and predatory action against different species. There are approximately 700 fungal species reported to be able to attack different life stages of nematodes (juveniles, adults, and eggs) (Li et al. 2015; Jiang et al. 2017). Over the decades, several researchers have worked on fundamental studies and their potential as biocontrol agents against different plant parasitic nematodes. Based on their infection mechanism, they are subdivided into four categories viz., nematode trapping fungi, endoparasitic fungi, egg and female parasitic fungi, and toxin producing fungi (Dackman et al. 1992; Nordbring-Hertz et al. 2006) (Table 10.1).

10.2.1 Nematode Trapping Fungi

These are soil borne fungi that have the ability to capture and kill nematodes by using trapping structures, including adhesive hyphae, adhesive knobs, constricting rings and non-constricting rings, and adhesive networks (Nordbring-Hertz et al. 2011; Jiang et al. 2017). The type of trapping structure formed mainly depends on the fungal species or strains of fungal species and both biotic and abiotic environmental factors (Nordbring-Hertz et al. 2006). Based on phylogenetic analysis results using ribosomal RNAs (rRNAs) and protein coding genes, these trapping devices could serve as indicators for generic delimitation among these fungi (Ahren et al. 1998; Scholler et al. 1999; Li et al. 2005). There are about 380 species of nematode trapping fungi have been reported from different regions of the world (Zhang et al. 2011). They are usually non-host specific and can infect all soil dwelling nematodes. All the known nematode trapping fungi belong to the order Orbiliales of the phylum Ascomycota (Zhang and Hyde 2014). These fungi can live both saprophytically on organic matter and as predatory by capturing tiny animals. However, they can shift from saprophytic to predatory lifestyle in the presence of nematode prey by the production of trapping structures (Li et al. 2011; Yang et al. 2012; Zhang and Hyde 2014). The application of these fungi for nematode suppression was accompanied by addition of large amounts of organic matter and in most cases the levels of nematode control were unpredictable (Stirling 1991).

10.2.1.1 Adhesive Hyphae

These are mostly produced by lower fungi belongs to the genera *Stylopage* and *Cystopage* under phylum Zygomycota (Table 10.1). They cannot produce complex devices for capturing nematodes due to the absence of septa (Barron 1977). However, septate fungi such as *Arthrobotrys botryospora*, *Dactylaria psychrophila,*

Table 10.1 Different categories of nematophagous fungi

Category	Nematode trapping structure	Name of fungi	Phylum
Nematode trapping fungi	Adhesive hyphae	*Stylopage hadra*	Zygomycota
		Cystopage cladospora	Zygomycota
	Adhesive knobs	*Dactylellina ellipsospora*	Ascomycota
		Dactylellina drechsleri	Ascomycota
		Dactylaria candida	Ascomycota
		Monacrosporium haptotylum	Ascomycota
		Gamsylella querci	Ascomycota
		Gamsylella robusta	Ascomycota
		Gamsylella parvicollis	Ascomycota
		Nematoctonus sp.	Basidiomycota
	Non-constricting rings	*Dactylaria candida*	Ascomycota
		Dactylaria lysipaga	Ascomycota
	Adhesive knobs + non-constricting rings	*Dactylellina appendiculata*	Ascomycota
		Dactylellina haptotyla	Ascomycota
	Constricting rings	*A. dactyloides*	Ascomycota
		A. brochopaga	Ascomycota
		Drechslerella stenobrocha	Ascomycota
		Drechslerella brochopaga	Ascomycota
		Drechslerella dactyloides	Ascomycota
	Adhesive knobs + adhesive spores	*Nematoctonus concurrens*	Basidiomycota
	Adhesive networks	*Arthrobotrys oligospora*	Ascomycota
		Arthrobotrys musiformis	Ascomycota
		Arthrobotrys conoides	Ascomycota
		Arthrobotrys vermicola	Ascomycota
		Arthrobotrys superba	Ascomycota
		Dactylaria scaphoides	Ascomycota

(continued)

Table 10.1 (continued)

Category	Nematode trapping structure	Name of fungi	Phylum
Endoparasitic fungi	Adhesive conidia	*Drechmeria coniospora*	Ascomycota
		Hirsutella rhossiliensis	Ascomycota
		Hirsutella minnesotensis	Ascomycota
		Cephalosporium balanoides	Ascomycota
	Adhesive spores	*Nematoctonus concurrens*	Basidiomycota
		Nematoctonus haptocladus	Basidiomycota
		Nematoctonus leiosporus	Basidiomycota
	Ingested conidia	*Harposporium anguillulae*	Ascomycota
		Harosporium cerbri	Ascomycota
	Zoospores	*Catenaria auxillaris*	Blastocladiomycota
		Catenaria anguillulae	Blastocladiomycota
		Myzocytiopsis glutinospora	Oomycota
		Myzocytiopsis vermicola	Oomycota
		Myzocytiopsis enticularis	Oomycota
		Myzocytiopsis humicola	Oomycota
Egg parasitic fungi	Appresoria	*Pochonia chlamydosporia*	Ascomycota
		Purpureocillium lilacinum (=*Paecilomyces lilacinus*)	Ascomycota
		Acremonium (=*Cephalosporium*) sp.	Ascomycota
		Dactylella oviparasitica	Ascomycota
		Dactylella lysipaga	Ascomycota
		Lecanicillium psalliotae	Ascomycota
		Lecanicillium lecanii	Ascomycota
	Zoospores	*Nematophthora gynophila*	Oomycota
Toxin producing fungi	Toxic droplets	*Pleurotus ostreatus*	Basidiomycota
	Toxin, spiny structures	*Coprinus comatus*	Basidiomycota
Endophytic fungi		*Fusarium oxysporum*	Ascomycota
		Neotyphodium spp.	Ascomycota
		Acremonium	Ascomycota
		Penicillium oxalicum	Ascomycota

and *A. superba* can capture nematodes with adhesive hyphae under certain conditions (Chen and Dickson 2004). The infection begins with the capture organ being adhered by nematode. Within few minutes, the nematodes added to a fungal colony were captured and penetrated within 1 h by the trap forming cell hyphae. After 6 h, the whole nematode body was filled with hyphae. The dead nematode did not induce traps but developed a large number of thin hyphae around the nematode.

10.2.1.2 Adhesive Knobs

These are very effective trapping structures and nematodes are often attacked at more than one infection site (Barron 1977). These knobs are covered by a thin layer of adhesive materials and the infection process involves one knob and several associated hyphal elements. These adhesive knobs produce an infection peg and infection bulb. From this bulb, the infection hyphae proliferate within the nematode and digest the inner contents. The adhesive knobs are found in Ascomycota and Basidiomycota (Table 10.1). This group of fungi is unique in forming clamp connections on the secondary hyphae (Chen and Dickson 2004). The genomic studies of adhesive knob forming species, *Monacrosporium haptotylum* indicated the enrichment of small secreted proteins (SSPs) that were highly and differentially expressed during the interaction with nematode hosts (Meerupati et al. 2013).

10.2.1.3 Adhesive Networks

This is the most common type of nematode trapping structure observed in *Arthrobotrys* spp. (Table 10.1). The trap may consist of a single ring or a three-dimensional network. *A. oligospora*, a model organism for understanding the interaction between fungi and nematodes, forms a three-dimensional adhesive network during infection process. The genomic and proteomic analyses of this fungus provide insights into nematode trap formation including G-protein coupled receptors, adhesive proteins, cell division cycle, peroxisome related proteins, and proteins involved in energy supplementation (Yang et al. 2011).

10.2.1.4 Constricting Rings

Among different trapping structures, constricting rings are probably the only ones that actually capture the nematodes and considered to be the lineal strategy after which other trapping structures evolved (Yang et al. 2007a; Liu et al. 2012). In general, trapping fungi that form constricting rings are more abundant in soils rich in organic matter and influenced by the population density of nematodes (Linford 1937; Gray 1985). However, the trapping mechanism is completely different in contrast to others. When a nematode passing into the ring, it stimulates the inner face of the ring such that the three cells comprising the ring inflate centripetally to about three times and get trapped within 0.1 s. The pressure exerted by nematode on the ring during this process causes the activation of G-protein coupled receptors which leads to an increase in cytoplasmic Ca^{2+}, and activation of calmodulin that opens the water channels, and thereby inflates the ring trapping the nematode (Chen et al. 2001). The genome sequence of *Drechslerella stenobrocha* constricting ring forming fungus revealed that the downregulation of saprophytic enzyme genes and the upregulation of infection related genes during the capture of nematodes indicated a transition between saprophagous and predatory life strategies. This study also indicated that protein kinase C (PKC) signal pathway and Zn (2)-C6 type transcription factors were responsible for trap formation in *D. stenobrocha* (Liu et al. 2014). Following the capture an infection peg is produced by one of the three ring cells and a small globose infection bulb develops after the penetration of infection peg into the body cavity of the nematodes. Trophic hyphae quickly digest and absorb the internal contents of nematode leaving only the cuticle structures.

10.2.1.5 Non-constricting Rings

Non-constricting rings are generally produced by erect lateral branches produced from septate hyphae. When a nematode thrusts its head inside the non-constricting ring, it gets wedged and held by friction. During this, the ring often breaks at the point of weakness near the stalk apex and this process may be repeated until several rings are wedged around the host. Following capture, the fungi penetrate and consume the inner contents of the host (Zaki 1994). *Dactylaria candida* and *D. lysipaga* usually generally form non-constricting rings during infection process (Table 10.1).

10.2.2 Endoparasitic Fungi

These are a group of fungi that infect nematodes mainly by conidia (*Drechmeria coniospora*), ingestive spores (*Harposporium* spp.), adhesive spores (*Nematoctonus concurrens*) or zoospores (*Catenaria anguillulae*) (Table 10.1). Their spores either adhere to the nematode cuticle or swallowed by the host and then germinate inside the nematode body which finally result in the death of nematode. In *D. coniospora* surface proteins and chymotrypsin-like proteases were involved in the infection process (Lopez-Llorca et al. 2008; Jansson and Friman 1999). Although some of these like *Nematophthora gynophila* could parasitize a large number of nematodes viz., *Heterodera avenae*, *H. trifolii*, *H. schachtii*, *H. goettengiana*, *H. cruciferae*, etc., and their bioefficacy was dependent on adequate soil moisture and on the relative number of nematodes and endozoic units present in the soil. Besides, their obligate nature posed a problem for mass production (Kerry 1987).

10.2.3 Egg and Female Parasitic Fungi

The research on egg and female parasitic fungi has been initiated in the 1990s. These fungi use either appressoria (*Purpureocillium* spp., *Pochonia* spp.,) or zoospores (*Nematophthora gynophila*) to kill different life stages (Lopez-Llorca et al. 2008) (Table 10.1). The relationship between nematodes and these fungi was variable, but as some of the isolates were highly virulent, they were extensively used and are still available as formulations in the market, especially for sedentary endoparasites. However, it is important to ascertain the quality parameters, namely colony forming units (CFU), presence of contaminants of these formulations before application in the field for control of nematode population. Among different egg parasitic fungi, *P. chlamydosporia* and *P. lilacinum* are widely used as biocontrol agents.

10.2.3.1 Pochonia chlamydosporia

P. chlamydosporia is considered as potential biocontrol agent of endoparasitic nematodes due to their ability to colonize the rhizosphere of plants and cultivars, to produce chlamydospores in vitro and to infect eggs of endoparasitic nematodes such as root knot (*Meloidogyne* spp.) and cyst nematodes (*Heterodera avenae*, *H. glycines*, *H. schachtii*) (Manzanilla-Lopez et al. 2013; Dallemole-Giaretta et al. 2015). In addition, this fungus has shown activity against false root-knot nematode, *Nacobbus aberrans*, burrowing nematode, *Radopholus similis*, citrus nematode, *Tylenchulus semipenetrans,* and reniform nematode, *Rotylenchulus* spp. (Manzanilla-Lopez et al. 2013; Abd-Elgawad and Askary 2018). The specificity of this fungus towards sedentary endoparasitic nematodes is associated with the recognition of both quantitative and qualitative changes in root exudates patterns during nematode infection (Wang and Bergeson 1974). Crops such as beans, cabbage, crotalaria, kale, pigeon pea, potato, pumpkin, and tomato are considered as good hosts (200 CFU/cm^2 of root) for colonization of this fungus in the rhizosphere. Whereas, chilli, sweet potato, cowpea, rye, tobacco, and cotton are considered as moderate hosts (100–200 CFU/cm^2 of root) and poor hosts (<100 CFU/cm^2 of root) include aubergine, okra, soybean, sorghum, and wheat (de Leij 1992; Bourne et al. 1996).

P. chlamydosporia infects nematode eggs through the development of appressoria at the hyphal tip and the presence of mucilaginous material between appressoria and surface of the egg shell appear to assist in egg shell penetration (Lopez-Llorca et al. 2002). A post infection bulb leads to the development of a mycelium within the egg and destruction of internal contents (Segers 1996; Kerry and Hirsch 2011). The fungus produce extracellular enzymes such as Serine proteases (VCP1) and chitinases which are involved in degradation of egg shells (Segers 1996). SCP1, a serine carboxypeptidase from *P. chlamydosporia* was immunolocalized in *M. javanica* eggs infected by fungus (Escudero et al. 2016).

The ability to produce chlamydospores in vitro without the addition of other energy sources lead to the consideration of this fungus as biocontrol agent. Hence application of chlamydospores at the rate of 5000 spores/g soil in aqueous suspension is recommended to test the efficacy of fungus but it may vary according to the strain and target nematode (de Leij et al. 1992; Stirling and Smith 1998; Bourne and Kerry 2000; Kerry and Hidalgo-Diaz 2004). Application of organic amendments may increase fungal abundance in soil and fungus remains in saprophytic phase but not necessarily increase in nematode parasitic activity (Atkins et al. 2003). Gene expression studies showed differences among several genes involved in cellular signals, transport or DNA repair, with a distinct cluster of genes commonly expressed during transition from saprophytic to parasitic phase of this fungus (Rosso et al. 2011). Niu (2017) reviewed that the secondary metabolites released from *P. chlamydosporia* and other species such as resorcylic acid lactone, pyranones, alkaloid, phenolics, etc. may act as virulence factors to plant and animal-parasitic nematodes parasitized by the fungus.

10.2.3.2 *Purpureocillium lilacinum* (=*Paecilomyces lilacinus*)

P. lilacinum is a soil inhabiting fungus reported from different parts of the world and widely used as potential biocontrol agent against plant parasitic nematodes (Vasanthi and Kumaraswamy 1999; Brand et al. 2010). This fungus infects eggs, egg masses, females, and cysts of many plant parasitic nematodes such as *Meloidogyne* spp., *Globodera* spp., *Heterodera* spp., *Tylenchulus* sp., and *Nacobbus* sp. The fungus first colonizes gelatinous matrix of different nematodes and penetrate the eggs with the help of appressoria or hyphae. In addition, the fungus produce several extracellular enzymes such as serine proteases, chitinases depending on the recognition of the host surface hydrophobicity and these were purified and characterized from different strains (Bonants et al. 1995; Lopez-Llorca et al. 2002; Khan et al. 2003; Huang et al. 2004; Khan et al. 2004). Enzymes produced by *P. lilacinum* strain 251 resulted in reduction of egg hatching in *M. javanica* (Khan et al. 2004). Similarly, the secondary metabolites produced by the fungi (Australian isolate), such as leucinostatins, have significant effect on the colonization of *M. javanica* eggs (Park et al. 2004).

In addition to control of plant parasitic nematodes, species of this fungus produce several metabolites which promote plant growth and defensive substances against biotic and abiotic stresses (Khan et al. 2012). Further, this fungus promote plant growth by performing Phosphorus solubilization in soil (Rinu and Pandey 2011; Lima-Rivera et al. 2016).

10.2.4 Toxin Producing Fungi

This group of fungi produces toxic metabolites which act as nematicidal toxins before the penetration of hyphae into nematode body through cuticle. The toxic effects on nematodes include reduced egg hatching, immobility, mortality, etc. The productions of toxins also help in preventing the consumption of fungal colonies by fungivorous nematodes and other invertebrates (de Freitas Soares et al. 2018). So far more than 200 compounds have been identified from nearly 280 fungal species (Li et al. 2007a; Li and Zhang 2014). The commonly included genera under this category are *Nematoctonus*, *Pleurotus,* and *Penicillium,* etc. (de Freitas Soares et al. 2018). These toxic metabolites include peptides, terpenoids, alkaloids, quinines, sterols, etc. (Li and Zhang 2014). Table 10.3 shows a list of toxic metabolites identified in different fungi and their effect on different nematode species. The discovery of these toxic metabolites further lead to the development of these chemicals as biocontrol agents against plant parasitic nematodes (Guo et al. 2012) (Table 10.2).

10.2.5 Endophytic Fungi

The approach of using endophytic fungi as biocontrol agents of plant parasitic nematodes has gained attention in recent years to rectify the difficulties involved in establishing an introduced organism in the rhizosphere environment. Endophytes have the benefit that they occur in the same ecological niche as endoparasitic nematodes but are not subject to competition from microorganisms in the soil and rhizosphere (Stirling 2011; Yadav et al. 2019a, b; 2020c). The most research work has focused on the strains of *Fusarium oxysporum* that reduce the infection and reproduction of burrowing nematode, *Radopholus similis* (Athman et al. 2007), root-knot nematode, *M. incognita* (Hallmann and Sikora 1994; Dababat and Sikora 2007), lesion nematode, *Pratylenchus goodeyi* (Waweru et al. 2014), spiral nematode, *Helicotylenchus multicinctus* (Waweru et al. 2014).

Trichoderma spp. are endophytic and mycoparasitic fungi that have been described as biocontrol agent against plant parasitic nematodes (Zhang et al. 2014; Li et al. 2015; Dandurand and Knudsen 2016). *Trichoderma* parasitizes nematode eggs by the secretion of chitinolytic enzymes encoded by two genes chi 18-5 and chi 18-12 (Szabó et al. 2012). In addition, trypsin like protease (PRA1) and serine protease (SprT) were also observed against *Meloidogyne* juveniles during infection by the fungi (Suarez et al. 2004; Chen et al. 2009). Further, Szabó et al. 2013 reported that comparative analysis of protease expression profiles in *T. harzianum* revealed 13 peptidase encoding genes, suggesting that these genes might play an important role in infection process by the fungi. In addition to direct antagonism, nematophagous activity has also observed on eggs of *M. incognita*, *M. javanica*, *M. arenaria,* and *M. exigua* (Windham et al. 1989; Eapen et al. 2005; Sharon et al. 2007; Spiegel et al. 2007; Ferreira et al. 2008).

Table 10.2 Nematicidal toxic metabolites identified in nematophagous fungi

Toxin	Fungi	Test nematode	Reference
Secalonic acid D, Oxalin	*Penicillium anatolicum*	*Globodera rostochiensis*, *Heterodera avenae* spp	Steyn (1970)
	Penicillium vermiculatum, Penicillium oxalicum	*Globodera rostochiensis, Globodera pallida*	
	Penicillium chrysogenum	*Meloidogyne javanica*	
trans-2-decenedioic acid	*Pleurotus ostreatus* NRRL 3526	*Panagrellus redivivus*	Kwok et al. (1992)
S-coriolic acid	*Pleurotus pulmonarius*	*Caenorhabditis elegans*	Stadler et al. (1994a)
Linoleic acid	*Pleurotus pulmonarius*	*Caenorhabditis elegans*	Stadler et al. (1994a)
p-Anisaldehyde	*Pleurotus pulmonarius*	*Caenorhabditis elegans*	Stadler et al. (1994a)
1-(4-Methoxyphenyl)-1,2-propanediol	*Pleurotus pulmonarius*	*Caenorhabditis elegans*	Stadler et al. (1994a)
2-Hydroxy-(4′-methoxy)_propiophenone	*Pleurotus pulmonarius*	*Caenorhabditis elegans*	Stadler et al. (1994a)
Dihydropleurotinic acid	*Nematoctonus robustus*		Stadler et al. (1994b)
Pleurotin	*Nematoctonus robustus*		Stadler et al. (1994b)
Leucopleurotin	*Nematoctonus robustus*		Stadler et al. (1994b)
T2 toxin, Moniliformin, Fusarenone, Neosolaniol, Verrucarina,	*Fusarium solani*	*Meloidogyne javanica*	Ciancio (1995)
Cheimonophyllon E; 5α,8α-epidioxyergosta-6,22-dien-3-β-ol; 5-hydroxymethyl-furancarbaldehyde	*Pleurotus eryngii* var. *ferulae* L14	*Bursaphelenchus xylophilus*	Li et al. (2007b)
5-methylfuran-3- carboxylic acid; 5-hydroxy-3,5-dimethylfuran-2 (5H)-one	*Coprinus comatus*	*Meloidogyne incognita* and *Panagrellus redivivus*	Luo et al. (2007)

The future market for fungal products may be improved by commercializing several virulent strains for nematode pests. Zhao et al. (2013) reported that the culture filtrates of new fungal species, *Simplicillium chinense* (strain-Snef5) showed potential effect against soybean cyst nematode, *Heterodera glycines*, root-knot nematode *M. incognita*, white tip nematode *Aphelenchoides besseyi* and *Caenorhabditis elegans*. Whereas, *Trichoderma* sp. KAV1 and *C. rosea* KAV2 showed 100% mortality to second stage juveniles of *M. incognita* and *M. javanica* under in vitro conditions (Migunova et al. 2018). Further, the fungal isolate, *Mortierella globalpina* proved pathogenic to *M. chitwoodi* in vitro using trapping structures and subsequently reduced root galls in vivo on the roots of tomato (*Solanum lycopersicum* var. Rutgers) (DiLegge et al. 2019). Recently, Du et al. (2019) reported inhibition rate of 84.61%. 78.91% and 84.25% and 79.48% for adult females, juveniles, egg mass, and gall index of *M. incognita* under greenhouse experimental conditions at a concentration of 3 × 10^8 cfu mL-1 *Phanerochaete chrysosporium* (strain B-22) in tomato.

10.3 Nematode-Fungal Interaction

The infection process of nematophagous fungi to nematodes involves a variety of virulence factors which have been studied by various techniques such as electron microscopy, bioassays, and several biochemical, physiological, immunological, and molecular techniques (Thorn and Barron 1984; Murray and Wharton 1990; Singh and Yadav 2020). In general, the interaction of fungi with nematode species involves five different stages, viz., recognition, attraction, adhesion, penetration, and digestion.

10.3.1 Recognition

The mechanism of host recognition by fungi is not completely understood. However, few reports suggested that lectin, a carbohydrate binding protein plays an important role in nematode–fungal interaction (Borrebaeck et al. 1984; Rosenzweig and Ackroyd 1983; Nordbring-Hertz and Mattiasson 1979; Nordbring-Hertz and Chet 1986). For example, the interaction between *A. oligospora* and nematode was mediated by GalNAc-(*N*-acetyl-D-galactosamine) specific lectin which binds to carbohydrate on the nematode surface (Nordbring-Hertz and Mattiasson 1979). Whereas, Hsueh et al. (2013) reported that ascarosides, a group of glycolipids constitutively secreted by soil dwelling nematodes could trigger the trap formation in *A. oligospora*. This type of ascaroside induced morphogenesis is conserved in several closely related species of nematophagous fungi and occurs under nutrient stress conditions (Jiang et al. 2017).

10.3.2 Attraction

Nematodes are attracted by the culture filtrates and living mycelia of several nematophagous fungi (Li et al. 2015). The volatile compounds such as monoterpenes (α-pinene and β-pinene) and a terpenoid (camphor) produced by an endoparasitic fungus *Esteya vermicola* hypothesized to be involved in the interaction of pinewood nematode, *Bursaphelenchus xylophilus* to *E. vermicola*. Fungi which have more parasitic ability, i.e., endoparasitic fungi are more effective in attracting nematodes than saprophytic fungi and it was tested in soil microcosms (Tunlid et al. 1992; Dijksterhuis et al. 1994; Nordbring-Hertz et al. 2006). In the same way, the volatile compounds produced by host plant roots could also play a role in the interaction of nematode and fungi (Zhao et al. 2007).

10.3.3 Adhesion

The adhesion of nematodes to the spores and trapping structures is an essential requirement in the infection process. The presence of extracellular fibrillar layer with residues of neutral sugars, uronic acid and proteins on the surface of adhesive traps, spores and appresoria mediates the adhesion of fungi to the nematode cuticle surface (Tunlid et al. 1991; Whipps and Lumsden 2001; Su et al. 2015).

10.3.4 Penetration and Digestion

During this stage the nematophagous fungi penetrate the host by mechanical pressure and the activity of several extracellular hydrolytic enzymes that can degrade the polysaccharides and proteins of the nematode cuticle and egg shells. These extracellular enzymes include proteases, collagenases, and chitinases that have identified in different nematode trapping fungi, which act as key factors in the penetration process. After penetration, the nematode is digested by the fungus.

10.4 Extracellular Enzymes

Extracellular hydrolytic enzymes such as proteases, chitinases, and collagenases produced by nematophagous fungi play an important role in nematode cuticle penetration and host cell digestion (Åhman et al. 2002; Huang et al. 2004; Morton et al. 2004). Among these, proteases produced more rapidly in higher concentrations by nematophagous fungi than collagenases and chitinases. So far, more than 20 serine proteases have been detected, characterized, and cloned from different nematode trapping and egg parasititc fungi by several researchers (Tunlid et al. 1994; Yang et al. 2007c, 2008). Lopez-Llorca (1990) first isolated serine protease P32 from *Pochonia rubens* (*Verticillium suchlasporium*). With the availability of genomic data, the number of genes encoding serine proteases have been identified in different nematophagous fungi (Table 10.3).

Chitinases are the enzymes usually produced by nematophagous fungi to penetrate the nematode eggshell during infection (Gortari and Hours 2008). The first chitinase (Chi43) was purified from *P. chlamydosporia* and *P. suchlasporia* (Tikhonov et al. 2002). So far, 20 chitinases have been purified or cloned from

Table 10.3 Serine proteases purified/cloned in nematophagous fungi

Fungi	Protease	Testing nematode	Fungal activity against nematode	Reference
Pochonia rubescens	P32	*Globodera pallida*	Degradation of proteins in nematode eggs	Lopez-Llorca (1990)
Pochonia chlamydosporia	VCP1	*Meloidogyne incognita*	The purified enzyme hydrolysed proteins in situ from the outer layer of the egg shell and exposed its chitin layer	Segers et al. (1994)
Arthrobotrys oligospora	PII	*Panagrellus redivivus*	76.8% immobilized nematodes after 20–22 h of treatment	Tunlid et al. (1994)
Paecilomyces lilacinus	pSP-3	*Meloidogyne hapla*	Significantly affect the development of eggs	Bonants et al. (1995)
Arthrobotrys oligospora	Aoz1	*Panagrellus redivivus*	Immobilization of nematodes	Zhao et al. (2004)
Clonostachys rosea	Lmz1 (Serine like protease)		Immobilization of nematodes after 24 h of treatment	Zhao et al. (2005)
Lecanicillium psalliotae	Ver112	*Panagrellus redivivus*	81% of cuticle degradation after treating with ver112 for 12 h	Yang et al. (2005)
Clonostachys rosea	PrC	*Panagrellus redivivus*	80 ± 5% of J2 were immobilized and degraded after treating with PrC for 48 h	Li et al. (2006)
Monacrosporium microscaphoides	Mlx	*Panagrellus redivivus*	Immobilization of nematodes after 24 h of incubation in purified protease and nematode cuticle degradation	Wang et al. (2006a)
Dactylella shizishanna	Ds1	*Panagrellus redivivus*	>60% of nematodes were killed and degraded after being treated with crude extract or the purified enzyme for 12 h	Wang et al. (2006b)
Hirsutella rhossiliensis	Hnsp	*Panagrellus redivivus*, *Heterodera glycines*	100% mortality of *H. glycines* J2 was observed in 100 μl crude enzyme solution after incubation for 12 h	Wang et al. (2007)

(continued)

Table 10.3 (continued)

Fungi	Protease	Testing nematode	Fungal activity against nematode	Reference
Arthrobotrys conoides	Ac1	*Panagrellus redivivus, Bursaphelenchus xylophilus*	Immobilization of 60–80% *P. redivivus* population after treated with crude enzyme for 24 h. Whereas, 40–50% of *B. xylophilus* nematode population was immobilized after 24 h of treatment	Yang et al. (2007b)
Dactylella varietas	Dv1	*Panagrellus redivivus* and *Caenorhabditis elegans*	50–100% tested nematodes were killed and degraded after being treated with either the crude extract or the purified enzyme for 12 h	Yang et al. (2007c)
Monacrosporium cystosporium	Mc1	*Panagrellus redivivus, Bursaphelenchus xylophilus*	70–80% of *P. redivivus* were immobilized after being treated with the crude and the purified proteases for 24 h, but only 50–60% of *B. xylophilus* were immobilized	Yang et al. (2008)
Cordyceps sinensis	Csp1	*Hepialus* spp.	Loosening and degradation of cuticle in larvae	Zhang et al. (2008)
Cordyceps sinensis	Csp2	*Hepialus* spp.	Loosening and degradation of cuticle in larvae	Zhang et al. (2008)
Hirsutella rhossiliensis	Hasp	*Heterodera glycines*	The mortality of J2 was significantly higher in purified hasp solutions (43 ± 5% mortality at 4 U/ml and 53 ± 4% mortality at 8 U/ml) than in the buffer control (22 ± 2%)	Wang et al. (2009)
Monacrosporium thaumasium	Mt1	*Angiostrongylus vasorum*	23.9% reduction in the number of L1 larvae, compared with control	Soares et al. (2012)
Duddingtonia flagrans	Df1	*Cyathostomin*	58% reduction of L3 larvae, after 24 h of treatment compared with control	Braga et al. (2012)
Esteya vermicola	Evsp	*Bursaphelenchus xylophilus*		Wang et al. (2015)

Table 10.4 Chitinases purified/cloned in nematophagous fungi

Nematophagous fungi	Chitinase	Testing nematode	Fungal activity against nematode	Reference
Pochonia chlamydosporia (=*Verticillium chlamydosporium*) *P. suchlasporia* (*V. suchlasporium*)	Chi43	*Globodera pallida*	Treated eggs showed surface damage	Tikhonov et al. (2002)
Paecilomyces lilacinus (strain 251)	Plc			Khan et al. (2003)
Lecanicillium lecanii (*Verticillium lecanii*)	Chi2			Lu et al. (2005)
Lecanicillium psalliotae	LpChi1	*Meloidogyne incognita*	Inhibition of egg hatching by 38.2% after 3 days of treatment	Gan et al. (2007a)
Clonostachys rosea (=*Gliocladium roseum*)	CrChi1			Gan et al. (2007b)
Paecilomyces variotii	Chi 32	*Meloidogyne incognita*		Nguyen et al. (2009)
Paecilomyces variotii	Chi 46	*Meloidogyne incognita*		Nguyen et al. (2009)
Pochonia chlamydosporia	PcChi44	*Meloidogyne incognita*	Scars on the surface and peeling of eggshells was observed for about 24 h after treatment	Mi et al. (2010)

various nematophagous fungi (Li et al. 2015). Table 10.4 showed a list of chitinases either purified or cloned from different nematophagous fungi and their activity on different species of nematode eggs under in vitro conditions.

Collagenases are another group of enzymes which are suspected to play a role in nematode infection. Initially Schenck et al. (1980) reported that eight nematophagous fungi could secrete collagenases. Later Tosi et al. (2002) reported that *Arthrobotrys* genus could produce collagenases.

10.5 Commercialization

The development of a biocontrol agent needs several steps aimed at isolation in pure culture and screening by different bioassay tests under in vitro, in vivo, and ex vivo conditions (Montesinos 2003). For commercialization of any product, the bioagent must be produced in a large scale, formulated by means of biocompatible additives to improve the storage capacity of the product. Further, quality control, registration of the particular formulated product and implementation are required (Ravensberg 2011).

In case of nematophagous fungi, various species have been tested for their efficacy in control of plant parasitic nematodes. However, only a few species have been commercialized for large scale multiplication and field application. Table 10.5 demonstrates a list of commercial products of nematophagous fungi produced by various companies under different trade names. Among these, the formulations of

Table 10.5 Commercial products of fungal biocontrol agents developed against plant parasitic nematodes

Fungal species	Trade name	Formulation type	Target nematode	Producer/country
Purpureocillium lilacinum (=Paecilomyces lilacinus)	Bioact	Water dispersible granule, water dispersible powder	Root-knot nematodes, cyst nematodes, reniform nematode, burrowing nematode, citrus nematode, golden cyst nematode and lesion nematode	Bayer Crop Science/ USA
	PL Gold	Granulate, WP		BASF Worldwide/ Germany
	PL 251	Water dispersible granule		Biological Control Products/South Africa
	Biocon	WP		Asiatic Technologies, Inc./Philippines
	Shakti Paecil	WP		Shakti Biotech/India
	Yorker	WP		Agriland Biotech Limited/India
	Pl plus	Wettable powder		Biological Control Products/South Africa
	Miexianning	Talc		Agricultural Institute, Yunnan Academy of Tobacco Science/ China
	Melocon	Water dispersible granule		Prophyta GmbH/ Germany; Certis/ USA
	Nematofree	WP		International Panaacea Ltd./India
	Paecilo	WP		Agri life/India
	Gmax bioguard	Talc		GreenMax AgroTech/ India
	Green Nemagon	Liquid		
	Bio-Nematon	Liquid/ powder		Imported from T. Stanes and company limited, India by Gaara company, Egypt
	Biostat			LAM International/ USA

(continued)

Table 10.5 (continued)

Fungal species	Trade name	Formulation type	Target nematode	Producer/country
Pochonia chlamydosporia	Xianchongbike	Liquid	Root-knot nematodes, cyst nematodes, false root-knot nematode, reniform nematode	Laboratory for Conservation and Utilization of Bio-resources, Yunnan University/ China
Pochonia chlamydosporia (IMI SD 187)	KlamiC®	Granulate		CENSA/Cuba
P. chlamydosporia (Pc-10)	Rizotec®			Rhizoflora, Viçosa (Brazil)
	PcMR-1 strain	Liquid		Clamitec, Myco solutions, lda/ Portugal
Arthrobotrys robusta	Royal 300		Unspecified	France
Arthrobotrys irregularis	Royal 350		Root-knot nematodes	France
Myrothecium verrucaria	DiTera®	Dry flowable	Root-knot nematode, cyst nematode, root-lesion nematode, stubby-root nematode, citrus nematode, burrowing nematode, sting nematode	Valent Biosciences Corp/USA
Trichoderma harzianum	Romulus	WP	Root-knot nematodes, cyst nematodes	Dagutat Biolab/South Africa
	Ecosom-TH	Wettable powder, liquid, lyophilized		Agri Life SOM Phytopharma Limited/India
	Commander	Unknown		HTC Impex Private Limited/India
	Trichobiol	WP		Control Biológico Integrado; Mora Jaramillo Arturo Orlando—Biocontrol/ Colombia
Trichoderma viride (strain 2684)	Trifesol	WP		BioCultivos S.A., Bogotá, Colômbia

(continued)

Table 10.5 (continued)

Fungal species	Trade name	Formulation type	Target nematode	Producer/country
Trichoderma lignorum	Mycobac	Unknown		Laboratórios Laverlam/Colombia
Beauveria bassiana strain GHA	Botanigard	ES/WP	Root-knot nematodes	
B. bassiana strain GHA	Mycotrol	ES	Root-knot nematodes	
Verticillium lecanii	Mycotal	WP	Root-knot nematode (*Meloidogyne incognita)*	
Consortium (*Bacillus subtilis, Trichoderma* spp., *Paecilomyces* spp. and extracts of *Tagetes* sp.)	Nemaxxion Biol	Liquid	Root-knot nematodes	GreenCorp/Mexico.
Consortium (*Arthrobotrys* spp., *Dactylella* spp., *Paecilomyces* spp., Mycorrhiza (*Glomus* spp.), and bacteria (*Bacillus* spp. and *Pseudomonas* spp.))	Rem G			Green Solutions/Italy

P. chlamydosporia, *P. lilacinum*, and *A. robusta*, *A. irregularis* have been widely used for nematode management in vegetables and fruit crops.

Although, nematophagous fungi provides several advantages over traditional products, the Commercialization of these bioproducts lags far behind due to inconsistent performance, quality control issues, limited shelf life of product, slow rate of kill, lack of field persistence of some formulations, difficulties in scale-up production, expensive and time consuming registration process and marketable issues, etc. (Moosavi and Askary 2015; Venkatesan and Pattar 2017). There is a need to focus on improving the formulation and manufacturing technologies that reduce costs and enhance shelf life of the commercial product.

The development and success of a biocontrol agent for plant parasitic nematodes require a better knowledge on the biology and ecology of the nematophagous fungi and the nematode, its host cultivar, method and time of application, and the various biotic and abiotic factors regulating the efficacy of biocontrol agent, the root diffusates differ markedly between plant species and cultivar which influences the proliferation of fungi (Tunlid and Ahrén 2001; Morton et al. 2004; Davies 2005). In addition, several soil microbes or their metabolites compete with the introduced bioagents for scarce energy sources. These can significantly affect the efficacy of the agent even when added to soil in a pre-colonized substrate. For example, egg masses of *Meloidogyne* spp. harbored 122 bacteria and 19 fungi, 23% and 74% of which, respectively, were antagonistic to *P. chlamydosporium* (Kok and Papert 2001). *Bacillus* sp. strain H6 isolated from a fungistatic soil produced iturin like compounds from that caused swelling in the conidia and germ tube of nematophagous fungi (Li et al. 2007a). Such sensitivity of a biocontrol agent to antagonism by an isolate of another microbe varies with the isolate (Montfort et al. 2006).

10.6 Conclusion and Future Prospects

Over the past 50 years, the number of scientists involved in research on the biocontrol of nematodes has increased significantly. Although several biocontrol agents for nematodes have been reported, only few organisms were developed as commercial bioagents. Surveys and empirical tests are being replaced by quantitative experimentation and basic research at genomic levels is being undertaken. Such information is essential for a realistic appraisal of the impact of microbial agents on nematode pests and for monitoring the spread and survival of the releases organisms. Our research efforts need to be directed towards identifying the factors governing their proliferation in soil and to remove the constraints wherever feasible. With the application of molecular biology, the molecular mechanisms of the interaction between nematode and fungal species can be understood, which further helps to develop new screening procedures of nematophagous fungi to control plant parasitic nematodes.

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Chapter 11
Global Scenario of Advance Fungal Research in Crop Protection

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Contents

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11.1 Introduction

Sustainable agriculture is one of the major challenges today, considering food security to growing human population and dependence of crop productivity on chemicals (Challa et al. 2019a) and (Kour et al. 2020). The ecological costs of the conventional agriculture approaches are largely underestimated. There are five billion kilograms of pesticides being annually used worldwide (Verger and Boobis 2013) and it is estimated to result in around two lakh deaths every year (WHO 2004). There are number of rules and legislations implemented for limiting the usage of these harmful chemical insecticides to protect human health as well as our environment; however, a lot of efforts are still required to minimize the usage of insecticides. At the same time, there is a requirement of more sustainable methods for resolving these agronomic challenges and reducing the chemical pollution.

Insect herbivory causes severe damage to plant in the natural systems, and their impact on agroecosystems is even more destructive (Meehan et al. 2011). Root pests have always caused huge damage to crops and the herbivores below ground sustain a wide diversity and feed on numerous plant tissues (Koppenhofer et al. 2000a; Hunter 2001). The biological control is challenging and scientifically based risk analysis is required, i.e. to be experimented extensively before releasing the biological control agents into the field. Classical method is based on the capability of a pathogen to control host populations, depending on its ability to perpetuate and disperse. This method needs special care in selecting the agents that are strongly pathogenic; and ecologically and climatically apt for the target location. The pathogen has to be specific to the host and may also include their relatives if they do not have any economic or environmental importance. This review discusses in detail about global scenario of advance fungal research in biocontrol or crop protection as shown in Fig. 11.1.

11.2 Fungi as Biocontrol Agents

Fungi are a phylogenetically diverse group of microorganisms which are heterotrophic in nature (absorptive nutrition). Fungi are employed for industrial or other applications like biocontrol, biomass degradation, bioremediation, bioenergy (biofuel), chemicals (organic acids), detergents, enzymes, food and feed, proteins, paper and pulp, pharmaceuticals (antibiotics, secondary metabolites, statins), and textiles due to its eco-friendly nature or bringing down greenhouse gas emissions (Lalitha et al. 2011, 2013; Challa et al. 2019a; Yadav et al. 2019b, c). Entomopathogenic hyphomycetes are known to be active against a number of insects or pests, weeds, soil borne pathogens, nematodes, etc. in the agricultural ecosystems (Fig. 11.2).

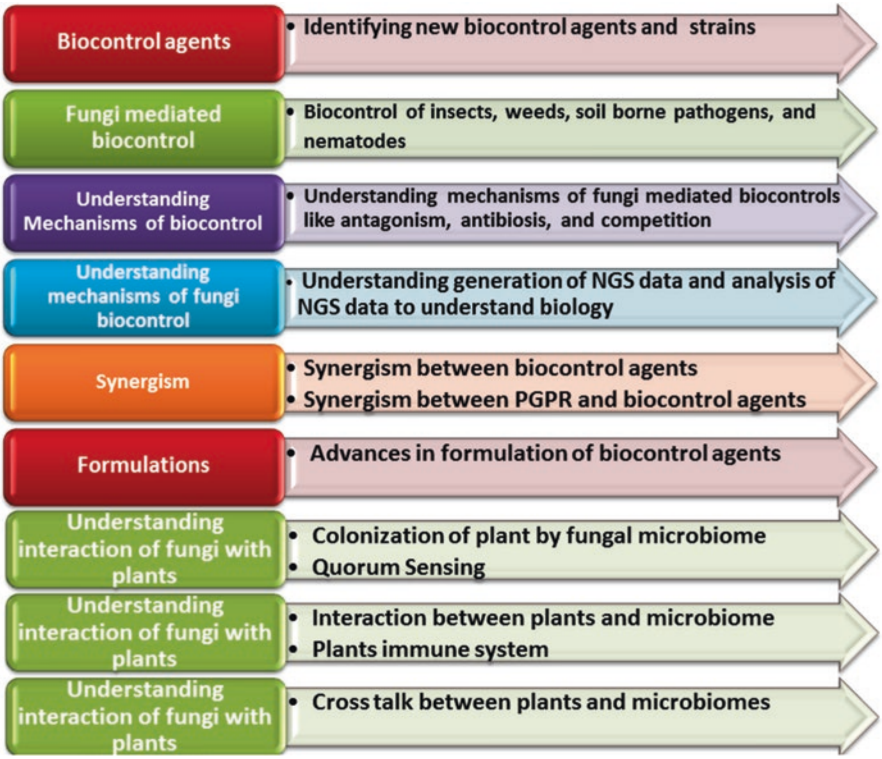


Fig. 11.1 Global scenario of advance fungal research in biocontrol or crop protection

11.2.1 Fungi Mediated Biocontrol of Pests

Entomopathogenic fungi are majorly known to be the natural enemies of pests of agricultural crops (Hajek and Leger 1994; Singh and Yadav 2020). Hyphomycetous fungi like *Aspergillus*, *Beauveria*, *Culicinomyces*, *Hirsutella*, *Metarhizium*, *Nomuraea*, *Paecilomyces*, *Tolypocladium,* and *Verticillium* are capable of causing natural outbreaks in the populations of the insects (Jyoti and Singh 2017). Entomopathogenic fungi *Beauveria*, *Metarhizium*, *Nomuraea*, *Paecilomyces*, and *Verticillium* belong to family Clavicipitaceae (Neelapu et al. 2009; Challa and Neelapu 2019). The reproductive biology of the entomopathogenic fungi *Beauveria bassiana* and *Nomuraea rileyi* was reported to be both clonal and recombination (Padmavathi et al. 2003; Devi et al. 2006, 2007). Devi et al. (2004) reported that *Beauveria bassiana* is resistance to organophosphate based insecticide and this

Fig. 11.2 Fungi mediated biocontrol of insects or pests, weeds, soil borne pathogens, and nematodes in the agricultural ecosystems

resistance is mediated by esterase. Thus, these can be used for efficacious management of insect pests; however, they are not easy to produce at mass scale. They are host specific and have a huge impact on the host pest populations. These fungi have life cycles that coordinate with insect host stages and the environmental conditions. All the stages of insects can be killed by these pathogens. Fungi unlike other pathogens do not ingest to infect and kill the host; thus sap sucking phytophagous insects are also a target to them. They infect either by primary contact with fungal spore or by uptake of spores when sprayed on crops (Moore and Prior 1993). "Some entomopathogenic fungi have restricted and varied host ranges, for example, *Aschersonia aleyrodes* infects only scale insects, and whiteflies, whereas other fungal species have a wide host range" (Sandhu et al. 2012) (Fig. 11.3).

11.2.2 Fungi Mediated Biocontrol of Soil Borne Plant Pathogens

Soil food chain includes an array of predators (herbivore pests), like carabid, centipedes, mites, spiders, and beetles (Symondson et al. 2002). Till date, small number of commercial products based on arthropod predators had success. There are several reasons aligned for it and one among them is that interactions between predators and their prey cannot be predicted easily when multi-trophic systems are considered

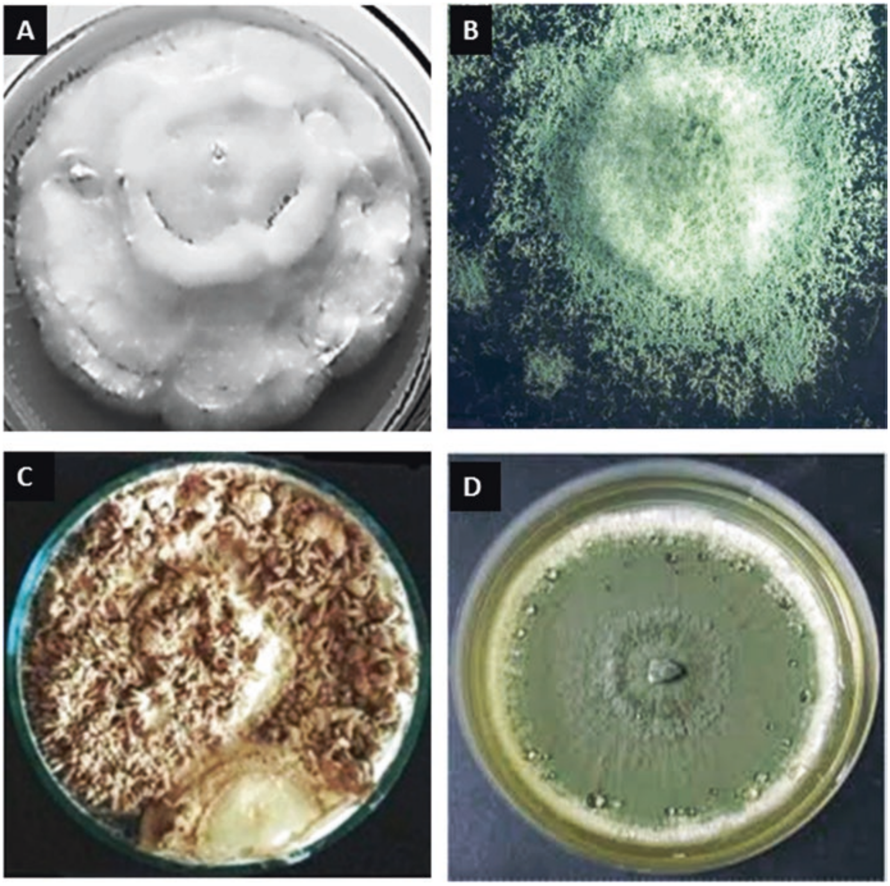


Fig. 11.3 Morphology of (**a**) *Beauveria bassiana*, (**b**) *Nomuraea rileyi*, (**c**) *Paecilomyces fumoroseus*, and (**d**) *Metarhizium anisopliae*

which are under the influence of constantly changing biotic and abiotic parameters. The developing commercial products are based on the soil macro-fauna and numerous venues can be investigated (Yadav et al. 2020c, d). *Trichoderma* and *Gliocladium* are the fungal biocontrol agents which are used to control weeds (Bhuiyan et al. 2012). *Gliocladium* was known to control *Pythium* damping-off (Wilhite et al. 1994). These BCAs produce antimicrobial compounds and suppress disease via antibiotics like gliovirin and gliotoxin.

11.2.3 Fungi Mediated Biocontrol of Weeds

Weeds are the major constraint to the worldwide agricultural production and impact of weeds on crop production is calculated with average losses of around 20%. Human resources can be better invested in more meaningful pursuits; but the social costs are hindering their development. The use of herbicides has limited due to the increase in population of herbicide-resistant weeds, majorly in wheat and maize (Rastegari et al. 2020a, b). This has led to the development of new strategies for long-term management of agricultural weeds. The result of global trade is that more plant species with potentially weedy traits are on move, resulting in the rise of new weed issues mainly in natural ecosystems and non-agricultural lands. Such situations lead to exotic weeds that contribute to the massive threat to our biodiversity after habitat destruction (Yadav et al. 2019a).

Fungal biological control agents (BCAs) are exploited for the management of weed. The risk analysis and safety issues of biological control using fungal pathogens are still in the learning phase. The two major methods for biological control are (1) classical biological control for management of exotic or alien weeds and (2) inundative application of BCAs for biological control of endemic weeds. The potential of fungal pathogens as classical BCAs is aptly defined as the "use of living organisms to control pest species" (Waage and Greathead 1988; Watson 1991). Fungi *Colletotrichum gloeosporioides* f.sp. malvae is used for the control of round leaf mallow (*Malva pusilla*) (Mortensen 1988; PMRA 2006). Same fungi *C. gloeosporioides f.sp. aeschynomene* was used to control *Aeschynomene virginica*. BCA, *Colletotrichum gloeosporioides* f.sp. is commercially available in the name of BioMal. Similarly, fungi *Sclerotinia minor* was used to control broadleaf plantain (*Plantago major*), dandelion (*Taraxacum officinale*), white clover (*Trifolium repens*), and in turf (PMRA 2010). BCA, *Sclerotinia minor* is commercially available in the name of Sarritor.

11.2.4 Fungi Mediated Biocontrol of Nematodes

Nematophagous fungi are the potential biological control agents to control nematodes effectively. Phytophagus nematodes, migrating in soil to new host plants or deprived of proper hosts, face survival in an environment abundantly populated with fungal enemies. Fungal spores of *Harposporium* are ingested by nematode and these spores germinate in the esophagus to develop and consume the nematode (Aschner and Kohn 1958). These fungi then recycle carbon, nitrogen, and other important elements from biomass of nematodes. Fungal species such as *Arthrobotrys*, *Verticillium chlamydosporium*, *Acremonium*, *Fusarium oxysporum*, and *Dactylella oviparasitica* are used to control nematodes. *Arthrobotrys* which is commercially available in the name of Royal 350 is used to control root-knot nematode against tomato crop (Cayrol and Frankowski 1979). *Verticillium chlamydosporium* and another nonsporulating "contortion fungus" are used to control eggs of *Heterodera schachtii* and *H. avenae* cysts (Tribe 1977). Further, *Acremonium* and *Fusarium oxysporum* are also used to control *H. schachtii* in sugar beet soils of California (Nigh 1979). Furthermore, these fungi are used to control *Sarisodera africanus* cysts of Panicum roots in West Africa. *Dactylella oviparasitica* is used to control root-knot nematode *Meloidogyne* populations and their eggs in peach orchards on Lovell rootstock in California's San Joaquin valley (Stifling 1978).

11.2.5 Mechanisms of Fungi Mediated Biocontrols

Biological control is an outcome of many different types of interactions among the organisms. The different biocontrol mechanisms are antagonism, antibiosis, and competition (Fig. 11.4).

11.2.5.1 Antagonism

Antagonism is defined as "lysis of the pathogen by other microorganism. This is also called as hyperparasitism and fungi that are parasitic on other fungi are known as mycoparasites" (Bakers and Cook 1974). Cook (1993) classified the mycoparasitic interactions as (a) unilateral antagonism, (b) mutual antagonism, and (c) no antagonism. *Ampelomyces quisqualis* has been the subject of numerous investigations on biological control of powdery mildews for over the 50 years. The fungus *Ampelomyces quisqualis* occurs on Erysiphales (powdery mildews) which is a naturally occurring deuteromycete hyperparasite and it infects to form pycnidia (fruiting bodies) within powdery mildew hyphae, conidiophores, and cleistothecia (the closed fruiting bodies of powdery mildews). Hyperparasitism "reduces the growth and eventually kills the mildew colony. The mycoparasitic competence of

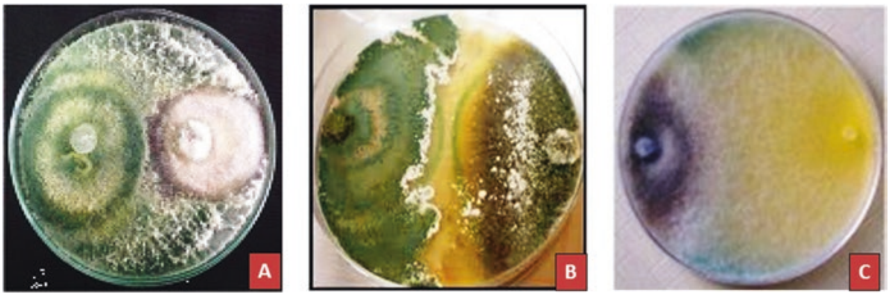


Fig. 11.4 Mechanisms of biological control (**a**) antagonism (*Tricohoderma viride* vs *Fusarium solani*) (Source: Villamizar-Gallardo et al. 2017), (**b**) antibiosis (*Trichoderma* spp. on *M. phaseolina*) (*Source:* Mendoza et al. 2015), and (**c**) competition (*Trichoderma harzianum* and *Ambrosiella grosmanniae*) (*Source:* Castrillo et al. 2016)

Trichoderma species against economically important plant pathogens has allowed the development of biocontrol strategies" (Harman et al. 2004; Motlagh and Samimi 2013). Weindling in 1932, "observed and reported that the *Trichoderama lignorum* (*T. viride*) parasitize the hyphae of *Rhizoctonia solani* and recommended that the *Trichoderma* can be used control damping-off of citrus seedlings" (Lo 1997). There are several fungal parasites like *Coniothyrium minitans* which attack plant pathogen like sclerotia, while *Pythium oligandrum* attack living hyphae belonging to *Botrytis, Fusarium,* and *Phytophthora*. Single fungal pathogen "can be attacked by multiple hyperparasites, for example, *Acremonium alternatum*, *Acrodontium crateriforme*, *Ampelomyces quisqualis*, *Cladosporium oxysporum*, and *Gliocladium virens* have the capacity to parasitize powdery mildew pathogens" (Kiss 2003).

11.2.5.2 Antibiosis

Antibiosis is the "procedure of secretion of antimicrobial compounds by fungi to suppress or kill pathogenic fungi in the vicinity of its growth area. Most fungi are capable of secreting one or more compounds. The secondary metabolites with the antibiotic activity are often correlated to specific stages of morphological differentiation, and are associated with the phase of active growth. Interestingly, some fungal secondary metabolites can modify the growth and the metabolism of plants, while others seem to target specific fungal processes such as sporulation and hyphal elongation. Thus, the expression of secondary metabolites may occur at a predictable point during the normal life cycle of some fungi, including those used for agriculture applications" (Keller et al. 2005). Menendez and Godeas (1998) reported "a biocontrol study of *Trichoderma harzianum* against *Sclerotinias clerotiorum*—a soil borne plant pathogen attacking many economically important crops, such as soybean". Menendez and Godeas (1998) studied "about antibiosis of *T. harzianum* against the plant pathogen and assumed that the beneficial effect was due to concurrent mycoparasitism and competition" (Inbar et al. 1996; Ghisalberti 2002). In another example, despite close contact between hyphae of *Trichoderma* spp. and *Fusarium moniliforme/Aspergillus flavus* on coculturing, hyphal penetration was absent. This suggested that mycoparasitism was not the sole cause for the observed inhibitory effects (Calistru et al. 1997). Therefore, metabolites produced by *Trichoderma* spp. (e.g., volatiles, extracellular enzymes, and/or antibiotics) were considered to be the probable elements involved in antibiosis.

Trichoderma spp. has been effective against a wide host range and in hindering the longevity of sclerotia of pathogenic fungi. Szekeres et al. (2005) reviewed about "antagonistic metabolites produced by *Trichoderma* spp. The metabolites are linear, amphipathic polypeptides, namely peptaibols and peptaibiotics. The physico-chemical and biological properties of these antibiotic compounds included disruption of lipid membranes, antimicrobial activities, and induction of plant resistance. Some biocontrol agents exhibit predatory behavior under nutrient-limited conditions. However, such activity generally is not expressed under typical growing conditions. For example, some species of *Trichoderma* produce a range of enzymes that are directed against cell walls of fungi. Peptaibols and the related peptaibiotics are linear, amphipathic polypeptides and the compounds are composed of 5–20 amino acids. These are generally produced in microheterogeneous mixtures that have strong antimicrobial activity". Gram-positive bacteria and fungi act synergistically with cell-wall-degrading enzymes (CWDEs) to inhibit the growth of fungal pathogens and elicit plant resistance to pathogens (Wiest et al. 2002; Szekeres et al. 2005). Peptaibols and peptaibiotics with unusual amino acid content are the result of non-ribosomal biosynthesis.

Large multifunctional enzymes known as peptide synthetases assemble these molecules by the multiple carrier thio-template mechanism from a remarkable range of precursors, which can be N-methylated, acylated, or reduced (Szekeres et al. 2005). Peptaibols and peptaibiotics show interesting physico-chemical and biological properties including the formation of pores in bilayer lipid membranes. In tobacco plants, exogenous applications of peptaibols trigger a defense response and reduce susceptibility to tobacco mosaic virus (Wiest et al. 2002). A peptaibol synthetase from *T. virens* has been purified, and the corresponding gene, when cloned, will facilitate studies of this compound and its contribution to biocontrol. An extensive review on antibiosis and production of *Trichoderma* secondary metabolites elaborated the significance of secondary metabolites (antibiotic activity) in antagonistic action of *Trichoderma* spp. against pathogenic fungi *Pythium ultimum* and *Rhizoctonia solani* (Hutchinson 1999; Hanson and Howell 2002). However, there seems to be a general consent on the combined synergistic effect of the two factors (enzymes and antibiotic compounds) (Schirmbock et al. 1994).

11.2.5.3 Competition

Starvation is the most "common cause of death for microorganisms, so that competition for limiting nutrients results in biological control of fungal phytopathogens" (Chet et al. 1997). Celar (2003) directed a study on the forms of nutrients mostly available to phytopathogenic and antagonistic fungi. Earlier study reconfirmed the findings of Blakeman (1978) that shortage of easily accessible nutrients for microorganisms, especially of those living in soil and on plant surfaces, results in open nutrient competition among microorganisms (Sivan and Chet 1986; Lewis and Papavizas 1991). Biocontrol based on competition for rare but essential micronutrients, such as iron, which is extremely limited in the rhizosphere, depending on soil pH has been observed. In highly oxidized and aerated soil, iron is present in ferric form (Lindsay 1979), which is insoluble in water (pH 7.4) and the concentration may be as low as 10–18 M. This concentration is too low to support the growth of microorganisms, which generally need concentrations approaching 10–6 M. To survive in such an environment, organisms were found to secrete iron-binding ligands called siderophores having high affinity to sequester iron from the micro-environment. Largely most filamentous fungi uptake iron as essential mineral for viability and under iron starvation, and mostly fungi excrete low-molecular-weight ferric-iron specific chelators, termed siderophores, to mobilize environmental iron (Eisendle et al. 2004).

Then, iron from the ferri-siderophore complexes is recovered via specific uptake mechanisms. In *Aspergillus fumigates* and *Aspergillus nidulans*, siderophore biosynthesis is negatively regulated by carbon source (Eisendle et al. 2004). In *Ustilago maydis*, gene products related to iron uptake affect the development of plant (McIntyre et al. 2004). Some *Trichoderma* and biocontrol agents produce highly efficient siderophores that chelate iron and stop the growth of other fungi (Chet and Inbar 1994). For this reason, soil composition influences the biocontrol effectiveness of *Pythium* by *Trichoderma* according to iron availability. In addition, *T. harzianum* T35 controls *Fusarium oxysporum* by competing for both rhizosphere colonization and nutrients, with biocontrol becoming more effective as the nutrient concentration decreases (Tjamos 1992). Competition has proved to be particularly important for the biocontrol of phytopathogens such as *Botrytis cinerea*, the main pathogenic. The increased efficiency in iron uptake of the commensal microorganisms is thought to be a contributing factor to their ability to aggressively colonize plant roots and an aid to the displacement of the deleterious organisms from potential sites of infection. Thus, the cited examples confirm the significance of competition for nutrients during biocontro.

11.2.5.4 Biocontrol Agents

This section discusses in detail about biocontrol agents like *Beauveria bassiana*, *Paecilomyces fumosoroseus*, *Nomuraea rileyi*, *Metarhizium anisopliae*, *Verticillium lecanii*, and *Trichoderma. Beauveria bassiana* is a filamentous entomopathogenic fungus which is highly adapted to specific insect hosts. This fungus naturally grows in soil and is a well-known pathogen on insects that causes white muscardine disease (Sandhu et al. 2001; Thakur et al. 2005; Jain et al. 2008). *Paecilomyces fumosoroseus* is a both nematophagous and entomopathogenic fungus, which kills harmful nematodes and insects by pathogenesis and causes disease in them. This fungus is used as a bionematicide for controlling nematodes by applying it directly to the soil. *P. lilacinus* infects and ingests the eggs of root-knot and even cyst nematodes. Hyphomycetes are the natural enemies of whiteflies worldwide and cause "Yellow Muscardine" disease (Nunez et al. 2008). Usually, certain species of fungi are known for their competence causing high level mortality, and developing natural epizootics that is dependent on the environmental conditions and also biased by various practices of crop production. *P. lilacinus* is known for its potential as biological control agent specifically in subtropical and tropical soils. *P. lilacinus* has the ability to grow on leaf surface in humid conditions and it is known to spread rapidly in whitefly populations (Wraight et al. 2000).

Nomuraea rileyi is dimorphic hyphomycetous fungi that cause epizootic on numerous insects and arthropods and thus it is a very efficient biocontrol agent against insects and arthropods. It is known that many insect species that belong to

Lepidoptera including *Spodoptera litura* and some to Coleoptera are very susceptible to *N. rileyi*. The host specificity and the eco-friendly nature of *N. rileyi* fortify its use in insect pest management. On the other hand, its mode of infection and development is examined and reported for numerous insect hosts (for instance, *Trichoplusia ni*, *Heliothis zea*, *Plathypena scabra*, *Bombyx mori*, *Pseudoplusia*). In another example, insect *Spilosoma* was found to be severely attacked by *N. rileyi* (Mathew et al. 1998). *Metarhizium anisopliae* is a pathogen for insect pests and is very well known for biological control of notorious insect pests (Sandhu et al. 1993; Sandhu and Mishra 1994). This species is specifically used for the control of locusts, grasshoppers, cockroaches, termites, and other major pests worldwide. Oil is used for spreading the green spores to the parts of the insect with high relative humidity (parts like the back of the neck or under the wing where cuticle is thin) where the fungus can grow easily. This fungus is very effective; it holds the capability to kill 90% of locusts with its application in 7–21 days, depending on the number of infected spores. Complete biological activity of *M. anisopliae* is tested on *Eutectona machaeralis* (teak skeletonizer) and is analyzed to be a potential fungal biological control agent of teak pest (Sandhu et al. 2000).

Verticillium lecanii is widely distributed entomopathogenic fungus that causes large epizootic in warm and humid environments (Nunez et al. 2008, Kim et al. 2002). It is known to be a very effective agent of biological control against *Trialeurodes vaporariorum* in South Korean greenhouses. In the year 1970, *V. lecanii* was developed for controlling whitefly and several aphids species including green peach aphids for use in greenhouse *Chrysanthemums* (Hamlen 1979). It is considered to be major parasite and can cause massive fall in cereal-cyst nematode populations (Kerry et al. 1982). Another species *V. chlamydosporium* has an extensive host range among cyst and root-knot nematodes. It is not much consistent and only few isolates have potential as commercial biological control agents. Species of *Trichoderma* are used in biological control of pests and soil borne pathogens, and as PGPR. This mechanism of biological control has led to improvement in application of the different strains as biocontrol agents. These are developed into commercial products of biocontrol that are used in the fields, greenhouse systems (Harman et al. 2004), and also well known for controlling various soil borne diseases. The soil borne diseases known are "*Pythium ultimum* Trow. (Naseby et al. 2000), *Sclerotinia sclerotiorum* (Lib.) de Bary (Inbar et al. 1996) and *Fusarium oxysporum* Schlechtend (Sivan and Chet 1993)" *Trichoderma* spp. easily extracts nutrients from complex substrates (e.g. protein, glucosamine, and tannin) in the soil. *Trichoderma viride* mediated reprogramming of plant defense mechanism in *Vigna mungo, Cajanus cajan*, *Vigna radiata*, was reported against plant pathogens *Fusarium oxysporum* and *Alternaria alternata* (Surekha et al. 2013, 2014; Rao et al. 2015). Thus, this potential is an additional advantage as it leads to improvement in soil minerals where excessive use of herbicides needs to be limited.

11.2.6 Advantages and Disadvantages of Fungi as Biocontrol Agents

Fungi as biocontrol agents have number of features that gathers public support. The best part is the usage of these has limited the chemical products that are poisonous to human population as well as to environment. Currently these biocontrol products are just 2% in global pesticide market. Chemical approach is easier and more effective on pests which actually led to chemical revolution from green revolution (Pimentel et al. 1992; Yadav et al. 2020a)**.** Fungi are dignified biological agents with diverse benefits such as they are self-generating either on the surface of plants or inside them which efficiently provide protection constantly and are absolutely safe to use. Fungi are easy to produce and also quite adaptable with current application technology. Additionally, vast usage of fungi can lead in control of numerous pests with a single product. There are certain limitations with biocontrol fungi like narrow host range of the beneficial organisms, and increase in mortality rate with age of biocontrol fungi. Environmental factors play a huge role in their success, for example, biocontrol to be effective, moist/humid weather is necessary. The above-mentioned major reasons limit their usage in pest control (Yadav et al. 2020b, e).

11.3 Understanding the Biology of the Biocontrol Agents

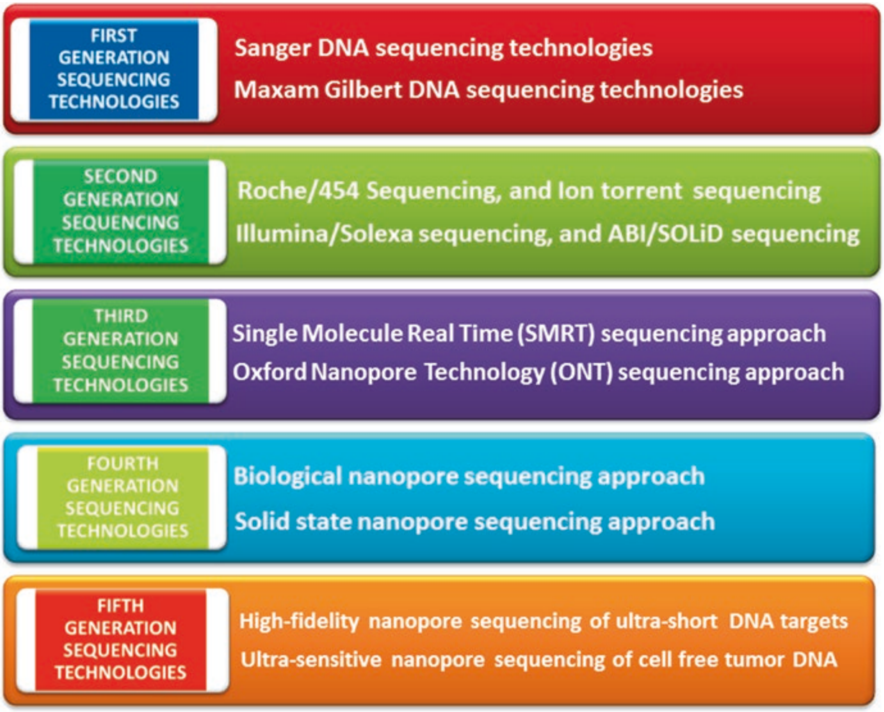
Understanding the biology of the biocontrol agents is possible when we understand the next generation sequencing (NGS) technologies and NGS data.

11.3.1 Next Generation Sequencing Technologies

Deoxyribonucleic acid (DNA) is the ultimate code of any living organisms genome and is composed of four bases [A, T, G, C] in enormous numbers and in different combinations. DNA sequencing utilizes the DNA composition for analysis and translates the code of all the biota on earth. The emergence of sequencing technologies performed a substantial role in studying genomic sequences of individuals. The sequence constitutes string of nucleotides [A,T,G,C] and N [represent ambiguity]. The first sequencing technologies were developed by Sanger et al. in the year 1977 and later by Maxam et al. in the year 1980. Their discovery unlocked the door for genetic code studies and lead to the development of faster and competent sequencing technologies. As we are heading towards the age of synthetic genomics and personalized medicine, there is an increased need of highly efficient sequencing technologies. Determination of order and composition of nucleic acid in a sample is a vital element for a number of research applications. Since, five decades large numbers of researchers are involved in advancements of these technologies for fast and accurate results. Also there is a stupendous improvement in recorded with time from sequencing short oligonucleotides to millions of bases. There was also hard time in deducing coding sequence of a single gene to broadly available data of whole genomes (Neelapu and Surekha 2016; Kchouk et al. 2017). This section discusses in detail about the next generation technologies used for generation of NGS data (Fig. 11.5).

11.3.2 First Generation Sequencing Technologies

First generation sequencing technology includes Sanger and Maxam Gilbert DNA sequencing technologies introduced in the year 1977. Sanger sequencing follows the chain termination method, i.e. dideoxynucleotide method (Sanger et al. 1977). Sanger sequencing uses oligonucleotide primers to find certain specific regions of DNA. The process is initiated with denaturation of double stranded to single stranded DNA which forms the template for the process of sequencing. The resultant single strand is then annealed with oligonucleotide primers. Later, elongated in



FIRST GENERATION SEQUENCING TECHNOLOGIES	Sanger DNA sequencing technologies Maxam Gilbert DNA sequencing technologies
SECOND GENERATION SEQUENCING TECHNOLOGIES	Roche/454 Sequencing, and Ion torrent sequencing Illumina/Solexa sequencing, and ABI/SOLiD sequencing
THIRD GENERATION SEQUENCING TECHNOLOGIES	Single Molecule Real Time (SMRT) sequencing approach Oxford Nanopore Technology (ONT) sequencing approach
FOURTH GENERATION SEQUENCING TECHNOLOGIES	Biological nanopore sequencing approach Solid state nanopore sequencing approach
FIFTH GENERATION SEQUENCING TECHNOLOGIES	High-fidelity nanopore sequencing of ultra-short DNA targets Ultra-sensitive nanopore sequencing of cell free tumor DNA

Fig. 11.5 Next generation sequencing technologies used for generation of NGS data

the mixture of deoxynucleotide triphosphates (dNTPs) that provides the nucleotides (A,T,G,C) to build new double stranded model. Along with these a few chain terminating dideoxynucleotide triphosphates (dNTPs) of each nucleotide are added, which help in termination of the strand. Each strand will be varying in their length depending on the ddNTPs attaching. Each ddNTP is associated with a fluorescent marker, when attached to the sequence will emit and illuminate light depending on the nucleotide base. According to the protocol each nucleotide is associated with specific color fluorescence, namely A by green, T by red, G by black, and C by blue. And then a laser depicts the sequence depending on the intensity color of light emitted and which is translated into peak. If a heterozygous variant is present in the sequence, peak will be captured by two fluorescent dyes and the dye color is replaced by completely new base pair's color. The types of variants include silent, missense, nonsense, truncating, deletion, insertion, and splicing. Sanger sequencing is the robust testing strategy that has the capability to diagnose point mutation/deletion or duplication. It is definitely a promising approach to cover desired regions but is costly for multiplex testing systems. Therefore, the latest Sanger sequencing approach is gene specific (Masoudi-Nejad et al. 2013; El-Metwally et al. 2014).

Maxam–Gilbert sequencing is another method that belongs to the first generation of sequencing which was developed in the year 1976–1977 by Allan Maxam and Walter Gilbert. It is well known as chemical degradation/chemical cleavage method for DNA sequence determination. The method depends on nucleotide cleaving and is most efficient with small nucleotide polymers. This method permits sequencing of at least 100 bases from the point of labelling (Maxam and Gilbert 1977). In accordance to this method, the sequence of the nucleotides is determined by terminally labelled DNA molecule by breaking it at any of the bases (ATGC) with the aid of chemical agents (Shackelford 2019). It is gel based sequencing method which uses four different base specific enzymes known as restriction endonucleases for cleaving at specific sequence. Postpurification, phosphate from 3′ end is cleaved with the help of phosphatase and replaced with radioactive phosphate 32P. Then the radioactive DNA fragment is treated with restriction endonucleases and the resultant DNA fragments are ran through gel electrophoresis to separate labelled and unlabelled end subfragments. And the fragment is purified whose sequence needs to be identified from its other end labelled subfragment. Four base specific samples are prepared and the end labelled DNA fragment is divided further and placed in these chemical solutions. Each solution treats a particular base and the bond of that specific base is broken and the base is removed. Electrophoresis is performed for the DNA fragments in the four reaction samples, and by autoradiography, the bands of DNA fragments are revealed according to their length in each individual lane. The sequence is read depending on the density of bands. The dark band in each reaction depicts the base present in position. Maxam–Gilbert method was more popular when compared to Sanger, but was not preferred because of its technical complexity and extensive usage of hazardous radioactive chemicals (Mahboob 2010).

11.3.3 Second Generation of Sequencing Technologies

The first generation sequencing technologies remained prominent for almost three decades, specifically Sanger sequencing. However, cost and time were the major drawbacks that have led to development of second generation sequencing technologies which are based on two approaches, namely sequencing by ligation and sequencing by synthesis. The basic characteristics of the second generation of sequencing are (1) generation of millions of short reads in parallel, (2) speeding up the process of sequencing when compared to first generation, and (3) detection of sequencing output directly without electrophoresis. The second generation sequencing technologies include Roche/454 sequencing, Ion torrent sequencing, Illumina/Solexa sequencing, and ABI/SOLiD sequencing.

Roche/454 sequencing was introduced in the market in the year 2005 and uses pyrosequencing technique which follows sequencing by synthesis method and detects pyrophosphate released after each nucleotide is incorporated in the new synthetic DNA. Each of the randomly fragmented DNA samples is attached to a bead which carries primers carrying oligonucleotides complementary to the DNA fragment. Each fragment is associated with a single bead and each bead is isolated, amplified using PCR producing a million copies of each fragment. The beads are now transferred onto a plate of wells which undergoes a series of reactions producing light at addition of each nucleotide that in turn deduce the sequence of DNA fragments. It has the capability to generate long reads which are easier to map a reference genome (Mardis 2008)

Ion torrent semiconductor sequencing technology was bought into market by Life Technologies in the year 2010. It is similar to 454 pyrosequencing, except that it does not use fluorescent labelled nucleotides. It is particularly based on hydrogen ion detection that is released during the process of sequencing. It uses microwell containing chip that has bead with several identical fragments. The change in pH while incorporating each nucleotide with fragment in the pearl is detected by the sensor and converted into a voltage signal that is proportional to the number of nucleotides incorporated. This method holds the capability to produce read of 200–600 base pairs. The major benefit of this technology is longer read length and speed of sequencing. The disadvantage on the other hand is difficulty in interpreting homopolymer sequences that cause indel errors (Rothberg et al. 2011).

Illumina/Solexa sequencing by synthesis approach is developed by Solexa which was acquired by Illumina and commercialized the sequencer Illumina/Solexa Genome Analyzer (GA) (Shendure and Ji 2008; Balasubramanian 2015). The DNA samples are fragmented and adapters ligated to either ends. These adapters are fixed to respective complementary adapters, then hooked on a slide with number of variants on a solid plate. Then each sequence attached to the solid plate is amplified by PCR bridge amplification creating several identical copies of sequences that are known as cluster and each cluster contains almost a million copies of the original sequence. Then sequence of nucleotide is determined via sequencing by synthesis approach of Illumina. This approach employs reversible terminators, add primers, modified nucleotides along with DNA polymerase. The modified nucleotide sequence helps in extending primers by polymerases. Each nucleotide is labelled with a fluorescent so that each one is unique and has one 3′-hydroxyl group assuring addition of a single nucleotide. Clusters are excited by lasers for emitting a signal that is unique for each nucleotide. The signal is then detected by a coupled-charge device (CCD) camera which is in turn translated by certain computer programs. Initially, it produces very short reads of 35 bp and they had the advantage in which they could produce paired end (PE) short reads. The sequence of both ends of each DNA cluster is recorded. However, the latest version is capable of sequencing more than 600 Gbp and short read length is about 125 bp (Reuter et al. 2015; Heo 2015)**.**

ABI/SOLiD sequencing is incorporated in market by Life Technologies which was later taken over by Applied Biosystems (ABI) in the year 2007. Supported Oligonucleotide Ligation and Detection (SOLiD) developed sequencing technique following the Sequencing By Ligation (SBL) approach which supports oligonucleotide ligation and detection. This process consists of multiple sequencing rounds which starts by attaching adapters to the DNA fragment, fix on beads, and then clone by PCR emulsion. Then the beads are placed on glass slide consisting of 8-mer with fluorescent label at the end of the fragment and the emitted color is recorded (Alic et al. 2016; Goodwin et al. 2016).

11.3.4 Third Generation of Sequencing Technologies

The third generation sequencing technologies run at low cost and are significantly faster when compared to second generation sequencing technologies. The sample preparation is easy without the need of PCR amplification. These advanced methodologies produce long reads in kilobases resolving the assembly problem and repetitive regions of complex genome. The two major approaches in third generation sequencing are Single Molecule Real Time (SMRT) sequencing approach and Oxford Nanopore Technology (ONT) sequencing approach. SMRT was developed by Pacific Biosciences and uses same fluorescent labelling as other technologies, but instead of executing cycles of amplification nucleotide, it detects signals in real time. Pacific biosciences sequencing platforms have a high error rate about 13% dominated by insertions and deletion errors. These errors are randomly distributed along the long read (Kchouk et al. 2017).

Oxford Nanopore Technology sequencing (ONT) was developed for determining the order of nucleotides in a DNA. MinION, the device that promised generation of long reads and enhanced resolution of structural genomic variants, was released by Oxford Nanopore Technologies in the year 2014 (Mikheyev and Tin 2014; Laehnemann et al. 2015). It is a small 4 in device that can be connected to a system (Laver et al. 2015). In this technique the initial DNA strand is linked to its complementary strand by a hairpin. A protein nanopore is used to pass the DNA fragment (Heo 2015). With the action of motor protein DNA fragment is translated through the pore generating ionic current variations that are caused by differences in moving nucleotides in the pore. The variance is recorded and then interpreted to analyze the sequence. In this the direct strand is sequenced to generate "template read" followed by hairpin and then the inverse strand that generates "complement read," the resulting consensus sequence is the "two direction read (2D)" (Jain et al. 2016; Lu et al. 2016). Low cost, small sizes are the major advantages of this technique over the rest. Also, the sequenced data is displayed on the screen for the sample loaded which is easy to read and reduces delay. MinION is capable of obtaining very long reads of more than 150 kbps, however, has a pretty high error rate ~12% (Ip et al. 2015). This technology has evolved and another device "PrometION" was released which is a sequencer with 48 individual flow cells and each one with 3000 pores that operates at 500 bp/s. Thus it holds the capability to sequence huge genomes (such as the human genome) (Lu et al. 2016).

11.3.5 Fourth Generation of Sequencing Technologies

Nanopore based sequencing is considered as the fourth generation sequencing technology which is also known as single molecule nanopore technology. The significance of the technology can be analyzed by its applications and this technology has a major impact on personalized medicine. It holds the capability to sequence the entire human genome in less than $1000 and at the same time is very quick and reliable. DNA that is the blueprint of life is the molecule that encodes genetic instructions. The other technologies require sample preparation and complex data processing algorithms resulting in low throughput, short read lengths, and high cost. The advantage of this technology over other generations is it is label-free; high-throughput generating ultra-long reads with minimum requirement of materials. This technology originated from Coulter counter and ion channels and the external voltage is applied and the particles that are smaller than pore are passed through. These pores are either made of solid state film or embedded in biological membrane which separates the reservoir with cis and trans compartments consisting of conductive electrolytes. Electrodes are immersed in each chamber and biased voltage is passed which results in electrolyte ions in the solution to pass through the pores electrophoretically resulting in ionic current signal. The pore is blocked by an analyte and the negatively charged cis DNA is added to the chamber blocking the current flowing through the chamber. The properties (physical and chemical) can be statistically calculated by analyzing duration and amplitude of current blockades with these translocation events. Nanopore technology can be broadly classified into two categories: biological nanopore technology and solid state nanopore technology.

Biological nanopores are the transmembrane protein channels that are usually inserted in the substrate (bilipid layer, polymer films, or liposomes). The major advantages with biological nanopore are reproducibility, size and structure along with the ability of modifying in combination with molecular biology techniques. The common biological nanopores include α-Hemolysin, MspA (for reading info from 4 nucleotides simultaneously), Bacteriophage phi29, and Oxford Nanopore

Technologies (ONT). α-Hemolysin also known as α-toxin is the most common biological nanopore, and it is an exotoxin secreted by a human pathogenic bacterium *Staphylococcus aureus*. The inner diameter of α-HL and size of ss-DNA are pretty close in size that aids in identifying the identifying nucleotides using ionic current in the nanopore making it a promising tool for the molecular interaction analyses. The only limitation is its limited pore size restricting it to the analysis of ss DNA or RNA or small molecules or length of β-barrel which is very long to distinguish each nucleotide in long chain DNA.

Solid state nanopore are nano-sized holes formed from drilling the opening in a solid substrate (Dekker 2007; Storm et al. 2003). These are specifically used in the study of molecular translocation. Growth in microfabrication technologies has gained more attention towards solid state nanopore. The advantage over biological nanopore is its thermal, chemical, and mechanical stability; along with size adjustability (Cheley et al. 2002; Abiola et al. 2003; Venkatesan et al. 2009), additionally they can even work under various experimental conditions and can be produced in bulk. Over the past few years the method is also applied in multiple fields such as DNA sequencing, protein detection, and disease diagnosis (Traversi et al. 2013). Some of the major examples of solid state nanopore include: Si3N4 and SiO2 nanopores (widely used a substrate because of their high chemical stability and low mechanical stress) (Kim et al. 2007), Al2O3 membranes (have improved electrical performance, low noise in DNA translocation, and higher signal-to-noise ratio (Feng et al. 2015), over single layer membranes, hybrid biological/solid state nanopore.

11.3.6 Fifth Generation Sequencing Technologies

Fourth generation sequencing technologies suffer with lower accuracy and cannot sequence ultra-short DNA. An alternative to sequencing-by-synthesis methods, a portable and affordable is offered by nanopore sequencing. There are two approaches—high-fidelity nanopore sequencing of ultra-short DNA targets and cyclomics and ultra-sensitive nanopore sequencing of cell free tumor DNA. High-fidelity nanopore sequencing of ultra-short DNA targets is a nanopore based sequencing strategy that has been reported to overcome the shortcomings in which short target sequences are first circularized and then amplified via rolling-circle amplification to produce long stretches of concatemeric repeats. These are sequenced on the MinION platform and the resulting repeat sequences are aligned in order to obtain highly accurate consensus which reduces the error rate in the individual repeats. For the first time the ability to obtain unbiased and accurate nanopore data for target DNA sequences of <100 bp has been demonstrated using this approach. This approach is sensitive enough to achieve single nucleotide variants (SNVs) discriminating them in mixtures of sequences. Also, enables quantitative detection of specific variants present at ratios of <10%. This method is simple, cost-effective, and only needs well-established processes. Therefore, it expands the utility of nanopore sequencing for molecular diagnostics and other applications, especially in resource-limited settings (Wilson et al. 2019).

Cyclomics: ultra-sensitive nanopore sequencing of cell free tumor DNA uses backbone and rolling-circle amplification to capture short molecules into circular molecules, giving multiple copies of the original molecule in long stretches. Cyclomics sequencing is an enrichment strategy which is possible with circumventing any random sequencing error by producing a per-molecule consensus sequence, and then these molecules can be prepared for sequencing on the MinION. This would create a sensitive, fast, and flexible workflow that allows to tell if a mutation is present in the patient molecule in an accurate fashion (De Jereon 2019).

11.4 Genome to Phenome Projects of Fungi

Next generation sequencing technologies are used to generate NGS data (genomes, epigenomes, transcriptomes, proteomes, metablomes, interactomes, and phenomes). Analysis of the NGS data (Challa and Neelapu 2018) will help us in understanding the biology of the fungi, including the fungi related to biocontrol agents. This section will discuss in detail about genome sequencing projects, transcriptome sequencing projects, proteome sequencing projects, etc.

11.4.1 Genome Sequencing Projects

This section will discuss in detail on genome sequencing projects like 1000 Fungal Genomes Project, and Ensembl Fungi. Fungi are the largest branch of tree of life with almost 1.5 million species. Their impact on human affairs and the ecosystem is enormous because of their diverse activities as pathogens, symbiont, and decomposers (Grigoriev et al. 2014). They form the most essential components of the carbon cycle and all of these together have the ability to degrade almost any polymer. Joint Genome Institute (JGI) of the Department of Energy has initiated a 5 year project for sequencing thousand fungal genomes. JGI Genome Portal is available at http://1000.fungalgenomes.org/home/. The objective of the project is to address gaps in the fungal tree of life by sequencing at least two reference genomes from around five hundred recognized families of fungi. The aim of the project is to provide genomic information for each family of fungi. Precise understanding of how fungi interact in natural and synthetic communities is crucial for the use of it and for the progress of humankind. The possibility to sample environments for complex fungal metagenomes is in place and it will be a major help in harnessing fungi for industrial, energy, and climate management tasks.

The accurate analysis of the data depends on characterization of fungi with reference to data of fungal genomes. The purpose of analyzing the data is to work on phylogenetic and comparative genomics data to understand evolution and biology of fungi at the most (Grigoriev et al. 2014). The large-scale genomics initiatives like the 1000 Fungal Genomes Project augmented data requirements and new approaches for data integration and analysis. An integrated fungal genomics resource MycoCosm was designed which allowed researchers to access and analyze large amounts of genomic data using web-based analytical tools. MycoCosm portal enables efficient comparative genomics of fungi and in-depth multidimensional analysis of individual genomes, which may be applied to phylogenetically related fungi or to those sharing the same lifestyle, ecological niche, or phenotypic trait. The efficient tools enable comparisons between the groups of genomes, providing an opportunity to create wealth of genomes in MycoCosm. Tools integrate single genomes into a comparative context and have the ability to visualize variations in gene counts in different GO, KEGG, and KOG categories across a user-selected assortment of genomes comprised in MycoCosm. MycoCosm also includes predefined groups of fungi to enable users to ask questions for fungal genomes in a group context. Two types of genome groups are available in MycoCosm (1) PhyloGroups, consisting of phylogenetically related species (corresponding to the nodes of the MycoCosm tree) and (2) EcoGroups, containing fungi of similar lifestyle or ecology (but which may be phylogenetically distant) (Grigoriev et al. 2014).

Ensembl Fungi is a browser for fungal genomes and is developed by EMBL-EBI for analysis and visualization of genomic data. Most of the fungal genome data retrieved are taken from the databases of the International Nucleotide Sequence Database Collaboration (European Nucleotide Archive at the EBI, GenBank at the NCBI, and DNA Database of Japan) and integrated into Ensembl Fungi. In some cases, the annotation has been directly retrieved from the websites of the data generators. Data can be visualized through the Ensembl genome browser and accessed at http://fungi.ensembl.org/index.html**.**

11.4.2 Transcriptome Sequencing Projects

Cordyceps militaris, an ascomycete caterpillar fungus parasitizes insects and this is used as a traditional Chinese medicine for many decades. The medicinal properties are anticancer and immunomodulatory activities. Systematic molecular studies on the improving stages of cultured *C. militaris* at both translational and transcriptional levels have been sorted (Yin et al. 2012). Functional annotations were performed for analyzing the protein expression difference between each development stage mycelium and fruiting body. Transcriptomes belonging to categories like intracellular nucleotide binding and metabolism, transcription regulator activity, cell growth and maintenance, transport were more active in mycelium. While carbohydrate binding and metabolism, lipid metabolism, signal transduction were more active in fruiting body at both transcriptional and translational level (Yin et al. 2012).

11.4.3 Proteome Sequencing Projects

Cordyceps militaris has two development stages mycelium and fruiting body. Clear view about the differences of two stages mycelium and fruiting body in the proteomes of *C. militaris* was observed. The protein count of mycelium and fruiting body are separated on SDS PAGE gel. The proteins were identified by searching against *C. militaris* genome database using Mascot program after in-gel trypsin-digested peptides were subjected to nESI-LC-MS/MS. This information can be used in identifying or extrapolating proteins related to different development stages in biocontrol fungi. Nearly 261 proteins responsible for mycelium stage, 116 proteins responsible for fruiting body stage, and 98 proteins responsible for both stages were observed during expression. Glycoside hydrolases are among the recognized protein which catalyze the hydrolysis of the glycoside linkage and release smaller sugars and play significant role in biomass degradation by some fungi (Martinez et al. 2008). Heat shock proteins were required for protecting the cells against stress conditions to the maximum in host–pathogen interactions (Largeteau et al. 2010). Enolase, glucose-6-phosphate isomerase, and tansketolase are involved in the processes of sugar metabolism playing a crucial in both the development stages. This information can be used in identifying or extrapolating proteins related to glycoside hydrolases, heat shock proteins, enolase, glucose-6-phosphate isomerase, and tansketolase in other biocontrol fungi.

11.5 Synergism Between Different Biocontrol Agents

The combination of biocontrol agents/organisms work synergistically together for protecting plants from root pest and this is a promising way for successful pest control below ground (Ansari et al. 2008; Jabbour et al. 2011; Ansari and Butt 2013). EPFs combined with pheromone of *Cosmopolites sordidus* (banana root borer) improved *Beauveria bassiana* dissemination and increased root pest infection by the fungus (Tinzaara et al. 2007). The combination of these EPNs and the control agents have proved to be synergistic and produce higher mortality compared to the individual agents (Koppenhofer and Kaya 1997). The synergisms of EPNs and the neonicotinoid insecticide imidacloprid were also reported (Koppenhofer and Kaya 1998; Koppenhofer et al. 2000b; Polavarapu et al. 2007). The synergism of *Dalotia coriaria* (predator) and *M. anisopilae* controlled *Frankliniella occidentalis* (western flower thrips) with significant mortality (>90%) (Saito and Brownbridge 2016). Thus, synergism between different biocontrol agents can improve biocontrol and crop protection.

11.6 Synergism Between Plant Growth Promoting Rhizobacteria and Biocontrol Agents

Synthetic elicitors, plant, and microfauna interactions limited the development of root pests by inducing phytohormonal defense pathways that include Jasmonic Acid (JA), Salicylic Acid (SA), Ethylene (ET), and some other metabolites (Orrell and Bennett 2013). This type of induction is divided into two major categories: Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR). SAR is the SA-dependent process and is induced by treatment with a variety of agents or chemicals (e.g. Acibenzolar-S-methyl, ASM). On the other side, ISR is mediated by ET and JA sensitive pathways that can be induced in plants by the application of a variety of abiotic or biotic agents (Spoel and Dong 2012). These biotic or abiotic agents include strains of Plant Growth Promoting Rhizobacteria (PGPR) (Van Loon et al. 1998). These antagonistic and resistance inducing bacteria can be good candidates for formulating new inoculants for biological control of plant disease (Beneduzi et al. 2012). Thus, synergism between different biocontrol agents like *B. bassiana* (entomopathogenic fungi) and *Trichoderma viride* can improve biocontrol (control pests above ground) and crop protection (ISR can protect below and above ground).

11.7 Advances in Formulation of Biocontrol Agents

Entomopathogenic fungi have great potential for control of insects, soil borne pathogens, weeds, and nematodes. The storage of biocontrol product or formulation at room temperatures is very important. However, more research is still required for isolating new and effective strains for developing biocontrol product or formulation (Wakefield 2006; Kour et al. 2020; Yadav et al. 2018). Future research projects should aim towards integration of various effective formulations of entomopathogenic fungi in managing stored products. But, the use of registered projects of these formulations might face challenges in the real world (Kour et al. 2019a, b). Thus, in order to achieve effective control of these insects, the following research areas should be prioritized (1) screening for the new and effective EPF strains in addition to the formulations, (2) application of most effective formulations and strains in various storage conditions, (3) looking for cheap substrates for growing biocontrol agents (like corn cob residues for growing *Trichoderma viride* (Lalitha et al. 2013), (4) optimizing the ingredients proportion in the formulations, and (5) integration of these products after registration and commercialization in pest management programmes (Yacoub and Batta 2016).

11.8 Understanding Interaction of Fungi with Plants

Understanding interaction of fungi with plants requires the knowledge of colonization of plant by fungi; quorum sensing among fungal biofilms (microbiome); interaction between plants and microbiome; and cross talk between plants and microbiome (Kaur et al. 2020; Kumar et al. 2019; Singh et al. 2020). This section of the chapter elaborates on the above aspects to improve our understanding on interaction of fungi with plants.

11.8.1 Colonization of Plant by Fungal Microbiome

Microbes colonize roots, leaves, and stem of plants at various developmental phases (Yadav et al. 2017). Microbes enter (a) roots of plants via primary root, horizontal roots, root hair, root crack, wounds, and nodules (Baldotto et al. 2011; Huang et al. 2011; Prieto et al. 2011) and (b) leaves via stomata in leaves. Microbes live in symbiosis (mutual association), or as epiphytes (surface of plant parts) or as endophytes ("in ethereal parts of the plant and vascular tissue cortex") *B. bassiana* and *Trichoderma viride* were the known endophytes and understanding the colonization of these fungi is very important. Once the plants are colonized by microbiomes, two possible parallel events occur in the nature. The first event allows microbes to interact among themselves via quorum sensing mechanism and the second event is cross talk between plants and microbiomes.

11.8.2 Quorum Sensing Among Plant Microbiome and Interkingdom Species

Microbes in the microbiome establish a communication process or system known as quorum sensing. N-acyl-homoserine lactones (AHLs), 2-heptyl-3-hydroxy-4-quinoline, and autoinducer-2 are the well-known signalling molecules, which are used by microbes for communication (Challa et al. 2018, 2019b; Challa and Neelapu 2018a; Mohana Sheela et al. 2018; Neelapu et al. 2018). AHLs in *Proteobacteria*, gamma-butyrolactones in *Streptomyces*, cis-11-methyl-2-dodecanoic acid in *Xanthomonas*, and oligopeptides in gram-positive microorganisms act as signalling molecules (Danhorn and Fuqua 2007). The three types of communication systems used by the plant microbiome are intraspecies communication system, interspecies communication systems, and interkingdom communication system; as the microbiome is made up of multiple microbial species in the plant habitat (Mohana Sheela et al. 2018). Intraspecies communication system enables effective communication among the same species of microbes in the microbiome. This allows detecting cell densities of the same species of microbes in the microbiome, to synchronize and control several cellular and physiological processes (Mohana Sheela et al. 2018). Interspecies communication system enables effective communication between different species of microbes in the microbiome. This allows detecting cell densities of different species of microbes in the microbiome to control global gene expression in the microbiome (Mohana Sheela et al. 2018). Interkingdom communication system enables effective communication between different species (bacteria and fungi) of microbes in the microbiome, and also between microbiome and the plant (Mohana Sheela et al. 2018). The best known example for interkingdom communication is between *Agrobacterium* and plant (Neelapu et al. 2018). Both interspecies and intraspecies communication help in horizontal gene transfer of genetic material from the donor to the host leading to evolution in nature. The ultimate use of quorum sensing in plant–microbiome interactions is to sense the surrounding environment and adjust to changing ecological conditions by enhancing supplement uptake or other means which are described above and below. Though we can understand that these three different mechanisms of quorum sensing exist in the nature when microbes colonize plant, still there is need to establish the evidence in favor of these communication systems.

11.8.3 Interaction Between Plants and Fungal Microbiome

Pathogen Associated Molecular Patterns (PAMPs) or Microbe Associated Molecular Patterns (MAMPs), are the molecular patterns on microbes and these patterns are recognized or detected by plants. These patterns can either be located on cell surface or located within the cell. The well-known PAMPs or MAMPs are bacterial flagellin, Ef-TU proteins, intracellular effector proteins, lipopolysaccharides, peptidoglycans, or tissue damage (Allen et al. 2004; Rivas and Thomas 2005; Boller and Felix 2009). These PAMPs or MAMPs are recognized by pattern recognition receptor (PRR) of plants (Allen et al. 2004; Rivas and Thomas 2005; Boller and Felix, 2009) and thereby activate plant immune system.

11.8.4 Plants Immune System

The plant immune system comprises of four levels (Jalil and Ansari 2018). In level 1, PAMPs of microbes are recognized and bind to specific PRRs located on the cell surface that triggers the plant immune system and leads to enhanced immunity (PTI), which prevents colonization and proliferation (Boller and Felix 2009; Tör et al. 2009; Bakker et al. 2012; Newman et al. 2013). In level 2, several pathogens induced effectors enhance virulence. The effectors hinder with PTI and lead to effector-triggered susceptibility. In level 3, nucleotide-binding leucine rich repeat receptor proteins recognize the effector, which activate the effector-triggered immunity (ETI) that leads to disease resistance. In level 4, natural selection has motivated pathogens to conquer ETI by emerging effectors promoting virulence until plants have developed new receptors (Jalil and Ansari 2018).

11.8.5 Cross Talk Between Plants and Microbiomes

Apart from interaction between fungal microbiome and plants, there are several cross talks between plants and other microbes during their interaction using different signalling molecules. Various microbes are harmful to plants that limit growth and development. In general, plant root exudates comprising of sugars, amino acids, and organic acids attract the microbes. Plants have mechanism to recognize certain compounds released by microbes and enhance defense responses. During plant–microbe interaction, once the plant recognizes microbe; plant signalling hormones, such as salicylic acid, jasmonic acid, and ET activate the defense machinery in response to salt stresses (Koornneef and Pieterse 2008; Yi et al. 2014; Jalil and Ansari 2018). In case of fungi–plant interactions, sugar levels are increased during fungi–plant interactions where sugars molecules act as priming molecules and are sensed by plant cell and act as a signalling molecule. This subsequently interacts with plant hormone signalling network thereby reprogramming the plant cells (Morkunas and Ratajczak 2014). When fungi are in the proximity of a plant cell, then sugar levels are increased which are important for providing energy and structural material for plants defense processes. Sugar priming increases oxidative burst, cell walls (lignification), flavonoids synthesis; and also induces pathogenesis related proteins. This induces plant immune system and also provides resistance to plants against fungi (if it is a pathogen) (Morkunas and Ratajczak 2014).

11.9 Conclusion and Future Directions

Fungi mediate biocontrol of insects, soil borne pathogens, weeds, and nematodes. The fungal biocontrol agents used to control insects are *Beauveria*, *Culicinomyces*, *Hirsutella*, *Metarhizium*, *Nomuraea*, *Paecilomyces*, *Tolypocladium,* and *Verticillium*. The fungal biocontrol agents which are used to control weeds are *Trichoderma* and *Gliocladium*. The fungal biocontrol agents used to control weed are *Colletotrichum gloeosporioides* f.sp. *Sclerotinia minor*. Fungal species such as *Arthrobotrys*, *Verticillium chlamydosporium*, *Acremonium*, *Fusarium oxysporum*, and *Dactylella oviparasitica* are used to control nematodes. The different mechanisms used by fungi for biocontrol are antagonism, antibiosis, and competition. In order to fullfill some of our knowledge gaps on fungi it is essential to continually explore fungal whole genomes. There are five next generation sequencing technologies available to generate NGS data: first, second, third, fourth, and fifth generation sequencing technologies. The first generation sequencing technologies include Sanger sequencing and Maxam–Gilbert sequencing method. The second generation sequencing method includes Roche/454 sequencing, Ion torrent sequencing, Illumina/Solexa sequencing, and ABI/SOLiD sequencing. The third generation sequencing method includes Single Molecule Real Time (SMRT) sequencing approach and Oxford Nanopore Technology (ONT) sequencing approach. The fourth generation sequencing method includes nanopore based sequencing by biological nanopores and solid state nanopores. The fifth generation sequencing method includes high-fidelity nanopore sequencing of ultra-short DNA targets and cyclomics and ultra-sensitive nanopore sequencing of cell free tumor DNA. Better understanding of fungal genomes has truly opened another door to improving our utilization and reservation for fungi despite of several bioinformatics challenges regarding sequence assembly, gene annotation, and genome comparison. The growth in number of genome, transcriptome, and proteome data from fungi has created additional opportunity to evaluate, compare, and formulate an optimal product. The other global research areas in the biocontrol are synergies between different biocontrol agents, synergies between biocontrol agents and PGPR, and advances in the formulation of biocontrol agents.

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Chapter 12

Functional Annotation of Agriculturally Important Fungi for Crop Protection: Current Research and Future Challenges

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

Contents

This book contains current knowledge about functional annotation of agriculturally important fungi for crop protection. The communities of fungi associated with plant as well as different ecosystems play important role in the protection and growth of plant through different plant growth promoting mechanisms. The beneficial plant growth promoting fungal communities may be utilized as microbial bioresources for agricultural sustainability in eco-friendly manners. The book covers the current knowledge of agriculturally important fungi (AIF) and their biotechnological applications for crop protection. The book will be highly useful to the faculty, researchers, and students associated with microbiology, biotechnology, agriculture, molecular biology, environmental biology, and related subjects.

The rapid increase in the global population is becoming a widespread and expected to grow around 8 billion people by 2020 (Scherbov et al. 2011). Feeding this gigantic population with limitations of the resources is a foremost challenge for the global community. During green revolution high yielding varieties and excessive use of agrochemicals undoubtedly increased the production of food simultaneously leading to gradual loss of natural soil microbiota and the fertility of soil

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(Tewari et al. 2019). Further, pathogenic microbes greatly affect the health of plant and have become a major threat to production of food and also ecosystem stability. To combat with pathogens, the pesticides use has become more reliable method for protecting crops. The unabated pesticides use led to numerous negative effects such as the development of resistance against pathogen and also their non-environmental impacts (Gerhardson 2002). Despite adopting different strategies, plant pathogens still account for more than 15% losses in the global harvest and fungal pathogens lead to about 30% reduction of the crop yield (Shaikh and Sayyed 2015b).

Sustainable farming systems endeavor to minimize the pesticides exercise by optimizing the use of alternative strategies to deal with plant pathogens (Yadav et al. 2020d). Biocontrol using antagonistic fungal communities is an effectual, environment friendly, and cost effective approach to chemical pesticides. Plant associated fungi are efficient competitors and can establish and persist on diverse crop plants (Yadav et al. 2019a, b, 2020a). These microbiomes avail number of services such as uptake of minerals, absorption of water, and decomposition of organic matter (Ansari et al. 2013; Das et al. 2012; Yadav et al. 2017). Fungi may also bind physically to few other fungi and do not allow the destructive fungi to colonize the area of root and are useful as biocontrol agents (Singh and Yadav 2020). The research on mechanisms of plant growth promoting microbiomes has provided a greater understanding of diverse features of disease suppression by these biocontrol agents (Compant et al. 2005). Revelations about the mechanisms of action open new doors for designing strategies to improve the efficiency of biocontrol agents (Morrissey et al. 2002). Further, it will also facilitate different strains combinations to hit pathogens with a broader spectrum of microbial weapons (Lutz et al. 2004).

Pest and plant pathogens (bacteria, fungi, viruses) affecting the crop are the major threat to agriculture. In order to attain the high yielding and healthy crops, the foremost factor is to control the pest and different diseases. Most of the farmers around the globe are dependent upon chemical based pesticides to control the pest and pathogens. However use of chemical based pesticides without recommended and dose safety norms has caused some severe health issues to humans as well as other organisms and these chemicals also affect the environment (Damalas 2009). In recent years, the increased awareness about the adverse pesticides effects has changed the market and now the peoples are more inclined towards the biopesticides. Currently, 90% of the microbial biopesticides are available in market and comprises about $3 billion to total market of crop protection (Marrone 2014). Fungi are one of the microbial agents that plays crucial role in agriculture as this organism can be used as a biofertilizers as well as biopesticide (Yadav et al. 2019b). Various fungi have been reported that inhibit the growth of pest and other agricultural microorganisms like *Cladosporium cladosporioides* (Paul and Park 2013), *Trichoderma asperellum* (El_Komy et al. 2015), *T. harzianum* (Sala et al. 2020), *T. lignorum* (Mostafa et al. 2012), *T. virens* (Christopher et al. 2010), *T. viride* (John et al. 2010), *Beauveria Bassiana* (Mahmood et al. 2019), *Nomuraea rileyi* (Perinotto et al. 2012), *Metarhizium anisopliae* (Howard et al. 2010), *Verticillium lecanii* (Aqueel and Leather 2013), *Paecilomyces lilacinus* (Lopez et al. 2014). Fungi as a biocontrol agent are widely used and also their products are commercially available in markets. The fungus *Beauveria bassiana* is one that has been commercialized under several trade names like Mycotrol® (Mycotech), Organiguard® (Emerald BioAgriculture). Also, another species of *Beauveria* that is *Beauveria brongniarti* is commercialized under the trade name of Betel® (NPP now Arysta Life Science) (Regnault-Roger 2012).

Siderophore is low molecular weight organic compound which produces by several bacteria and fungi. This compound helps in chelation of iron which is one of the important micronutrients for plants. Siderophores play a major role in the enhancement in growth of plant and also control the certain biological organisms (Yadav et al. 2018, 2020b, c). This mechanism facilitates the killing of phytopathogens by reducing the availability of iron as siderophores binding tightly with iron which is present in soil (Ahmed and Holmström 2014). Very few reports are available on fungi that helps in pathogen biocontrol by producing siderophores. In a study, *Trichoderma* species were reported for producing siderophores and stimulating the growth as well as protecting bean from phytopathogenic fungi (Hoyos-Carvajal et al. 2009). In another report, *Trichoderma* sp. and *T. harzianum* were producing siderophores and protecting chickpea (*Cicer arietinum* L.) crop from two phytopathogens, namely *Sclerotium rolfsii* and *Rhizoctonia solani* (Rawat and Tewari 2011). In a study, another species *Trichoderma* named *Trichoderma asperellum* was reported for producing siderophores and were protecting tomato crop from *Fusarium oxysporum* f.sp. *lycopersici* that was causing *Fusarium* wilt disease (Segarra et al. 2010). In a study also, *Trichoderma asperellum* was reported for producing siderophores and helping the growth of cucumber seedling (Qi and Zhao 2013). One more study was conducted and found that *Trichoderma virens* was producing siderophores (Babu et al. 2014). In another report, *Aspergillus* spp. and *A. parasiticus* were reported for producing siderophores and enhancing the growth of mung bean (Patel et al. 2017).

Several chemical compounds are produced by the fungi which benefits in the plant growth. Among which hydrogen cyanide (HCN) is one such compound that helps in biocontrolling of certain plant pathogens (Rastegari et al. 2020a, b). There are very limited reports available of fungi that are producing HCN. In a report, *Trichoderma* spp. obtained from rice rhizosphere were reported for producing HCN and this strain was showing antagonist activity against bakanae disease pathogen named *Fusarium fujikuroi* (Ng et al. 2015). In another report, also different strain of *Trichoderma* spp. was reported for HCN production and protecting chickpea plant from chickpea wilt complex (Rawat and Tewari 2011).

In 1928 Alexander Fleming invented the first medically useful antibiotics as a result of the fungus *Penicillium notatum*. Antibiotics have been used since 1950s to control several diseases caused by bacteria. Today, streptomycin and oxytetracycline are the most commonly used antibiotics on plants. In the USA, plant based antibiotics account for less than 0.5% of overall antibiotics use. Although there are a huge amount of species of fungi, only a comparative some have been found to produce antibiotics, and only seven antibiotics are commercially produced. Antibiotics are the most significant of all microbial products manufactured commercially. Thousands of antibiotics are manufactured commercially using microbial fermentation. The first antibiotics discovered in history were used to cure diseases, but nowadays more antibiotics are utilized for therapeutic applications. Antibiotics, being the most studied secondary metabolites in history, possess many valuable pharmacological properties in the medical field (Hassan et al. 2012). This study goal is therefore to present a review on antibiotics that includes the description of antibiotics, classification, and mode of action, uses, antibiotics resistance, side effects, and type of antibiotics, metabolism, and method of determining an antibiotic.

Worldwide, fungi produce lots of antibiotics that are widely used as drugs which have antibacterial and antifungal activity, especially drugs of penicillin, fusidic acid, and cephalosporin (Al-Enazi et al. 2018). Novel antibacterial, anticancer, antifungal, anti-inflammatory, antimalarial, and antiviral compound have been reportedly developed by fungal endophytes (Rana et al. 2019a, b, c). Al-Daamy et al. (2018) had been screened the filtrates of fungi like as *Trichoderma* sp., *Penicillium notatum*, *Cladosporium* sp., *Bacillomyces* sp., *Aspergillus niger*, *Aspergillus ochraceus*, *Aspergillus flavus* for its antimicrobial activity against *Streptococcus agalactiae, Staphylococcus* sp., *Pseudomonas* sp., *Klebsiella* sp., *Enterobacter* sp., and *Bacillus* sp., through the disc technique. In this study *Bacillus* sp. was found to be the most susceptible. *Trichoderma viride* has been tested as an anticancer, antioxidant, and antimicrobial agent isolated from rhizospheric soil (Awad et al. 2018).

Only fewer plant diseases are caused by bacteria and phytoplasmas are recently treated with antibiotics; therefore, development of mostly crops would be unaffected. A minority of all hectares are treated even for crop such as pear, peach, and apple to which the mass of plant grade streptomycin and oxytetracycline are applied (McManus et al. 2002) until recently, antibiotics use on plant has largely gone unnoticed by those outside the plant farming community. However, the alarming rise in humans antibiotic resistant bacteria pathogen and effort to conserve the efficacy of antibiotics in human medicine have drawn attention to the use of non-medicinal antibiotics. De Siqueira et al. (2011) reported *Alternaria alternata* from *Lippia sidoides* that showed antimicrobial activity. Another investigation of (Zhang et al. 2008) reported *Aspergillus sydowii* showing cytotoxic activity. Donald et al. (2005) observed *Aspergillus flavus* and *Fusarium verticillioides* from maize that produced mycotoxins and showed antifungal activity. Another fungus reported *Trichoderma brevicompactum* from garlic showed antifungal activity against *Rhizoctonia solani* (Shentu et al. 2014). We have finally envisioned a future without antibiotics. There are some new fire blight products for apples and pears that significantly decreases the quantity of antibiotics applied in farming. Nevertheless, from a practical perception, antibiotics appliance remnants the mainly successful and commercial method for controlling fire blight, the major antibiotic-targeted plant disease.

Hydrolytic enzyme is a type of enzyme that catalyzes the transition from the substratum molecules to the acceptor water molecule of the specified chemical molecules. In some cases, hydroxyl compound can be active as other acceptors. These enzymes are produced by rhizospheric microbes that inhibit the phytopathogens growth through hydrolyzing their cell wall, DNA, and protein (Jadhav and Sayyed 2016). Their hydrolytic enzyme producing fungi plays significant and sustainable function in controlling under phytopathogens versus chemical fungicides. The large amount of microbes that have potential to control pathogens have been found (Kour et al. 2020; Verma et al. 2016; Yadav et al. 2016). In a report, oxygenic photosynthetic prokaryotes were first time reported on the production of hydrolytic enzymes, which may be potential candidates for the improvement of biocontrol beside selected phytopathogenic fungi (Prasanna et al. 2008). The application of producing hydrolytic enzyme by rhizospheric microbes is an eco-friendly resolution to this problem, as they are completely natural and eco-friendly (Kour et al. 2019). Recently hydrolytic enzymes have demonstrated their capability to control pathogens in plants (Shaikh and Sayyed 2015a; Shaikh et al. 2016).

Hydrolytic enzyme such as chitinase, cellulose, glucanase, hemicellulose, and protease can be degraded the fungus cell wall and caused cell lysis of fungal pathogens. Phytopathogens biocontrol using rhizospheric microbes involves the hydrolytic enzymes development which degraded the cell wall (Verma et al. 2019; Yadav 2019; Yadav and Yadav 2018). There are many rhizobia that are capable to synthesize extracellular enzymes which have been hydrolyzed some variety of polymeric compounds like as chitin, cellulose, proteins, hemicelluloses, and DNA of phytopathogens (Kobayashi et al. 2002). Chitinase lyses the fungal cell wall by degrading the chitin polymer present in the cell wall of fungal phytopathogen. Enzymes can be used straightly on the phytopathogens, and indirectly used purified chitinase proteins, or by controlling the chitinase coding genes (Kim et al. 2003). Chitinase degradation has been involved incremental splitting of chitin polymer into monomer, spontaneous cleavage at internal chitin microfibril sites, or progressive release of diacetylchitobiose without releasing monosaccharides or oligosaccharides.

The commercially hydrolytic enzyme production is done by solid state fermentation in *Aspergillus awamori*, *Sporotrichum thermophile*. Exogenous hydrolytic enzymes help in the breakdown of complex cell wall polymers into sugar which may then be fermented and convert into ethanol (Willis et al. 2016). It has long been believed that engineered feedstock processing of cell wall degradation enzyme could be an effective medium for exogenous hydrolytic enzymes development. The genus *Trichoderma* is a much known biocontrol agent, that controls numerous phytopathogenic fungi and substantial production of hydrolytic enzymes is a parameter for its success. Couri et al. (2000) have been reported fungi *Aspergillus niger* that produces hydrolytic enzymes in solid state fermentation. dos Reis Almeida et al. (2007) have been reported several *Trichoderma harzianum* species that are used as a biological control agent, various phytopathogenic fungi like as *Rhizoctonia solani* have evaluated for coiling and hydrolytic enzyme production. Another investigation Bala and Singh (2016) reported *Sporotrichum thermophile* that produces xylanase enzymes. Botella et al. (2005) have reported *Aspergillus awamori* that produces hydrolytic enzymes.

Tang et al. (2008) induced ectomycorrhizal fungi hydrolytic enzymes against *Rhizoctonia solani* pathogen. In another investigation by Urquhart and Punja (2002) it have been isolated five species of yeast like fungus *Tilletiopsis* Derx (*Tilletiopsis fulvescens* Gokhale, *Tilletiopsis pallescens* Gokhale, *Tilletiopsis washingtonensis* Nyland, *Tilletiopsis minor* Nyland, *Tilletiopsis albescens* Gokhale) that produce antifungal compound and hydrolytic enzyme which are antagonists of fungi that causes powdery mildew disease. El-Shishtawy et al. (2015) have reported *Trichoderma virens* under solid state fermentation condition that was produced hydrolytic enzyme of alkali pre-treated carboxymethyl cellulase (CMCase), filter paperase (FPase), pectinase (PGase), and xylanase (Xylase). In a reported fungi *F. proliferatum* and *Fusarium verticillioides* produce hydrolytic enzyme, N-acetyl-b-glucosaminidase, b-d-glucosidase, and a-d-galactosidase (Reynoso et al. 2002). In overall study data information presented that new biocontrol strategies can be used to effectively control pest in agriculture using the cuticle degrading enzymes complex of entomopathogenic fungi.

Fungi no doubt are one of the appropriate substitutes for pesticides for improving the performance of crop particularly as biocontrol agents but still there are certain issues which have to be resolved like success or failure of commercial product (Owen et al. 2015). The commercial product must fulfill the requirements of farmers such as the repeated positive results, easy handling, and reasonable price and prolong product shelf-life (Murphy et al. 2018). Adding more, biocontrol agent with microbial inoculants and/or microbial secondary metabolites has specific problems of viability loss and reduced product effectiveness against pest or pathogen during storage (Vurukonda et al. 2018). Though a numeral of studies have been done for the investigation of efficient fungi as biocontrol agents but most of them are restricted to controlled conditions. Thus, field trials and complete data analysis will open doors for reliable biocontrol agents that are compatible with the crop and environment. Otherwise, lack of understanding regarding the biocontrol utilization methods may end up with reduced confidence for usage and demand in the product (De Silva et al. 2019). Finally, the awareness among the farmers about the efficient use of products is very important.

Studies clearly indicate that fungi have a potential as biocontrol agents and a tremendous progress has been made over past few years. The biological control agent application in agriculture for management of plant diseases is in fact gaining greater attention. Further, research is essential for their commercialization that will not only minimize the economic costs but will also maintain the ecosystem stability. This can easily be achieved through ecological dynamics, metagenomics, and statistical advances. Thus, in future, screening and selection of efficient bioagents with dual activities of biocontrol and plant growth promotion will be very beneficial for achieving sustainability in agriculture.

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Index

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