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Tarek A. A. Moussa *Editors*

Plant Mycobiome

Diversity, Interactions and Uses

Springer

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We dedicate this book to our families, friends, and colleagues. The editors would like to express their sincere gratitude to all authors, contributors, and the Springer team. We appreciate the time and effort they have put into this book. We also dedicate this book to all scientists who spend their life serving science, especially those who have worked on fungi all over the world.

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January 2023

Preface

Plant mycobiome represents a diverse array of plant-associated communities of endophytic and epiphytic fungi. These communities fundamentally affect plant health, development, adaptation, and communication with the surrounding ecosystem. Furthermore, they have key roles in the establishment, diversification, productivity, and sustainability of different natural ecosystems. However, some of these plant mycobiome are pathogenic for the plant itself or dangerous for the consumers, due to the production of toxins. In other words, plant mycobiome represents two faces of a coin. This book aims to explore contributions of plant mycobiome in plant-environment interactions from different perspectives. Chapters of this book address numerous themes covering the recent advances in the field of roles, diversity, and dynamics of plant mycobiome as biocontrol agents, biofertilizers, growth promoters, and their secondary metabolites in the area of sustainable crop improvement and biotechnology, as well as the plant pathogenic and toxigenic fungi. This book will be useful to postgraduate students, botanists, mycologists, ecologists, plant pathologists, and physiologists.

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New Damietta, Egypt — Zakaria A. M. Baka

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January 2023

Introduction

Plant microbiome is a huge community of microbes that live near or on plants, or colonize their tissues. The plant microbiome, which consists of all microbial genomes, can enhance the plant's genomic and metabolic capabilities enabling a number of crucial functions such as nutrient uptake, immunological regulation, and stress tolerance. These varied species that make up the plant microbiota can spread horizontally through the environment or vertically through the seeds. Numerous studies have recently focused on the makeup, dynamics, and usefulness of the bacterial components involved in the plant microbiome. Understanding other plant microbiome components, such as fungi, as well as archaea, protists, and viruses, is, however, far less developed. Although the potential biotechnological uses of fungi in the industry have long been recognized, research on the microbiome typically overlooks the importance of the microbial communities that live in the soil and on plants, known as mycobiota. Because of technical problems resulting from the phenotypic/genotypic diversity of the mycobiota, our comprehension of it lags considerably behind that of the bacteriota.

Plant mycobiome is one of the most important topics for ecological management and sustainable agriculture in the twenty-first century. Through the cycling of organic matter and the distribution of nutrients across the trophic levels, a plant-associated fungal community significantly contributes to the preservation of ecological fitness. Numerous studies have emphasized the importance of plant mycobiome research for improved disease control, best ecological practices, and the adoption of eco-friendly crop production techniques. High-throughput sequencing techniques reveal fungal variety, functionality, and relationships with other microbiome creatures and plants that enhance our understanding of the significance of fungi to plants. By enhancing plant nutrition, stress tolerance, and defense, endophytic and epiphytic fungi can dramatically boost plant resilience. The significance of the plant mycobiome within the plant microbiome has been underestimated, even though some of these interactions have been recognized for decades. The creation of the best biotechnological applications in agro-systems and natural environments has been hampered by our inadequate understanding of fungal biology and its interactions with plants in the context of the broader phytobiome.

The three main compartments that house the plant mycobiota are the rhizosphere, phyllosphere, and endosphere. The composition of mycobiota assemblages varies depending on the plant compartment and is influenced by several variables, including plant genotype, biogeography, environmental conditions, nutrition availability, and interactions with other microbiota species. In this book, the editors and authors tried to take an overview of the plant mycobiome, covering all subjects related to it.

Younes M. Rashad

Zakaria A. M. Baka

Tarek A. A. Moussa

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Mycotoxins and Their Producers: Diversity, Side Effects and Control

Younes M. Rashad, Zakaria A. M. Baka, and Tarek A. A. Moussa

1 Introduction

Mycotoxins can be defined as natural, poisonous, low molecular weight secondary metabolites which are synthesized by a group of filamentous fungi (molds), mainly species of the genera *Aspergillus, Penicillium, Fusarium,* and *Alternaria* which can infect crops in the field (pre-harvest), in the store (post-harvest), and/or in any processing stages (Shabana et al. 2021). However, a mycotoxin may be synthesized by many fungal species, and one fungus may produce more than one type of mycotoxines (Palumbo et al. 2020). In contrary, not all fungi are toxigenic and not all toxins can be considered a mycotoxin, for example, antibiotics such as cephalosporins and griseofulvin which produced by fungi are toxic to bacteria but not considered as mycotoxins. Until now, over four hundred mycotoxins have been reported such as aflatoxins, ochratoxins, zearalenone, fumonisins, trichothecenes, and patulin. These poisonous metabolites have deleterious effects on human and livestock health causing acute or chronic mycotoxicosis, oncogenesis, mutagenesis, hepatotoxicity, nephrotoxicity, immunosuppression, or embryotoxicity (Pietsch 2020; Kyei et al. 2020). Mycotoxins can occur in our food via products derived from originally infected plants (field or post-harvest infection) or by contamination of food products such as grain-based foods, dairy products, legumes, flour, oilseeds, or fruits due

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to growth of mycotoxigenic fungi at any stage of production, transportation, or storage. In addition, mycotoxins may be indirectly transferred to humans through consumption of animal-derived products such as eggs, meats and dairy products which derived from animals that fed with mycotoxines-contaminated feed (Kępińska-Pacelik and Biel 2021). Based on reports of Food and Agriculture Organization (FAO), more than 25% of the global crops are affected by different mycotoxins (Eskola et al. 2020). However, their type and extent of production vary based on the climatic variables in the field. Various factors can regulate their production such as temperature, wind, humidity (Shabana et al. 2022), agricultural practices, susceptibility of the plant/fruit in the field or under storage conditions, penetrability of the processed food products, fungicides/preservatives application, distribution, density, type of fungal species, genetic ability of the fungal isolate for mycotoxins accumulation, dissemination rate of the fungal spores, and storage conditions of the food products such as aeration and duration (Vogelgsang et al. 2019). However, mycotoxines may be found singly or in co-occurrence (more than one type). Co-occurrence of mycotoxines is a frequent phenomenon which can be explained on the basis of the ability of some toxigenic fungi to produce more than one type, contamination of the food/feed with more than one kind of toxigenic fungi at any production or processing stages, or mixing of multiple raw ingredient in preparing composite feed which results in different mycotoxines combinations (Pinotti et al. 2016).

Different and variable techniques have been developed for quantitative and qualitative detection of mycotoxines including chromatographic techniques such as HPLC, TLC, GC, ELISA, and biosensor-based techniques. However, detection of mycotoxines is limited by many factors such as sensitivity of the analytical method especially at low concentrations of mycotoxines so that in food industry, prevention of contamination with mycotoxines is more favorable than their detoxification (Bueno et al. 2015). Annually, high percentages of the harvested crops have been contaminated with mycotoxigenic fungi causing high economic losses in the agricultural and food industrial sectors. For example, United States of America (USA) has yearly lost up two billions of dollars in maize industry due to contamination by mycotoxins (Mitchell et al. 2016). In this chapter, diversity and occurrence of mycotoxins, their side effects, producing fungi, as well as their control measures in foodstuffs will be highlighted.

2 Economic Importance of Mycotoxins

Every year, the global agricultural and health sectors have incurred high economic losses due to mycotoxins. Economic influences of mycotoxins can be investigated according to two vital aspects; (i) market costs due to crop losses, trade losses, or income losses of contaminated food commodities, and (ii) health impacts on humans and animals due to consumption of mycotoxin-contaminated food.

2.1 Market Losses

Every year, considerable market losses are incurred due to contamination of foodstuffs with mycotoxins worldwide, specially cereals, coffee, peanut and nut crops. Data illustrated in Fig. 1 indicates the estimated global annual quantities of major food grains subjected to contamination with mycotoxins.

Mycotoxins-contaminated foodstuffs are subjected to rejection or at least sold at reduced prices for else use due to their lowered value. The economic losses can be occurred at various trade levels such as reduction in the crop yield quantity or value, monitoring and control costs, grain elevators costs (assessment and management), livestock losses, exportation market losses, and crop insurance costs (Mitchell et al. 2016). According to the Food and Drug Administration (FDA), USA annually have incurred economic losses up to 1.7 billion dollars due to contamination of maize, wheat, and peanut grains with aflatoxins, fumonisins, and deoxynivalenol, while the annually incurred losses in livestock and poultry due to mycotoxins are estimated to be around 6 million dollars (Villafana et al. 2019). In addition, about 0.5 billion dollars are also costed for management of mycotoxin contamination in USA. While, in the developing countries, little data about the economic losses due to mycotoxins are available.

One of the economic loss components due to mycotoxins is the lowered crop value, either in local or export market, due to elevated concentration of mycotoxins in the produced grains even if they appear healthy. In some cases, contamination with mycotoxins may lead to sever reduction in the grain quality and result in a bad appearance. In this regard, various crop producers have lost their deals with buyers due to elevated mycotoxins levels in their commodities over the regulatory limits. In other situations, they have been obligated to accept reduced prices for their commodities. In the developing countries, they may be enforced to export their best quality foodstuffs and keep the lowest quality foods for local use.

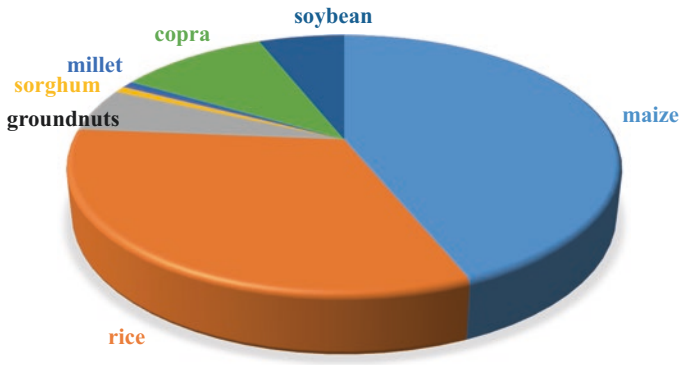

Fig. 1 Global annual estimation of mycotoxins-affected food grains

2.2 Health Influences of Mycotoxins on Humans and Animals

According to World Health Organization (WHO), impacts of intake of mycotoxins-contaminated food include some acute illness which rapidly appears or chronic (long-term influences) such as oncogenesis and immunosuppression. In general, ingestion of the mycotoxin-contaminated foods may cause mycotoxicosis, oncogenesis, mutagenesis, hepatotoxicity, nephrotoxicity, immunosuppression, or embryotoxicity. Risks to humans vary from one person to another according to different factors such as ingestion dose, duration, mycotoxin type, and immunity of the person ranging from catching allergies, in case of non-immune people, to sever cancer and finally death. However, human health impacts are not easy to be quantified.

Contamination of food commodities with mycotoxins is more common in developing countries where application of the regulatory limits is infrequent. Avoiding food contamination is a function of setting up of regulatory standers and their implementation. In a recent study conducted in Kenya, the authors reported 84% contamination with aflatoxin in Kenyan wheat, in addition, 50% of the baby food samples were found to have high failure rates, based on the European Union (EU) regulatory limits. The study ended to a conclusion that the Kenyan humans and livestock are severely subjected to mycotoxin hazards and in extremely need to apply high quality monitoring and enforcement of strict regulatory standards (Kibugu et al. 2019).

Since the earliest reported toxicosis disaster in Britain in 1960s, where more than 100 thousands of turkeys died (Blount 1961), an elevated attention has been attracted in mycotoxicosis and their effects on animal production. Mycotoxins may influence animals health either singly or additively, in case of contamination of more than one type of mycotoxins, affecting their liver, immunity, fertility, or gastrointestinal tract leading to dangerous diseases and reductions in their productivity (Mavrommatis et al. 2021). Several symptoms have appeared on animals as a result to the mycotoxicosis including reduction in feeding (appetite), decrease in growth and performance, sick appearance, absence of response to antibiotics, convulsion, paralysis, gangrene, spasms, hyperthermal fever, abortion, reduced fertility, diarrhea, and mouth blistering (Table 1).

On the other hand, poultry and their derived products such as meat, egg and their processed products represent a great importance in the food chain and poultry industry. Hence, a considerable attention has been received and directed to the risk of contamination of their feed with dangerous mycotoxins due to the deleterious health effects they inflect. However, toxicity degree may vary depending on various factors such as the dosage and period of mycotoxin intake, susceptibility, animal sex, age, immunity, as well as other environmental factors (Murugesan et al. 2015).

Table 1 Deleterious effects of mycotoxins-contaminated feed in cattle

Target organ	Mycotoxins	Adverse effect
Liver	AFB, FUM	Liver cancer
		Increased liver weight
		Liver lesions
		Hepatocellular injuries
Kidney	AFB, FUM	Increased kidney weight
		Kidney lesions
Gastrointestinal tract	AFB, DON, T-2, HT-2, OTA, Ergots	Gastroenteritis
		Gastrointestinal lesions
		Intestinal hemorrhages
		Impaired rumen function
		Decreased rumen motility
		Shifts in rumen pH and fatty acids production
		Decreased dry matter digestibility
		Decreased in crude protein and fiber digestibility
		Diarrhea
		Ketosis
Reproduction system	AFB, ZEN, T-2, HT-2, Ergots	Irregular heats
		Low conception rates
		Decreased milk production
		Ovarian cysts
		Embryonic loss
		Abortions
		Early development of mammary gland
		Low testicular development
		Low sperm production
		Low semen quality
Common complications	AFB, Don, T-2, HT-2, Ergots, OTA	Impaired thermoregulation
		Convulsions and neurological signs
		Mastitis and laminitis
		Decreased milk production
		Residues in milk
		Immunosuppression
		Hematological alterations
		Growth inhibition

3 The Major Families of Mycotoxins

3.1 Aflatoxins

It is the first known family of mycotoxines, and is considered one of the most poisonous families which is produced mainly by *A. flavus*, *A. parasiticus* and *A. nomius.* The family name is composed of three parts "A" which derived from the genus

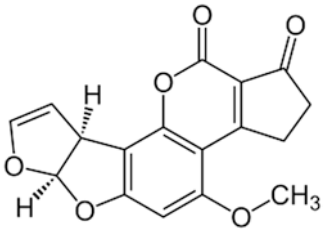

Fig. 2 Chemical structure of aflatoxin B1

Aspergillus, "fla" which derived from the species *flavus*, and toxin which means poison (Kumar et al. 2017). In 1960s, about 100,000 domestic turkeys died in England due to "turkey X disease" and after 2 years the causative agent was recognized and named "aflatoxin" (Blount 1961). Up to date, at least 20 members have been identified in this family, among them, the main members are B1, B2, G1, and G2, in addition to M1 and M2 which are hydroxylated forms of B1 and B2, while the most toxic one is B1 (Nazhand et al. 2020).

The chemical structure of aflatoxin B1 is illustrated in Fig. 2. The most foodstuffs usually contaminated with aflatoxins B1, B2, G1, and G2 are cereals such as wheat, maize, sorghum and rice, oilseeds such as cotton, sunflower, soybean, peanut, spices such as ginger, black pepper and turmeric, and eggs, milk and dairy products, while aflatoxins M1 and M2 are found in ruminant milk and milk products as a result of consuming feed which contaminated with aflatoxins B1 and B2 (Martinez-Miranda et al. 2019).

This family of mycotoxines is highly toxic, which mainly affecting the liver and causing hepatocellular carcinoma, mutagenesis, immunosuppression, and aflatoxicosis. In this concern, the International Agency of Research on Cancer (IARC) has classified aflatoxin B1 in group 1 carcinogen, while aflatoxin M1, hydroxylated form of B1, has been listed in group 2B (Ostry et al. 2017). Owing to their extreme toxicity, aflatoxins are the only group among all mycotoxins that have been closely regulated by the FDA action levels, while the other groups are controlled to advisory levels. The US regulatory limit for aflatoxins B1, B2, G1, and G2 in food products is 20 μg/kg for total and 0.5 μg/kg for M1, while the EU limits are 2–12 μg/kg for B1 and 4–15 μg/kg for total (B1, B2, G1, and G2), 0.05 μg/kg for M1 in milk and 0.025 μg/kg in infant milk (Alshannaq and Yu 2017).

3.2 Ochratoxins

This family is one of the most common mycotoxins in foodstuffs which is produced by different members of the genera *Aspergillus* and *Penicillium*, particularly *A. ochraceus,* from which the family name was derived, *A. carbonarius* and *P. verrucosum* (Alshannaq and Yu 2017). The most important member in this family is

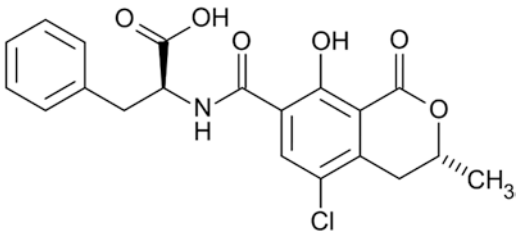

Fig. 3 Chemical structure of ochratoxin A

ochratoxin A which was first discovered in South Africa in 1965 from corn meal contaminated with *A. ochraceus* (Leitão 2019). Ochratoxins can contaminate several foodstuffs such as cereals, coffee, flour, red pepper, beans, wine, grape juice, in addition, they may be found in animal-derived products such as milk, cheese and meat (Malir et al. 2016; Palumbo et al. 2020).

Ochratoxin A has high stability against acidity and heat, so that it is very difficult to be eliminated from the contaminant food by cooking. The chemical structure of ochratoxin A is illustrated in Fig. 3. Ochratoxin A has intense nephrotoxicity, hepatotoxicity, neurotoxicity, and embryotoxicity. It has been listed by IARC in group 2B. The mode of action of ochratoxin A toxicity is by interfering with phenylalanine hydroxylase activity leading to inhibition in protein synthesis. Moreover, it inhibits nucleic acids biosynthesis. While FDA did not set any regulatory limits for ochratoxin A, the EU limits for ochratoxin A are 2–10 μg/kg (Muñoz et al. 2014).

3.3 Zearalenone

Zearalenone is one of the most abundant estrogenic mycotoxins in foodstuffs. It is produced by many species in the genus *Fusarium*, mainly *F. graminearum, F. semitectum, F. moniliforme,* and *F. oxysporum.* It can contaminate different foodstuffs such as cereals including wheat, oat, barley, sorghum, maize and their products, particularly under a high humidity and low temperature conditions. Although it shows heat stability (up to 160 °C), it can be partially eliminated by very high temperatures (Piacentini et al. 2019). The chemical structure of zearalenone is illustrated in Fig. 4.

Zearalenone has a close similarity with the natural mammalian estrogen, the main female sex hormone, so it can induce reproductive disorders (hyperestrogenism) affecting the female reproductive system (Kowalska et al. 2016; Zhang et al. 2018). Moreover, its toxicity may extend to severely destroy the intestinal mucosal membrane and disturb the microecological balance of the intestine (Wang et al. 2018). Due to their toxicity, zearalenone is listed by IARC in group 3 carcinogen. To date, FDA did not set any regulatory limit for zearalenone, however, their EU limits are 20–100 μg/kg in any foodstuffs (Ostry et al. 2017).

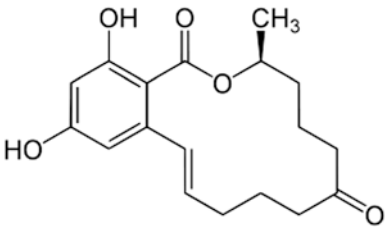

Fig. 4 Chemical structure of zearalenone

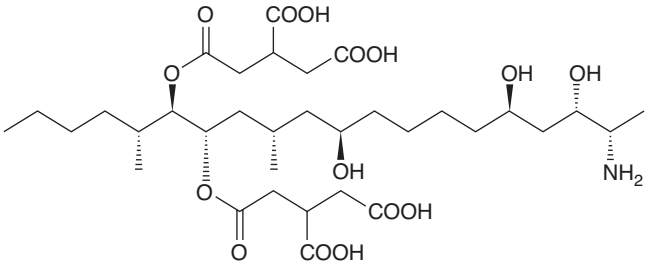

Fig. 5 Chemical structure of fumonisins B1

3.4 Fumonisins

This family comprises a set of non-fluorescent mycotoxins, commonly known as *Fusarium* toxins, because they are produced by members of the genus *Fusarium*, mainly *F. verticillioides* and *F. proliferatum* (Ji et al. 2019). Fumonisins were first discovered in South Africa in 1970, on maize kernels contaminated with *F. verticillioides*, formerly *F. moniliforme*, as the causal agent of leukoencephalomalacia in horses (Kellerman et al. 1972). To date, more than 28 types of fumonisins were identified, and categorized in four groups; fumonisins A, fumonisins B, fumonisins C, and fumonisins P with three subtypes in each group. However, the most abundant group is fumonisins B (B1, B2, and B3) which form 75% of the family. The major foodstuffs which contaminated with fumonisins mycotoxins are wheat, maize, sorghum, rice, oat, soybean, milk, food products such as cornflakes, bread, flour, popcorn, oil, and some medicinal plants (Kamle et al. 2019).

Fumonisins B1 is the most toxic one, so it has been listed by IARC in group 2B (probably carcinogenic). The chemical structure of fumonisins B1 is illustrated in Fig. 5. Recent researches reported that it can lead to carcinoma of esophageal and liver and sever toxicosis in kidney, lung, and nervous system (Braun and Wink 2018; Feijó Corrêa et al. 2018). Although fumonisins exhibit relative heat-stability, their chemical structure can be altered during food systems which reduces their toxicity, so many studies have investigated their fate during different food industrial processes (Bordini et al. 2019). The US regulatory limits for fumonisins B1, B2, and B3 in foodstuffs are 2000–4000 μg/kg, while the EU limits are 200–1000 μg/kg.

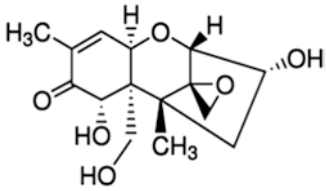

Fig. 6 Chemical structure of deoxynivalenol

3.5 Trichothecenes

Trichothecenes family comprises a large and diverse set of sesquiterpenoid mycotoxines which is produced mainly by members of genus *Fusarium* such as *F. graminearum, F. poae* and *F. culmorum*. However, they have been produced also by members of various genera including *Trichoderma*, *Trichothecium*, *Stachybotrys*, *Myrothecium*, *Acremonium*, and *Cylindrocarpon* (Zhu et al. 2020). To date, over 200 trichothecenes have been identified and classified into four groups (A, B, C, and D). Among them, deoxynivalenol is the most abundant one, particularly in cereals. The chemical structure of deoxynivalenol is illustrated in Fig. 6. Trichothecenes were first recognized in the Soviet Union in 1932 from grains contaminated with *F. sporotrichioides* and *F. poae* as the causal agent of alimentary toxic aleukia. Trichothecenes can contaminate wheat, oat, maize, rice, barley, soybean, peanut, legumes, fruits, vegetables and cereals products (Alshannaq and Yu 2017). Trichothecenes are highly toxic causing neurotoxigenic, immune suppression, cytotoxic, anemia, and skin necrosis. The FDA regulatory limit for trichothecenes in food products is 1000 µg/kg, while the EU limits are 200–500 µg/kg for B1 and 4–15 µg/kg (Habrowska-Górczyńska et al. 2019).

3.6 Patulin

Patulin is a polyketide mycotoxin, which is produced by various members of the genera *Penicillium*, and *Aspergillus*, mainly by *P. expansum* and *P. patulinum,* from which the mycotoxin name was derived. Patulin was first isolated from *P. griseofulvum* in 1943 as an antibiotic against gram +ve and gram -ve bacteria, but later it was recognized as a mycotoxin in 1944 (Sadok et al. 2019). The chemical structure of patulin is illustrated in Fig. 7. Patulin has been found to be associated with different rotten fruits such as apples, grapes, bananas, peaches, pineapple, blueberries, pears, their processed products, as well as vegetables, and cereals kernels (Ji et al. 2017).

Patulin was found to cause toxicosis, mutagenesis, carcinogenesis, and teratogenesis in humans. In addition, it can affect the immune system, the nervous system, and may led to DNA damage (Assunção et al. 2016). However, it has been listed by IARC in group 3 carcinogen. The US regulatory limit for patulin in foodstuffs is 50 µg/kg, while the EU limits are 10–50 µg/kg (Alshannaq and Yu 2017).

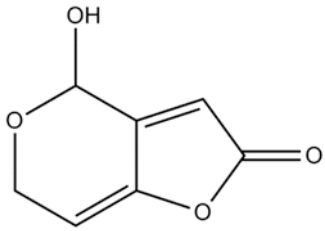

Fig. 7 Chemical structure of patulin

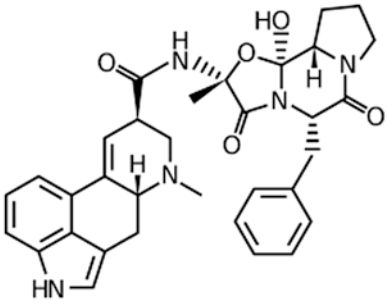

Fig. 8 Chemical structure of ergotamine

3.7 Ergot Alkaloids

This family comprises tryptophan-derived alkaloid mycotoxins which are produced by members of the genus *Claviceps* such as *C. purpurea, C. sorghi, C. sorghicola,* and *C. Africana* (Topi et al. 2017). These pathogenic fungi are the causal agents of ergot disease on cereals and forage grasses, where the fungal sclerotia (dark, thick mass of fungal mycelia) are produced instead of the plant grains/seeds. Wheat, rye, barley, millet, and oats are the most common contaminated crops, where the ergot alkaloid mycotoxins still affect the plant grains, even if the fungal sclerotia are physically eliminated. However, wheat yield is considered "ergoty" if it includes at least 0.05% ergot sclerotia (Shi et al. 2019).

Various mycotoxins are known in this family such as α-ergocryptine, α-ergosine, ergometrine, secalonic acids, ergoflavin, ergocristine, and ergotamine. The chemical structure of ergotamine is illustrated in Fig. 8. Ingestion of ergot-contaminated grains causes ergotism disease, commonly known as ergot toxicosis, in humans which may result in gangrenous, hyperthermic, reproductive, or convulsive toxicosis and finally the death of the animal or human (Flieger et al. 2019). The US regulatory limit for ergot is 300 mg sclerotia/kg grain, while the EU limit is 0.5 g/kg for the sum alkaloids (Agriopoulou et al. 2020).

4 Mycotoxins-Producing Fungi

Various fungal species which have the ability to produce mycotoxins are identified and studied by many researchers (Greco et al. 2014; Ayofemi Olalekan Adeyeye 2020). The most common toxigenic fungi include members of the genera *Aspergillus*, *Penicillium*, *Fusarium*, and *Claviceps,* in addition to some minor toxigenic fungi from the genera *Trichoderma*, *Trichothecium*, *Stachybotrys*, *Myrothecium*, *Acremonium*, and *Cylindrocarpon* (Zhu et al. 2020). These toxigenic fungi can infect crops in field causing serious diseases which affect the host yield quantity and quality (field fungi), or they may contaminate the yield or its products in the post-harvest, or at any processing stages under storage conditions causing spoilage and deterioration of stored foods/feeds (storage fungi).

4.1 Aspergillus *spp.*

Members of this genus are widely distributed worldwide and can be found in soil, air, on plant debris, and woods, growing in a wide range of climates from moderate to high temperatures. Most of them are saprophytic, which live on plant debris or stored foodstuffs, in addition to few pathogenic species that can infect living plants in the field causing different diseases including black rot of grapes and molding of cereals. Among them, some members have the ability to produce mycotoxins, which have adverse effects on humans and animal health, specially aflatoxins and Ochratoxins. Table 2 represents the most common mycotoxigenic species in genus

Table 2 Most common mycotoxigenic *Aspergillus* spp. and their produced mycotoxins

Aspergillus species	Produced mycotoxins
Aspergillus flavus	Aflatoxin B1, Aflatoxin B2
Aspergillus nomius	Aflatoxin B1, Aflatoxin B2
Aspergillus parasiticus	Aflatoxin G1, Aflatoxin G2
Aspergillus ochraceus	Ochratoxins
Aspergillus niger	Ochratoxins
Aspergillus japonicas	Ochratoxins
Aspergillus carbonarius	Ochratoxins
Aspergillus glaucus	Ochratoxins
Aspergillus candidus	Ochratoxins
Aspergillus fumigatus	Ochratoxins
Aspergillus chevalieri	Sterygmatocystin
Aspergillus versicolor	Sterygmatocystin
Aspergillus amstelodami	Sterygmatocystin
Aspergillus terreus	Patulin
Aspergillus clavatus	Patulin

Aspergillus. In this regard, some isolates of *A. flavus* and *A. nomius* have the ability to produce aflatoxin B1 and aflatoxin B2, other isolates of *A. parasiticus* can produce aflatoxin G1 and aflatoxin G2. While, some isolates of *A. ochraceus*, *A. niger*, *A. japonicas*, and *A. carbonarius* produce ochratoxins and other species produce patulin and sterygmatocystin mycotoxins.

4.2 Penicillium *spp.*

Genus *Penicillium* compresses the highest number of species which inhabiting a wide range of habitats and different climates, especially that pose heavy rainfall and mild temperature. While, few members of this genus are highly destructive pathogens of post-harvest diseases. Many members in this genus can cause decay of fruits, kernels, and vegetables in the field, at harvesting, and in the storage. The main diseases caused by *Penicillium* spp. include molding of cereals, and blue and green molds of orange, and apple. In addition, they may decay other processed foods such as meat, dairy products, juices, and cereals products. This group of fungi can produce several mycotoxins including ochratoxins, patulin, citrinin, and penicillic acid. Table 3 represents the most common mycotoxigenic species in genus *Penicillium.*

4.3 Fusarium *spp.*

Members of this genus have global distribution as one of the most important pathogenic fungi affecting various crops in filed, foods, and feeds. In addition, they may live as saprophytes on plant debris. *Fusarium* species can cause many plant diseases

Table 3 Most common mycotoxigenic *Penicillium* spp. and their produced mycotoxins

Penicillium species	Produced mycotoxins
Penicillium verrucosum	Ochratoxins, Citrinin
Penicillium expansum	Patulin
Penicillium patulinum	Patulin
Penicillium griseofulvum	Patulin
Penicillium roquefiortii	Patulin
Penicillium citrinum	Citrinin
Penicillium aurantiogriseum	Penicillic acid
Penicillium variabile	Penicillic acid
Penicillium islandicum	Penicillic acid
Penicillium purpurogenum	Penicillic acid
Penicillium chrysogenum	Penicillic acid
Penicillium capsulatum	Penicillic acid

Table 4 Most common mycotoxigenic *Fusarium* spp. and their produced mycotoxins

Fusarium species	Produced mycotoxins
Fusarium acuminatum	T-2 toxin, moniliformin, HT-2 toxin, diacetoxyscirpenol, monoactoxycirpenol, neosolaniol, beauvericin
Fusarium anthophilum	Beauvericin
Fusarium avenaceum	Moniliformin, enniatins, beauvericin
Fusarium cerealis	Nivalenol, fusarenone-X, zearalenone, zearalenols
Fusarium chlamydosporum	Moniliformin
Fusarium culmorum	Deoxynivalenol, zearalenone, nivalenol, fusarenone-X, zearalenols, mono-acetyldeoxynivalenols
Fusarium equiseti	Zearalenone, zearalenols, monoactoxycirpenol, fusarenone-X, diacetoxyscirpenol, nivalenol, diacetylnivalenol, fusarochromanone, beauvericin
Fusarium graminearum	Deoxynivalenol, zearalenone, fusarenone-X, diacetylnivalenol, mono-acetyldeoxynivalenols, nivalenol, di-acetyldeoxynivalenol
Fusarium heterosporum	Zearalenone, zearalenols
Fusarium nygamai	Beauvericin, fumonisin B1, fumonisin B2
Fusarium oxysporum	Moniliformin, enniatins, beauvericin
Fusarium poae	Diacetoxyscirpenol, monoactoxycirpenol, nivalenol, fusarenone-X, T-2 toxin, HT-2 toxin, neosolaniol, beauvericin
Fusarium proliferatum	Beauvericin, fumonisin B1, fumonisin B2, moniliformin
Fusarium sambucinum	Diacetoxyscirpenol, T-2 toxin, neosolaniol, monoactoxycirpenol, beauvericin
Fusarium semitectum	Beauvericin
Fusarium sporotrichioides	T-2 toxin, HT-2 toxin, neosolaniol, diacetoxyscirpenol, monoactoxycirpenol
Fusarium subglutinans	Beauvericin, moniliformin, fusaproliferin
Fusarium tricinctum	Moniliformin, beauvericin
Fusarium verticillioides	Fumonisin B1, fumonisin B2, fumonisin B3

such as wilt, rots of stalk, crown, and root, head blight, endosepsis, cereals ear rots in the field, as well as fruits and vegetables rots under storage conditions. Various mycotoxins can be produced by members of *Fusarium* genus including fumonisins, zearalenones, trichothecenes, moniliformins, beauvericin, and fusaproliferin. Table 4 shows the most common mycotoxigenic species in genus *Fusarium.*

4.4 Claviceps *spp.*

Species of this genus can infect more than six hundreds of plant species such as wheat, rye, oats, and grasses. *Claviceps* spp. infect cereals plants producing t heir hard sclerotia instead of the grains in the spikes causing the ergots disease. Ergot alkaloids accumulate in produced sclerotia, which harvested within the cereal

grains, and when ingested by animals or humans they result in ergotism disease that may end with the death. A diverse set of mycotoxins is produced by members of the genus including α-ergocryptine, α-ergosine, ergometrine, secalonic acids, ergoflavin, ergocristine, and ergotamine. Genus *Claviceps* includes many mycotoxigenic fungi such as *C. purpurea*, *C. sorghi*, *C. sorghicola*, *C. fusiformis*, *C. cyperi*, *C. paspali* and *C. Africana.*

5 Occurrence in Foodstuffs

Various foodstuffs can be contaminated with mycotoxins, single or in co-occurrence, based on different ecological factors and geographical locations worldwide.

5.1 Cereals and Cereal Based-Products

Cereals and their processed products represent the most vital food source regarding to human and animal consumption, however, they are one of the highly foodstuffs groups regarding contamination with mycotoxines-producing fungi, among them, wheat and maize are the highest in this concern (Park et al. 2018). Indeed, all cereal crops can be contaminated with mycotoxines-producing fungi in field, particularly in the temperate and tropical areas, and when the plant is subjected to stress conditions such as drought, irregular irrigation, and insects attack. Postharvest contamination is more favorable in storage under low aeration, high relative humidity and temperature conditions (Iqbal et al. 2016). The main mycotoxigenic fungi reported on cereals include *A. flavus, A. ochraceus, A. versicolor, F. armeniacum, F. graminearum, F. proliferatum, F. subglutinans, P. aurantiogriseum, P. citreonigrum, P. citrinum, P. verrucosum, A. infectoria,* and *Ustilaginoidea virens* (Gonçalves et al. 2019; Palumbo et al. 2020). The most prevalent mycotoxines detected in cereals grains and their products include aflatoxin B1, fumonisins B1, ochratoxin A, zearalenone, and deoxynivalenol (Kaltner et al. 2017; Carballo et al. 2018; Wan et al. 2020). These mycotoxines may be found in a single form or in co-occurrence with each other. In this regard, Chen et al. (2016) reported the presence of aflatoxin B1 and zearalenone in maize, rice and peanut samples. Co-occurrence of fumonisins and deoxynivalenol in 11% of the investigated samples of maize, sorghum, and millet was also reported by Chilaka et al. (2016). Moreover, co-occurrence of at least two mycotoxines was also reported in 43% of the analyzed samples in this study.

5.2 Meat and Processed Meat Products

Mycotoxines may be transferred to human consumers indirectly through animal-derived products, which prepared from animals that were fed with contaminated feeds such as meat and milk products from cows and cattle, or eggs and flesh from poultry. In a recent study, the analyzed samples of chicken meat were found to be contaminated with 35%, 41%, and 52% of aflatoxins, ochratoxin A, and zearalenone, respectively, while occurrence of these mycotoxins in the egg samples was 28%, 35%, and 32%, respectively (Iqbal et al. 2014). The most abundant mycotoxines in animal-derived products include aflatoxins, ochratoxins, zearalenone, fumonisins, and trichothecenes, however, they may be found singly or in a co-occurrence (Pereira et al. 2019). Co-occurrence of mycotoxines in animal feed is of a great danger because it provides a synergistic toxic effect, whether sum of the same actions or different mode of actions (Zachariasova et al. 2014). In addition, these mycotoxines that pass through the animal digestive system may be detoxified, or in the contrary, transformed to more toxic forms. Moreover, some mycotoxines may be synthesized during processing of the animal-derived products (Wen et al. 2016). Although selection of the fungal ferments should be lack of any mycotoxigenic fungi, various studies have indicated that the mycoflora isolated from meat-derived products is usually contain some probable toxigenic fungi. So that, keeping the hygienic and nutritional quality of animal feeds is of an extreme importance, guaranteeing the animal health and productivity (Greco et al. 2014). Among 98 samples of sausage and burger analyzed for mycotoxins, 11.2% were found contained aflatoxin B1 (>1 ng/g), and 8.9% contaminated with *A. flavus, A. niger, Mucor* sp., and *Penicillium* sp. (Maktabi et al. 2016).

5.3 Milk and Dairy Products

History of dairy products contamination with mycotoxins backs to the 1960s, where the first report of contamination by aflatoxin M1 (metabolized form of aflatoxin B1) in milk which resulted in sever health hazards. Feeding of lactating animals such as buffalos and cows with aflatoxin B1-contaminated fodder results in metabolizing of the ingested mycotoxin in the animal liver and its transformation into aflatoxin M1 which is highly water soluble and more excretable in the animal milk (Becker-Algeri et al. 2016). In addition, aflatoxin M1 is highly stable against pasteurization, sterilization, or other processing treatments (Iha et al. 2013). However, rate of biotransformation of aflatoxin B1 to aflatoxin M1 varies between animals depending on the animal type, nutritional and physiological factors (Iqbal et al. 2013). In a 2-years survey study conducted in Egypt, 302 of raw milk and dairy products were

sampled and analyzed for aflatoxin M1. Of them, 21.6% and 18.3% of raw milk samples were found contaminated with aflatoxin M1 at concentrations exceed EU limits, respectively. While, 33.9% and 44.6% of karish cheese samples were found also contaminated at concentrations above EU limit, respectively (Ismaiel et al. 2020).

Although they have not been widely studied as aflatoxin M1, other mycotoxins such as ochratoxin A, zearalenone, fumonisins, and deoxynivalenol have also been reported in milk samples and dairy products even in non-significant concentrations. In this regard, of 38 milk samples, 84.2% of the samples were contaminated with ochratoxin A at 3.32–6.02 ng/ml which higher than EU limits.

5.4 Fruits and Fruit-Based Products

Fruits and vegetables are subjected to attack by many toxigenic fungi including *P. expansum, P. claviforme, P. viridicatum, P. urticae, A. clavatus, A. niger, A. tubingensis, A. terreus, A. flavus, A. parasiticus, A. ochraceus, A. carbonarius,* and *Byssochlamys* sp. Among the known mycotoxines, patulin, aflatoxins, ochratoxin A, alternariol, and citrine are the most prevalent in vegetables and fruits (Nan et al. 2022).

However, the rate and level of contamination process in fruits and vegetables are affected by different factors such as susceptibility of the kind and cultivars of the plant, climatic variables, geographical site, pre- and post-harvest treatments, surface damage, and storage conditions (Oteiza et al. 2017). Occurrence and co-occurrence of various mycotoxins have been widely investigated in different fruits and their products juices. In this regard, Carballo et al. (2018) studied the occurrence of 15 mycotoxins in different fruit juices of pineapple, orange, apple, apricot, pear, and mixed juice. Of them, 36% were found contaminated with mycotoxins. Patulin was the most prevalent with frequency of 14–86%, while 43% of the mixed juice were contaminated with HT-2 toxin. In another study, Juan et al. (2017) studied mycotoxins presence in berries jam and juice. Of fifty-two analyzed samples, 53% of berries juice were found contaminated with aflatoxins, alternariol and alternariol monomethyl ether. Among them, 43% exhibited co-occurrence of two or more of the analyzed mycotoxins. As mentioned before, the mycotoxines are heat resistance molecules, not reduced by sterilization or pasteurization. In addition, drying of fruits or vegetables, which are contaminated with toxigenic fungi, does not prevent toxin production. Even deep freezing does not limit the mycotoxin concentration, just inhibits additional production of the mycotoxins through suppression of the fungal growth (Nan et al. 2022).

6 Factors Affecting Mycotoxin Production and Occurrence in Foodstuffs

Production and contamination of a mycotoxin can be influenced by a diverse set of physical factors such as climatic conditions favored by the producing fungus (temperature, moisture, humidity, and aeration of stored foods), chemical factors such as application of suitable fungicides, and biological factors related to the toxigenic fungi and their substrates (Tola and Kebede 2016).

6.1 Pre-harvest Conditions

Growth and occurrence of aflatoxin-producing fungi are highly occurred in temperate regions with warm climate so these areas are more exposed to this problem particularly due to global warming. Moreover, wounding by insects and herbivores or hot condition stress may affect plant susceptibility and lead to sever fungal infection in the field. In this regard, the best conditions for growth of the aflatoxigenic fungi *A. flavus* and *A. parasiticus* are 35 °C and 0.95 water activity, whereas, the optimum conditions for aflatoxin production are 33 °C and 0.99 water activity (Jackson and Al-Taher 2008). Other chemical components of the plant/fruit may induce/inhibit these fungi and their mycotoxin production such as soluble solids content (carbohydrates, and organic and amino acids). For example, 1% concentration of three sugars (sucrose, fructose, glucose) enhances the fungal growth but not their toxigenic activity, while, raising sucrose concentration to 20% leads to doubling of the produced toxin. In addition, application of suitable fungicides at proper doses and susceptibility of the plant cultivar can influence the fungal growth and mycotoxigenic activity.

6.2 Harvest and Post-harvest Conditions

Health and ripening status of grains/fruits at harvesting has a great importance in limiting/enhancing infection of the toxigenic fungi and accumulation of their toxins during post-harvest and next processing stages. Excluding of rotten, abnormal, and insect-damaged fruits should be applied at harvesting. Good storing conditions such as aeration, temperature, humidity percentage, careful handling, and applying sanitary procedures have also a great importance in suppression/enhancement of fungal contamination. During processing stages, quality control should be established to prevent mycotoxin contamination. For example, fruits drying should begin immediately after the fruit harvest and for sufficient period at proper moisture content. However, raining during the drying period enhances the possibility of mycotoxin contamination (Jackson and Al-Taher 2008).

7 Control Strategies of Mycotoxins

The high stability of different mycotoxins during harvesting, storage, and processing stages indicates the necessity for prevention of the fungal infection in the field, and contamination of the stored foodstuffs through utilizing safe agricultural and manufacturing practices and applying quality control during all stages (Ayofemi Olalekan Adeyeye 2020). However, if the mycotoxins are already occurred, decontamination/detoxification strategies should be followed which include suppression or reduction their absorption, induction of their excretion, or interfering their mode of action through addition of various food additives (Luo et al. 2018).

7.1 Pre-harvest Strategies

Prevention of infection with toxigenic fungi in the field rather than mycotoxin detoxification in the next stages is more favored in mycotoxins control. The pre-harvest strategies include application of good agricultural practices such as use of resistant cultivars, disinfected seeds, crop rotation, suitable fungicides, insecticides, and herbicides (Alberts et al. 2017). In addition, the use of biological control products during the agricultural process such as antagonistic beneficial bacteria and fungi, or natural plant origin products is of a great importance to guarantee mycotoxins-free food (Sarrocco and Vannacci 2018). Many beneficial microorganisms (bacteria and fungi) have been widely studied as biocontrol agents against toxigenic and phytopathogenic fungi. In this concern, *Bacillus*- and *Trichoderma*-based products share the vast majority of the biocontrol agents market (Rashad and Moussa 2020). These biocontrol agents pose potential antifungal activity against toxigenic fungi through multiple modes of action including competition for nutrients and/or space, antibiosis by (volatile, nonvolatile compounds, and lytic enzymes), and mycoparasitism (such as some *Trichoderma* spp.). In addition, most of the beneficial biocontrol agents have the ability to trigger the plant resistance against the attacking fungi (Köhl et al. 2019). Moreover, the biocontrol ability of some antagonistic microorganisms may exceed the fungal-growth-inhibitory activity to the anti-mycotoxigenic activity through suppression of the toxin biosynthesis process. In a recent study, twenty-nine strains of *Bacillus* spp., isolated from rice fields, were screened for their antagonistic and anti-aflatoxigenic activities against *A. flavus*. Of them, fifteen isolates inhibited the fungal growth of *A. flavus*, while twenty six isolates exhibited considerable anti-aflatoxigenic activity, some of which did not suppress the fungal growth (Chalivendra et al. 2018).

7.2 Post-harvest Strategies

Elimination or alleviation of mycotoxin contamination during post-harvest and processing stages are considered one of the most serious challenges. Various techniques have been suggested in this concern including physical (such as radiation and thermal insulation), chemical (such as treating with bases, ozone or mycotoxin binders), and biological methods (such as microbial degradation or detoxification) (Agriopoulou et al. 2020). Whereas the chemical and physical methods have different limitations owing to their high cost and time-consumption, biological methods provide more potential, economic, and eco-friendly option (Wang et al. 2019).

7.2.1 Physical Methods

Different physical methods are used to eliminate/minimize mycotoxins-contaminated foodstuffs such as washing, sieving, sorting, flotation and density segregation, peeling, irradiation, cold plasma, heating, drying, and use of mycotoxin binders. Washing and sorting represent the first stages of the mycotoxins control process. In this regard, Pascale et al. (2020) reported a reduction up to 94% in the aflatoxin content of maize batches when industrially processed by application of cleaning, mechanical (based on gravity), and optical sorting (using digital cameras) techniques. In contrast, elevated levels of aflatoxins (≈490 μg/kg) were reported in the rejected parts. Elimination of rotten fruits significantly reduces the patulin mycotoxin content in the fruit batches fruit juice processing steps (Agriopoulou et al. 2020). On the other hand, solar irradiation, ɣ-irradiation, and microwave irradiation are effective methods in detoxification of mycotoxins (Peng et al. 2018). Utilization of gamma irradiation at 5 kGy, as decontamination method, had considerable reduction in the toxicity of aflatoxin B1 and ochratoxin A molecules (Domijan et al. 2019). In addition, cold plasma, the fourth state of matter, which is an ionized gas with a mixture of reactive charged ions, UV photons, and electrons has been used as an alternative physical method for mycotoxins control. Cold plasma has the potential to detoxify the mycotoxins and suppress growth of the mycotoxigenic fungi (Pankaj and Keener 2017). In this concern, Casas-Junco et al. (2019) reported a complete inhibition of the mycotoxigenic fungi *A. westerdijikiae, A. steynii, A. versicolor,* and *A. niger,* and 50% reduction in the content of ochratoxin A in roasted coffee when treated with cold plasma for 30 min. Another alternative physical method of mycotoxins control which is the addition of mycotoxins binders to the contaminated foods, which bind to the mycotoxin molecules suppressing their absorption from the gut of livestock. A diverse set of adsorbents substances has been utilized such as activated clays, activated charcoal, clays, cholestyramines, graphene oxides, zeolites, and aluminosilicates (Ji and Xie 2020). Horky et al. (2020) reported rapid and efficient adsorption rates for application of graphene oxide against aflatoxins, zearalenone, and deoxynivalenol mycotoxins in crushed wheat in vitro.

7.2.2 Chemical Methods

Mycotoxins eradication in foodstuffs using chemical treatments is another choice for mycotoxins control including ammoniation, ozonation, oxidation, and addition of antifungal preservatives. However, the chemical treatments are not favored by FAO owing to their probable roles in producing new toxic compounds, and lowering the nutritional values of the treated food (Peng et al. 2018). Detoxification (chemical inactivation/degradation) of mycotoxins in foods using ammonia as a gas or substance has been widely studied by many researchers leading to these mycotoxins to undetectable levels and suppress growth of the toxigenic fungi (Haque et al. 2020). Ammonization of aflatoxin B1 leads to its degradation through hydrolysis of lactone ring and decarboxylation to aflatoxin D1 but this hydrolysis process is reversible, so the ammonization process must continue for a long enough time. Ozonation of the foodstuffs such as cereals and vegetables is another reported method for degradation of many mycotoxins owing to its safety and efficiency (Conte et al. 2020). Li et al. (2019a, b) used gaseous ozone in order to detoxify deoxynivalenol in wheat scab and analyzed their degradation products. Their toxicities were found significantly lowered by ozone attack to deoxynivalenol. These results are in accordance with that obtained by Wang et al. (2016) on wheat grains. Application of eco-friendly antifungal chemicals as food preservatives such as chitosan for inhibition growth of the toxigenic fungi was also reported. Zachetti et al. (2019) investigated the synergistic effect of using chitosan and water activity on growth of *F. proliferatum* and *F. verticillioides* on maize and *F. graminearum* on wheat as well as their mycotoxins production. A growth reduction of *F. graminearum* as a result of application of chitosan at 0.5 mg/g, and suppression in the growth of *F. proliferatum* and *F. verticillioides* at 0.98 water activity and chitosan at 2 mg/g were obtained. In addition, a reduction in deoxynivalenol and fumonisins production on maize and wheat was also achieved.

7.2.3 Biological Methods

Using microorganisms such as bacteria and fungi, or their enzymes in detoxification of mycotoxins has been heavily studied by many researchers (Ben Taheur et al. 2019; Wang et al. 2019). Detoxification/degradation of mycotoxins using microorganisms usually compresses converting them to less/non-toxic forms, which called biotransformation, through hydrolysis, hydroxylation, oxidation, methylation/demethylation, or glycosylation processes (Li et al. 2020). In this regard, Wang et al. (2017) screened the zearalenone-degrading bacteria *B. pumilus* ES-21 based on their esterase activity. A degradation rate up to 95.7% for zearalenone in the culture medium was achieved. The probiotic yeast (*Saccharomyces cerevisiae*) was studied by Liu et al. (2019) and showed a significant mycotoxin degradation ability against deoxynivalenol. In another study, a degradation up to 90% of patulin to dexipitulic acid was also reported by the yeast *Rhodotorula mucilaginosa* (Li et al. 2019a, b). Bio-adsorption using microorganisms has been also described as another

mode of action for inactivation of mycotoxines. In this regard, Haidukowski et al. (2019) studied adsorption activity of *Pleurotus eryngii* mycelium, and reported an aflatoxin B1 removal of 85%. Bio-adsorption activity of lactic acid bacteria (*Lactobacillus fermentum*) for mycotoxins has been investigated by Adebo et al. (2019) achieving up to 98%, 84% and 82% reduction in aflatoxin B1, T-2, and alpha-zearalenol respectively through fermentation of sorghum grains. Using non-toxigenic fungal isolates from genera *Aspergillus*, *Rhizopus*, and *Trichoderma* to compete with the toxigenic ones is another form of biological control of mycotoxins (Sarrocco et al. 2019). Enzymatic detoxification is one of the most studied methods of biological control of mycotoxins. In this regard, detoxification of fumonisins mycotoxins by enzymes produced by *Aspergillus* spp. was reported (Burgess et al. 2016). The antifungal activity of β-glucanase and chitinase enzymes was tested by Cence et al. (2019) against the spoilage fungi *P. simplicissimum, P. nalgiovense, A. niger* and *A. flavus,* isolated from salami surface. A Highly growth inhibition for all tested fungi was obtained by application of both enzymes at 50% concentration indicating their efficacy in the fermented sausage industry. Plant extracts and essential oils are used also for their antifungal and anti-mycotoxins activities. Clove and turmeric essential oils have been reported as inhibitors for *A. flavus* and *P. citrinum* as well as suppressor for aflatoxin B1 production (Luo et al. 2018).

8 Future Perspectives

Contamination of crops and foodstuffs with mycotoxins represents a great sanitary and economic problem and big challenge, particularly for developing countries, where there is a weak monitoring for the mycotoxin contents in the foodstuffs, and limited application of regulatory levels of mycotoxins. To overcome this challenge, a multi-aspect approach should be established. A research capacity buildings and research centers must be developed to set a food-borne-mycotoxins database and research expertise in areas of detection, analyzing, monitoring, and control of mycotoxins. Implementation of strict regulatory system to monitor and regulate trade, exportation, and importation of foods and feeds must be applied. Application of good agriculture practices and quality control procedures in all storage and processing stages should be enforced. Developing community knowledge and interest, especially farmers, for mycotoxins risk and ways to prevent their contamination should be implemented.

On the other hand, another problem should be addressed. It is about mitigation the adverse effects of global climate change, on the long-term, on occurrence and distribution of toxigenic fungi and their toxigenicity. Management control systems are needed to be applied including control measures of plant pathogens, as well as growing awareness of growers, breeders, and agronomists to overcome this challenge. Global warming may promote the growth, distribution, or translocation of toxigenic fungi, or it may alter their toxigenicity or pathogenicity.

9 Conclusions

Mycotoxins represent a hazardous threat for humans and animals causing adverse health effects and considerable economic losses. Control of food contamination with mycotoxins and toxigenic fungi is a tremendous challenge, which requires applying of good quality control measures in order to prevent the infection with the toxigenic fungi in the field, storage, and food processing stages. Various control strategies have been described every year; however, there is a continuous demand to find new safe, effective, and low cost methods to control contamination of mycotoxins in foodstuffs to maintain the global food security.

References

Adebo OA, Kayitesi E, Njobeh PB (2019) Reduction of mycotoxins during fermentation of whole grain sorghum to whole grain ting (A Southern African food). Toxins (Basel) 11. https://doi.org/10.3390/toxins11030180

Agriopoulou S, Stamatelopoulou E, Varzakas T (2020) Advances in occurrence, importance, and mycotoxin control strategies: prevention and detoxification in foods. Foods 9. https://doi.org/10.3390/foods9020137

Alberts JF, Lilly M, Rheeder JP et al (2017) Technological and community-based methods to reduce mycotoxin exposure. Food Control 73:101–109. https://doi.org/10.1016/j.foodcont.2016.05.029

Alshannaq A, Yu JH (2017) Occurrence, toxicity, and analysis of major mycotoxins in food. Int J Environ Res Public Health 14. https://doi.org/10.3390/ijerph14060632

Assunção R, Alvito P, Kleiveland CR, Lea TE (2016) Characterization of in vitro effects of patulin on intestinal epithelial and immune cells. Toxicol Lett 250–251:47–56. https://doi.org/10.1016/j.toxlet.2016.04.007

Ayofemi Olalekan Adeyeye S (2020) Aflatoxigenic fungi and mycotoxins in food: a review. Crit Rev Food Sci Nutr 60:709–721. https://doi.org/10.1080/10408398.2018.1548429

Becker-Algeri TA, Castagnaro D, de Bortoli K et al (2016) Mycotoxins in bovine milk and dairy products: a review. J Food Sci 81:R544–R552. https://doi.org/10.1111/1750-3841.13204

Ben Taheur F, Kouidhi B, Al Qurashi YMA et al (2019) Review: biotechnology of mycotoxins detoxification using microorganisms and enzymes. Toxicon 160:12–22. https://doi.org/10.1016/j.toxicon.2019.02.001

Blount WP (1961) Turkey "X" disease. J Br Turk Fed 9:52–61

Bordini JG, Ono MA, Garcia GT et al (2019) Transgenic versus conventional corn: fate of fumonisins during industrial dry milling. Mycotoxin Res 35:169–176. https://doi.org/10.1007/s12550-019-00343-1

Braun MS, Wink M (2018) Exposure, occurrence, and chemistry of fumonisins and their cryptic derivatives. Compr Rev Food Sci Food Saf 17:769–791. https://doi.org/10.1111/1541-4337.12334

Bueno D, Istamboulie G, Muñoz R, Marty JL (2015) Determination of mycotoxins in food: a review of bioanalytical to analytical methods. Appl Spectrosc Rev 50:728–774. https://doi.org/10.1080/05704928.2015.1072092

Burgess KMN, Renaud JB, McDowell T, Sumarah MW (2016) Mechanistic insight into the biosynthesis and detoxification of fumonisin mycotoxins. ACS Chem Biol 11:2618–2625. https://doi.org/10.1021/acschembio.6b00438

Carballo D, Moltó JC, Berrada H, Ferrer E (2018) Presence of mycotoxins in ready-to-eat food and subsequent risk assessment. Food Chem Toxicol 121:558–565. https://doi.org/10.1016/j.fct.2018.09.054

Casas-Junco PP, Solís-Pacheco JR, Ragazzo-Sánchez JA et al (2019) Cold plasma treatment as an alternative for ochratoxin a detoxification and inhibition of mycotoxigenic fungi in roasted coffee. Toxins (Basel) 11:337

Cence K, Santos P dos, Garcia MV et al (2019) Enzymatic biocontrol of spoilage fungi from salami. Lwt 115:108457. https://doi.org/10.1016/j.lwt.2019.108457

Chalivendra S, DeRobertis C, Pineda JR et al (2018) Rice phyllosphere bacillus species and their secreted metabolites suppress *Aspergillus flavus* growth and aflatoxin production in vitro and in maize seeds. Toxins (Basel) 10:159

Chen Y, Chen Q, Han M et al (2016) Development and optimization of a multiplex lateral flow immunoassay for the simultaneous determination of three mycotoxins in corn, rice and peanut. Food Chem 213:478–484. https://doi.org/10.1016/j.foodchem.2016.06.116

Chilaka CA, De Boevre M, Atanda OO, De Saeger S (2016) Occurrence of Fusarium mycotoxins in cereal crops and processed products (Ogi) from Nigeria. Toxins (Basel) 8. https://doi.org/10.3390/toxins8110342

Conte G, Fontanelli M, Galli F et al (2020) Mycotoxins in feed and food and the role of ozone in their detoxification and degradation: an update. Toxins (Basel) 12:486

Domijan AM, Marjanović Čermak AM, Vulić A et al (2019) Cytotoxicity of gamma irradiated aflatoxin B 1 and ochratoxin A. J Environ Sci Heal – Part B Pestic Food Contam Agric Waste 54:155–162. https://doi.org/10.1080/03601234.2018.1536578

Eskola M, Kos G, Elliott CT et al (2020) Worldwide contamination of food-crops with mycotoxins: validity of the widely cited 'FAO estimate' of 25%. Crit Rev Food Sci Nutr 60:2773–2789. https://doi.org/10.1080/10408398.2019.1658570

Feijó Corrêa JA, Orso PB, Bordin K et al (2018) Toxicological effects of fumonisin B1 in combination with other Fusarium toxins. Food Chem Toxicol 121:483–494. https://doi.org/10.1016/j.fct.2018.09.043

Flieger M, Stodůlková E, Wyka SA et al (2019) Ergochromes: heretofore neglected side of ergot toxicity. Toxins (Basel) 11. https://doi.org/10.3390/toxins11080439

Gonçalves A, Gkrillas A, Dorne JL et al (2019) Pre- and postharvest strategies to minimize mycotoxin contamination in the rice food chain. Compr Rev Food Sci Food Saf 18:441–454. https://doi.org/10.1111/1541-4337.12420

Greco MV, Franchi ML, Rico Golba SL et al (2014) Mycotoxins and mycotoxigenic fungi in poultry feed for food-producing animals. Sci World J 2014:968215. https://doi.org/10.1155/2014/968215

Habrowska-Górczyńska DE, Kowalska K, Urbanek KA et al (2019) Deoxynivalenol modulates the viability, ROS production and apoptosis in prostate cancer cells. Toxins (Basel) 11. https://doi.org/10.3390/toxins11050265

Haidukowski M, Casamassima E, Cimmarusti MT et al (2019) Aflatoxin B1-adsorbing capability of pleurotus eryngii mycelium: efficiency and modeling of the process. Front Microbiol 10:1386

Haque MA, Wang Y, Shen Z et al (2020) Mycotoxin contamination and control strategy in human, domestic animal and poultry: a review. Microb Pathog 142:104095. https://doi.org/10.1016/j.micpath.2020.104095

Horky P, Venusova E, Aulichova T et al (2020) Usability of graphene oxide as a mycotoxin binder: in vitro study. PLoS One 15:e0239479. https://doi.org/10.1371/journal.pone.0239479

Iha MH, Barbosa CB, Okada IA, Trucksess MW (2013) Aflatoxin M 1 in milk and distribution and stability of aflatoxin M 1 during production and storage of yoghurt and cheese. Food Control 29:1–6. https://doi.org/10.1016/j.foodcont.2012.05.058

Iqbal SZ, Asi MR, Jinap S (2013) Variation of aflatoxin M1 contamination in milk and milk products collected during winter and summer seasons. Food Control 34:714–718. https://doi.org/10.1016/j.foodcont.2013.06.009

Iqbal SZ, Nisar S, Asi MR, Jinap S (2014) Natural incidence of aflatoxins, ochratoxin A and zearalenone in chicken meat and eggs. Food Control 43:98–103. https://doi.org/10.1016/j.foodcont.2014.02.046

Iqbal SZ, Selamat J, Ariño A (2016) Mycotoxins in food and food products: current status. In: Selamat J, Iqbal SZ (eds) Food safety: basic concepts, recent issues, and future challenges. Springer, Cham, pp 113–123

Ismaiel AA, Tharwat NA, Sayed MA, Gameh SA (2020) Two-year survey on the seasonal incidence of aflatoxin M1 in traditional dairy products in Egypt. J Food Sci Technol 57:2182–2189. https://doi.org/10.1007/s13197-020-04254-3

Jackson LS, Al-Taher F (2008) Factors affecting mycotoxin production in fruits. In: Barkai-Golan R, Paster NBT-M (eds) Mycotoxins in fruits and vegetables. Academic, San Diego, pp 75–104

Ji J, Xie W (2020) Detoxification of Aflatoxin B1 by magnetic graphene composite adsorbents from contaminated oils. J Hazard Mater 381:120915. https://doi.org/10.1016/j.jhazmat.2019.120915

Ji X, Li R, Yang H et al (2017) Occurrence of patulin in various fruit products and dietary exposure assessment for consumers in China. Food Control 78:100–107. https://doi.org/10.1016/j.foodcont.2017.02.044

Ji F, He D, Olaniran AO et al (2019) Occurrence, toxicity, production and detection of Fusarium mycotoxin: a review. Food Prod Process Nutr 1:6. https://doi.org/10.1186/s43014-019-0007-2

Juan C, Mañes J, Font G, Juan-García A (2017) Determination of mycotoxins in fruit berry by-products using QuEChERS extraction method. LWT Food Sci Technol 86:344–351. https://doi.org/10.1016/j.lwt.2017.08.020

Kaltner F, Rampl C, Rychlik M et al (2017) Development and validation of a cost-effective HPLC-FLD method for routine analysis of fumonisins B1 and B2 in corn and corn products. Food Anal Methods 10:1349–1358. https://doi.org/10.1007/s12161-016-0688-y

Kamle M, Mahato DK, Devi S et al (2019) Fumonisins: impact on agriculture, food, and human health and their management strategies. Toxins (Basel) 11. https://doi.org/10.3390/toxins11060328

Kellerman TS, Marasas WF, Pienaar JG, Naudé TW (1972) A mycotoxicosis of equidae caused by Fusarium moniliforme Sheldon. A preliminary communication. Onderstepoort J Vet Res 39:205–208

Kępińska-Pacelik J, Biel W (2021) Alimentary risk of mycotoxins for humans and animals. Toxins (Basel) 13. https://doi.org/10.3390/toxins13110822

Kibugu JK, Mburu D, Munga LK et al (2019) Food-borne mycotoxin hazards in the Kenyan market-a retrospective study. bioRxiv:773747. https://doi.org/10.1101/773747

Köhl J, Kolnaar R, Ravensberg WJ (2019) Mode of action of microbial biological control agents against plant diseases: relevance beyond efficacy. Front Plant Sci 10:845

Kowalska K, Habrowska-Górczyńska DE, Piastowska-Ciesielska AW (2016) Zearalenone as an endocrine disruptor in humans. Environ Toxicol Pharmacol 48:141–149. https://doi.org/10.1016/j.etap.2016.10.015

Kumar P, Mahato DK, Kamle M et al (2017) Aflatoxins: a global concern for food safety, human health and their management. Front Microbiol 7:2170. https://doi.org/10.3389/fmicb.2016.02170

Kyei NNA, Boakye D, Gabrysch S (2020) Maternal mycotoxin exposure and adverse pregnancy outcomes: a systematic review. Mycotoxin Res 36:243–255. https://doi.org/10.1007/s12550-019-00384-6

Leitão AL (2019) Occurrence of ochratoxin a in coffee: threads and solutions – a mini-review. Beverages 5:36

Li M, Guan E, Bian K (2019a) Structure elucidation and toxicity analysis of the degradation products of deoxynivalenol by gaseous ozone. Toxins (Basel) 11. https://doi.org/10.3390/toxins11080474

Li X, Tang H, Yang C et al (2019b) Detoxification of mycotoxin patulin by the yeast Rhodotorula mucilaginosa. Food Control 96:47–52. https://doi.org/10.1016/j.foodcont.2018.08.029

Li P, Su R, Yin R et al (2020) Detoxification of mycotoxins through biotransformation. Toxins (Basel) 12. https://doi.org/10.3390/toxins12020121
Liu Y, Chang J, Wang P et al (2019) Effects of Saccharomyces cerevisiae on alleviating cytotoxicity of porcine jejunal epithelia cells induced by deoxynivalenol. AMB Express 9:137. https://doi.org/10.1186/s13568-019-0863-9
Luo Y, Liu X, Li J (2018) Updating techniques on controlling mycotoxins – a review. Food Control 89:123–132. https://doi.org/10.1016/j.foodcont.2018.01.016
Maktabi S, Fazlara A, Ghorbanpoor M et al (2016) Measurement and assessment of aflatoxin B1 and its producing molds in Iranian sausages and burgers. J Kerman Univ Med Sci 20:74–78
Malir F, Ostry V, Pfohl-Leszkowicz A et al (2016) Ochratoxin a: 50 years of research. Toxins (Basel) 8. https://doi.org/10.3390/toxins8070191
Martinez-Miranda MM, Rosero-Moreano M, Taborda-Ocampo G (2019) Occurrence, dietary exposure and risk assessment of aflatoxins in arepa, bread and rice. Food Control 98:359–366. https://doi.org/10.1016/j.foodcont.2018.11.046
Mavrommatis A, Giamouri E, Tavrizelou S et al (2021) Impact of mycotoxins on animals' oxidative status. Antioxidants 10:1–24. https://doi.org/10.3390/antiox10020214
Mitchell NJ, Bowers E, Hurburgh C, Wu F (2016) Potential economic losses to the US corn industry from aflatoxin contamination. Food Addit Contam – Part A Chem Anal Control Expo Risk Assess 33:540–550. https://doi.org/10.1080/19440049.2016.1138545
Muñoz K, Blaszkewicz M, Campos V et al (2014) Exposure of infants to ochratoxin A with breast milk. Arch Toxicol 88:837–846. https://doi.org/10.1007/s00204-013-1168-4
Murugesan GR, Ledoux DR, Naehrer K et al (2015) Prevalence and effects of mycotoxins on poultry health and performance, and recent development in mycotoxin counteracting strategies. Poult Sci 94:1298–1315. https://doi.org/10.3382/ps/pev075
Nan M, Xue H, Bi Y (2022) Contamination, detection and control of mycotoxins in fruits and vegetables. Toxins (Basel) 14:309
Nazhand A, Durazzo A, Lucarini M et al (2020) Characteristics, occurrence, detection and detoxification of aflatoxins in foods and feeds. Foods 9. https://doi.org/10.3390/foods9050644
Ostry V, Malir F, Toman J, Grosse Y (2017) Mycotoxins as human carcinogens – the IARC monographs classification. Mycotoxin Res 33:65–73. https://doi.org/10.1007/s12550-016-0265-7
Oteiza JM, Khaneghah AM, Campagnollo FB et al (2017) Influence of production on the presence of patulin and ochratoxin A in fruit juices and wines of Argentina. LWT Food Sci Technol 80:200–207. https://doi.org/10.1016/j.lwt.2017.02.025
Palumbo R, Crisci A, Venâncio A et al (2020) Occurrence and co-occurrence of mycotoxins in cereal-based feed and food. Microorganisms 8:74. https://doi.org/10.3390/microorganisms8010074
Pankaj SK, Keener KM (2017) Cold plasma: background, applications and current trends. Curr Opin Food Sci 16:49–52. https://doi.org/10.1016/j.cofs.2017.07.008
Park J, Kim DH, Moon JY et al (2018) Distribution analysis of twelve mycotoxins in corn and corn-derived products by LC-MS/MS to evaluate the carry-over ratio during wet-milling. Toxins (Basel) 10. https://doi.org/10.3390/toxins10080319
Pascale M, Logrieco AF, Graeber M et al (2020) Aflatoxin reduction in maize by industrial-scale cleaning solutions. Toxins (Basel) 12:331
Peng WX, Marchal JLM, van der Poel AFB (2018) Strategies to prevent and reduce mycotoxins for compound feed manufacturing. Anim Feed Sci Technol 237:129–153. https://doi.org/10.1016/j.anifeedsci.2018.01.017
Pereira CS, Cunha SC, Fernandes JO (2019) Prevalent mycotoxins in animal feed: occurrence and analytical methods. Toxins (Basel) 11. https://doi.org/10.3390/toxins11050290
Piacentini KC, Ferranti LS, Pinheiro M et al (2019) Mycotoxin contamination in cereal-based baby foods. Curr Opin Food Sci 30:73–78. https://doi.org/10.1016/j.cofs.2019.06.008
Pietsch C (2020) Risk assessment for mycotoxin contamination in fish feeds in Europe. Mycotoxin Res 36:41–62. https://doi.org/10.1007/s12550-019-00368-6

Pinotti L, Ottoboni M, Giromini C et al (2016) Mycotoxin contamination in the EU feed supply chain: a focus on cereal byproducts. Toxins (Basel) 8:45. https://doi.org/10.3390/TOXINS8020045

Rashad YM, Moussa TAA (2020) Biocontrol agents for fungal plant diseases management. In: El-Wakeil N, Saleh M, Abu-hashim M (eds) Cottage industry of biocontrol agents and their applications. Springer, Cham, pp 337–363. https://doi.org/10.1007/978-3-030-33161-0_11

Sadok I, Stachniuk A, Staniszewska M (2019) Developments in the monitoring of patulin in fruits using liquid chromatography: an overview. Food Anal Methods 12:76–93. https://doi.org/10.1007/s12161-018-1340-9

Sarrocco S, Vannacci G (2018) Preharvest application of beneficial fungi as a strategy to prevent postharvest mycotoxin contamination: a review. Crop Prot 110:160–170. https://doi.org/10.1016/j.cropro.2017.11.013

Sarrocco S, Mauro A, Battilani P (2019) Use of competitive filamentous fungi as an alternative approach for mycotoxin risk reduction in staple cereals: state of art and future perspectives. Toxins (Basel) 11:701

Shabana YM, Rashad YM, Ghoneem KM et al (2021) Biodiversity of pathogenic and toxigenic seed-borne mycoflora of wheat in Egypt and their correlations with weather variables. Biology (Basel) 10(10):1025. https://doi.org/10.3390/biology10101025

Shabana YM, Ghoneem KM, Rashad YM et al (2022) Distribution and biodiversity of seed-borne pathogenic and toxigenic fungi of maize in Egypt and their correlations with weather variables. Plants 11(18):2347. https://doi.org/10.3390/plants11182347

Shi H, Schwab W, Liu N, Yu P (2019) Major ergot alkaloids in naturally contaminated cool-season barley grain grown under a cold climate condition in western Canada, explored with near-infrared (NIR) and Fourier transform mid-infrared (ATR-FT/MIR) spectroscopy. Food Control 102:221–230. https://doi.org/10.1016/j.foodcont.2019.03.025

Tola M, Kebede B (2016) Occurrence, importance and control of mycotoxins: a review. Cogent Food Agric 2:1191103. https://doi.org/10.1080/23311932.2016.1191103

Topi D, Jakovac-Strajn B, Pavšič-Vrtač K, Tavčar-Kalcher G (2017) Occurrence of ergot alkaloids in wheat from Albania. Food Addit Contam – Part A Chem Anal Control Expo Risk Assess 34:1333–1343. https://doi.org/10.1080/19440049.2017.1307528

Villafana RT, Ramdass AC, Rampersad SN (2019) Selection of Fusarium trichothecene toxin genes for molecular detection depends on TRI gene cluster organization and gene function. Toxins (Basel) 11. https://doi.org/10.3390/toxins11010036

Vogelgsang S, Beyer M, Pasquali M et al (2019) An eight-year survey of wheat shows distinctive effects of cropping factors on different Fusarium species and associated mycotoxins. Eur J Agron 105:62–77. https://doi.org/10.1016/j.eja.2019.01.002

Wan J, Chen B, Rao J (2020) Occurrence and preventive strategies to control mycotoxins in cereal-based food. Compr Rev Food Sci Food Saf 19:928–953. https://doi.org/10.1111/1541-4337.12546

Wang L, Luo Y, Luo X et al (2016) Effect of deoxynivalenol detoxification by ozone treatment in wheat grains. Food Control 66:137–144. https://doi.org/10.1016/j.foodcont.2016.01.038

Wang G, Yu M, Dong F et al (2017) Esterase activity inspired selection and characterization of zearalenone degrading bacteria Bacillus pumilus ES-21. Food Control 77:57–64. https://doi.org/10.1016/j.foodcont.2017.01.021

Wang X, Yu H, Shan A et al (2018) Toxic effects of zearalenone on intestinal microflora and intestinal mucosal immunity in mice. Food Agric Immunol 29:1002–1011. https://doi.org/10.1080/09540105.2018.1503233

Wang L, Wu J, Liu Z et al (2019) Aflatoxin B1 degradation and detoxification by Escherichia coli CG1061 isolated from chicken cecum. Front Pharmacol 9:1548

Wen J, Mu P, Deng Y (2016) Mycotoxins: cytotoxicity and biotransformation in animal cells. Toxicol Res (Camb) 5:377–387. https://doi.org/10.1039/c5tx00293a

Zachariasova M, Dzuman Z, Veprikova Z et al (2014) Occurrence of multiple mycotoxins in European feeding stuffs, assessment of dietary intake by farm animals. Anim Feed Sci Technol 193:124–140. https://doi.org/10.1016/j.anifeedsci.2014.02.007

Zachetti VGL, Cendoya E, Nichea MJ et al (2019) Preliminary study on the use of chitosan as an eco-friendly alternative to control fusarium growth and mycotoxin production on maize and wheat. Pathogens 8. https://doi.org/10.3390/pathogens8010029

Zhang GL, Feng YL, Song JL, Zhou XS (2018) Zearalenone: a mycotoxin with different toxic effect in domestic and laboratory animals' granulosa cells. Front Genet 9:667

Zhu M, Cen Y, Ye W et al (2020) Recent advances on macrocyclic trichothecenes, their bioactivities and biosynthetic pathway. Toxins (Basel) 12. https://doi.org/10.3390/toxins12060417

Seed-Borne Mycoflora and Their Management

Satriyas Ilyas and Dyah Manohara

1 Introduction

Seeds are the most important input for plant production and crop health. According to Anwar et al. (2013), about 90% crops of in the world use seeds as planting materials.

Seed-borne mycoflora are important not only have the potential to affect the seed quality causing germination failure but also can become a source of primary inoculum, causing new diseases and as inoculums that contaminate the soil can persist permanently (Kesho and Abebe 2020). Therefore, seed-borne mycoflora have to be managed, and seed health testing is an important step in managing seed-borne diseases.

In this chapter, we gather the previous research findings on the detection of seed-borne mycoflora in various crop species with standard methods or a new approach using a multispectral imaging technique. The effect of seed-borne mycoflora on seed quality, plant growth, and yield is another concern. Finally, we present the findings on various seed treatments to overcome the seed-borne mycoflora.

A meta-analysis covering 396 studies globally shows that biological seed treatments can be a sustainable solution to increase crop yield under climate change while ensuring environmental sustainability and preventing negative effects on human health (Lamichane et al. 2022). Biological seed treatments can be done through biomatriconditioning or biopriming (Ilyas et al. 2015). The most common

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use is biopriming, which is a seed treatment that incorporates biological agents such as plant growth-promoting rhizobacteria (PGPR), involving the hydration of seeds and inoculation with beneficial microbes. Seed biopriming improves seed viability and vigor, plant growth, yield, and disease resistance through the production of growth regulators and protecting seedlings/plants from seed- or soil-borne pathogens (Ilyas et al. 2015; Mitra et al. 2021). Biopriming using PGPR inoculants is becoming more common in modern agriculture as an alternative to chemical treatments, thus being more environmentally sustainable and safer for future agriculture while improving plant growth and soil health (Mitra et al. 2021).

2 Detection of Seed-Borne Mycoflora

Mycoflora as a seed-borne may be divided into two groups such as pathogenic and non-pathogenic fungi. Pathogenic fungi are fungi as the causal agent of disease in plants such as *Fusarium*, *Phytophthora*, and *Colletotrichum*. Non-pathogenic fungi are usually said as weak pathogenic or saprophytic such as *Penicillium, Aspergillus, Mucor,* and *Rhizopus* that colonize seeds as a result of physical damage or unfavorable environments that affect seeds during harvesting and storage (Gyasi et al. 2020). Detection of seedborne mycoflora is usually conducted using either a blotter test or agar plate method as recommended by International Seed Testing Association (ISTA).

Mycoflora of soybean seeds was observed by blotter test and agar plate method against eight varieties collected from central Java, Indonesia. Eight fungal species were found from the blotter test viz. *Aspergillus flavus, Aspergullus niger, Cladosporium oxysporum, Colletotrichum dematium, Curvularia pallescens, Fusarium solani, Melanospora zamiae and Nigrospora* sp. In contrast, only four species were detected by the agar plate method, *Aspergillus niger, Cladosporium oxysporum, Colletotrichum dematium,* and *Fusarium solani* (Soesanto et al. 2020). Ramdan and Kalsum (2017) also used the blotter test method to detect seeds' mycoflora, which were collected from West Java, Indonesia. They identified *Fusarium* spp., as the significant population, followed by *Colletotrichum* sp., *Rhizopus* sp., *Curvularia* sp., *Aspergillus* sp., and *Penicillium* spp. Amongst those seed mycoflora, the common pathogenic fungi against soybean in Indonesia were *Colletotrichum dematium* and *Fusarium* spp. Sajesh et al. (2014) revealed that *C. dematium* survived in the pericarp and hilum of soybean seed whereas *Fusarium* spp. was found in the pericarp and hilum and also embryo. Four seed-borne fungi species namely *Aspergillus* spp., *Penicillium* spp., *Cladosporium* spp., and *Fusarium* spp. were detected from soybean seeds by agar plate method in Turkey. Based on the pathogenicity test, *F. proliferatum* (RU1) and *C. clodosporioides* (AC1) isolates caused the seed rot. The other isolates, *Aspergillus* spp. and *Penicillium* spp., did not cause seed rot disease (Ustum et al. 2021), in other words, both were non-pathogenic.

Chang et al. (2020) conducted a screening of 12 soybean cultivar seeds in China using the agar plate method. The soybean plants were planted as intercropping with maize. In general, they found 148 isolates consisting of 13 fungal genera such as *Fusarium* spp., *Colletotrichum* spp., *Alternaria* sp., *Diaporthe/Phomopsis,* and nine genera in fewer populations. *Fusarium* was the dominant population (55%) followed by *Colletotrichum.* Two species of *Fusarium* viz. *F. fujikuroi* and *F. asiatum* had the highest pathogenicity compared to others. *F. fujikuroi* has been found in almost soybean cultivars. Alemu (2014) reported the result of detecting soybean seed-borne fungus by agar plate and blotter test method in Ethiopia. The fungus consisted of *Aspergillus flavus*, *Aspergillus niger*, *Fusarium* spp., *Penicillium* sp., and *Rhizopus* spp. Two fungi such as *A. flavus* and *A. niger* were dominant in both methods, and belong to saprophytic fungi. *A. flavus* occupied all parts of the soybean seed, while *A. niger was* found only on the pericarp and embryo (Sajeesh et al. 2014).

The cowpea cv. Phule Vithai seed-borne mycoflora was detected in India using five standard methods. The methods were the standard blotter test, agar plate method, blotter soak method, test tube water agar seedling symptom test, and standard deep freeze blotter method. They concluded that the standard blotter test without pre-treatment seeds in advance was the best because it could detect almost all the seed-borne fungi viz. *Alternaria alternata*, *Aspergillus flavus*, *Aspergillus niger*, *Fusarium oxysporum*, *Penicillium* spp. and *Fusarium moniliforme* (Zanjare et al. 2020). A similar result was found when 16 white cowpea seed samples collected from various cities in Pakistan were investigated for seed-borne fungi. Agar plate was the best method for the detection of *Macrophomina phaseolina* and *Rhizoctonia solani*, and deep-freezing and blotter methods were best for *Fusarium oxysporum.* The most dominant fungal species in all three methods used *were Aspergillus flavus* followed by *A. niger*. Surface sterilization of seeds with 1% sodium hypochlorite greatly reduced the incidence of saprophytic fungi (Dawar et al. 2015).

Screening seed-borne fungi of several legume species (*Pisum sativum*, *Macrotyloma uniflorum*, *Lens culinaris*, *Phaseolus vulgaris*, *Vigna unguiculata, Cajanus cajan*, *Cicer arietinum*) using blotter plate indicated that untreated seeds showed the highest number of seed-borne fungi than the seeds treated with 1% sodium hypochlorite for 10 min (Ghangaokar and Kshirsagar 2013). Pre-treatment with sodium hypochlorite by soaking the seeds is generally used to sterilize the surface of the seed so that the mycoflora attached to the seed surface will be lost. Dhakar et al. (2018) detected eight mycoflora using the agar plate method *Alternaria alternata, Aspergillus flavus, A. niger, Curvularia lunata, Fusarium moniliforme, Rhizopus stolonifer, Mucor* spp., and *Trichoderma viride* from wheat seeds in two districts in India. However, *T. viride* was not found when using the blotter test. The percentage incidences of all mycoflora isolated from sterilized seeds were lower than unsterilized ones. Rahim and Dawar (2015) investigated seed-borne mycoflora associated with okra (*Abelmoschus esculentus* (L.) Moench) seeds of 18 samples obtained from 13 areas of Pakistan. Among the ISTA seed health test methods used to detect the fungi, the agar plate method (59 species) was the best followed by the standard blotter method (35 species), only 5 fungi species were isolated by deep

freezing. Species of *Aspergillus* and *Chaetomium* were the most dominant fungi isolated from the okra seeds. The incidence of storage fungi was reduced by surface sterilization of seeds with 1% sodium hypochlorite.

Mycofloral capsicum pepper seeds collected from three different agroecological regions in Sri Lanka were identified by Welideniya et al. (2019). They used several methods: the standard blotter method, agar plate, seed wash method, and deep-freezing method. They identified *Colletotrichum capsici* and *C. gloeosporioides* as pathogenic fungi, that cause anthracnose disease; *Fusarium* and *Aspergillus* as non-pathogenic or saprophytes on pepper seeds or fruits. Furthermore, they also observed the location of fungi in seeds by separating the parts of a seed. The result showed that *C. capsicum* and *C. gloeosporioides* were found in the seed coat, pericarp, and embryo of the diseased pepper plant but not in the healthy plant. *Fusarium* and *Aspergillus* were detected only on the seed coat of sick and healthy pepper plants.

Birla et al. (2020) identified seed mycoflora of two chili varieties (Garima-12 and HPH-12) by agar plate method, blotter paper method, and rolled paper towel method in India. The result revealed five seed-borne fungi viz. *Aspergillus flavus, A. niger, Colletotrichum capsici, Penicillium citrinum*, and *Fusarium annum.* Amongst the three methods, the agar plate method was the best for detecting the mycofloral of chili seeds. Ramdan and Kalsum (2017) identified the chili seed-borne fungal by blotter paper method, two kinds of fungus were the dominant population, viz. *Colletotrichum* sp. was a pathogenic fungus and *Rhizopus* sp. was a saprophyte fungus usually found in storage as the contamination.

Assessment of seed health specifically the seed-borne fungi on hybrid cacao seeds was done using water agar (WA), potato dextrose agar (PDA), and filter paper (FP). Thirteen species of seed-borne fungi were identified by WA and PDA media, and eight species by FP. The 13 seedborne fungi potentially reduced the physiological seed quality and yield of cacao. Predominant fungi were *Aspergillus* spp., *Penicillium chrysogenium*, *Colfoundetotrichum acutatum*, *Curvularia geniculata*, and *Fusarium* spp. However, these fungi need to be further tested for their pathogenic, saprophytic, or antagonistic properties towards other fungi on cacao seeds (Baharudin et al. 2012).

Welideniya et al. (2019) stated that many researchers have observed mycoflora on seeds using many kinds of methods. Hence, the results were quite varied since each method has advantages and disadvantages depending on the type of plant, cultivation, and location. Pathogenic fungi such as *Colletotrichum* spp. may settle in soybean and chili seeds internally and/or externally. The non-pathogenic or weak pathogenic, namely *Fusarium* and *Aspergillus* found on the seed coats of soybean and chili seeds. Both of them attached the seed coat during the processing of harvesting or storage so it is well-known as storage fungi besides *Penicillium* spp., *Mucor* spp., and *Rhizopus* spp. (Amza 2018).

Regular methods known as seed health test for detecting and identifying seed-borne fungi is time-consuming and requires highly trained specialists for the characterization of the pathogens. Therefore, a new approach using a multispectral vision system for identifying surface properties of different fungal infections was tested in spinach seeds. It was shown that multispectral imaging with wavelengths

ranging from 395–970 nm could be used to distinguish between uninfected seeds and seeds infected with *Verticillium* spp., *Fusarium* spp., *Stemphylium botryosum*, *Cladosporium* spp. and *Alternaria alternata* (Olesen et al. 2011). Recently, Rego et al. (2020) used the multispectral imaging technique at 19 wavelengths (365–970 nm) in combination with statistical models for evaluating the health status of cowpea seeds. The seeds were artificially inoculated with *Fusarium pallidoroseum*, *Rhizoctonia solani*, and *Aspergillus* sp. A model based on linear discriminant analysis (LDA) was developed using the reflectance, color, and texture features of the seed images. Results demonstrated that the LDA-based models were efficient with high accuracy (92–99%) in detecting and identifying different species of fungi in cowpea seeds. This confirms that the new method is promising for further development to evaluate seed-borne fungi rapidly.

3 Effect of Mycoflora on Seed Health and Viability, Plant Growth, and Yield

High-quality seed alone is estimated to contribute 18–20% to increasing crop yield with other production inputs fulfilled. However, many biotic and abiotic factors affect seed quality. Seed health is one important aspect of seed quality. The presence of seed-borne pathogens may reduce seed germination and seed vigor resulting in a low yield of up to 15% to 90% (Gebeyaw 2020).

A s*eed* is a small embryonic plant that is a basic unit of production for all plants. Seed health is essential for plants to produce good products (Tsedaley 2015). Almost all seeds are contaminated by mycoflora, amongst which there is a seed-borne pathogen. The fungal pathogen interferes with seeds, decreasing seed germination and vigor, thus reducing seed quality (Chang et al. 2020). Furthermore, during germination, it may cause seed rot and seed mortality or inhibit plant growth and decrease productivity (Amza 2018). However, a fungal pathogen stays in the seed without showing symptoms as a latent infection (Boufleur et al. 2021; de Silva et al. 2017), so it could be a primary inoculum disease in new planting areas. Seed-borne diseases are the major production constraint for almost all crops, for instance, soybean dan chili.

Chang et al. (2020) studied the soybean seed mycoflora cultivated by relay strip intercropping with maize in Southwest China. *Fusarium* was the dominant population, followed by *Colletotrichum.* Further study against five *Fusarium* species found that it caused significantly reduced the germination percentage and vigor of soybean seedlings. In the previous reports (Pedrozo and Little 2017; Naeem et al. 2019), as pathogenic fungi, *Fusarium* could infect almost all the growth stages of soybean plants causing pod rot and seed decay. *Colletotrichum* spp. is a fungal pathogen usually found in soybean seeds (Dias et al. 2019). According to Boufleur et al. (2021), the main limiting factor of soybean production is caused by *Colletotrichum,* which causes anthracnose disease and the loss of production of up to 50%. As a seed-borne

pathogen, the fungal causes pre and/or postemergence damping-off. Besides that, *Colletotrichum* also can carry out systemic infections in all parts of the soybean plant as a latent or silent infection, meaning without causing visible symptoms (de Silva et al. 2017; Dias et al. 2016). The potential of inoculum carrier seeds to spread to various areas will threaten the loss of soybean production in new areas (Naeem et al. 2019). The anthracnose incidence of about 1% can cause soybean production loss of up to 90 kg/ha (Dias et al. 2016). Soybean anthracnose is caused by *C. truncate* (Dias et al. 2019), although other *Colletotrichum* species have also been reported as causal agents of this disease. Boufleur et al. (2021) declared that at least 12 *Colletotrichum* lineages are associated with soybean; among them, *C. truncatum* is considered the most important causal agent of soybean anthracnose. According to Jauhari and Majid (2019), production loss due to soybean anthracnose may be up to 95%. Besides the pathogenic fungi, saprophytic fungi were frequently found dominant as mycofloral soybean seeds such as *Aspergillus, Penicillium,* and *Rhizopus.* Those fungi could reduce the germination of seeds and damage the seeds in storage (Alemu 2014).

Colletotrichum spp. is also found as seed mycoflora on chili pepper (*Capsicum annuum* L.), causing the disease known as anthracnose. Severe losses will occur if chili pepper is cultivated in tropical and subtropical areas due to anthracnose, which can occur during the preharvest or post-harvest period as fruit rot (Welideniya et al. 2019). *Colletotrichum* is a seed and air-borne, can infect chili from an early stage and continue until harvest (Saxena et al. 2016; Manda et al. 2020). According to Welideniya et al. (2019) in Sri Lanka, two species of *Colletotrichum are* usually found as the causal agent of anthracnose on chili pepper viz. *Colletotrichum capsici* (*Colletotrichum truncatum*) and *C. gloeosporioides*, decreased the quality and quantity of the harvesting. Germination of infected seeds ranges between 30.0% and 33.3%. Pre-emergence and postemergence losses range between 66.7–70.0% and 27.8–68.6%, respectively. In contrast, the sample from healthy seeds showed a germination range between 93.3% and 96.7%. Pre-emergence and post-emergence losses were between 3.3–6.7% and 0.0–11.1%, respectively.

Abdulwehab et al. (2015) investigated seed-borne mycoflora on six Sudanese leguminous crops *Cajanus cajan*, *Cicer aritinum*, *Dolichos lablab*, *Medicago sativa*, *Phaseolus vulgaris*, and *Vigna unguiculata* and their effect on seed germination and seedling emergence. *Alternaria*, *Aspergillus,* and *Fusarium* (four species each) were the most dominant fungi among others. The seeds contaminated with both saprophytic and pathogenic mycoflora (17–64%) reduced seed germination (41–86%), and seedling emergence (29–81%). Chaudhari et al. (2017) did a seed health test on pigeon pea (*Cajanus cajan* L.) using the agar and blotter method and detected *Alternaria alternata, Aspergillus flavus, A. niger, Fusarium moniliforme, Fusarium oxysporum,* and *Fusarium udum*. The seed mycoflora caused a reduction in seed germination and seedling vigor as compared to the healthy seeds (control), and the most prominent reduction was caused by *Aspergillus* spp. Sahu and Lakpale (2020) examined the seed health of lentil (*Lens culinaris* Medik.) seed lots of six varieties. When the roll paper towel method was used, the maximum frequency of

mycoflora was observed from local variety (110%) i.e. *Aspergillus flavus* (26%), *Fusarium* sp. (24%), *Rhizopus stolonifer*, *Penicillium* sp. (18%), *Chaetomium globosum* (12%), *Aspergillus niger*, and *Alternaria alternata* (6%) with minimum germination percentage (80%). Whereas the JL-3 variety recorded higher germination due to lower frequencies of detected mycoflora as compared to other varieties in the study. The presence of mycoflora may cause abnormalities and failure in seed germination. Hussain et al. (2009) examined the incidence of seed-borne fungi and their impact on the seed germination of pearl millet (*Pennisetum typhoides*). By use of the blotter test method, three fungi species were detected predominantly *Alternaria alternata* (35.5%), *Fusarium semitectum* (33.5%), and *Curvularia lunata* (23.5%), and other species of mycoflora were less than 20%. The roll paper method for the germination test showed that the percentage of abnormal seedlings resulting from naturally infected seeds was higher than normal ones.

Seed health tests were conducted on sorghum and foxtail millet seeds collected from different growing areas in South Korea using dry inspection, standard blotter, and the agar plate method. Five dominant seed-borne fungi species (*Alternaria alternata*, *Aspergillus flavus*, *Curvularia lunata*, *Fusarium moniliforme,* and *Phoma* sp.) were observed in sorghum and four dominant species (*Alternaria alternata*, *Aspergillus flavus*, *Curvularia lunata*, *Fusarium moniliforme*) were recorded in foxtail millet. Inoculation of the dominant seed-borne fungi increased infected and dead seedlings and reduced the rate of seedling emergence (Yago et al. 2011). Wheat seeds tested with blotter test indicated the presence of field fungi was high initially in the storage, however, storage fungi were increased at the end of storage. The seed germination decreased as the storage duration increased (Habib et al. 2011).

4 Management of Seed-Borne Mycoflora

Crop seeds are subjected to pathogen attack during seed development and before or after harvest by many species of mycoflora. Seed-bearing pathogen serves as the primary source of infection and has a very important role in the epidemiology of the disease because it is a very effective means for transporting the pathogen over long distances (Dhakar et al. 2018). It is well-known that the seed-borne pathogen can affect seed quality, plant growth, and crop productivity. Therefore, preventive action must be taken to anticipate the spread of the disease.

The most basic seedborne disease management in the seed production chain is analyzing seed lots for the presence of pathogens. Langeraak (1998) suggested that management of seedborne disease includes: (1) prevention of seed infection or contamination during seed establishment, (2) control of pathogens from developing further in seeds after harvest, (3) prevention of contamination between seed lots during processing, packaging, storage, and distribution; (4) reduction of infection or contamination levels in infected seed lots (disinfection, eradication), (5) do not send infected seed lots to areas at risk of disease, (6) never use infected seeds in disease-free areas, (7) production of next-generation seeds from healthy seeds in

disease-free areas or areas with low disease incidence/frequency, (8) development and use of disease-resistant varieties, and (9) field inspection, roguing, disease and weed control. The most effective way to protect from seedborne diseases at an early stage is by detecting and controlling pathogens (Rai et al. 2020). Gupta and Kumar (2020) stated that strategies and techniques for disease management can be categorized into prevention and therapy or curative (treatment or cure). Prevention includes practices undertaken for the management of plant diseases before the infection occurs, whereas curative action refers to practices undertaken after the pathogen encounters. For example, quarantine helps in the prevention of disease in any region, whereas seed treatment help in the elimination of established phytopathogens.

Management of seed-borne mycoflora should be conducted from the beginning, that is, before planting. It is recommended to use certified seeds or a location free from major pathogens. Seed health testing should be done before planting by conducting direct and indirect observation of seed samples. Direct observation is carried out to examine the shape and color of seeds. Good seeds commonly perform a uniform shape dan color. Indirect observation is conducted through incubation with the blotter method, for instance. The result of seed health testing determines the seed treatment method used afterward. Seed treatment aims to reduce or eliminate seed-borne mycoflora, which consists of physical, chemical, and biological practices (Amza 2018). Seed health tests followed by appropriate seed treatments are effective strategies for controlling seed-borne pathogens (Gebeyaw 2020).

Seed-borne mycoflora can be divided into two categories, originating from the field and storage infestation (Amza 2018). In the field, the origin of seeds, soil microflora, and plant cultivation techniques are the factors that can be the source of seed-borne mycoflora, especially pathogenic fungi. Seed-borne mycoflora can be air-borne mycoflora after planting in the field and spreading. Storage mycoflora usually belongs to the saprophytic or weak pathogen group of fungi.

Hot water treatment included in physical seed treatment is an old practice. However, it is an efficient method to eliminate seed-borne pathogens both inside and on the surface of the seed and an eco-friendly control method. The temperature is hot enough to kill the pathogens but does not affect the germination of the seed, so the seed soaking duration depends on the crop and the type of the pathogen (Singh et al. 2020a, b). Hot water treatment of carrot seeds at 54 °C for 20 min controlled *Alternaria dauci* as the causal agent of *Alternaria* leaf blight without affecting germination and yield (Amza 2018; Singh et al. 2020a, b). Maize seeds of three varieties were evaluated on the major seed-borne mycoflora *Bipolaris maydis*, *Cuvularia lunata,* and *Fusarium*. Seeds treated with hot water at 50 °C provided the best results for controlling the fungal infections while improving seed germination percentages as compared to other hot water treatments of 45 °C and 55 °C and untreated (Rahman et al. 2008). Hot water treatment at 54 °C for 15 min also controlled the chili seed-borne fungi (Alam et al. 2014).

According to Ayesha et al. (2021), heat treatment has generally been used as a seed treatment that can eliminate some seed-borne pathogens without interfering with seed germination. Besides hot water treatment, physical treatment can be done through hot air, aerated steam, and radiation. Those treatments have been used to

eliminate seed-borne fungi in some crops, but the results are variable and, in some cases, inconsistent.

Seeds can also be treated with a microwave to combat seed-borne fungi. Szopinska and Dorna (2021) investigated the effect of dry and wet microwave treatments on carrot seeds cv. Amsterdam, the seeds were naturally infected with *Alternaria radicina* at 38% and seed germination was 50%. Microwave-wet treatment (the seeds were soaked in water) at different output levels (500 W, 650 W, 750 W) for 45–90 s, significantly reduced the infection. The germination percentages reached the highest from the 650 W for 45 s treatment (85%) followed by 500 W for 75 s (81%) and 750 W for 60 s (77%), and the water temperature in those microwave radiation treatments was 58, 66, and 67 °C, respectively.

Seed disinfectant treatment of soybean had proved to reduce the number of seeds contaminated with mycoflora. In non-treated soybean seeds, the number of seeds that were contaminated with fungi was 58.7%. The number of contaminated seeds was reduced to 4%, 14.7%, and 16.7% after treatment in hot water at 60 °C for 2 min, 2% calcium hypochlorite for 10 min, and 5% acetic acid for 2 min, respectively. The data showed a decrease of 93.2%, 74.9%, and 71.6% of the total initial seed-borne fungi due to treatment in hot water at 60 °C for 2 min, 2% calcium hypochlorite for 10 min, and acetic acid 5% for 2 min, respectively. Based on the data, physical seed treatment practice for soybean was soaking in hot water at 60 °C for 2 min, or chemical seed treatment such as soaking in 2% calcium hypochlorite for 10 min, or 5% acetic acid for 2 min were recommended as potential seed disinfection treatments for soybean seeds, which no effect to germination seeds (Escamilla et al. 2019). Six fungi species (*Aspergillus flavus*, *Rhizopus stolonifera*, *Colletotrichum capsici*, *Curvularia lunata*, *Alternaria alternata*, and *Fusarium moniliforme*) isolated from chili seeds were effectively suppressed in vitro by 3% hydrogen peroxide compared to lower concentration (1% and 2%). However, the highest seed germination and vigor index was obtained in 1% H_2O_2-treated chili seed (Nandi et al. 2017).

Rahim and Dawar (2012) treated lentil seeds with NaCl or KCl 0.1% (w/w) before storage. Both seed treatments were effective to combat storage fungi observed after up to 80 days of seed storage at room temperature of 25–30 °C. Sterilization of the seed surface with 1% $Na(OCl)_2$ reduced the infestation of the fungi. Although KCl was more effective than NaCl against *Aspergillus* spp., NaCl was the best in increasing seed germination as compared to KCl seed treatment and control.

Fungicides have been used routinely to control seed-borne fungi; sometimes, it is the cheapest and most effective in eliminating or inhibiting the growth of seed-borne fungi compared to other seed treatment methods (Ayesha et al. 2021). Three groups of fungicides are used as seed treatment based on their mobility. The first groups are fungicides that act by contact, the action is surface protectants of seed-borne and soil-borne pathogens. The second groups are locally systemic, surface, and internal seed-borne pathogens targeted. The third groups are xylem mobile and systemic translocation. The systemic fungicide, such as carboxin and thiabendazole reduced both seed-borne and soil-borne fungal pathogens. Besides that, some

fungicide seed treatments can improve seed emergence and plant vigor (Lamichhane et al. 2020).

Several mycoflora species infected the seeds of three rice cultivars in India. Seed treatment with 2 g carbendazim (kg seed)$^{-1}$ was more effective than mancozeb in inhibiting the seed-borne pathogen activity during the 9 months storage period. These chemicals possess antimicrobial agents hence the deterioration level in these treated seeds was less (Pedireddi et al. 2018). The incidences of downy mildew caused by *Peronosclerospora maydis*, seed-borne fungi in sweet corn grown in plastic-house and field experiments were reduced by seed treatment with synthetic fungicides combination of 3 g metalaxyl 25% (kg seed)$^{-1}$ and 5 g dimethomorf 60% (kg seed)$^{-1}$ (Sonhaji et al. 2013).

Working on lentil seeds, Hoque et al. (2014) found *Aspergillus flavus*, *A. niger*, *Penicillium* spp., and *Fusarium* spp. as seed-borne pathogens. Seed treatment with fungicide Secure 600 WG (0.2%) (fenamidone + mancozeb) was the most effective in controlling the fungi. Chaudhari et al. (2017) applied seed treatment on pigeon pea (*Cajanus cajan* L.) infected with several seed-borne mycoflora. A combination of metalaxyl and mancozeb 0.2% was the most effective seed treatment in improving seed germination and seedling vigor.

Complete elimination of seed-mycoflora through seed disinfectant seems impossible, so it has to be supported by other strategies such as Good Agriculture Practices/GAP (Amza 2018; Chang et al. 2020). Cultural management is one of the most critical factors in preventing disease in seed production, so good care and maintenance of the crops must be applied to obtain good seed quality.

5 Biological Seed Enhancement Treatment to Control Seed-Borne Mycoflora and Improve Seed Quality, Plant Growth, and Yield

Seed quality comprises genetic, physical, physiological, and pathological quality or seed health. The use of healthy seeds will result in healthy seedlings, good plant performance, and a high yield. On the other hand, unhealthy seeds or seeds with seed-borne pathogens may reduce seed viability, germination will fail or die. The seed germination may not be affected but the pathogens may develop and result in abnormal seedlings. One infected seed can infect many seedlings in the seedbed before being transplanted to the field. A few infected plants can be the source of inoculum to spread the disease to other plants. Therefore, the seed-borne pathogens must be eradicated by seed treatments before the seeds are used for planting. Many studies have been done on developing various seed enhancement treatments to control seed-borne mycoflora or fungi while improving seed vigor as well.

Biological seed treatments are an alternative to chemical seed treatments. Chemical seed treatments harm human health and the environment. Seed treatment using biological agents such as antagonists of the fungal pathogen in

seed-mycoflora has been developed as eco-friendly control management. *Trichoderma viride* was reported to eliminate seed-borne pathogens such as *Colletotrichum dematium, Alternaria alternata, and Phyllosticta cajani,* and reduce seed-borne saprophytic such as *Aspergillus flavus* (Amza 2018). According to Lamichhane et al. (2022), biological seed treatments significantly improve seed germination (7 ± 6%), seedling emergence (91 ± 5%), plant biomass (53 ± 5%), disease control (55 ± 1%), and crop yield (21 ± 2%) compared to untreated seeds.

Seed dressing with fungicides combined with natural bio-formulants such as *Pseudomonas, Trichoderma,* and rhizobia enhanced crops' field performance (Ayesha et al. 2021). Seed dressing of chili (*Capsicum annuum*) with *Trichoderma* and fungicide carboxin, metalaxyl, and carbendazim effectively reduced seed-borne mycoflora that were *A. flavus, A. niger, Colletotrichum capsici, Penicillium citrinum,* and *Fusarium annum.* Besides that, it also reduced soil-borne fungi and increased seed germination (Birla et al. 2020).

Ilyas et al. (2015) incorporated biological agents *Trichoderma harzianum* or *T. pseudokoningii* in matriconditioning, so-called biomatriconditioning, the best treatment to reduce *Colletotrichum capsici* contamination level. However, biopriming showed better than biomatriconditioning in improving percent germination and index of vigor. Biopriming with a mixture of *Bacillus polymixa* BG25 and *Pseudomonas fluorescens* PG01 reduced anthracnose disease incidence and improved plant growth, fruit yield, and seed quality of harvested seeds. According to Sutariati et al. (2014), biological seed treatment with *P. fluorescens* PG01 only or a mixture with *B. polymixa* BG25 led to the induction of resistance against *C. capsici*, as a result of the increase in peroxidase activity and phytoalexin biosynthesis that have been considered as resistance mechanisms against plant diseases. Amin et al. (2014) found that *Colletotrichum lindemuthianum* the seed-borne fungi causing anthracnose in common beans (*Phaseolus vulgaris* L.) was suppressed by bioagent seed treatments using either *Pseudomonas fluorescence*, *Trichoderma harzianum* or *Trichoderma viride*s. The lowest percentages of disease severity, disease incidence, and infected pods per plant, and the highest yield were shown by the *P. fluorescence* treatment. While the untreated plots had the maximum disease incidence and severity levels, and the lowest yield.

Mastouri et al. (2010) examined the effects of seed treatment with *T. harzianum* strain T22 on the germination of tomato seed cv. Jubilee. The seeds were treated with the conidial *T. harzianum* suspension of 2×10^7 CFU g^{-1} seed and then were exposed to biotic stress (seed and seedling disease caused by *Pythium ultimum*) and abiotic stresses (osmotic, salinity, chilling, or heat stress). The treated seeds germinated faster and more uniformly under abiotic stress and improved the seedling vigor of aged seeds. This study indicated that the beneficial fungi ameliorate both biotic and abiotic plant stresses.

Phytophthora capsici, a seed-borne, and soil-borne fungal pathogen is the cause of phytophthora blight on chili. The disease is difficult to control because of the resistant varieties' unavailability in Indonesia. From our study, *P. capsici* fungus was found in all samples of sick plants in several chili planting areas in East Java-Indonesia, and there were three rhizobacterial isolates (E1, E3C2, and F2B1), out of

78 isolates from rhizosphere soil and 174 isolates from the rhizoplane of the healthy plants, that can inhibit *P. capsici* in vitro (Zakia et al. 2018). Biopriming of chili seeds with the rhizobacteria combination of E1 + F2B1 isolates after transplanting was capable to improve plant growth and control phytophthora blight disease in the greenhouse while 800 ppm metalaxyl seed treatment did not effective (Zakia et al. 2017). Furthermore, seed coating and biopriming of the chili seeds with those rhizobacteria were able to maintain seed viability (79–89%) for 24 weeks of storage at 27–30 °C as compared to metalaxyl seed treatment that reduced the viability down to 54% (Madyasasi et al. 2017). And when the bioprimed seeds were planted after being stored for 7 months, the plant growth was increased although the soil was inoculated with *P. capsici*. Bioprimed or coated seeds reduced the disease incidence by 28.3% while metalaxyl did not (Hikmawati et al. 2019). Our previous studies also proved that biopriming with rhizobacteria isolated from healthy pepper (*Piper nigrum*) plants, reduced the phytophthora blight disease incidence as compared to metalaxyl treatment (Rosadiah et al. 2015; Ibrahim et al. 2014), and there was no significant difference whether the rhizobacteria applied singly or combination of two isolates (Rosadiah et al. 2015).

Biopriming of tomato seeds with a combination of ascorbic acid and antagonistic microbes *Trichoderma asperellum* BHU P-1 and *Ochrobactrum* sp. BHU PB-1 improved plant growth, increased total phenol and lignin content in the plant, and induced pathogenesis-related proteins' gene expression in response to the *Fusarium oxysporum* f. sp. *lycopersici* challenge, which reduced Fusarium wilt disease incidence in tomato (Singh et al. 2020a, b).

Another sustainable and environmentally safe approach for controlling seedborne fungal diseases is the use of natural products, especially plant-derived compounds. They have played a significant role in reducing the incidence of seedborne pathogens and improving seed quality and seedling establishment (Bello and Sisterna 2010). Chitosan, a natural product, is known to have antimicrobial properties and has been used to control fungi pathogens. *Jatropha curcas* seeds applied with chitosan before inoculating with *Fusarium equiseti* and *Curvularia lunata* inhibited their pathogenic activities without reducing seed germination (Pabón-Baquero et al. 2015). Chitosan and yeast elicitor at 2000 ppm are potential compounds for seed-priming biopolymer agents to control seed-borne fungi (*Aspergillus flavus, A. niger, Botrytis cinerea, Fusarium moniliforme, F. oxysporum, Phoma exigua, Rhizopus stolonifer*, *Macrophomina phaseolina, Penicillium* spp., *Curvularia lunata, Chaetomium spp., Colletotrichum* spp., *Cercospora* spp. and *Alternaria alternata*) of cucurbits (cucumber, bottle gourd, sweet gourd, snake gourd, wax gourd). The seeds were soaked for 2 h in chitosan or yeast elicitor solution at room temperature before sowing. Antimicrobial activity of chitosan resulting from positively charged amino groups that respond to negatively charged cell membranes of microorganisms. This reaction leads to the leakage of intracellular protein components and other microorganism components. Yeast extract may contain vitamin B complex and glucan that elicit plant defense responses by triggering metabolite synthesis (Tumpa et al. 2018).

Plant-derived compounds including plant extracts and essential oils have been known to have antifungal properties that are potentially used as seed treatment replacing synthetic fungicides to protect seeds against seed-borne pathogens. Among plant-derived products, essential oils are used widely as a method of controlling plant diseases. Major active compounds from essential oils are known to have broad-spectrum antifungal activity against plant pathogens (Bello and Sisterna 2010).

Seed treatment with some botanical extracts potentially proved to control seed-borne mycoflora. Gyasi et al. (2020) found that the effectivity of garlic (*Allium sativum*) aqueous extract (60% (w/v)) and mancozeb suspension was the same in eliminating *C. capsici* and *C. gloeosporioides* when the chili pepper seeds were soaked for 24 h. Ginger (*Zingiber officinale*) aqueous extract (60% (w/v)) was effective against seed-borne *Fusarium* and *Aspergillus* spp. whereas aqueous neem (*Azadirachta indica*) extract (60% (w/v)) was effective in controlling *A. flavus* and *A. niger*. Based on that result, garlic aqueous extract (60% (w/v)) can be used to control chili seed-borne fungi, replacing mancozeb (synthetic fungicide), so that to be an eco-friendly control method. Alam et al. (2014) studied some botanical seed treatments against chili seed-borne fungi, such as neem leaf extract (1:1 w/v), garlic clove extract (1:3 w/v), and ginger extract (1:2 w/v), and the result showed that three extracts eliminated *C. capsici* and *Fusarium moniliforme* seed-borne fungi. Besides that, neem leaf extract increased seed germination, healthy seedling, and seedling vigor. Working with pigeon pea seed, Chaudhari et al. (2017) showed that neem seed extract as well as *Trichoderma viride* were effective in reducing the seed-borne mycoflora and increasing seed germination and seedling growth. Investigating sunflower seeds, Afzal et al. (2010) found that *Azadirachta indica* and *Allium sativum* (0.015%) were the best antifungals against all the fungi tested (*Alternaria alternata* and *A. helianthi, Aspergillus flavus, A. fumigatus,* and *A. niger, Curvularia lunata, Drechslera tetramera*, *Fusarium solani,* and *F. moniliforme*, *Macrophomina phaseolina*, *Mucor mucedo, Penicillium* and *Rhizopus* spp.). Therefore, both plant extracts could substitute the systemic fungicides Topsin and Bayleton which were very effective in eradicating the phytopathogens.

Ilyas et al. (2015) found that matriconditioning using burned rice hull (65 mesh) plus 0.1% clove oil was the best seed enhancement treatment that significantly reduced infection levels of *C. capsici* in infected hot pepper seeds and increased the index of vigor and relative speed of germination. When clove leaf powder was used as a botanical fungicide integrated into matriconditioning it showed better for reducing the *C. capsici* infection level of hot pepper seeds than matriconditioning plus fungicide. This treatment also improved the storability of infected hot pepper seeds.

Gyasi et al. (2022) identified seed-borne fungi on 200 accessions of cowpea under cold storage at CSIR-Plant Genetic Resources Research Institute (PGRRI), Ghana. Amongst botanical fungicides which have an antifungal effect on the major seed-borne fungi of the cowpea seeds, the most effective one, *Aframomum melegueta* extract was highly recommended as a seed protectant. Mancini and Romanazzi (2013) revealed that among the plant extracts, thyme oil for seed treatment was

more frequently effective than other natural compounds against various seedborne pathogens in vegetable crops.

6 Concluding Remarks and Future Research

Seed is an effective medium in carrying the seed-borne mycoflora and infected other seeds, transmitting them through the plant and finally to the seeds. Infestation of mycoflora can also occur during harvest and post-harvest handling. Furthermore, mycoflora can be developed faster during the non-optimum storage condition, resulting in deteriorated or damaged seeds. The presence of mycoflora may cause abnormalities and failure in seed germination. If the germination is not affected, the fungi pathogens may show symptoms either at the vegetative or generative stage which cause yield reduction.

Among management strategies for controlling seed-borne mycoflora is an assessment of seed health to detect seed-borne pathogens. The blotter test and agar plate test are the most effective methods to detect seed-borne mycoflora. Determination of the seed's health status can be used as a guide to provide appropriate seed treatments. Chemical seed treatment is commonly used to combat seed-borne fungi. However, due to environmental safety or eco-friendly and sustainable considerations, the use of plant-derived protectants including plant extracts and essential oil, and biological agents increased. *Trichoderma* spp. are the most widely used biological agents to control seed-borne diseases, improve seed quality, plant growth promotion, and eventually increase yield. The efficacy of biological seed treatments needs to be investigated further on finding a more precise formula for application in the field on a large scale.

References

Abdulwehab SA, El-Nagerabi SAF, Elshafie AE (2015) Leguminicolous fungi associated with some seeds of Sudanese legumes. Biodiversitas 16:269–280. https://doi.org/10.13057/biodiv/d160223

Afzal R, Mughal SM, Munir M, Sultana K, Qureshi R et al (2010) Mycoflora associated with seeds of different sunflower cultivars and its management. Pak J Bot 42(1):435–445

Alam MZ, Hamim I, Ali MA, Ashrafuzzaman M (2014) Effect of seed treatment on seedling health of chili. J Environ Sci Nat Resour 7(1):177–181

Alemu K (2014) Seed-borne fungal pathogen associated with soybean (*Glycine max* L.) and their management in Jimma, Southwestern Ethiopia. J Biol Agric Healthcare 4(25):14–19

Amin A, Teshele J, Tesfay A (2014) Evaluation of bioagents seed treatment against *Colletotrichum lindemuthianum* in haricot bean anthracnose under field condition. Plant Sci 2(1):22–26. https://doi.org/10.12691/plant-2-1-5

Amza J (2018) Seed borne fungi; food spoilage, negative impact, and their management: a review. Food Sci Qual Manag. ISSN 2224-6088 (Paper) ISSN 2225-0557 (Online) Vol 81. Accessed 25 August 2020

Anwar SS, Riaz S, Ahmad CA, Subhani MN, Chattha MB et al (2013) Mycoflora associated with stored seeds of soybean. Mycopathologia 11(2):85–90

Ayesha MS, Suryanarayanan TS, Nataraja KN, Prasad SR, Shaanker RU (2021) Seed treatment with systemic fungicides: time for review. Front Plant Sci 12:654512. https://doi.org/10.3389/fpls.2021.654512

Baharudin SMR, Ilyas S, Purwantara A (2012) Isolasi dan identifikasi cendawan terbawa benih kakao hibrida. J Littri 18(1):40–46

Bello GD, Sisterna M (2010) Use of plant extracts as natural fungicides in the management of seedborne diseases. In: Arya A (ed) Management of Fungal Pathogens. CAB International, Wallingford, pp 51–68. ISBN-13: 978 1 84593 603 7

Birla M, Singh RK, Barade N (2020) Validation of detection techniques and management of seed-borne diseases of chili (*Capsicum annum*). J Pharmacogn Phytochem 9(6):168–171

Boufleur TR, Ciampi-Guillardi M, Tikami Í et al (2021) Soybean anthracnose caused by Colletotrichum species: Current status and future prospects. Mol Plant Pathol 22:393–409. https://doi.org/10.1111/mpp.13036

Chang X, Li H, Naeem M, Wu X, Yong T et al (2020) Diversity of the seedborne fungi and pathogenicity of Fusarium species associated with intercropped soybean. Pathogens 9:531. https://doi.org/10.3390/pathogens9070531

Chaudhari A, Sharma H, Jehani M, Sharma JK (2017) Seed mycoflora associated with pigeon pea [*Cajanus cajan* (L.) Millsp.], their significance and the management. J Pure Appl Microbiol 11(1):567–575

Dawar S, Kulsoom M, Rahim S (2015) Seed-borne fungi associated with cowpea (*Vigna unguiculata* L.) WALP. Int J Biol Biotechnol 12(4):565–569

De Silva DD, Crous PW, Ades PK, Hyde KD, Taylor PWJ (2017) Lifestyles of Colletotrichum species and implications for plant biosecurity. Fungal Biol Rev 31:155–168. https://doi.org/10.1016/j.fbr.2017.05.001

Dhakar H, Ratnoo RS, Jat A (2018) Detection and identification of seed borne mycoflora of wheat (*Triticum aestivum* L. em. The ll.) seed samples. J Pharmacogn Phytochem 7(3):3164–3170. www.phytojournal.com

Dias MD, Pinheiro VF, Café-Filho AC (2016) Impact of anthracnose on the yield of soybean subjected to chemical control in the north region of Brazil. Summa Phytopathol 42:18–23

Dias MD, Dias-Neto JJ, Santos MDM, Formento AN, Bizerra LVAS et al (2019) Current status of soybean anthracnose associated with *Colletotrichum truncatum* in Brazil and Argentina. Plan Theory 8(11):459. https://doi.org/10.3390/plants8110459

Escamilla D, Rosso ML, Zhang B (2019) Identification of fungi associated with soybeans and effective seed disinfection treatments. Food Sci Nutr 7:3194–3205

Gebeyaw M (2020) Review on: impact of seed-borne pathogens on seed quality. American Journal of Plant Biology 5(4):79–83. https://doi.org/10.11648/j.ajpb.20200504.11

Ghangaokar NM, Kshirsagar AD (2013) Study of seed-borne fungi of different legumes. Trends Life Sci 2(1):32–35

Gupta A, Kumar R (2020) Management of seed-borne diseases: an integrated approach. In: Kumar R, Gupta A (eds) Seed-borne diseases of agricultural crops: detection, diagnosis & management. Springer Nature, Singapore. https://doi.org/10.1007/978-981-32-9046-4_25

Gyasi E, Kwoseh C, Moses E (2020) Identification of seed-borne fungi of farmer-saved seeds of pepper and their control with some selected botanicals. Ghana J Agric Sci 55(1):43–53. https://doi.org/10.4314/gjas.v55i1.5

Gyasi E, Kotey DA, Adongo BA, Adams FK, Owusu EO et al (2022) Management of major seed-borne fungi of cowpea (*Vigna unguiculata* (L.) Walp) with four selected botanical extracts. Adv Agric 2022., Article ID 3125240:8. https://doi.org/10.1155/2022/3125240,8

Habib A, Sahi ST, Javed N, Ahmad S (2011) Prevalence of seed-borne fungi on wheat during storage and its impact on seed germination. Pak J Phytopathol 23(1):42–47

Hikmawati ANM, Ilyas S, Manohara D (2019) Efektivitas pelapisan rizobakteri pada benih cabai setelah disimpan dalam meningkatkan pertumbuhan tanaman serta mengendalikan penyakit busuk phytophthora. Bul Agrohorti 7(1):100–107. https://doi.org/10.29244/agrob.v7i1.24434

Hoque MA, Ali MA, Mahfuzul Haque AHM, Mehraj H, Jamal Uddin AFM (2014) Efficacy of some fungicides for the improvement of seed quality in lentil. Int J Sustain Crop Prod 9(3):22–26

Hussain A, Anwar SA, Sahi GM, Abbas Q, Imran (2009) Seed-borne fungal pathogens associated with pearl millet (*Pennisetum typhoides*) and their impact on seed germination. Pak J Phytopathol 21(1):55–60

Ibrahim A, Ilyas S, Manohara D (2014) Perlakuan benih cabai (*Capsicum annuum* L.) dengan rizobakteri untuk mengendalikan *Phytophthora capsici*, meningkatkan vigor benih dan pertumbuhan tanaman. Bul Agrohorti 2(1):22–30. https://doi.org/10.29244/agrob.2.1.22-30

Ilyas S, Asie KV, Sutariati GAK, Sudarsono (2015) Biomatriconditioning or biopriming with bio fungicides or biological agents applied on hot pepper (*Capsicum annuum* L.) seeds reduced seedborne *Colletotrichum capsici* and increased seed quality and yield. Acta Hortic 1105(13):89–96. https://doi.org/10.17660/ActaHortic.2015.1105.13

Jauhari C, Majid A (2019) Kajian jenis fungisida dan interval aplikasi terhadap perkembangan penyakit antraknosa pada kedelai. J Bioindustri 2(1):308–317

Kesho A, Abebe W (2020) Detection of seed-borne fungi associated with some cereals and legume crops of seeds grown in main season at Holetta Agricultural Research Center. Am J Life Sci 8(5):91–95. https://doi.org/10.11648/j.ajls.20200805.11

Lamichhane JR, You MP, Laudinot V, Barbetti MJ, Aubertot JN (2020) Revisiting sustainability of fungicide seed treatments for field crops. Plant Dis 104:610–623. https://doi.org/10.1094/PDIS-06-19-1157-FE

Lamichhane JR, Corrales DC, Soltani E (2022) Biological seed treatments promote crop establishment and yield: a global meta-analysis. Agron Sustain Dev 42:45. https://doi.org/10.1007/s13593-022-0076-z

Langeraak K (1998) Seedborne diseases in the 21st century: the economical importance and the role of the Plant Disease Committee of the International Seed Testing Association in their management. In: International workshop on seedborne diseases, 25–27 March 1998. Nagoya, pp 91–97

Madyasari I, Budiman C, Syamsuddin MD, Ilyas S (2017) Efektivitas seed coating dan biopriming dengan rizobakteri dalam mempertahankan viabilitas benih cabai dan rizobakteri selama penyimpanan. J Hort Indonesia 8(3):192–202. https://doi.org/10.29244/jhi.8.3.192-202

Mancini V, Romanazzi G (2013) Seed treatments to control seedborne fungal pathogens of vegetable crops. Pest Manag Sci 70:860–868. https://doi.org/10.1002/ps.3693

Manda RR, Pavithra G, Addanki VA, Srivastava S (2020) Anthracnose of *Capsicum annuum* L. (chili). Int J Curr Microbiol App Sci 9(11):749–756

Mastouri F, Björkman T, Harman GE (2010) Seed treatment with *Trichoderma harzianum* alleviates biotic, abiotic, and physiological stresses in germinating seeds and seedlings. Am Phytopathol Soc 100(11):1213–1221. https://doi.org/10.1094/PHYTO-03-10-0091

Mitra D, Mondal R, Khoshru B, Shadangi S, Mohapatra PKD, Panneerselvam P (2021) Rhizobacteria-mediated seed bio-priming triggers resistance and plant growth for sustainable crop production. Curr Res Microb Sci 2:100071

Naeem M, Li H, Yan L, Raza MA, Gong G et al (2019) Characterization and pathogenicity of Fusarium species associated with soybean pods in maize/soybean strip intercropping. Pathogens 8(4):245. https://doi.org/10.3390/pathogens8040245

Nandi M, Pervez Z, Alam MS, Islam MS, Mahmud MR (2017) Effect of hydrogen peroxide treatment on health and quality of chili. Int J Plant Pathol 8:8–13

Olesen MH, Carstensen JM, Boelt B (2011) Multispectral imaging as a potential tool for seed health testing of spinach (*Spinacia oleracea* L.). Seed Sci Technol 39:140–150

Pabón-Baquero D, Velázquez-del Valle MG, Evangelista-Lozano S, León-Rodríguez R, Hernández-Lauzardo AN (2015) Chitosan effects on phytopathogenic fungi and seed germination of

Jatropha curcas L. Revista Chapingo Serie Ciencias Forestales y del Ambiente 21(3):241–253. https://doi.org/10.5154/r.rchscfa.2014.10.051

Pedireddi UR, Rao LVS, Choudhary R, Patroti PD, Pallay S et al (2018) Effect of seed infection on seed quality and longevity under storage of three rice varieties produced at different environments. J Pharmacogn Phytochem 1(7):3289–3298

Pedrozo R, Little CR (2017) *Fusarium verticillioides* inoculum potential influences soybean seed quality. Eur J Plant Pathol 148:749–754

Rahim S, Dawar S (2012) Treatment of lentil (*Lens culinaris* L.) seeds with various concentrations of salts to check their efficiency against seed-borne mycoflora during storage. Arch Phytopathol Plant Prot 451(6):1891–1901. https://doi.org/10.1080/03235408.2012.718180

Rahim S, Dawar S (2015) Seed-borne mycoflora associated with okra [*Abelmoschus esculentus* (L.) MOENCH]. Pak J Bot 47(2):747–751

Rahman MME, Ali ME, Ali MS, Rahman MM, Islam MN (2008) Hot water thermal treatment for controlling seed-borne mycoflora of maize. Int J Sustain Crop Prod 3(5):5–9

Rai S, Kumar A, Singh IK, Singh A (2020) Seedborne disease and its management. In: Tiwari AK (ed) Advances in seed production and management. Springer, Singapore. https://doi.org/10.1007/978-981-15-4198-8_31

Ramdan EP, Kalsum U (2017) Inventarisasi cendawan terbawa benih padi, kedelai, dan cabai. J Pertanian Presisi 1(1):48–58

Rego CHQ, França-Silva F, Gomes-Junior FG, de Moraes MHD, de Medeiros AD, da Silva CB (2020) Using multispectral imaging for detecting seed-borne fungi in cowpea. Agriculture 10(8):361. https://doi.org/10.3390/agriculture10080361

Rosadiah FN, Ilyas S, Manohara D (2015) Perlakuan benih cabai (*Capsicum annuum* L.) dengan rizobakteri secara tunggal atau kombinasi dapat mengendalikan *Phytophthora capsici* dan meningkatkan pertumbuhan tanaman. J Hort Indonesia 6(1):1–10. https://doi.org/10.29244/jhi.6.1.1-10

Sahu D, Lakpale N (2020) Seed health evaluation of different varieties of lentil by incubation methods. Int J Chem Stud 9(1):416–421. https://doi.org/10.22271/chemi.2021.v9.i1f.11263

Sajeesh PK, Rao MSL, Jahagirdar S (2014) Molecular detection, transmission and histopathological studies of seed-borne fungal infection of soybean (*Glycine max* (l.) Merill). Bioscan 9(1):247–251

Saxena A, Raghuwanshi R, Gupta VK, Singh HB (2016) Chilli anthracnose: the epidemiology and management. Front Microbiol 7:1527

Singh P, Singh J, Ray S, Rajput RS, Vaishnav A, Singh RK, Singh HB (2020a) Seed biopriming with antagonistic microbes and ascorbic acid induce resistance in tomato against Fusarium wilt. Microbiol Res 237:126482. https://doi.org/10.1016/j.micres.2020.126482

Singh S, Singh H, Bharat NK (2020b) Hot water seed treatment: a review. https://doi.org/10.5772/intechopen.91314

Soesanto L, Hartono ARR, Mugiastuti E, Widarta H (2020) Seed-borne pathogenic fungi on some soybean varieties. Biodiversitas 21(9):4010–4015. https://doi.org/10.13057/biodiv/d210911

Sonhaji MY, Surahman M, Giyanto IS (2013) Perlakuan benih untuk meningkatkan mutu dan produksi benih serta mengendalikan penyakit bulai pada jagung manis. J Agron Indonesia 41(3):243–249. https://doi.org/10.24831/jai.v41i3.8103

Sutariati GAK, Widodo S, Ilyas S (2014) Biological seed treatment for controlling anthracnose disease of hot pepper. Int J Sustain Trop Agric Sci 1(1):29–43

Szopinska D, Dorna H (2021) The effect of microwave treatment on germination and health of carrot (*Daucus carota* L.) seeds. Agronomy 11(2):2571. https://doi.org/10.3390/agronomy11122571

Tsedaley B (2015) Review on seed health tests and detection methods of seed-borne diseases. J Biol Agric Healthcare 5(5) ISSN (Paper) 2224-3208 ISSN (Online) 2225-093X. Accessed 23 Aug 2022

Tumpa FH, Alam MZ, Hossen K, Khokon MAR (2018) Chitosan and yeast elicitor in suppressing seed-borne fungi of cucurbitaceous vegetables. J Bangladesh Agril Univ 16(2):187–192. https://doi.org/10.3329/jbau.v16i2.37959

Üstün R, Çat A, Çatal M, Uzun B (2021) Identification of seed-borne fungi on soybean (*Glycine max* L.) seeds grown in mediterranean region of Turkey. Turk J Agric Res 8(3):367–373. https://doi.org/10.19159/tutad.1014598

Welideniya WA, Rienzie KDRC, Wickramaarachchi WART, Aruggoda AGB (2019) Characterization of fungal pathogens causing anthracnose in capsicum pepper (*Capsicum annuum* L.) and their seed-borne nature. Ceylon J Sci 48(3):261–269. https://doi.org/10.4038/cjs.v48i3.7650

Yago JI, Roh J, Bae S, Yoon Y, Kim H, Nam M (2011) The effect of seed-borne mycoflora from sorghum and foxtail millet seeds on germination and disease transmission. Mycobiology 39(3):206–218. https://doi.org/10.5941/MYCO.2011.39.3.206

Zakia A, Ilyas S, Budiman C, Syamsuddin MD (2017) Peningkatan pertumbuhan tanaman cabai dan pengendalian busuk phytophthora melalui biopriming benih dengan rizobakteri asal pertanaman cabai Jawa Timur. J Hort Indonesia 8(3):171–182. https://doi.org/10.29244/jhi.8.3.171-182

Zakia A, Ilyas S, Budiman C, Syamsuddin MD (2018) Exploration and selection of rhizobacteria that inhibit *Phytophthora capsici in vitro*. J HPT Tropika 18(1):83–94. https://doi.org/10.23960/j.hptt.11883-94

Zanjare SR, Balgude YS, Zanjare SS, Suryawanshi AV, Shelar VR (2020) Detection of seed-borne myco-flora associated with cowpea (*Vigna unguiculata* L. Walp). Int J Chem Stud 8(1):1585–1587

Rhizosphere Mycobiome: Roles, Diversity, and Dynamics

Tarek A. A. Moussa, Akram H. Mohamed, and Mohamed S. Zaky

1 Introduction

A variety of fungi live in numerous compartment niches generated by plants, including the rhizosphere, endosphere, and phylloplane (Trivedi et al. 2020). The health, productivity, secondary metabolism, and biogeochemical cycling of plants are significantly influenced by a variety of interactions between these plant mycobiomes and their hosts (Vandenkoornhuyse et al. 2015; Frantzeskakis et al. 2020).

We are significantly less knowledgeable about the ecological characteristics of plant mycobiomes and their interactions with hosts, particularly in the context of coevolution, even though they are important, and fungi contribute more terrestrial biomass than bacteria do (Bar-On et al. 2018).

The evolutionary traits of plant-microbe interaction patterns have been studied very infrequently, even though many studies have estimated correlations between host evolutionary changes and microbiome variations to demonstrate evidence for phylosymbiosis (Vincent et al. 2016; Kim et al. 2020). The vast diversity of the microbial community and the intricacy of the underlying chemical pathways make this big (Upson et al. 2018). However, by focusing on whether bacteria that have been selected for or against different plant species are ecologically similar, we can simplify this investigation and arrive at a fundamental understanding because

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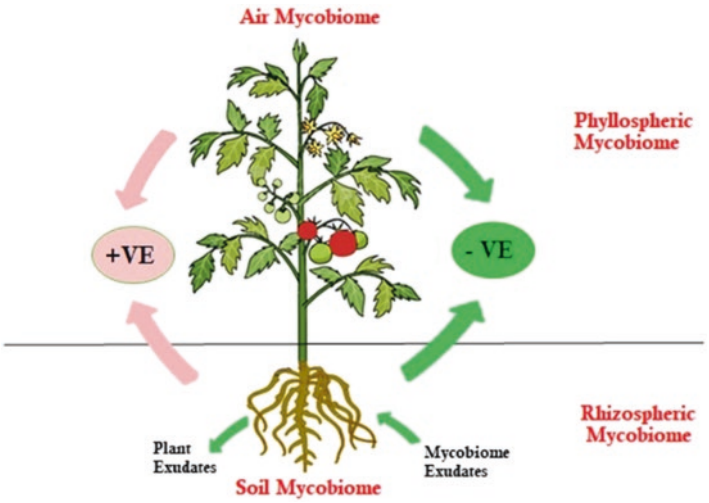

Fig. 1 The interaction of mycobiome with the plant

selection and exclusion of microbes are two important outcomes of plant-microbe interactions (Fig. 1).

2 Neutral Processes

The neutral model offers a powerful sampling theory-based tool to assess the relative importance of these ecological processes. The neutral model is used because it is straightforward and effective in simulating microbial communities, even though the basic idea of ecological equality between species seems overly straightforward (Zhou and Ning 2017). More importantly, this model may be used as a null model to derive particular hypotheses regarding the roles of those taxa by examining how microbial taxa differ from the neutral prediction (Burns et al. 2016).

The relative simplicity of neutral and other sampling-based theories makes them a good starting point for studying assembly patterns. The similar per-capita rates of species' development, death, and dispersal, which assume species are "neutral" in their ecological fitness, are the basis for the neutral theory, which gets its name. Without these distinctions, community assembly is the consequence of the stochastic processes of dispersal and drift, in which organisms in the community randomly die and are replaced by individuals from the same community or by individuals dispersing from another community. Neutral models have accurately predicted the patterns of many communities, including microbial communities, even though their ecological equivalency assumptions may seem oversimplified (Ofiţeru et al. 2010; Östman et al. 2010; Venkataraman et al. 2015). These models are especially helpful when simulating microbial systems, where the enormous diversity of communities makes it challenging to characterize the precise ecological characteristics of each

individual taxon. Additionally, they enable researchers to gauge the significance of processes like dispersal that are challenging to detect firsthand but can nevertheless have significant effects on microbial communities (Lindström and Östman 2011).

3 Selective Processes

3.1 The Biotic Effects Among Microbes

Rhizosphere and soil mycobiome interact with other soil species, therefore, changes in the microbial community may have an impact on how well the entire soil ecosystem functions (Yang et al. 2017). Mycologists must therefore evaluate the interactions between the mycobiome and other pedologic organisms in order to create a clear and complete picture of a soil and rhizosphere mycobiome community. Functional soil biodiversity and soil ecosystem function were found to be strongly correlated (Delgado-Baquerizo et al. 2017; Morriën et al. 2017).

3.1.1 Interaction with Other Microorganisms

The rhizosphere, where plant exudates are generated by roots and serve as the primary food supply for microorganisms as well as a driving force behind their population density and activities, is also thought to be a hot zone for interactions between microbial species of various genera. The rhizosphere not only harbors and suppresses the existence of numerous species that have a neutral effect on the plant, but it also draws in organisms that have both negative and positive effects on the plant. These interactions combined create a dynamic zone of microbial conflict. Many pathogenic fungi, oomycetes, bacteria, and nematodes are present in the rhizosphere and soil, which would negatively affect plant growth and the health of the soil due to their functions in antagonism, pathogenicity, decomposing plant wastes, and giving nutrients (Ehrmann and Ritz 2014).

There are a ton of taxonomically different organisms living in the rhizosphere. A huge number of taxonomically arranged fungi live in the rhizosphere, where they serve a crucial role in absorbing nutrients and giving resistance to pathogen invasion and other abiotic stresses related to the host crops (Stringlis et al. 2018; Pérez-Jaramillo et al. 2019). For instance, (AMF) arbuscular mycorrhizal fungi form mutualistic endosymbiosis with their particular host crop to improve disease resistance, as well as abiotic stressors within the host plant, and the absorption of mineral nutrients (mostly phosphate) (Akiyama et al. 2005; Luginbuehl et al. 2017; Wang et al. 2017; Jia-Dong et al. 2019; Gao et al. 2020). As symbiotic fungi, several Glomeromycota species, such as AMF, are regarded as natural biofertilizers that make up the mycorrhizosphere. On the other hand, some soilborne fungi have the ability to cause illness in crops because they are plant-pathogenic (Delgado-Baquerizo et al. 2020). Fungi-fungi interaction dynamics are recognized to perform significant symbiotic

microbial roles for supporting crop health and constitute a key component of the rhizosphere fungal community. Characterizing these interactions has provided fresh insight into how pathogen infection and AMF symbiosis work (Agler et al. 2016). But even though more research is needed, and we don't yet fully understand how fungi interact with one another in the rhizosphere, understanding the mechanisms underlying pathogen infection and AMF symbiosis would be of great importance.

Different roles are played by saprotrophic fungi and non-symbiotic microorganisms in the plant-soil compartment that is advantageous to both the plant and other microbes. Trichoderma species are commercial bio-fungicides, biofertilizers, and soil amendments in addition to being natural biocontrol agents (Harman et al. 2004; Vinale et al. 2008). Trichoderma is widespread and is the dominating species in various ecosystems across a wide range of climate zones. Furthermore, it is possible to isolate and recognize these adaptable fungi from various agricultural fields. Such species are influenced by a variety of variables, such as microclimate, substrate accessibility, and complex ecological relationships. The rhizosphere is a typically ecological soil niche where other soil fungi that can serve as their prey and rich plant root-derived material are also important factors (Kredics et al. 2014); However, it can also be separated from synthetic substrates when xenobiotics are present. Some species exist as plant endophytes, which promote plant development, lessen the impacts of drought stress, and shield plants from disease (Zaidi et al. 2014). Most soilborne pathogens are adapted to grow and survive in the bulk soil, but the rhizosphere also serves as the pathogen's play area and infection court as it forms a parasitic bond with the plant. The diverse rhizosphere community, which includes microflora and microfauna, engages in interactions with pathogens and influences the course of pathogen infection in the rhizosphere.

3.1.2 Plant Type Effect on Rhizosphere Community

Plant species have an impact on the rhizosphere's microbial population because when root exudates are released into the rhizoplane, many exoenzymes, fatty acids, chemotaxis, and secondary metabolites do as well (Hartmann et al. 2009). Roots offer a very attractive, nutrient-rich niche for microbes throughout the plant's life cycle and seasonal environment responses (Baetz and Martinoia 2014), where the interactions of both partners are also facilitated by the requirement for highly active transport of water and soluble molecules by roots, in addition to exudation of reactive carbon compounds and uptake of mobile nutrients and water (George et al. 2008; Hartmann et al. 2009). Plants have a significant impact on soil biology and structure in addition to being the main source of organic molecules, assisting in gas exchange, and reducing the need for inorganic fertilizers. Roots are thought of as the plant organs that typically harbor the largest numbers of microbes in the rhizosphere and rhizoplane due to the secretion of large amounts of exudates containing photosynthetically fixed carbon in the form of a wide range of molecules such as carbohydrates, amino acids, organic acid ions, and vitamins (Bais et al. 2006; Andreote et al. 2014).

Physical, chemical, and biological soil processes that support biodiversity enable soil carbon sequestration and cycle nutrients in natural and agricultural systems all depend heavily on the co-evolution of the rhizosphere and plant roots (Hinsinger et al. 2009; Lambers et al. 2009). The rhizosphere and soil mycobiome play essential roles in biogeochemical cycles, organic matter decomposition, plant growth, disease development, and control. Plant microbiota health and growth are closely linked to the rhizosphere and soil mycobiome, so the plant-rhizosphere system strongly influences the biomass and activity of soil mycobiome (Raaijmakers et al. 2009).

Because roots generate a variety of organic chemicals that contributed to a distinct rhizosphere nutrient pool that is available to soil microorganisms, it is hypothesized that plant-dependent fungal community diversity occurs in the rhizosphere (Han et al. 2017; Jiang et al. 2017). It is well known that changes in the rhizosphere fungal community are highly connected with soil's physical and chemical qualities (Schappe et al. 2017).

The impact of plant type on its rhizosphere microorganisms as a biotic factor impacting the soil mycobiome was examined in a dozen to hundreds of researches. The mycobiome composition in the rhizosphere is thought to be shaped and formed by changes in the pH and redox gradients as well as the available nutrients released by the plant, as the plants have an impact on soil microorganisms near their roots through the architecture of their roots, exudates, and mucilage (Bais et al. 2006; Badri and Vivanco 2009; Schmidt et al. 2011). The number of microorganisms that take advantage of the chemical changes near the roots and use these substances rises, and they often exhibit increased metabolic activity (Schreiter et al. 2014) (Table 1).

It is well known that the plant's endophytic microbiota is dynamically linked to the soil microbiomes in the rhizosphere and the rhizoplane surrounding it. However, despite the significance of the plant microbiome and its impact on the other soil microbiomes nearby, the rhizosphere mycobiome has only recently been

Table 1 Average maximum depth of rooting and depth of deepest root for 11 terrestrial biomes from Canadell et al. (1996)

Biome	Average maximum rooting depth (m)	Deepest root (m)
Tundra	0.5 ± 0.1	0.9
Boreal forest	2.0 ± 0.3	3.3
Cropland	2.1 ± 0.2	3.7
Temperate grassland	2.6 ± 0.2	6.3
Temperate deciduous forest	2.9 ± 0.2	4.4
Tropical deciduous forest	3.7 ± 0.5	4.7
Temperate coniferous forest	3.9 ± 0.4	7.5
Sclerophyllous shrubs and trees	5.2 ± 0.8	40.0
Tropical evergreen forest	7.3 ± 2.8	18.0
Desert	9.5 ± 2.4	53.0
Tropical grassland/savanna	15.0 ± 5.4	68.0

acknowledged as the second genome of plants themselves. The notion to incorporate the plant microbiome as a crucial component of plant breeding programs came about as a result of numerous recent research demonstrating the importance of the plant microbiome for plant development and health (Berendsen et al. 2012).

Conservative tillage, a widely used agricultural practice that alters soil texture and nutrient conditions as well as is confirmed to significantly modify the microbial community's composition in the soil, is a crucial mycobiome diversity determinant and effective factor. In order to shed light on the changes in the mycobiome during conservative tillage, high-throughput sequencing of the internal transcribed spacer (ITS) gene and quantitative PCR are now being used. Until now, it has been unclear how conservation tillage affects the rhizosphere and bulk soil fungal communities during plant growth. When compared to other tilling techniques, zero tillage greatly increased the variety of fungi in the bulk soil and rhizosphere. Additionally, there was a noticeable difference in the amount of fungal alpha diversity between the rhizosphere and bulk soils, with the latter showing the most diversity, even though tillage had no discernible impact during the blooming stage. The phylogenetic structure of the communities also showed this, with rhizosphere soil communities going through a higher transition from tillering to blooming than bulk soil communities. In summary, the alterations in soil characteristics brought on by plant development probably had an impact on the mycobiome populations of the soil under the plowing (Naumova et al. 2022).

3.2 The Abiotic Effects Among Microbes

3.2.1 Temperature, pH, and Moisture Effect on Mycobiome Diversity

Besides the cultivation types, soil profile, and surrounding microorganisms, climatic factors also have been proven to have a driving force on mycobiome diversity as well (Crowther et al. 2016; Newsham et al. 2016; Větrovský et al. 2019). Screening and surveying the whole soil mycobiome distribution on the planet earth didn't take much more concern due to the difficulties in unifying the sampling conditions everywhere, the tremendous amount of representative samples to all biogeographical regions needed to be captured, the process's cost, and time needed to accomplish sampling and data analysis… etc. (Bahram et al. 2018; Egidi et al. 2019; Větrovský et al. 2019). Recently several researchers exploited the HTS technique to end up the dominance of some fungal phyla on earth soil, mainly *Basidiomycota* and *Ascomycota* which is explained in reference to their capabilities to adapt and accommodate a wide range of climatic conditions, and on the other hand confirm the correlation between other phyla distributions according to the suitable climatic conditions (Maestre et al. 2015; Větrovský et al. 2019).

In order to capture the comprehensive attributes of the climatic factors on the mycobiome biodiversity, even to anticipate the upcoming mycobiome alteration combined with changing one factor or more of climatic ones, first, we have to deeply understand mycobiome communities. Understanding of mycobiome population

depends not only on its identification and classification, yet also, on studying its dynamics, functions, and roles in the ecosystem where they exist, all would have a great impact in visualizing and interpreting the full picture of the mycobiome community. Not only the prevalence of fungal species was correlated to the soil type and cultivation, but the climatic factors also showed to be as a driving factor of mycobiome biodiversity and determinant not only to the abundance but also to the community's function performance, so any proposed environmental changes lead to changes in biodiversity and functions of mycobiome (Fernandes et al. 2022).

In an attempt to understand the relationship between the environmental climatic factors and mycobiome population, so, screening of the metaproteomic of soil mycobiome in different environmental and climatic parameters across; forests, grasslands, and shrublands systems, the analysis led to the thorough functional profile of mycobiome in accordance to each and every ecosystem, where the forests had the highest protein intensity may due to the higher mycobiome abundance than another ecosystem, not only the environmental variable but also it was so clear that protein richness was linked to temperature, pH and moisture (Fernandes et al. 2022).

3.2.2 Soil Type as a Factor Affecting the Mycobiome Diversity

Out of being in a dynamic and complex biosphere system, soil as a component is a crucial parameter influencing the mycobiome biodiversity (Targulian et al. 2019). Activities and research conducted to investigate the soil mycobiome on-field conditions are not enough to unveil the whole soil's effects on its different types of mycobiome biodiversity (Schreiter et al. 2014). Each soil system is distinguished by its own unique chemical and physical structure, which lead to the alluring of a specific group of fungi sharing the same characteristics or life pattern as each definite soil ecosystem, and on the other side may repel away or suppress other fungal species to specific soil, such behavior would lead to the creation of soil-dependent mycobiome community (Neumann et al. 2014).

The soil profile including different texture layers, porosity, organic matter composition, and soil particle size, in addition to particle shape, altogether are representing a big impact on the soil living inhabitants and leads to specifying and shaping the rhizosphere mycobiome accordingly (Singh et al. 2007; Wang et al. 2009). It wasn't surprising to tell that microbial diversity increases with decreasing particle size and different organisms can occupy niches of different soil textures of specific particle size (Sessitsch et al. 2001).

In spite of its remarkable role in architecting the mycobiome, but it is still undetermined specifically the range to which the influences of soil on the mycobiome population on-field has reached, due to the multifactorial condition including the cultivated plant type, the irrigation system management, the climatic factors, fertilizers exposure history and protocol of cultivation, all sharing great impact on the mycobiome abundance, so it is hard to generalize the results of investigating a specific region to global scale (Costa et al. 2006, 2007). Many human activities like deforestation and reclamation also act as drivers for soil mycobiome diversity and abundance (Ceballos et al. 2015; Seddon et al. 2016).

4 Inferences in Microbial Community Assembly

Utilizing theoretical frameworks and statistical methods refined over years in community ecology. The complicated process of microbial community building is influenced by stochasticity, species diversity, and habitat filtering.

4.1 Community Assembly in Host-Associated Systems

Process-based modeling of biogeochemical cycles suffers from a critical information gap related to the collective effects of community assembly mechanisms (such as dispersal, drift, and selection) on microbial metabolism of carbon and nutrients in the environment. Rates of microbial metabolism may be impacted by both dispersal and selection. For instance, dispersal limitation can prevent the immigration of metabolic diversity and, in some cases, result in a maladapted and poorly functioning community (Lindström and Östman 2011; Hanson et al. 2012; Peres et al. 2016). Selection, on the other hand, can enhance metabolism via species-sorting mechanisms that optimize the microbiome for a given environment (Lindström and Langenheder 2012). Numerous spatiotemporal dynamics, such as the distance between communities, the rate of environmental change, and historical abiotic conditions, affect how much community assembly processes control metabolism (Graham et al. 2014, 2016; Nemergut et al. 2014; Hawkes and Keitt 2015). However, a conceptual framework for how various community-building mechanisms interact to affect microbial metabolism is still lacking (Gonzalez et al. 2012; Shade et al. 2013; Graham et al. 2016).

Processes of community assembly have an impact on community membership via geography and time, which then has an impact on microbial metabolism (Nemergut et al. 2013). For instance, taxa that are well suited to their environment and have high metabolic rates may exist in communities that have seen a history of strong and consistent selection. As an alternative, microbial taxa that degrade scarce resource pools and hinder community metabolic functioning may be eliminated by harsh, unrelenting selection (Knelman and Nemergut 2014). In this situation, it would be predicted that more diversified communities—those with higher rates of dispersal or opposing selected pressures, for example—would show higher and more dependable rates of metabolism than those shaped by a single dominating selective pressure. Lower rates of community metabolism can result from dispersal limitations that prevent organisms from reaching their ideal environments, whereas high rates of dispersal can either reduce or enhance microbial metabolism, depending on whether they allow for the immigration of organisms that are not adapted to their environment or increase biodiversity (Hooper et al. 2012; Nemergut et al. 2014).

4.2 Host Development

4.2.1 Metabolites

Phytohormone Production

Phytohormone production by rhizosphere mycobiome could be synthesized via tryptophan which is excreted as exudates from the host plant through the host-fungal symbiotic relationships (Bartel 1997; Zhao 2014). Eighty percent of rhizospheric microbes could produce auxins as secondary metabolites (Patten and Glick 1996).

Indole acetic acid (IAA) is the most abundant auxin that plays a crucial role in cell division and elongation, root systems induction, leaves development, plant flowering, and fruiting of the plant (Duca et al. 2014). This auxin is considered a key hormone that could control the synthesis of other phytohormones such as ethylene (Woodward and Bartel 2005). Rather than the role of IAA in cell division and elongation, it could alleviate salinity stress and induce plant defense system through cell-cell signaling (Wang et al. 2016, 2021). Fungi have the ability to the production of IAA via both tryptophan-dependent and independent pathways which are similar to that produced by plants (Tsavkelova et al. 2012).

Phosphate Solubilization

Phosphorus is one of the most limiting elements which is required for many vital plant physiological processes (Ha and Tran 2014). It resembles about 0.2–0.8% of plant dry weight (Sharma et al. 2013). Phosphorus is very important for plant cell viability as its included in nucleic acids, enzymes, coenzymes, nucleotides, and phospholipids as well as root growth, flower formation, and nitrogen fixation in legumes in addition to increasing the resistance of plants against to phytopathogens (Bechtaoui et al. 2019). It is found that phosphorus forms an insoluble complex with iron, aluminum, and calcium making it unavailable for plants. So, it's necessary to apply phosphate solubilizing microorganisms (PSM) to the soil to make phosphorus available to plants through different mechanisms such as lowering soil pH, chelation as well as mineralization (Kalayu 2019).

ACC Deaminase Production by Rhizospheric Fungi

ACC (1-aminocyclopropane-1-carboxylic acid) is the precursor of ethylene production which play a vital role in many physiological processes in plants such as leaves, flowers, and fruits development, although the production of ethylene hormone could suppress or minimize plant growth. As reported in many studies that Plant growth promoting fungi (PGPF) have the ability to the production of ACC deaminase which

acts on the ACC substrate and degrades it into NH_3 (ammonia) and α-ketobutyrate (Nascimento et al. 2014). So, Fungi producing ACC deaminase could regulate plant growth by cleaving the ACC and minimizing the ethylene level when its concentration exceeds the optimal levels. Acds gene which is responsible for the encoding of ACC deaminase production by *Trichoderma asperellum* T203 correlated with the high plant growth ability of this fungus, while when this gene is knocked out its plant growth-promoting ability decreased (Brotman et al. 2013; Glick 2014). In addition, ACC deaminase was reported in other fungi including *Penicillium citrinum* and *Phytophthora sojae* (Singh and Kashyap 2012). Interestingly, ACC deaminase-producing microorganisms gained competitive activity in the soil rhizosphere over the non-ACC–deaminase producers since ACC deaminase supports soil with nitrogen source as by-products of ACC cleavage (Nascimento et al. 2014).

5 Geographic Distribution

There are active and passive drivers that could lead to the mycobiome prevalence and abundancy somewhere over others, active ones include the fungal capability to spread and extend, the ability to adapt whatever the biogeographic and climatic factors, and finally the functioning performance, the other passive drivers recognized by long-distance wind dispersing mechanisms such as genera of *Alternaria, Cladosporium* and *Fusarium* (Pringle et al. 2016).

To a large extent, several fungal families are recognized as dependent on some hosts and counterparts, or even their existence limited to some conditions, or finite to some restrictions (Crowther et al. 2014). Much successive research hypothesized a coherent soil mycobiome network system, in addition to some fungal taxa propagations and prevalence covering a wide biogeographic range. For instance, genera of *Cladosporium*, and *Alternaria* accommodate and dominate different types of environments (Newsham et al. 2016), and the connected ground areas through neighbor continents ease the dissemination and invasion of some fungal families to accommodate vast areas of different ecosystems (Cox et al. 2016).

Universal dominant families and their characterization are of great importance to be understood could predict the mycobiome-ecosystem interactions and behavior in a different environment, in addition to the mycobiome pattern of feeding, breeding, and inhabits or even response to adverse events and harsh conditions (Peay et al. 2010). In accordance with their dynamic behavior and interaction activities with the surrounding organisms, any disturbance that appears in the mycobiome community may be reflected in the ecosystem functioning and stability (Hooper et al. 2012; Rivett and Bell 2018).

References

Agler MT, Ruhe J, Kroll S et al (2016) Microbial hub taxa link host and abiotic factors to plant microbiome variation. PLoS Biol 14:e1002352

Akiyama K, Matsuzaki K, Hayashi H (2005) Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature 435:824–827

Andreote FD, Gumiere T, Durrer A (2014) Exploring interactions of plant microbiomes. Sci Agric 71:528–539

Badri DV, Vivanco JM (2009) Regulation and function of root exudates. Plant Cell Environ 32:666–681

Baetz U, Martinoia E (2014) Root exudates: the hidden part of plant defense. Trends Plant Sci 19:90–98

Bahram M, Hildebrand F, Forslund SK et al (2018) Structure and function of the global topsoil microbiome. Nature 560:233–237. https://doi.org/10.1038/s41586-018-0386-6

Bais HP, Weir TL, Perry LG et al (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol 57:233–266

Bar-On YM, Phillips R, Milo R (2018) The biomass distribution on earth. Proc Natl Acad Sci 115:6506–6511

Bartel B (1997) Auxin biosynthesis. Annu Rev Plant Biol 48:51–66

Bechtaoui N, Raklami A, Tahiri A-I et al (2019) Characterization of plant growth promoting rhizobacteria and their benefits on growth and phosphate nutrition of faba bean and wheat. Biol Open 8. https://doi.org/10.1242/bio.043968

Berendsen RL, Pieterse CMJ, Bakker PAHM (2012) The rhizosphere microbiome and plant health. Trends Plant Sci 17:478–486

Brotman Y, Landau U, Cuadros-Inostroza Á et al (2013) Trichoderma-plant root colonization: escaping early plant defense responses and activation of the antioxidant machinery for saline stress tolerance. PLoS Pathog 9:e1003221. https://doi.org/10.1371/journal.ppat.1003221

Burns AR, Stephens WZ, Stagaman K et al (2016) Contribution of neutral processes to the assembly of gut microbial communities in the zebrafish over host development. ISME J 10:655–664

Canadell J, Jackson RB, Ehleringer JB et al (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583–595

Ceballos G, Ehrlich PR, Barnosky AD et al (2015) Accelerated modern human–induced species losses: entering the sixth mass extinction. Sci Adv 1:e1400253

Costa R, Salles JF, Berg G, Smalla K (2006) Cultivation-independent analysis of Pseudomonas species in soil and in the rhizosphere of field-grown Verticillium dahliae host plants. Environ Microbiol 8:2136–2149

Costa R, Gomes NCM, Krögerrecklenfort E et al (2007) Pseudomonas community structure and antagonistic potential in the rhizosphere: insights gained by combining phylogenetic and functional gene-based analyses. Environ Microbiol 9:2260–2273

Cox F, Newsham KK, Bol R et al (2016) Not poles apart: Antarctic soil fungal communities show similarities to those of the distant Arctic. Ecol Lett 19:528–536. https://doi.org/10.1111/ele.12587

Crowther TW, Maynard DS, Crowther TR et al (2014) Untangling the fungal niche: the trait-based approach. Front Microbiol 5:579. https://doi.org/10.3389/fmicb.2014.00579

Crowther TW, Todd-Brown KEO, Rowe CW et al (2016) Quantifying global soil carbon losses in response to warming. Nature 540:104–108. https://doi.org/10.1038/nature20150

Delgado-Baquerizo M, Powell JR, Hamonts K et al (2017) Circular linkages between soil biodiversity, fertility and plant productivity are limited to topsoil at the continental scale. New Phytol 215:1186–1196

Delgado-Baquerizo M, Guerra CA, Cano-Díaz C et al (2020) The proportion of soil-borne pathogens increases with warming at the global scale. Nat Clim Chang 10:550–554. https://doi.org/10.1038/s41558-020-0759-3

Duca D, Lorv J, Patten CL et al (2014) Indole-3-acetic acid in plant-microbe interactions. Antonie Van Leeuwenhoek 106:85–125. https://doi.org/10.1007/s10482-013-0095-y

Egidi E, Delgado-Baquerizo M, Plett JM et al (2019) A few Ascomycota taxa dominate soil fungal communities worldwide. Nat Commun 10:2369. https://doi.org/10.1038/s41467-019-10373-z

Ehrmann J, Ritz K (2014) Plant: soil interactions in temperate multi-cropping production systems. Plant Soil 376:1–29. https://doi.org/10.1007/s11104-013-1921-8

Fernandes MLP, Bastida F, Jehmlich N et al (2022) Functional soil mycobiome across ecosystems. J Proteome 252:104428

Frantzeskakis L, Di Pietro A, Rep M et al (2020) Rapid evolution in plant–microbe interactions–a molecular genomics perspective. New Phytol 225:1134–1142

Gao X, Guo H, Zhang Q et al (2020) Arbuscular mycorrhizal fungi (AMF) enhanced the growth, yield, fiber quality and phosphorus regulation in upland cotton (*Gossypium hirsutum* L.). Sci Rep 10:1–12

George TS, Gregory PJ, Hocking P, Richardson AE (2008) Variation in root-associated phosphatase activities in wheat contributes to the utilization of organic P substrates in vitro, but does not explain differences in the P-nutrition of plants when grown in soils. Environ Exp Bot 64:239–249

Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol Res 169:30–39. https://doi.org/10.1016/j.micres.2013.09.009

Gonzalez A, King A, Robeson MS II et al (2012) Characterizing microbial communities through space and time. Curr Opin Biotechnol 23:431–436

Graham EB, Wieder WR, Leff JW et al (2014) Do we need to understand microbial communities to predict ecosystem function? A comparison of statistical models of nitrogen cycling processes. Soil Biol Biochem 68:279–282

Graham EB, Crump AR, Resch CT et al (2016) Coupling spatiotemporal community assembly processes to changes in microbial metabolism. Front Microbiol 7:1949

Ha S, Tran L-S (2014) Understanding plant responses to phosphorus starvation for improvement of plant tolerance to phosphorus deficiency by biotechnological approaches. Crit Rev Biotechnol 34:16–30. https://doi.org/10.3109/07388551.2013.783549

Han L-L, Wang J-T, Yang S-H et al (2017) Temporal dynamics of fungal communities in soybean rhizosphere. J Soils Sediments 17:491–498

Hanson CA, Fuhrman JA, Horner-Devine MC, Martiny JBH (2012) Beyond biogeographic patterns: processes shaping the microbial landscape. Nat Rev Microbiol 10:497–506. https://doi.org/10.1038/nrmicro2795

Harman GE, Howell CR, Viterbo A et al (2004) Trichoderma species – opportunistic, avirulent plant symbionts. Nat Rev Microbiol 2:43–56. https://doi.org/10.1038/nrmicro797

Hartmann A, Schmid M, van Tuinen D, Berg G (2009) Plant-driven selection of microbes. Plant Soil 321:235–257. https://doi.org/10.1007/s11104-008-9814-y

Hawkes CV, Keitt TH (2015) Resilience vs. historical contingency in microbial responses to environmental change. Ecol Lett 18:612–625

Hinsinger P, Bengough AG, Vetterlein D, Young IM (2009) Rhizosphere: biophysics, biogeochemistry and ecological relevance. Plant Soil 321:117–152. https://doi.org/10.1007/s11104-008-9885-9

Hooper DU, Adair EC, Cardinale BJ et al (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108. https://doi.org/10.1038/nature11118

Jia-Dong H, Tao D, Hui-Hui W et al (2019) Mycorrhizas induce diverse responses of root TIP aquaporin gene expression to drought stress in trifoliate orange. Sci Hortic (Amsterdam) 243:64–69

Jiang Y, Li S, Li R et al (2017) Plant cultivars imprint the rhizosphere bacterial community composition and association networks. Soil Biol Biochem 109:145–155

Kalayu G (2019) Phosphate solubilizing microorganisms: promising approach as biofertilizers. Int J Agron 2019:4917256. https://doi.org/10.1155/2019/4917256

Kim H, Lee KK, Jeon J et al (2020) Domestication of Oryza species eco-evolutionarily shapes bacterial and fungal communities in rice seed. Microbiome 8:1–17
Knelman JE, Nemergut DR (2014) Changes in community assembly may shift the relationship between biodiversity and ecosystem function. Front Microbiol 5:424
Kredics L, Naeimi S, Manczinger L, Druzhinina IS (2014) Biodiversity of the genus hypocrea/trichoderma in different habitats. In: Gupta V (ed) Biotechnology and biology of trichoderma. Elsevier, Waltham
Lambers H, Mougel C, Jaillard B, Hinsinger P (2009) Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective. Plant Soil 321:83–115. https://doi.org/10.1007/s11104-009-0042-x
Lindström ES, Langenheder S (2012) Local and regional factors influencing bacterial community assembly. Environ Microbiol Rep 4:1–9
Lindström ES, Östman Ö (2011) The importance of dispersal for bacterial community composition and functioning. PLoS One 6:e25883
Luginbuehl LH, Menard GN, Kurup S et al (2017) Fatty acids in arbuscular mycorrhizal fungi are synthesized by the host plant. Science 356(80):1175–1178
Maestre FT, Delgado-Baquerizo M, Jeffries TC et al (2015) Increasing aridity reduces soil microbial diversity and abundance in global drylands. Proc Natl Acad Sci 112:15684–15689. https://doi.org/10.1073/pnas.1516684112
Morriën E, Hannula SE, Snoek LB et al (2017) Soil networks become more connected and take up more carbon as nature restoration progresses. Nat Commun 8:1–10
Nascimento FX, Rossi MJ, Soares CRFS et al (2014) New insights into 1-aminocyclopropane-1-carboxylate (ACC) deaminase phylogeny, evolution and ecological significance. PLoS One 9:e99168. https://doi.org/10.1371/journal.pone.0099168
Naumova N, Barsukov P, Baturina O et al (2022) Soil mycobiome diversity under different tillage practices in the south of West Siberia. Life 12:1169
Nemergut DR, Schmidt SK, Fukami T et al (2013) Patterns and processes of microbial community assembly. Microbiol Mol Biol Rev 77:342–356
Nemergut DR, Shade A, Violle C (2014) When, where and how does microbial community composition matter? Front Microbiol 5:497
Neumann G, Bott S, Ohler MA et al (2014) Root exudation and root development of lettuce (*Lactuca sativa* L. cv. Tizian) as affected by different soils. Front Microbiol 5:2
Newsham KK, Hopkins DW, Carvalhais LC et al (2016) Relationship between soil fungal diversity and temperature in the maritime Antarctic. Nat Clim Chang 6:182–186. https://doi.org/10.1038/nclimate2806
Ofiţeru ID, Lunn M, Curtis TP et al (2010) Combined niche and neutral effects in a microbial wastewater treatment community. Proc Natl Acad Sci 107:15345–15350
Östman Ö, Drakare S, Kritzberg ES et al (2010) Regional invariance among microbial communities. Ecol Lett 13:118–127
Patten CL, Glick BR (1996) Bacterial biosynthesis of indole-3-acetic acid. Can J Microbiol 42:207–220. https://doi.org/10.1139/m96-032
Peay KG, Garbelotto M, Bruns TD (2010) Evidence of dispersal limitation in soil microorganisms: isolation reduces species richness on mycorrhizal tree islands. Ecology 91:3631–3640. https://doi.org/10.1890/09-2237.1
Peres CA, Emilio T, Schietti J et al (2016) Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. Proc Natl Acad Sci 113:892–897
Pérez-Jaramillo JE, de Hollander M, Ramírez CA et al (2019) Deciphering rhizosphere microbiome assembly of wild and modern common bean (*Phaseolus vulgaris*) in native and agricultural soils from Colombia. Microbiome 7:114. https://doi.org/10.1186/s40168-019-0727-1
Pringle A, Brenner MP, Fritz JA et al (2016) Chapter 20 reaching the wind: boundary layer escape as a constraint on ascomycete spore dispersal. In: Dighton J, White JF (eds) The fungal community: its organization and role in the ecosystem, 4th edn. CRC, Boca Raton, pp 309–320

Raaijmakers JM, Paulitz TC, Steinberg C et al (2009) The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. Plant Soil 321:341–361. https://doi.org/10.1007/s11104-008-9568-6

Rivett DW, Bell T (2018) Abundance determines the functional role of bacterial phylotypes in complex communities. Nat Microbiol 3:767–772. https://doi.org/10.1038/s41564-018-0180-0

Schappe T, Albornoz FE, Turner BL et al (2017) The role of soil chemistry and plant neighbourhoods in structuring fungal communities in three Panamanian rainforests. J Ecol 105:569–579

Schmidt MWI, Torn MS, Abiven S et al (2011) Persistence of soil organic matter as an ecosystem property. Nature 478:49–56. https://doi.org/10.1038/nature10386

Schreiter S, Ding G-C, Heuer H et al (2014) Effect of the soil type on the microbiome in the rhizosphere of field-grown lettuce. Front Microbiol 5:144

Seddon N, Mace GM, Naeem S et al (2016) Biodiversity in the Anthropocene: prospects and policy. Proc R Soc B Biol Sci 283:20162094

Sessitsch A, Weilharter A, Gerzabek MH et al (2001) Microbial population structures in soil particle size fractions of a long-term fertilizer field experiment. Appl Environ Microbiol 67:4215–4224

Shade A, Gregory Caporaso J, Handelsman J et al (2013) A meta-analysis of changes in bacterial and archaeal communities with time. ISME J 7:1493–1506

Sharma SB, Sayyed RZ, Trivedi MH, Gobi TA (2013) Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils. Springerplus 2:587. https://doi.org/10.1186/2193-1801-2-587

Singh N, Kashyap S (2012) In silico identification and characterization of 1-aminocyclopropane-1-carboxylate deaminase from Phytophthora sojae. J Mol Model 18:4101–4111. https://doi.org/10.1007/s00894-012-1389-0

Singh BK, Munro S, Potts JM, Millard P (2007) Influence of grass species and soil type on rhizosphere microbial community structure in grassland soils. Appl Soil Ecol 36:147–155

Stringlis IA, Zhang H, Pieterse CMJ et al (2018) Microbial small molecules–weapons of plant subversion. Nat Prod Rep 35:410–433

Targulian VO, Arnold RW, Miller BA, Brevik EC (2019) Pedosphere☆. In: Second E (ed) Fath BBT-E of E. Elsevier, Oxford, pp 162–168

Trivedi P, Leach JE, Tringe SG et al (2020) Plant–microbiome interactions: from community assembly to plant health. Nat Rev Microbiol 18:607–621. https://doi.org/10.1038/s41579-020-0412-1

Tsavkelova E, Oeser B, Oren-Young L et al (2012) Identification and functional characterization of indole-3-acetamide-mediated IAA biosynthesis in plant-associated Fusarium species. Fungal Genet Biol 49:48–57. https://doi.org/10.1016/j.fgb.2011.10.005

Upson JL, Zess EK, Białas A et al (2018) The coming of age of EvoMPMI: evolutionary molecular plant–microbe interactions across multiple timescales. Curr Opin Plant Biol 44:108–116

Vandenkoornhuyse P, Quaiser A, Duhamel M et al (2015) The importance of the microbiome of the plant holobiont. New Phytol 206:1196–1206

Venkataraman A, Bassis CM, Beck JM et al (2015) Application of a neutral community model to assess structuring of the human lung microbiome. MBio 6:e02284–e02214

Větrovský T, Kohout P, Kopecký M et al (2019) A meta-analysis of global fungal distribution reveals climate-driven patterns. Nat Commun 10:5142. https://doi.org/10.1038/s41467-019-13164-8

Vinale F, Sivasithamparam K, Ghisalberti EL et al (2008) Trichoderma–plant–pathogen interactions. Soil Biol Biochem 40:1–10. https://doi.org/10.1016/j.soilbio.2007.07.002

Vincent JB, Weiblen GD, May G (2016) Host associations and beta diversity of fungal endophyte communities in New Guinea rainforest trees. Mol Ecol 25:825–841

Wang G, Xu Y, Jin J et al (2009) Effect of soil type and soybean genotype on fungal community in soybean rhizosphere during reproductive growth stages. Plant Soil 317:135–144

Wang S, Ren X, Huang B et al (2016) Aluminium-induced reduction of plant growth in alfalfa (Medicago sativa) is mediated by interrupting auxin transport and accumulation in roots. Sci Rep 6:30079. https://doi.org/10.1038/srep30079

Wang M, Weiberg A, Dellota E Jr et al (2017) Botrytis small RNA Bc-siR37 suppresses plant defense genes by cross-kingdom RNAi. RNA Biol 14:421–428

Wang Z, Wang M, Yang C et al (2021) SWO1 modulates cell wall integrity under salt stress by interacting with importin α in Arabidopsis. Stress Biol 1:9. https://doi.org/10.1007/s44154-021-00010-5

Woodward AW, Bartel B (2005) Auxin: regulation, action, and interaction. Ann Bot 95:707–735. https://doi.org/10.1093/aob/mci083

Yang T, Adams JM, Shi Y et al (2017) Soil fungal diversity in natural grasslands of the Tibetan Plateau: associations with plant diversity and productivity. New Phytol 215:756–765

Zaidi NW, Dar MH, Singh S, Singh US (2014) Chapter 38 – Trichoderma species as abiotic stress relievers in plants. In: Gupta VK, Schmoll M, Herrera-Estrella A et al (eds) . Elsevier, Amsterdam, pp 515–525

Zhao Y (2014) Auxin biosynthesis. Arab B 12:e0173. https://doi.org/10.1199/tab.0173

Zhou J, Ning D (2017) Stochastic community assembly: does it matter in microbial ecology? Microbiol Mol Biol Rev 81:e00002–e00017

Phyllosphere Mycobiome: Diversity and Function

Teng Yang, Chao Xiong, Jiayu Zhou, Wei Zhang, and Xin Qian

1 Introduction

Fungi are one of most fascinating and enigmatic kingdoms on earth. They occupy enormous habitats in both terrestrial and aquatic environments, driving biogeochemical cycling and influencing the structures of plant and animal communities (Peay et al. 2016; Grossart et al. 2019). Even in extreme ecosystems, such as deep-sea sediments, volcanic vents, and dry valleys of Antarctica, fungi are still the key players of biodiversity and biochemistry (Coleine et al. 2022). Benefiting from the development of high-throughput sequencing and omics technics, we are redrawing the atlas of fungal kingdom on their taxonomic and functional diversity (Nilsson et al. 2019; Fernandes et al. 2021; Tedersoo et al. 2022). For example, current estimates based on high-throughput sequencing suggest that there are at least 6.28 million fungal species on earth (Baldrian et al. 2021), which is larger than the total

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species number previously estimated. In addition, the continuously updated fungal databases of functional traits, such as FUNGuild (Nguyen et al. 2016b), Fun^{Fun} (Zanne et al. 2020), and FungalTraits (Põlme et al. 2021), are designed for rapid functional assignments and predicting how fungal functional diversity varies along certain environmental gradients. Nevertheless, many previous studies focus on the underground fungal diversity and biogeography (Tedersoo et al. 2014, 2021; van der Linde et al. 2018) and mycorrhizal functional ecology (Tedersoo et al. 2020; Tedersoo and Bahram 2019; Genre et al. 2020). The surfaces of phyllosphere fungal diversity and function are barely scratched, despite the highest proportion of unknown fungal species is assumed in plant tissues and lichens (Baldrian et al. 2021).

Phyllosphere is termed as the aerial habitat influenced by plants (Lindow and Leveau 2002), and generally includes the endosphere and episphere (i.e., surface) of plants tissues. In some cases, phyllosphere also includes stems, buds, flowers, and fruits (Whipps et al. 2008); however, most studies on phyllosphere microbiology focus on leaves, the most dominant plant aerial organ. It is estimated that the terrestrial leaf surface area is close to 10^9 km^2 (Lindow and Brandl 2003). Previously, researchers performed lots of work on bacterial diversity and function in phyllosphere (Lindow and Leveau 2002; Lindow and Brandl 2003; Remus-Emsermann and Schlechter 2018). This is because bacterial community is regarded as the most predominant component of phyllosphere microbial community by the traditional view. For example, based on culture method, bacterial cell number was found about 100-fold larger than fungal cell number in the unit weight of the blade (Yang et al. 2013b); however, the difference between phyllosphere bacteria and fungi was not significant at the diversity level (Xiong et al. 2021b; Wei et al. 2022). As far as phyllosphere microbial functions are concerned, both bacteria and fungi play the crucial roles in plant fitness, health, and productivity (Bashir et al. 2022; Xu et al. 2022a, b).

Compared with phyllosphere bacteria, phyllosphere fungi may have the larger differences in morphology, such as filamentous and yeast forms. Moreover, fungi are supposed to more actively enter the internal tissues of plants through leaf stomata or cuticle wounds. Consequently, a large quantity of case studies and reviews on phyllosphere fungi are at the scope of foliar endophytic fungi, including foliar endophytic fungal diversity and their interactions with plant health and fitness (Arnold 2007; Rodriguez et al. 2009; Busby et al. 2016). For example, Busby et al. exemplified foliar endophytic fungi to clarify how the plant microbiomes facilitate reforestation and serve in long-term forest carbon capture and the conservation of biodiversity (Busby et al. 2022). For leaf episphere, Gouka et al. reviewed the updated ecology and functional potential of yeasts; using genomic surveys, they proposed that we only scratched the surface of the largely unexplored functional potential of phyllosphere yeasts (Gouka et al. 2022).

Fungi exhibit a spectrum of life strategies among saprotrophy, mutualism (at most of the time, commensalism), and parasitism in phyllosphere (Schulz and Boyle 2005). At the alive state of leaves, endophytic and epiphytic fungi can mediate host plant growth and health by affecting plant physiology, development, and tolerance to biotic and abiotic stresses (Yang et al. 2013a, 2014; Busby et al. 2016; Costa Pinto et al. 2000; Khan et al. 2015). When leaves fall, some phyllosphere (epiphytic

and endophytic) fungi, as the pioneer decomposers of leaf litter, drive the degradation of leaves, and facilitate the nutrient reflux to plants or soil organic matter accumulation (Voriskova and Baldrian 2013; Unterseher et al. 2013; Chen et al. 2022; Osono 2006). Consequently, phyllosphere fungi play a predominant role in global carbon-nitrogen cycle, which has been largely ignored in the past. It is noted that foliar endophytic fungi, epiphytic fungi and both of them can be all termed as phyllosphere fungi. In some studies, epiphytic fungi are also termed as phylloplane fungi (Xiong et al. 2021a, b). The usage of aforementioned terms is determined by the pre-process methods of samples (e.g., leaf surface sterilization or not). Investigations at different compartments (e.g., endosphere vs. episphere) may lead to the distinctive diversity levels, community compositions, and co-occurrence patterns (Yao et al. 2019).

Albert Einstein once said that it is more important to ask a question than to solve it. Around phyllosphere mycobiome, there are many questions that await to be solved. On one hand, high diversity of phyllosphere mycobiome spawns a series of questions about biogeographic patterns, temporal dynamics, and community assembly processes. For example, what are the main environmental factors driving phyllosphere fungal diversity and community composition at different temporal and spatial scales? What are the relative contributions of stochastic and deterministic processes to fungal community assembly in phyllosphere? What are the proportions of phyllosphere fungal community originating from soil, air and water, respectively? On the other hand, the essential functions of phyllosphere mycobiome trigger us to think about the complicated interactions of phyllosphere mycobiome with plant health, changing environments and other biological communities. For example, what are the key functional traits and genes of phyllosphere fungi that can significantly enhance plant fitness and health? Whether do global change factors, such as warming and drought, break the balance of original relationships between phyllosphere fungi and host plants, or impair the beneficial effects of phyllosphere mycobiome? What are the potential roles of phyllosphere mycobiome in future global carbon cycling? By reading the chapter, we are confident that the readers will find most of the answers to the above questions.

2 High Diversity of the Phyllosphere Mycobiome

The phyllosphere supports a massive diversity of yeasts and filamentous fungi. Many of them are epiphytic and then become endophytic by entering the internal tissues. Some phyllosphere fungi could turn to pathogens (Behnke-Borowczyk et al. 2019; Lazarevic and Menkis 2020), while others have antagonistic capacities and influence plant performance (Bashir et al. 2022). Yeasts are the major fungal epiphytes, among which *Cryptococcus*, *Sporobolomyces* and *Rhodotorula* are the commonly occurring genera (Glushakova and Chernov 2004). Yeast-like fungus *Aureobasidium pullulans* is also frequently found in phyllosphere (Inacio et al. 2002). Compared to yeasts, most filamentous fungi tend to be endophytic and

commonly belong to *Acremonium*, *Alternaria*, *Aspergillus*, *Cladosporium*, *Mucor* and *Penicillium* (Bashir et al. 2022). Here, we summarize and compare the community composition and diversity of phyllosphere fungi from various plant species in different ecosystems, including natural ecosystems, agroecosystems, and urban ecosystems. We focus on the representative fungal taxa at genus level and summarize the fungal diversities in Table 1.

2.1 Natural Ecosystems

A natural ecosystem is a relatively stable ecosystem maintained by natural regulation within a certain time and space scale. On land, natural ecosystems mainly include forests, grasslands, deserts and wetlands. Among them, forests represent the highly productive ecosystem with hierarchical structure, numerous species and essential ecological functions (Baldrian 2017; Pan et al. 2011). Forests are mainly consisted of and represented by coniferous and broad-leaved trees, and thus the diverse phyllosphere fungi related to these tall trees are summarized at first.

Conifer needles are long lived and thus may harbor diverse fungal taxa (Millberg et al. 2015). *Pinus* is one of the most widely distributed coniferous trees. Previous studies showed that *Alternaria*, *Aspergillus*, *Cladosporium*, *Cryptococcus*, *Lophodermium*, *Penicillium* and *Sydowia* were the most observed fungal genera in *Pinus* (Lazarevic and Menkis 2020; Behnke-Borowczyk et al. 2019; Millberg et al. 2015; Agan et al. 2021; Sun et al. 2021b; Lynikiene et al. 2020; Oono et al. 2015). In these cases, *Cladosporium* and *Lophodermium* were commonly observed in the phyllosphere of *P. sylvestris*, which was one of the most naturally widespread *Pinus* species (Behnke-Borowczyk et al. 2019; Millberg et al. 2015; Agan et al. 2021; Lynikiene et al. 2020). Moreover, higher fungal diversity was observed in needles with disease symptoms compared to healthy ones of *P. sylvestris*, indicating the enrichment of plant pathogens or decomposers (Millberg et al. 2015). In addition, the phyllosphere fungal diversities of *Picea abies* (Nguyen et al. 2016a), *Picea glauca* (Eusemann et al. 2016) and *Sequoia sempervirens* (Harrison et al. 2016) were also investigated. Generally, *Cladosporium* is the most common fungal genus in the phyllosphere of coniferous trees according to our summary. *Alternaria*, *Aspergillus*, *Aureobasidium*, *Cryptococcus*, *Exobasidium*, *Lophodermium*, *Penicillium*, *Phoma*, *Sydowia* and *Taphrina* were frequently observed in phyllosphere as well.

Most of coniferous tree leaves remain alive and green all the year around. Moreover, some broad-leaved tree species are also evergreen or semi-evergreen. It is interesting to explore their phyllosphere fungal composition and to compare the common fungal genera in the phyllosphere of coniferous and these broad-leaved trees. *Euterpe oleracea* is an arborescent multiple stemmed palm with *Xylaria* and *Letendraeopsis* as the most common foliar endophytic fungi (Rodrigues 1994). Another study isolated and identified the phyllosphere fungal communities of five evergreen or semi-evergreen plant species (*Acer monspessulanum*, *Quercus faginea*,

Table 1 Phyllosphere fungal diversity and dominant genera of typical plant species across ecosystems

Ecosystems	Plant Species	Diversity Statistics	Dominant Genera[a]	Detection Methods	Target Regions	References
Natural ecosystems	*Pinus heldreichii*	254 genera (excl. singletons)	*Lophodermium*, *Sydowia*, *Cyclaneusma*, *Phaeosphaeria*	PacBio sequencing	ITS2	Lazarevic and Menkis (2020)
	Pinus massoniana	2127 OTUs (excl. singletons)	*Camptophora*, *Cryptococcus*, *Dictyochaeta*, *Meliniomyces*, *Pestalotiopsis*, *Proliferodiscus*	Illumina HiSeq sequencing	ITS2	Sun et al. (2021b)
	Pinus sylvestris	2429 OTUs (excl. singletons)/602 OTUs (excl. singletons)	*Alternaria*, *Aureobasidium*, *Cladosporium*, *Cryptococcus*, *Coleosporium*, *Curvibasidium*, *Cyclaneusma*, *Phaeococcomyces*, *Lophodermium*, *Sydowia*	PacBio sequencing/454 Pyrosequcing	ITS1/ITS2	Lynikiene et al. (2020) and Millberg et al. (2015)
	Pinus taeda	118 OTUs	*Anthostomella*, *Nemania*, *Nigrospora*, *Podospora*, *Septorioides*	Isolation, cultivation and identification/restriction fragment length polymorphism (RFLP)	ITS–LSU	Oono et al. (2015)
	Picea abies	1737 OTUs (excl. singletons)	*Aureobasidium*, *Celosporium*, *Cladosporium*, *Ceramothyrium*, *Chrysomyxa*, *Epicoccum*, *Phaeocryptopus*, *Sydowia*, *Taphrina*, *Tumularia*	454 pyrosequencing	ITS2	Nguyen et al. (2016a)
	Picea glauca	2009 OTUs	*Articulospora*, *Aureobasidium*, *Catenulostroma*, *Constantinomyces*, *Gyoerffiella*, *Lemonniera*, *Meristemomyces*, *Perusta*, *Pseudocercospora*, *Venturia*, *Xenomycosphaerella*, *Xenophacidiella*, *Zasmidium*	Illumina MiSeq sequencing	ITS1	Eusemann et al. (2016)
	Sequoia sempervirens	1274 OTUs	*Arthroderma*, *Aspergillus*, *Batcheloromyces*, *Caloplaca*, *Catenulostroma*, *Cladophialophora*, *Phaeomoniella*, *Readeriella*, *Taphrina*, *Teratosphaeria*	Illumina MiSeq sequencing	ITS1	Harrison et al. (2016)
	Fagus sylvatica	3713 OTUs/414 OTUs (excl. singletons)	*Aureobasidium*, *Cryptococcus*, *Lalaria*, *Mycosphaerella*, *Penicillium*, *Taphrina*, *Venturia*, *Woollsia*, *Sphaerulina*, *Trametes*	454 pyrosequencing/Illumina MiSeq sequencing	ITS1	Cordier et al. (2012a) and Siddique and Unterseher (2016)

(continued)

Table 1 (continued)

Ecosystems	Plant Species	Diversity Statistics	Dominant Genera[a]	Detection Methods	Target Regions	References
	Betula ermanii	1275 OTUs (excl. singletons)	*Sphaerulina*, *Cylindrium*, *Mrakiella*, *Venturia*, *Allantophomopsis*, *Epicoccum*, *Cladosporium*, *Alternaria*, *Aureobasidium*, *Hymenoscyphus*	454 pyrosequencing	ITS1	Yang et al. (2016b)
	Mussaenda shikokiana	792 OTUs	*Cryptococcus*, *Hannaella*, *Kockovaella*, *Periconia*, *Phomopsis*, *Phoma*, *Rhodotorula*, *Stagonospora*, *Strelitziana*, *Trichomerium*, *Trimmatostroma*	Illumina MiSeq sequencing	ITS2	Qian et al. (2018a)
	Catharanthus roseus	16 species	*Alternaria*, *Chaetomium*, *Colletotrichum*, *Fusarium*, *Lasiodiplodia*, *Phoma*	Isolation, cultivation and identification	ITS full length	Dhayanithy et al. (2019)
Agroecosystems	*Triticum aestivum*	278 OTUs (excl. singletons)/284 OTUs	*Alternaria*, *Arthrinium*, *Ascochyta*, *Bipolaris*, *Blumeria*, *Cladosporium*, *Cryptococcus*, *Dioszegia*, *Epicoccum*, *Fusarium*, *Penicillium*, *Rhodotorula*, *Sporobolomyces*, *Udeniomyces*, *Zymoseptoria*	454 pyrosequencing	ITS1/ITS2	Sapkota et al. (2015) and Karlsson et al. (2017)
	Oryza sativa	45 OTUs	*Aspergillus*, *Bipolaris*, *Bullera*, *Cryptococcus*, *Curvularia*, *Eupenicillium*, *Fusarium*, *Hannaella*, *Hypocrea*, *Isaria*, *Leptosphaerulina*, *Metschnikowia*, *Meyerozyma*, *Penicillium*, *Pseudozyma*, *Sporidiobolus*, *Sporobolomyces*, *Trichoderma*, *Wickerhamomyces*	Restriction fragment length polymorphism (RFLP)	D1-D2 (LSU)	Nasanit et al. (2015)
	Vitis vinifera	897 OTUs for ITS2 and 615 OTUs for D2	*Alternaria*, *Aureobasidium*, *Cladosporium*, *Cryptococcus*, *Davidiella*, *Didymella*, *Endoconidioma*, *Lewia*, *Pleospora*, *Ustilago*	Illumina MiSeq sequencing	ITS2 and D2 (LSU)	Castaneda et al. (2018)
	Brassica oleracea	2038 ASVs	*Alternaria*, *Cystofilobasidium*, *Filobasidium*, *Papiliotrema*, *Purpureocillium*, *Sporobolomyces*	Illumina MiSeq sequencing	ITS2	Kim and Park (2021)
	Lactuca spp.	5 genera	*Cladosporium*, *Cryptococcus*, *Lewia*, *Sporobolomyces*, *Tilletiopsis*	Terminal restriction fragment length polymorphism (TRFLP)	ITS full length	Hunter et al. (2015)
	Cucurbita moschata	399 OTUs	*Alternaria*, *Aureobasidium*, *Davidiella*, *Leptosphaerulina*, *Peniophora*, *Phoma*, *Podosphaera*, *Pseudozyma*, *Rhodotorula*, *Strelitziana*	Illumina MiSeq sequencing	ITS1	Zhang et al. (2018d)

	Solanum lycopersicum	413 OTUs	*Bullera*, *Cladosporium*, *Curvularia*, *Dioszegia*, *Hannaella*, *Moesziomyces*, *Nigrospora*, *Papiliotrema*, *Pseudozyma*, *Saitozyma*,	Illumina MiSeq sequencing	ITS1	Toju et al. (2019)
	Atractylodes lancea	15 genera	*Absidia*, *Acremonium*, *Alternaria*, *Aspergillus*, *botrytis*, *Cephalosporium*, *Curvularia*, *Fusarium*, *Gilmaniella*, *Gliocladium*, *Mucor*, *Penicillium*, *Verticillum*	Isolation, cultivation and identification	SSU	Yang et al. (2013b)
Urban ecosystems	*Quercus macrocarpa*	1232 OTUs	*Alternaria*, *Aureobasidium*, *Cladosporium*, *Davidiella*, *Didymella*, *Epicoccum*, *Erysiphe*, *Mycosphaerella*, *Neofabraea*, *Sporobolomyces*	454 pyrosequencing	ITS1	Jumpponen and Jones (2010)
	Betula pendula	246 OTUs	*Pseudomicrostroma*, *Taphrina*, *Microstroma*, *Aureobasidium*, *Kondoa*, *Ampelomyces*, *Microstromatales*, *Exobasidium*, *Cephalosporium*, *Knufia*	Illumina MiSeq sequencing	ITS full length	Ivashchenko et al. (2022)
	Cinnamomum camphora	5132 OTUs	*Mycosphaerella*, *Zasmidium*, *Trimmatostroma*, *Epicoccum*, *Paraconiothyrium*, *Phoma*, *Cryptococcus*, *Villosiclava*, *Pholiota*, *Preussia*	Illumina MiSeq sequencing	ITS2	Tan et al. (2022)
	Lycoris radiata	27 species	*Colletotrichum*, *Fusarium*, *Gibberella*, *Glomerella*, *Phyllosticta*, *Stagonosporopsis*	Isolation, cultivation and identification	ITS full length	Zhou et al. (2020)

[a]For most studies, approximately ten most abundant fungal genera were listed. For some plant species, several studies were performed, so the most abundant fungal genera overlapped in the studies were listed. *OTUs* operational taxonomic units, *ASVs* amplicon sequence variants

Cistus albidus, *Pistacia lentiscus* and *Osyris quadripartita*) in a mediterranean-type ecosystem; they found that *Alternaria*, *Aureobasidium*, *Cladosporium* and *Penicillium* could be recovered from the leaf samples (Inacio et al. 2002). These four fungal genera were also frequently observed in the phyllosphere of coniferous species, indicating the long-life leaves might harbor the similar fungal taxa.

Although the leaves of some broad-leaved trees are evergreen or semi-evergreen, the leaves of most broad-leaved trees sprout in spring and fall in autumn. Thus, it is interesting to investigate whether these broad-leaved trees harbor different phyllosphere fungal communities compared to evergreen coniferous and broad-leaved trees. Some studies investigated phyllosphere fungal communities of *Fagus sylvatica* and showed that *Mycosphaerella* and *Pseudocercospora* were commonly observed in the phyllosphere (Cordier et al. 2012a, b; Siddique and Unterseher 2016; Unterseher et al. 2016). Other studies surveyed the phyllosphere fungal communities of more deciduous broad-leaved tree species, such as *Betula ermanii* (Yang et al. 2016b), *Mussaenda shikokiana* (Qian et al. 2018a), and *Swida controversa* (Osono and Mori 2005). Summarily, *Cladosporium* and *Phoma* were the most common fungal genera in the phyllosphere of deciduous broad-leaved trees according to our review. Moreover, *Alternaria*, *Aureobasidium*, *Cryptococcus*, *Mycosphaerella*, *Penicillium* and *Pseudocercospora* were frequently observed. Although the life cycles of evergreen and deciduous trees are quite different, they harbor the similar fungal taxa in their phyllosphere.

Besides trees, phyllosphere fungal diversities of shrubs and herbs were explored as well. For *Catharanthus roseus* in the coastal areas, *Alternaria*, *Cophinforma* and *Colletotrichum* were the only three fungal genera isolated from the sterilized leaves (Dhayanithy et al. 2019). The phyllosphere yeast populations of *Oxalis acetosella* were dominated by *Cystofilobasidium*, *Cryptococcus*, *Rhodotorula*, and *Sporobolomyces* (Glushakova and Chernov 2004).

Summarily, *Cladosporium* was the most common fungal genus in the phyllosphere of both coniferous and broad-leaved trees, which was not commonly observed in shrubs and herbs. This difference may be due to different sunshine conditions - the leaves of trees were commonly sampled from the canopy, while the leaves of shrubs and herbs most occupy the shade. In addition, *Alternaria* was frequently observed in the phyllosphere of trees and shrubs, while *Cryptococcus* was frequently observed in the phyllosphere of trees and herbs. It indicates some fungal taxa may horizontally transfer among different plant species. It is worth noting that different plant lineages harbor specific phyllosphere fungal taxa. Various morphological and metabolic characteristics of host plants' leaves may be one of important reasons behind the aforementioned patterns.

2.2 Agroecosystems

Agriculture practices can significantly influence phyllosphere fungal diversity and function. For example, conventional and organic agricultural management differentially affected the fungal community composition on the leaves of grapevines

(Castaneda et al. 2018). Organic farming could increase fungal richness in the phyllosphere of *Triticum aestivum* (Karlsson et al. 2017). Fungicide negatively affected the fungal richness and evenness as well as significantly changed the fungal composition in the phyllosphere of *T. aestivum* (Karlsson et al. 2014). Moreover, agroecosystems are supposed to harbor different fungal taxa compared to natural ecosystems. Recent studies showed that phyllosphere mycobiome is very important to crop health and growth (Sapkota et al. 2015). Thus, understanding the diversity of phyllosphere mycobiome in agroecosystems is crucial to develop new strategies for improving crop growth and adaptation.

In particular, phyllosphere fungal diversity in cereals has been largely explored, considering their importance to global food production. The phyllosphere mycobiome of *Avena sativa*, *Hordeum vulgare*, *Secale cereale*, *T. aestivum* and *Triticum* × *Secale* were explored, and 20 fungal genera were observed in phyllosphere (Sapkota et al. 2015). Each genus was observed at least in two plant species, indicating the possibility of core fungal community in the phyllosphere of diverse cereals. Among them, *Cladosporium* and *Cryptococcus* were the most common genera observed in the phyllosphere of *T. aestivum* (Karlsson et al. 2014, 2017; Larran et al. 2007; Sapkota et al. 2015). Other studies focused on the fungal diversity in the phyllosphere of *Oryza sativa*, the major cereal in Asia. For example, Venkatachalam et al. isolated and identified two morphologically different fungal strains, belonging to *Bipolaris* and *Curvularia* (Venkatachalam et al. 2016). Mwajita et al. showed that *Penicillium*, *Aspergillus* and *Trichoderma* were the common genera in the phyllosphere of *O. sativa* (Mwajita et al. 2013). Nasanit et al. focused on the epiphytic yeast diversity in *O. sativa*; they found that *Bullera*, *Pseudozyma* and *Cryptococcus* were the most common genera (Nasanit et al. 2015). The fungal genera observed in the aforementioned three studies were quite different; the reason may be the significant biogeographic isolation of phyllosphere fungal communities between nations that were revealed by culturable methods.

In addition, some studies explored the phyllosphere fungal communities across different grape species. For example, Singh et al. surveyed the fungal community composition in the phyllosphere of *Vitis pentagona*, *Vitis riparia*, *Vitis vinifera*, *Muscadinia rotundifolia* and *Parthenocissus quinquefolia* by Illumina MiSeq sequencing; they found that *Alternaria*, *Aureobasidium*, *Cladosporium* and *Lachnum* were the most abundant genera observed (Singh et al. 2019). *Alternaria*, *Davidiella* and *Didymella* were most abundant in the phyllosphere of Carménère grapevines (*V. vinifera*) (Castaneda et al. 2018). Moreover, the study showed that the diversity of phyllosphere fungi were highest in the wild, lowest in the conventional, and intermediate in the organic vineyard, respectively (Kernaghan et al. 2017). According to these studies, *Alternaria* was the most common fungal genus in the grape phyllosphere.

Besides cereals and fruits, vegetables are also important crops in agroecosystems. Kim and Park surveyed the fungal diversity in phyllosphere of preharvest and postharvest broccoli (*Brassica oleracea* var. italic); they found that *Cystofilobasidium* and *Purpureocillium* were the representative genera in phyllosphere of preharvest broccoli, while *Filobasidium* and *Sporobolomyces* were the most abundant genera

in the phyllosphere of postharvest broccoli (Kim and Park 2021). Another study surveyed 26 lettuce (*Lactuca* spp.) accessions and showed that *Sporobolomyces* and *Cladosporium* were the two dominant genera with significant different abundances among accessions (Hunter et al. 2015). In addition, the researchers analyzed the fungal diversity in the phyllosphere of pumpkin (*Cucurbita moschata*) showing powdery mildew symptoms; they found besides *Podosphaera* (the plant pathogen), *Alternaria*, *Aureobasidium* and *Davidiella* were the most observed genera (Zhang et al. 2018d). Toju et al. surveyed the leaf endophytic fungal community of tomato (*Solanum lycopersicum*) and found that *Cladosporium*, *Dioszegia* and *Moesziomyces* were the most frequently observed genera (Toju et al. 2019).

Moreover, many studies were performed on the phyllosphere mycobiome of medicinal plants, considering their contributions to human health. *Atractylodes lancea* is a traditional Chinese medicinal plant with abundant bioactive terpenoids. *Acremonium*, *Fusarium* and *Penicillium* were the most abundant fungal genera in the phyllosphere of *A. lancea*; besides, some special fungal genera, such as *Absidia*, *Gilmaniella* and *Verticillum*, were also observed in phyllosphere (Yang et al. 2013b). *Ginkgo biloba* is one of the most distinctive trees with an important position in plant evolution, and its dry leaves have multiple medicinal values (Lin et al. 2022). In the leaf interiors of *G. biloba*, *Alternaria*, *Colletotrichum*, *Fusarium* and *Phomopsis* were the most dominant fungal genera (Xiao et al. 2013). For the traditional Brazilian medicinal plant, *Solanum cernuum*, the dominant phyllosphere fungal genera differed between seasons: *Colletotrichum*, *Coprinellus* and *Phoma* were most frequently observed in summer; while *Arthrobotrys*, *Colletotrichum*, *Glomerella*, *Diatrypella*, and *Mucor* were most frequently observed in winter (Vieira et al. 2012). It is noteworthy that medicinal plants tend to harbor special fungal genera in their phyllosphere, which may facilitate the synthesis and accumulation of special bioactive secondary metabolites (Yang and Dai 2013).

Summarily, *Alternaria*, *Cladosporium* and *Cryptococcus* were frequently observed in both natural and agricultural ecosystems. However, *Exobasiduim, Lophodermium* and *Sydowia* were only enriched in natural ecosystems. The phyllosphere of agricultural crops, especially vegetables, harbored some unique fungal taxa, such as *Dioszegia* and *Sporobolomyces*, indicating the interactive effects of agriculture practices and plant species identity. In addition, for most cases, the observed numbers of genera and OTUs in agroecosystems were lower than those in natural ecosystems (Table 1).

2.3 Urban Ecosystems

With an increase in human population, urban area is expanding rapidly. Compared to other ecosystems, urban microbial communities are largely affected by anthropogenic activities, land management, urban heat island effect and air pollution (Perreault and Laforest-Lapointe 2022). For example, *Q. macrocarpa* is a native tree species in Manhattan and often used as an ornamental tree. Fungal richness and

other diversity indices in the phyllosphere of *Q. macrocarpa* grown in urban areas were lower than those trees grown in nonurban areas (Jumpponen and Jones 2009), and half of the phyllosphere fungal genera showed distinct and significant seasonal dynamics (Jumpponen and Jones 2010).

Many plant species are cultivated in urban area to purify the air and improve the environment. Some of them could release fragrant and antimicrobial volatiles. *Eucalyptus citriodora* is a widely cultivated tree in Indian cities; *Cladosporium* was dominant in its phylloplane, while *Botrytis* was dominant in its leaf interiors (Kharwar et al. 2010). For *Populus balsamifera* grown in a garden, *Leptosphaerulina* was dominant in the phyllosphere (Balint et al. 2013). Moreover, some flowers were also common ornamental plants cultivated in urban ecosystems, and their phyllosphere mycobiome were explored as well, such as *Camellia japonica* (Osono 2008) and *Lycoris radiata* (Zhou et al. 2020). Among their phyllosphere fungi, *Colletotrichum* was the genus observed in both of the two flowers.

Some studies revealed that the plants grown in polluted areas could harbor more pollutant-degrading microbes. For example, aromatic hydrocarbon (AH) degrading fungi were enriched in the phyllosphere of *Ixora chinensis*, *Ervatamia divaricata*, *Hibiscus rosa-sinensis* and *Amaranthus cruentus*, which were grown on the roadsides of polluted areas (Undugoda et al. 2016). Fungal communities in the phyllosphere of *Cinnamomum camphora* were surveyed in urban, suburban and rural area. The results showed that the fungal diversity was highest in the suburban areas and was strongly affected by the polycyclic aromatic hydrocarbon (PAH) concentrations (Tan et al. 2022); among the ten most abundant fungal genera, *Mycosphaerella*, *Zasmidium*, *Trimmatostoma*, *Epicoccum* and *Paraconiothyrium* were common in rural and suburban area, and *Phoma* was common in urban area.

Generally, all these studies showed that urban ecosystem could harbor special fungal taxa, and their enrichment was related to the environmental pollution induced by urbanization. In summary, common fungal genera could be observed in the phyllosphere of all the three ecosystems, but their abundances varied significantly. Thus, different ecosystems could enrich different fungal genera, indicating that different dominant environmental factors constrain and shape the fungal diversity and community composition accordingly.

3 Fungal Biogeographic Patterns in Phyllosphere

Fungal biogeography is the study of distribution of fungal diversity over space and time; the subject aims to reveal the general patterns and the underlying drivers (Martiny et al. 2006). It is necessary to know which fungi are where, and why they are found there and not somewhere else. These knowledges are the premise and foundation for the protection of fungal diversity and the utilization of fungal resources. The phyllosphere habitat provides an excellent platform to test the biogeographic hypotheses and formulate the associated theories (Andrews and Harris 2000). As early as 1987, researchers had used the theory of island biogeography to

explain the fungal distributions on apple leaves (Andrews et al. 1987); they proposed that leaves, like virtual islands, have the natural advantages for biogeographic studies, as they are accessible, replicated and easily manipulated. Other researchers corroborated the geographic isolation and size effect of islands by surveying foliar endophytic fungi of birch trees in the archipelago of Finland (Helander et al. 2007). Based on the framework of current microbial biogeography (Chu et al. 2020), phyllosphere fungal biogeographic distribution is constrained by multiple driving factors, such as plant host identity, leaf functional traits, climatic conditions, geographic distance and other microbial guilds. Of note, microbial biogeographic distribution is spatial scale dependent. At the different spatial scales, the main driving factors may be distinctive (Vaz et al. 2014b). In addition, different detection methods, e.g., culture-based and culture-free methods (e.g., 454 Pyrosequencing, MiSeq Sequencing, and PacBio Sequencing), may lead to the different observed patterns (Bowman and Arnold 2021).

3.1 Fine and Local Scales

At the local-scale tropical forests, there are strong evidence of host tree preference and spatial heterogeneity for phyllosphere fungal communities, regardless of using culture-based or culture-free methods (Arnold et al. 2000; Kembel and Mueller 2014). However, the aforementioned host- and habitat-specificity were not observed for phyllosphere fungal communities of grasses in tropical forests (Higgins et al. 2011, 2014). In other ecosystems, such as mountains, mangroves, and arctic zones, phyllosphere fungi also exhibited host-specificity, namely, different plant species have unique fungal partners (Arfi et al. 2012; Zhang and Yao 2015; Yao et al. 2019; Apigo and Oono 2022). The significant plant identity effect is partly attributed to leaf economic traits (Kembel and Mueller 2014; Tellez et al. 2022), and its extent varies by different plant abundances and lineages (Apigo and Oono 2022).

In order to deeply and extensively explore the other driving factors besides plant species identity, many studies focused on the phyllosphere fungal biogeography of single plant species. Across a Hawaiian landscape, foliar endophytic fungal communities of *Metrosideros polymorpha* were strongly driven by temperature and rainfall (Zimmerman and Vitousek 2012). In a subalpine timberline ecotone on Changbai Mountain, the alpha diversity of foliar endophytic fungi of *B. ermanii* significantly increased with increasing elevation, and fungal community composition differed between different elevation sites; leaf carbon was the main driver of alpha diversity and community composition (Yang et al. 2016b). For *Pinus muricata* and *Vaccinium ovatum* growing across a broad soil nutrient gradient, foliar endophytic fungal richness was constrained by leaf nitrogen-to-phosphorus ratio and sodium content (Oono et al. 2020). The effect of plant within-species variation (i.e., tree genotype) was not observed in the needle mycobiome-*Picea glauca* system at an arctic treeline ecotone (Eusemann et al. 2016). In addition, biotic interactions, such as neighboring plant diversity, fungal-fungal associations, mycorrhizal colonization, and inoculation of endophytes, were found to be significant drivers of

phyllosphere fungal communities (Pan and May 2009; Eschen et al. 2010; Nguyen et al. 2017; Yang et al. 2013b). Even at the fine scale, there are still the significant biogeographic patterns; e.g., fungal endophytes *Xylaria* associated with Myrtaceae exhibited leaf fragment preference to petiole and tip (Vaz et al. 2014a).

3.2 Regional Scales

Regional-scale biogeographic studies are commonly carried out over a span of more than 100 km, and thus have the larger geographic distance and broader environmental gradient compared with local-scale studies. Both host species identity and geographic locality were the primary drivers of fungal communities in phyllosphere at the regional scale (Hoffman and Arnold 2008). However, their relative effects were different, and most of the studies showed that host species identity played a more important role than dispersal limitation in shaping phyllosphere fungal biogeographic patterns (Lau et al. 2013; Sapkota et al. 2015; Vincent et al. 2016). Of note, with increasing urbanization, the community dissimilarity of foliar endophytic fungi among different tree species in urban zones significantly decreased compared with that in rural forests (Matsumura and Fukuda 2013). It indicates that human activity exerts a profound effect on fungal biogeographic patterns in phyllosphere, e.g., decrease beta diversity among different tree species (i.e., host specificity).

Strictly, site effect may result from two independent factors – one is geographic distance, and the other is environmental distance (e.g., climatic difference). By focusing on the phyllosphere fungal community of single plant species, researchers found that environmental filtering plays a greater role in structuring foliar fungal communities than dispersal limitation caused by geographic distance (Garcia et al. 2013; Barge et al. 2019; Bowman and Arnold 2021). In addition, fungal community composition in the phyllosphere of *Mussaenda pubescens* was significantly structured by host genotype, and less by geographic distance (Qian et al. 2018b). Manipulative experiments are the important supplement to field surveys in biogeographic studies, as it can uncouple multiple effects directly and test for causality. Commonly, the manipulative experiments are carried out at the local scale. Sometimes, for example, provenance-progeny trails can be carried out at regional scales. Based the provenance-progeny trails of sugar maple as well as switchgrass, researchers found that site effect was the main driver of the variation in phyllosphere fungal communities, whereas seed provenance or host ecotype has no significant effect (Whitaker et al. 2018; De Bellis et al. 2022). Recently, a 7-year old provenance-progeny trail showed that both site and host genetic variation shape the phyllosphere fungal communities of Scots pine (Schonrogge et al. 2022). Therefore, more experiments involving single plant species should be extensively performed to summarize the general pattern of phyllosphere fungal biogeography. In addition, aerial spore communities, rare fungal species and plant genetic distance among different host species were also reported as the drivers for phyllosphere fungal distributions (Oono et al. 2017; Redondo et al. 2022; Sarver et al. 2022; Teng et al. 2022).

3.3 Continental and Global Scales

Phyllosphere fungi cooccur with all major lineages of land plants and are widely distributed across every corner of the earth. However, few studies were really performed to reveal the biogeographic pattern of phyllosphere fungi at the global scale. Previously, Arnold and Lutzoni isolated, cultured and (Sanger) sequenced 1403 endophytic fungal strains involving 28 host plant species from the lowland tropical forest of central Panama to the Canadian arctic; they found the incidence, diversity, and host breadth of foliar endophytic fungi significantly decreased with the increasing latitude (Arnold and Lutzoni 2007). The diversity pattern of foliar endophytic fungi along latitude seems to be similar to the pattern of plants and animals. Later on, the research team examined 4154 endophytic and endolichenic fungal strains involving ca. 20 plant and lichen species across North America; climatic variables, geographic distance, and plant host identity together affected the fungal distributions at the continental scale, among which climatic variables more strongly affected the fungal distributions than geographic distance alone (U'ren et al. 2012). It indicates again that environmental filtering plays a greater role in structuring foliar fungal communities than dispersal limitation at the broad spatial scale. When we study the global-scale phyllophere fungal biogeography, one issue always exists. Considering the turnover of host plants with geography and climate, the relative effects of host species identity, geographic distance, and abiotic environmental variables on foliar fungal biogeography are not clear, especially at the global scale. Also from the progress of Arnold's team, they revealed that host availability, rather than turnover with geographic or environmental distance, drove distributions of foliar endophytic fungi in boreal forest ecosystems at the trans-continent scale (across North America and Eurasia) (U'Ren et al. 2019).

Although there has been a few continental- and trans-continental-scale studies on phyllosphere fungal biogeography, these studies are mainly carried out in the American continent and for foliar endophytic fungi. Therefore, more global-scale integrated studies are needed to form the fundamental knowledge on the biogeography of phyllosphere fungi. Meta-analysis is one of practical approaches to acquire the global-scale understanding. Starting from the raw sequencing data of 10 published studies, researchers corroborated the latitudinal diversity decline and distance-decay relationships, which indicates the similarity in biogeographic patterns between fungi and other organisms (Meiser et al. 2014). Recently, Bladrian et al. complied and analyzed fungal high-throughput sequencing data from 156 publications; they extrapolated fungal diversity to 6.28 million and highlighted the hotspot of unknow diversity in lichen and plant tissues (Baldrian et al. 2021). Of note, phyllophere samples only accounted for one part in the aforementioned meta-analysis studies. Fortunately, some citizen science projects (incl. Dataset construction; Franic et al. 2022) that specify phyllosphere fungi are in progress (https://sisu.ut.ee/funleaf/about). In the near future, it will definitely bring us more insights into the biogeographic patterns of phyllosphere fungi.

4 Fungal Temporal Dynamics in Phyllosphere

4.1 Temporal Factors Shaping Phyllosphere Mycobiome Assembly

A better understanding of fungal temporal dynamics in the phyllosphere is essential for uncovering fundamental ecological processes underpinning the assembly of the plant mycobiome. Changes in phyllosphere mycobiome assembly along plant growth are closely associated with many temporal factors, including plant age, host developmental stage, and seasonal climatic factors (Gao et al. 2020; Xiong et al. 2021b; Vacher et al. 2016; Remus-Emsermann and Schlechter 2018). Growing evidences on maize, sorghum, barley, *Arabidopsis*, and trees have revealed that plant developmental stage and growing season are important factors influencing structure and function of leaf-associated fungal communities and regulating the balance between deterministic and stochastic processes in phyllosphere mycobiome assembly (Table 2). For example, Gao and colleagues showed that leaf-associated fungal communities altered strongly across plant developmental stages (1st to 17th week), and stochastic forces (drift or stochastic dispersal) played a role in shaping leaf fungal community assembly at the early stage of plant development (Gao et al. 2020). Similarly, a recent work on maize grown under different fertilization practices at two contrast sites have suggested that plant developmental stage had the strongest effects on the phylloplane mycobiome, compared with other plant and soil compartments (Xiong et al. 2021b). Null model analysis further showed that the relative importance of deterministic and stochastic processes in the assembly of leaf-associated mycobiome were greatly influenced by plant developmental stage, with a higher relative contribution of stochastic processes mainly belonging to homogenizing dispersal and undominated (e.g., diversification and/or drift) observing for both epiphytic and endophytic phyllosphere fungal communities at the seedling stage (Xiong et al. 2021b). By contrast, deterministic processes dominated the assembly of endophytic phyllosphere fungal community at both tasseling and mature stages (Xiong et al. 2021b). Given that the phyllosphere is an important interface between the plant host and the environment, fungal community assembly in the phyllosphere is not only shaped by temporal factors but also influenced by other biotic and abiotic factors (Vacher et al. 2016; Remus-Emsermann and Schlechter 2018; Vorholt 2012). By using artificial plants made of plastic material as "background controls" in the field during maize developmental stages, Xiong and colleagues found that season-dependent environmental factors like air, dust and rainwater also played a role in phyllosphere fungal community assembly (Xiong et al. 2021b). Source tracking analysis further indicated that atmosphere environment contributed an increasing proportion as the source of the maize phylloplane fungal community across three plant developmental stages (from 86.6% to 92.4%) (Xiong et al. 2021b).

Table 2 Recent studies on fungal temporal dynamics in phyllosphere

Plant species	Leaf Compartment	Research content	Temporal factor	References
Arabidopsis thaliana	Episphere and endosphere	Fungal diversity, composition, and network properties	5 growing seasons	Almario et al. (2022)
45 subtropical tree species	Episphere	Fungal diversity and composition	Dry and wet seasons	Li et al. (2022a)
Hordeum vulgare	Episphere and endosphere	Fungal diversity, composition, and network properties	1st to 18th week	Sapkota et al. (2022)
Schefflera octophylla	Episphere	Fungal composition and network properties	2nd to 6th week	Song et al. (2022b)
Camellia sinensis	Episphere and endosphere	Fungal diversity and composition	4 developmental stages	Xu et al. (2022b)
Gingko biloba, *Pinus bungeana*, and *Sabina chinensis*	Episphere	Fungal diversity, composition, and network properties	2 growing seasons	Bao et al. (2022)
Zea mays	Episphere and endosphere	Fungal diversity, composition, assembly processes, and network properties	3 developmental stages	Xiong et al. (2021b)
Quercus robur	Episphere and endosphere	Fungal diversity and composition	3 growing seasons	Faticov et al. (2021)
Panicum virgatum	Episphere and endosphere	Fungal diversity, composition, and network properties	7 growing seasons	Bowsher et al. (2021)
Sorghum bicolor	Episphere and endosphere	Fungal diversity, composition, and assembly processes	1st to 17th week	Gao et al. (2020)
Olea europaea	Endosphere	Fungal diversity and composition	3 growing seasons	Materatski et al. (2019)
Olea europaea	Episphere and endosphere	Fungal diversity and composition	2 growing seasons	Gomes et al. (2018)
Fraxinus excelsior	Episphere and endosphere	Fungal diversity and composition	9 growing time points	Cross et al. (2017)

In addition, increasing studies indicated that effects of the temporal factors and other drivers on fungal community assembly in the phyllosphere largely depend on changes in plant growth and developmental stages, variation in host identity, and spatial scale (e.g., geographic distance). For example, previous work had showed that plant developmental stage (18–39%) dominated over site (3–26%) in shaping fungal communities in both epiphytic and endophytic phyllosphere of maize (Xiong et al. 2021b). At the plant level, it was reported that plant developmental stage (10.7%) played a more important role than drought treatment (2.6%) and plant

cultivar (0.2%) in structuring fungal communities across soil, root, and leaf of sorghum (Gao et al. 2020). Moreover, a recent work on oak had suggested that plant growing season (10%) explained more variation in leaf fungal communities than warming treatment (2%) and host genotype (1%) (Faticov et al. 2021). Study on spring barley reported that plant age (44%) played a more important role than host cultivar (1%) in shaping leaf fungal community (Sapkota et al. 2022). Gomes et al. examined fungal communities in endophytic and epiphytic phyllosphere and demonstrated that season was the major driver of fungal community composition, especially for epiphytic fungal community (Gomes et al. 2018). Wind speed and temperature were important environmental factors influencing epiphytic phyllosphere fungal community, while plant organ, rainfall, and temperature were the major drivers shaping endophytic phyllosphere fungal community (Gomes et al. 2018). All these results suggest that the temporal factors are vital drivers shaping the assembly of leaf-associated fungal communities under different host selection and environmental stresses.

4.2 Temporal Patterns of Fungal Diversity, Composition, and Networks

Increasing works have suggested that the temporal factors also significantly affected diversity, composition, and co-occurrence patterns of the phyllosphere mycobiome (Bowsher et al. 2021; Li et al. 2022a; Faticov et al. 2021; Almario et al. 2022). For instance, the study on the pedunculate oak (*Quercus robur*) across one growing season had showed that phyllosphere fungal species richness increased but evenness decreased during the growing season (Faticov et al. 2021). The relative abundance of Yeasts increased over the time, while putative fungal pathogens decreased (Faticov et al. 2021). A recent work analyzed leaf fungal community of *Arabidopsis thaliana* throughout the plant's natural growing season (extending from November to March) over three consecutive years, and demonstrated that the time of sampling had an important effect on fungal communities (32–40% explained variance) (Almario et al. 2022). The relative abundance of Microbotryales increased throughout the plant's growing season, while that of Sporidiobolales decreased (Almario et al. 2022). Sapkota and colleagues characterized the phyllosphere mycobiome of three spring barley cultivars at weekly intervals during a growth season from seedling emergence to senescence and seed maturity, and showed that the specific members like *Dioszegia* and *Sporobolomyces* of the mycobiome responded differently to plant developmental stage (Sapkota et al. 2022). Moreover, it was found that fungal seasonal dynamics in the phyllosphere differed between phylogenetic groups, with *Aureobasidium* and *Neoascochyta* sp. peaking in early summer and then decreasing across the growing season (Bowsher et al. 2021). By contrast, higher relative abundance of *Epicoccum* sp. were observed at the early stage and then steadily increased throughout much of the growing season (Bowsher et al. 2021). Moreover, previous studies explored fungal diversity and seasonal

succession in ash leaves infected by the invasive ascomycete *Hymenoscyphus fraxineus* by high-throughput sequencing and quantitative PCR profiling of *H. fraxineus* DNA, and indicated that plant growing season had a significant impact on fungal composition in the phyllosphere (Cross et al. 2017). Initiation of ascospore production by *H. fraxineus* after overwintering was followed by pathogen accumulation in asymptomatic leaves across plant growing seasons (Cross et al. 2017). Some fungal taxa like genera *Phyllactinia* and *Phoma* were more abundant at the late season and were positively correlated with *Hymenoscyphus*, while some taxa like *Taphrina*, *Tilletiopsis*, *Cladophialophora* were more abundant at the early season and were negatively correlated with *Hymenoscyphus* (Cross et al. 2017). These strong seasonal changes of the phyllosphere fungal community might be explained by the fact that plant metabolisms, leaf physical and chemical traits, and seasonal weather conditions significantly vary across different growing seasons and plant developmental stages (Xu et al. 2022b; Vacher et al. 2016). For example, theophylline was prevalent metabolite at the early shoot development stage and strongly affected fungal communities in the tea plant phyllosphere, in contrast, epigallocatechin gallate was more abundant at the late stage and was identified as the main driver of fungal community assembly (Xu et al. 2022b). Bowsher and colleagues investigated seasonal dynamics of epiphytic phyllosphere fungal communities of switchgrass, and observed a strong impact of plant growing season on fungal community composition, with multiple taxonomic levels exhibiting clear temporal patterns (Bowsher et al. 2021). It was shown that fungal richness index increased after the first time point and remained high until late summer, when it decreased across the final two time points (Bowsher et al. 2021). Further, seasonal patterns in fungal community were significantly correlated to leaf nitrogen concentration, leaf dry matter content, plant height, and minimum daily air temperature(Bowsher et al. 2021), indicating that both host selection and environmental changes contribute to phyllosphere fungal temporal dynamics.

Furthermore, it was reported that fungal network connectivity changed across plant growth stages, with a weak co-occurrence pattern early in the season but increasing dramatically at the late stage (Sapkota et al. 2022). A recent work on maize also revealed that bacterial-fungal interkingdom network patterns in both epiphytic and endophytic phyllosphere changed distinctly across three developmental stages (Xiong et al. 2021b). The fungal network connectivity and the proportion of fungal nodes increased over the time, indicating an increasing role of fungal taxa in the networks (Xiong et al. 2021b). The random forest modeling analysis further indicated that fungal community composition at the mature stage is a strong predictor for crop yield (Sapkota et al. 2022). Additionally, an increasing research effort is to explore core taxa of the phyllosphere mycobiome during plant developmental stages. For instance, six fungal taxa were identified as persistent core taxa (present in at least 95% of samples) for the phyllosphere mycobiome, including two ascomycetes (*Cladosporium* spp.) and four basidiomycete yeast (*Dioszegia* sp., *Itersonilia* sp., *Sporidiobolus* sp., and *Udeniomyces* sp.) (Almario et al. 2022). Taken together, these findings reveal the prominent roles of temporal factors in shaping diversity, composition and co-occurrence networks of the phyllosphere

mycobiome under various environmental conditions. These findings can help to form a systematic understanding on the fundamental ecological processes governing plant mycobiome assembly and to develop microbiome-based tools for sustainable plant protection and crop production.

5 Fungal Community Assembly in Phyllosphere

5.1 Community Assembly Processes

Microbial community assembly are driven by four ecological processes: selection, speciation, diversification, and drift based on the theory proposed by Vellend (2010). Selection mirrors deterministic fitness differences between species. Diversification represents evolutionary process of generating new genetic variants. Dispersal relates to the movement of organisms across space, and drift reflects stochastic changes in species abundance (Vellend 2010; Zhou and Ning 2017).

5.1.1 Selection

Leaves present as an extreme environment where phyllosphere fungi withstand low nutrient availability, large moisture fluctuation, intense ultraviolet radiation, and temperature oscillations. These leaf microclimate parameters vary with regional climate and exhibit fine-scale variations due to terrain, vegetation, and canopy structure (Vacher et al. 2016). Thus, environmental factors often exert important selective pressure on phyllosphere fungal communities. For example, climate warming altered the composition of fungal assemblages of *Mycosphaerella punctiformis* along an elevation gradient (Cordier et al. 2012b) or affected phyllophere fungal assemblages of *Quercus robur* in a multifactorial experiment (Faticov et al. 2021). Warming strengthened host plant defenses and filtered out the less adapted fungal taxa in the phyllosphere (Faticov et al. 2021). Precipitation also exerted a significant influence on phyllosphere fungal communities of *Mussaenda kwangtungensis* (Qian et al. 2018a) and *Panicum hallii* (Giauque and Hawkes 2016). Precipitation indirectly influenced fungal community assembly through variation in the local plant community structure (Hawkes et al. 2011). In addition, environmental changes were assumed to decrease the activity of host genes, resulting in the context-dependent expression of genetic variation for plant phenotypic features, which might further alter the community assembly processes of phyllosphere fungi (Wagner et al. 2016).

Since the phyllosphere is an ecological interface between air and host plants. Plant species identity should be an essential driver of community structure of phyllosphere fungi. Previous studies have shown significant different foliar fungal community composition among different plant species (Kembel and Mueller 2014; David et al. 2016) or plant genotypes (Qian et al. 2018b; Balint et al. 2013). Many phenotypic properties including leaf morphology, physiology, and chemistry

derived from the host genetic repertoire likely exert selective pressure on the phyllosphere fungal community assembly and the plant-fungal interactions (Friesen et al. 2011). Fungal cells and spores that land on the leaf surface initially contact with the trichomes and cuticles, whose architecture varies greatly depending on environmental conditions and plant identity. Trichomes or hairy extensions can protect the leaf against ultraviolet radiation, ensnare the water, and help spores adhere to the leaf surface (Qian et al. 2020). For instance, some endophytic *Trichoderma* species were found to be intimately associated with *Theobroma cacao* glandular trichomes (Bailey et al. 2009). Cuticle permeability and wettability can influence the diffusion rate of compounds from the apoplast onto the leaf surface and the retention of water droplets on the leaf surface, which will affect the colonization of microbes in the phyllosphere (Schlechter et al. 2019). Additionally, plant traits related to leaf sizes, foliar nutrients (e.g., sulfur, nitrate, and calcium) and leaf secretions (e.g., organic acids, sugars, and secondary metabolites) can also largely influence the phyllosphere fungal diversity and community composition (Larkin et al. 2012; Kivlin et al. 2019; Glushakova et al. 2007; Saunders and Kohn 2009).

5.1.2 Dispersal

Dispersal of foliar microbes is performed primarily by bioaerosols that contain fungal spores, single cells, and fragments of hyphae. Bioaerosols can deposit on nearby plants and travel over a long distance, which relies on the height of release occurs, environmental conditions, local vegetation structures, and the size and density of particles (Vacher et al. 2016). Dispersal limitation theory demonstrates that there will be a decay in the similarity of microbial communities with geographic distance (Hanson et al. 2012). This phenomenon has been found in the fungal communities inhabiting the leaves of *M. pubescens* var. *alba* (Qian et al. 2018b) and *Pinus taeda* (Oono et al. 2017) at regional scales, which highlights the importance of geographic distance as a driver in shaping regional foliar fungal communities.

5.1.3 Diversification and Drift

Given that the current microbial distribution patterns cannot be entirely explained by selection and dispersal, diversification or mutation at the gene level may also act an essential role in determining microbial community assembly (Zhou and Ning 2017). Phyllosphere fungi often cope with intense ultraviolet radiation and reactive oxygen that are considered to accelerate mutation rates (Vorholt 2012). However, we still lack the methods to calculate the relative contribution of diversification in shaping the community structure.

Drift is a purely stochastic process that can function on its own via probabilistic factors, especially in small communities or when the regional pool is enormous in comparison to the size of local communities (Chase 2003). Drift could interact with selection to create multiple stable equilibria and become more important when

selection is weak (Chase and Myers 2011). Generally, the majority of phyllosphere fungi are rare taxa, which may be easily influenced by drift, because slight changes in their abundance can lead to extinction on a local scale (Vacher et al. 2016). In addition, the functional redundancy of phyllosphere microbes could increase neutrality and makes functionally redundant members more vulnerable to drift (Zhou and Ning 2017).

5.2 Co-occurrence Networks

In phyllosphere environments, microbial members often interact with each other and live within complicated ecological networks rather than existing in isolation (Faust and Raes 2012). The microbial interactions can be classified as positive (mutualism), neutral (commensalism) or negative (competition, predation, parasitism) and play important roles in determining the fitness of phyllosphere microbes, selecting for specific microbial traits, and shaping the structure of microbial communities (Bashir et al. 2022; Vacher et al. 2016).

Co-occurrence network analysis can reveal how species coexist within a community, disentangle the microbe-microbe and microbe-host interactions, and thus provide comprehensive insights into the assembly process and ecological function of microbial communities (Banerjee et al. 2018). The co-occurrence pattern has been frequently visualized as a network of nodes (microbial taxa) connected by edges (microbial interaction) of varying strength that correspond to the frequency of paired species presence at a site (Kay et al. 2018). Ecological modules are comprised of closely connected microbes, and are usually considered as the result of phylogenetic relatedness, niche differentiation, and/or habitat heterogeneity of the microbial communities (Zhang et al. 2018a; Newman 2006). Network analysis can also help us identify keystone microbes that are highly connected; the keystone species may exert a great influence on the structure and functioning of microbial communities irrespective of their abundance (Banerjee et al. 2018). The removal of these taxa will lead to a dramatic shift in network topology. The network topological properties, such as clustering coefficient, average path length, mean connectivity, and edge density, can be used to speculate microbial assembly and interactions. In particular, co-occurrence network analysis based on amplicon sequencing data has been increasingly used to explore the ecological interactions among multiple-kingdom microbial members as well as microbe-host relationships in various habitats (Teng et al. 2022; Yang et al. 2022).

Recently, several studies have been conducted to explore co-occurrence networks of phyllosphere fungal communities. For instance, Yao et al. found foliar endophytic network had higher levels of specialization and modularity but lower connectance and stronger anti-nestedness than the epiphytic network in a local mangrove forest (Yao et al. 2019). Qian et al. found that the phyllosphere fungal networks of *Mussaenda kwangtungensis* in island regions showed less complex and coherent, but more modular structure than the mainland ones (Qian et al. 2020). At

the scale of more than 2000-km span of mountain forests in eastern China, Yang et al. demonstrated that the plant-fungus networks in leaves were significantly higher specialized, modular and stable, but less connected compared to the networks in soils (Teng et al. 2022). Phyllosphere fungal networks of *M. shikokiana* displayed a trend of reduced connectivity and integrity with increasing elevation (Qian et al. 2018a). Nevertheless, we still lack basic knowledge regarding the environmental factors that determine the network structure of phyllosphere fungi. Environmental drivers could influence phylogenetic congruence patterns and the rare taxa involved in coevolved interactions, but exploring the response of networks to environmental change will require linking network architecture with ecosystem functioning, and using multilayer network approaches (Tylianakis and Morris 2017).

5.3 Source Analyses of Phyllosphere Fungi

The phyllosphere recruits microbes via horizontal (from an environmental, free-living symbiont source) or vertical (from the inheritance of the symbiont from the mother or both parents) transmissions (Bright and Bulgheresi 2010; Bashir et al. 2022). Therefore, the sources of phyllosphere fungi are diversified. Epiphytic fungal residents originate from the air, water, or soil and can arrive at the leaf surface through wind, bioaerosols, raindrops or animals (especially insects and herbivores) (Whipps et al. 2008). Once deposited, their establishment and survival will further rely on microbial physiological and genetic features (e.g., acquisition of leaf nutrients, capability to adhere to leaf surface, and adaptation to leaf microclimate) and leaf phenotypic properties in the aspects of morphology, chemistry and physiology (Bashir et al. 2022). Some of them can pass through leaf epidermal openings structure like stomata or hydathodes and become endophytes (Bashir et al. 2022). Yang et al. found more phylogenetically clustered structure for epiphytic and endophytic fungi inhabiting the leaves of *B. ermanii* compared with the corresponding soil fungi, indicating a continuum acted by epiphytes and endophytes in the phyllosphere (Yang et al. 2016a). Some endophytic fungal species (e.g., clavicipitaceous endophytes) can transmit vertically, with maternal plants passing fungi on to offspring through seeds (Rodriguez et al. 2009). Additionally, there is increasing evidence that endophytic microbes in the roots could enter the vascular system and be transferred internally to the leaves where they develop as foliar endophytes (Whipps et al. 2008). For example, many fungal taxa of *Mussaenda kwangtungensis* were shared between the leaf and root endosphere compartments, although the overall community structure can differ significantly (Qian et al. 2019).

The advancement of statistical tools facilitates us to identify the sources of phyllosphere fungi more precisely. For example, SourceTracker is a Bayesian approach to estimate the proportion of contaminants in a given community (Knights et al. 2011); the approach was widely used in high-throughput metagenomic studies (Yang et al. 2021; Zhang et al. 2022). Using SourceTracker, the researchers found that 60% of the foliar endophytic fungal community of healthy Rice was derived

from the soil environment. FEAST (i.e., fast expectation-maximization microbial source tracking) is an alternative Bayesian approach to estimate the proportions of microbial sources in a given community based on Gibbs sampling; this method can deal with bigger data information in a timely manner (Shenhav et al. 2019). Using FEAST, the researchers surveyed the sources of the foliar fungal community along the burn severity gradient; they found that the percentages of these sources were strongly affected by the burn severity levels (Dove et al. 2021). In unburned plots, 40% of the foliar fungal taxa were derived from rhizosphere, while bulk soil was the main source of the foliar fungal taxa in burned plots. In addition, airborne fungal community was more derived from leaf surface than soils (Qi et al. 2020). Therefore, soil, air and other plant tissues are potential sources of phyllosphere mycobiome, but their relative contributions vary by plant growth stages and surrounding environments.

6 Fungal Functions in Phyllosphere

Phyllosphere fungi have intimate relationships with plants and exhibit diverse functions, which not only benefit their own survival and growth but also affect plant performance and even the whole ecosystem. They have been reported to increase plant access to nutrients and water, enhance plant resistance to biotic and abiotic stress, degrade organic matters or pollutants, drive plant population and community and so on (Busby et al. 2016; Khan et al. 2015; Rudgers et al. 2010; Russell et al. 2011). However, leaf fungal pathogens induce plant diseases and cause huge losses in agroecosystem (Chen et al. 2021a). Thus, understanding functional diversity of phyllosphere fungi is essential to maintain the sustainability of natural ecosystems, promote the yield in agroecosystems, and benefit to human health in urban ecosystems.

6.1 Functional Traits

Recently, more and more studies focus on fungal functional traits, which are the measurable characteristics that affect organism growth and adaptability in certain environments (Yang 2021). Functional traits can be analyzed based on phenotypic characteristics or inferred from microbial genomes. Microbial functional traits are more sensitive to environmental fluctuations compared to microbial taxonomic composition (Xiang et al. 2020). Currently, several databases of fungal functional traits have been established, including FUNGuild (Nguyen et al. 2016b), Fun^{Fun} (Zanne et al. 2020), and FungalTraits (Põlme et al. 2021), which make the quantification and prediction of diverse fungal traits under different conditions much quicker and easier.

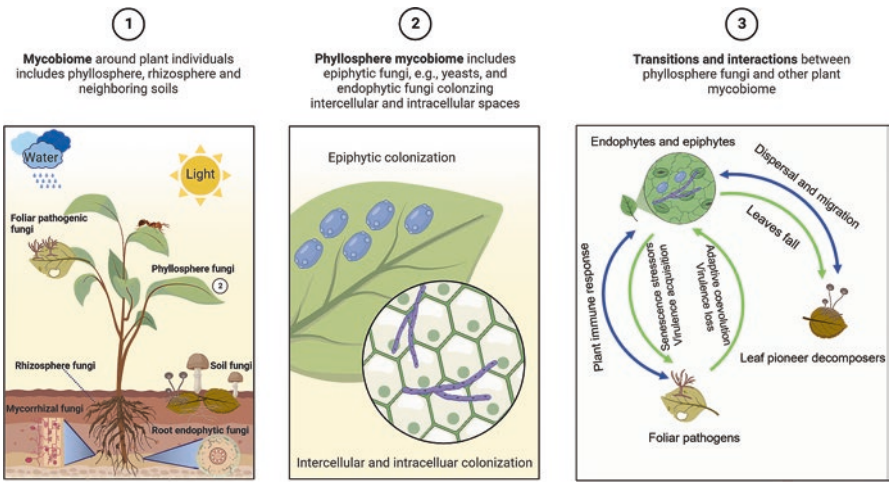

Fig. 1 Dimensions of mycobiome around plant individuals. The transitions in life history and biotic interactions among representative fungal guilds are shown in diagram ③. In the diagram, blue arrows represent biotic interactions between different fungal guilds. For example, endophytes (or epiphytes) and foliar pathogens affect each other by adjusting plant immune responses (Schulz and Boyle 2005). Green arrows represent the transitions in life history between phyllosphere fungi and other plant mycobiomes. For examples, endophytic fungal lineages frequently transit to and from pathogenicity, while endophytic lineages give rise to saprotrophs, but the revisions to endophytism are rare (Arnold et al. 2009). The diagrams are created with the help of BioRender.

Guild, also known as functional group, refers to a group of organisms that utilize the similar environmental resources or have certain niche overlaps, no matter these organisms are phylogenetic related or not (Nguyen et al. 2016b). In FUNGuild, 12 guilds were classified, among which endophytes, pathogens, saprotrophs, and mycorrhizal fungi are plant-associated fungi (Nguyen et al. 2016b). Nevertheless, there are the highly complicated plant mycobiome around plant individuals - different functional guilds (incl. endophytes and epiphytes) transform the life histories and interact with each other closely (Fig. 1). Some fungal endophytes in the phyllosphere could become saprotrophic decomposers after leaf fall (Suryanarayanan 2013). Moreover, *Colletotrichum* (Rojas et al. 2010; Mendgen and Hahn 2002) and Dothideomycetes fungi (Ohm et al. 2012) could transform between non-pathogens and pathogens in response to different environmental conditions or host cues. Dothideomycetes fungi are common in the phyllosphere of many plant species (Qian et al. 2018b; Yao et al. 2019; Teng et al. 2022). The comparison of genome features of 18 Dothideomycetes fungi showed that they could be classified as plant pathogens and saprotrophs, and these pathogens could be further divided into necrotrophs, biotrphs, and hemibiotrophs (Ohm et al. 2012). Further analysis showed that genes involved in carbohydrate degradation and secondary metabolism were expanded in necrotrophs; and necrotrophs also had higher number of genes encoding effectors compared to (hemi)biotrophs, which could lead to the death of leaves and benefit the survival and growth of necrotrophs. Thus, the shift among different life strategies could be predicted by measuring fungal functional traits,

such as the production and exudation of lytic enzymes, the suppression of host defenses, and so on (Mendgen and Hahn 2002).

Functional traits that are critical to fungal physiology were also summarized, such as growth rate, respiration rate, spore size and number, stress tolerance (especially through melanin synthesis), demand for nitrogen (N) and phosphorus (P), and extracellular enzyme activity (Zanne et al. 2020). Other functional traits are highly correlated with fungal interactions with plants. For example, some foliar endophytes inhibited *Rhizoctonia solani*, decreasing disease severity and increasing potato yield (Lahlali and Hijri 2010). Among the tested fungal endophytes, *Trichoderma atroviride* acted as a mycoparasite; *Alternaria longipes* and *Epicoccum nigrum* produced antagonistic secondary metabolites; *Phomopsis* sp. competes for nutrients and space with leaf pathogens. Thus, the aforementioned fungal functional traits could be used to predict three-way interactions among plants, pathogens, and mutualists.

As mentioned above, phyllosphere fungi may change their functional guilds in response to changed conditions. Zhang and Elser examined the stoichiometry of different fungal guilds and found that N content was higher while P content was lower in pathogens compared to saprophytes (Zhang and Elser 2017). However, the N/P ratio was much higher in saprophytes than pathogens (Zhang and Elser 2017). Moreover, saprophytes acquire carbon energy by decomposing dead plant matter, so they may harbor more abundant genes encoding carbohydrate-active enzymes (CAZymes) (Zanne et al. 2020). Therefore, for the fungal taxa that can transition from one guild to another, it is essential to understand which fungal traits can specify the guild changes. These functional traits may help to predict fungal functions in phyllosphere more precisely in the future.

6.2 Functional Genes

One microbial strain harbors thousands of functional genes, which are less evolutionarily conserved compared to phylogenetic biomarkers such as 18S rRNA gene or nuclear ribosomal internal transcribed spacer (ITS) gene (Yang 2021). The presence and expression levels of certain functional genes can be used to estimate the fungal functional traits (Zanne et al. 2020). Although the simplest trait is encoded by single genetic locus, most traits are complex (Martiny et al. 2015). Some phyllosphere fungi may obtain certain genes from their host plants and exhibit novel traits through horizontal gene transfer (HGT) (Tiwari and Bae 2020). Thus, it is difficult to summarize all the fungal functional traits by only one or several genes (Escalas et al. 2019). More approaches are needed to ensure the links between functional genes and traits, such as gene knockout and genetic mutant generation.

Fungal community, as a functional library, contains a collection of genes selected by certain environmental conditions (Escalas et al. 2019). A large collection of microbial functional genes have been summarized, which are mainly categorized into nutrient cycling, substance degradation, antibiotic resistance, stress response, and virulence (Escalas et al. 2019). Some functional genes are reported to enrich or

delete in phyllosphere mycobiome. For example, phyllosphere fungi harbored specific functional genes related to carbon (C), N, P, sulfur (S) cycles compared to the fungi in other habitats, because carbohydrates, amino acids, and organic acids were released by plants to leaf surface (Xiang et al. 2020). In contrast, powdery mildews lost genes encoding CAZymes, primary and secondary metabolism related enzymes, and transporters, which benefit its biotrophic pathogenicity (Spanu et al. 2010). Thus, the presence and absence of some unique genes in phyllosphere fungal communities can be used to assess their potential phenotypes, functional diversity as well as the healthy state of host plants.

6.3 Omics

Most fungi in the phyllosphere are unculturable in common media and under common culture conditions. Metagenomics is defined as the culture-independent genomic analysis of microbial community (Schloss and Handelsman 2003), which was followed by the emergence of metatranscriptomics, metabolomics, and metaproteomics (Schneider and Riedel 2010). The applications of aforementioned high-throughput techniques will promote the exploration of fungal functions in phyllosphere, providing more comprehensive and accurate information.

6.3.1 Metagenomics

Metagenomics can reveal a much higher fungal diversity in the phyllosphere compared to culture dependent methods (Quince et al. 2017), because the unculturable microbes occupy nearly 99.5% of the entire environmental microbiota (Lloyd et al. 2018). More importantly, metagenomics provides a powerful tool to extend the functional traits from individual to community at the extensive sampling effort (e.g., hundreds or thousands of samples) (Barberan et al. 2012). Individual microbial genomes could be assembled from community metagenomics data, referred to as metagenome-assembled genomes (MAGs), providing an essential basis for genome-centric functional analyses (Luo et al. 2012). Several steps are essential to the accuracy and efficiency of metagenomics. For example, the purity and quality of nucleic acid molecules extracted from environmental samples must be ensured (Hawkes et al. 2021). Then, the improvements in bioinformatic tools and pipelines will further identify and remove contamination sequences. These bioinformatic tools could mimic gene translation progress, converting raw reads generated from metagenomic sequencing into meaningful microbial features. Furthermore, metagenomic sequencing could avoid the biases of PCR amplification that result from the use of target-specific primers (Tedersoo et al. 2015).

Metagenomic analysis showed low functional diversity but highly redundant functions in phyllosphere mycobiome, which may be relevant to fungal adaption to low nutrients, high ultraviolet radiation, and changing temperature and humidity of

phyllosphere environment (Stone et al. 2018). Khoiri et al. analyzed the structure and function of microbial community in the sugarcane phyllosphere using the shotgun metagenomics, including archaea, bacteria, fungi, and viruses; they found that different farming practices strongly affected the taxonomic and functional diversity and co-occurrence interactions of phyllosphere microbes (Khoiri et al. 2021). However, several studies used metagenomics to explore fungal taxonomic diversity rather than functions. For example, Ottesen et al. combined amplicon and metagenomic sequencing to reveal the fungal and bacterial diversity in the surface of tomato leaves, stems, roots, flowers, and fruits (Ottesen et al. 2013).

It is noteworthy that metagenomics is the first step to understand microbial community, which could reveal the gene capacity of a community but not the expression of genes and their post-transcriptional modification. Thus, the metatranscriptomics, metabolomics, and metaproteomics should be applied to achieve a more comprehensive picture on the functions of phyllosphere mycobiome.

6.3.2 Metatranscriptomics

Metatranscriptomics could capture gene expression in the plant-associated microbial community, showing the functional profile under certain conditions (Aguiar-Pulido et al. 2016). Since fungal transcripts show different sequence length and GC content from plant transcripts, it is possible to analyze the transcriptome of plants and their phyllosphere fungi together (Delhomme et al. 2015). Delhomme et al. performed *de novo* transcript assembly of more than 1 billion reads from *Picea abies* and obtained a mix of plant and fungal transcripts (Delhomme et al. 2015). They found that fungal transcripts were predominantly from Dothideomycetes and Leotiomycetes, with functional annotation related to glucose intake and processing, indicating active fungal growth and metabolism in the phyllosphere. In other studies, metagenomics and metatranscriptomics were combined to analyze phyllosphere mycobiome. Camargos Fonseca et al. combined amplicon sequencing, shotgun metagenomics, and small RNA transcriptomics to explore the fungal diversity and functions of rubber trees (*Hevea brasiliensis*); they found that most phyllosphere fungi were assigned to saprotrophic ecological mode, with fewer to pathotrophic and symbiotrophic modes, or a combination among them (Camargos Fonseca et al. 2022).

6.3.3 Metabolomics and Metaprotemics

Metabolomics aims to analyze all the metabolites produced by an organism or a community, while metaproteomics aims to identify all the proteins and peptides in a microbial community. Unlike metagenomics and metatranscriptomics that heavily rely on sequencing, both metabolomics and metaproteomics have benefited from the improvement of mass spectroscopy technologies. Moreover, proteins and peptides could also be quantified by analyzing their individual intensity on gels. Generally,

metabolomics and metaproteomics provide a more accurate information to the metabolic pathways compared to metagenomics and metatranscriptomics (Levy et al. 2018).

Metabolomics is able to characterize and quantify the chemical outputs of microbial metabolism, which are highly related to the cellular processes under certain conditions (Fiehn 2002). In community, microbes would produce various metabolites, including signaling molecules to communicate with others as well as toxins to kill competitors (Aguiar-Pulido et al. 2016). As such, metabolomics analysis can reveal the role of phyllosphere fungi in the transformation of nutrients and degradation of pollutants. Some fungal endophytes could get host genes through HGT and synthesize plant metabolites (Kusari et al. 2012). Consequently, phyllosphere fungi may be one of most important factors for leaf phytochemical composition (Mogouong et al. 2021). In addition, metabolome is considered as the most direct indicator of the homeostasis of an environment, so certain microbial metabolites could be developed as predictive biomarkers for environmental fluctuations (Lankadurai et al. 2013).

Metaproteomics is defined as a large scale characterization of the entire proteins in microbial communities at a given time point (Wilmes and Bond 2004), which is necessary to reveal the physiology, ecology, and evolution of microbial communities (VerBerkmoes et al. 2009). Currently, metaproteomics has been used to analyze the bacterial functions in the phyllosphere (Lambais et al. 2017; Knief et al. 2012), few studies focused on fungal metaproteomic analysis. In addition, some studies used metaproteomics to reveal fungal functions in soil. For example, Fernandes and colleagues found that the protein functions of soil fungi shifted from metabolism in forests to information processing and storage in shrublands (Fernandes et al. 2021). These existing studies provide some essential technical references to advancing metaproteomics analyses for phyllosphere mycobiome, whose composition and diversity are much simpler than soil mycobiome.

In summary, integrated analysis of metagenomics, metatranscriptomics, metabolomics, and metaproteomics are enabled by the lower cost of sequencing and the advancement of bioinformatic platform. These omics approaches will accelerate our understanding of phyllosphere fungal diversity and functions greatly.

7 Interactions of Phyllosphere Mycobiome with Plants

Phyllosphere mycobiome intimately interacts with host plants and contributes to many processes, from the health of individual plant to the development and function of plant community. Some phyllosphere fungal taxa are reported as latent plant pathogens that may produce negative effects on plant development and growth in some cases. Most of phyllosphere fungi, especially for endophytic fungal group, are able to increase plant fitness by producing phytohormones, increasing plant nutrient uptake, reducing pathogen and herbivore damages, and enhancing plant adaption to stressful environments. Besides influencing the health of individual plant, phyllosphere fungi have a consequence on the plant population and community by

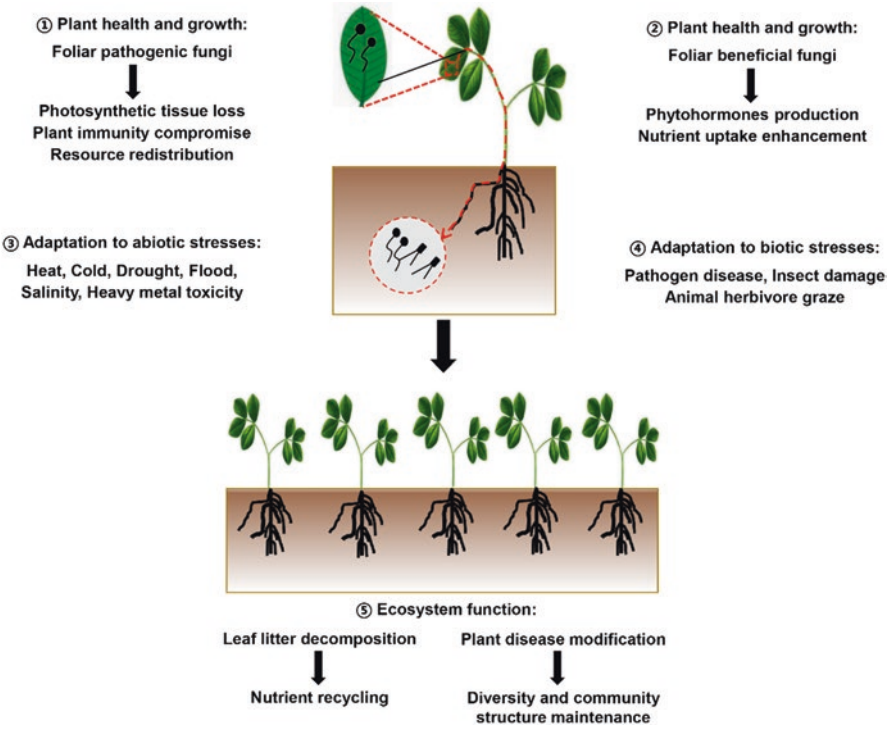

Fig. 2 Roles of phyllosphere mycobiome in plant health and plant community. Phyllosphere fungi can act as latent plant pathogens that produce negative effects on plant development and growth. Some foliar fungi are able to increase plant fitness by producing phytohormones, increasing plant nutrient uptake, reducing pathogen and herbivore damages and enhancing plant adaption to stressful environments. Besides influencing the health of individual plant, foliar fungi have a consequence on the plant population and community by decomposing leaf litter and modifying plant disease. Part ①–④ are at the plant individual level, while part ⑤ occurs at the plant population and community level

decomposing leaf litter (Osono 2006) and modify plant disease (Busby et al. 2016). Here, we focus on the effects of interactions of phyllosphere mycobiome with plants on plant health, growth, biomass, population and community (Fig. 2).

7.1 Roles in Plant Health

7.1.1 Phyllosphere Fungi as Pathogens that Inhibit Plant Health

In the last several decades, the ecology of phyllosphere inhabiting fungi has been studied extensively, but more attentions have been paid on fungal pathogens (Jia et al. 2020). This is not surprising, as 7 in the top 10 most important plant-pathogenic fungi are foliar infection, including *Magnaporthe oryzae, Puccinia* spp., *Fusarium*

graminearum, Blumeria graminis, Mycosphaerella graminicola, Colletotrichum spp., *Ustilago maydis* and *Melampsora Lini* (Dean et al. 2012). Many previous studies have revealed the molecular mechanisms underlying foliar infection of fungal pathogens, and identified fungal virulence effectors and plant resistance (R) proteins during infection process. For instance, fungal effector AvrPiz-t of *M. oryzae* suppresses rice immunity and promotes virulence by Ca^{2+} sensor-mediated ROS scavenging system (Gao et al. 2021).

Given that leaves are initial infection organ for foliar fungal pathogens, it is reasonable that photosynthesis system would be the prime target by the infection. Foliar fungal infection inevitably deters plant health by directly damaging photosynthetic organelle, chloroplasts, and indirectly interfering plant immunity. Photosynthesis is the fundamental process that fuels plant growth and development (Brestic et al. 2021). Foliar fungal disease causes substantial loss of photosynthetic tissue, reductions in chlorophyll content, net photosynthesis rate (Pn) and other photosynthesis-related parameters, and thus reduces the carbohydrates for plant growth. For instance, maize leaves infection with *Colletotrichum musae* and *Fusarium moniliforme* reduce photosynthetic capacity due to the reduction in chlorophyll content (Pinto et al. 2000). The negative effects on photosynthesis system by foliar fungal and oomycete pathogens are achieved by a cocktail of effectors. During infection, pathogens introduce effectors specifically into chloroplasts, which interact with chloroplast proteins to induce programmed cell death (PCD), interfere chloroplasts function and facilitate pathogen proliferation (Kretschmer et al. 2019). For example, *Pyrenophora tritici-repentis* (Ptr), a necrotrophic fungus, produces host-selective toxins ToxA and ToxB (Ciuffetti et al. 2010), of which ToxA interacts with chloroplast protein ToxA Binding Protein 1 (ToxABP1) in wheat, leading to reductions in levels of PSI and PSII protein (Manning et al. 2010). A haustorium-specific protein (Pst_12806) from wheat stripe rust fungus, *Puccinia striiformis* f. sp. Tritici (Pst) is transported into chloroplasts and interacts with the C-terminal Rieske domain of TaISP protein, which suppresses chloroplast function by reducing electron transport rate, photosynthesis and chloroplast-derived H_2O_2 accumulation (Xu et al. 2019). However, our knowledge of chloroplast-targeted effectors from fungi and oomycete pathogens has lagged behind our knowledge of cytoplasm-targeted effectors, as chloroplast-targeted effectors have not been identified in some of best-characterized fungal pathogens, such as *M. oryzae* and *U. maydis*.

Besides fueling the growth of plants, photosynthesis system also plays central role in early immune responses through the formation of ROS and NO, Ca^{2+} oscillations, and the synthesis of plant defensive phytohormones, including salicylic acid (SA) and jasmonic acid (JA) (Serrano et al. 2016). The biosynthesis of JA and SA is associated with chloroplast. Two different enzymatic pathways are responsible for SA biosynthesis: isochorismate (IC) and phenylalanine ammia-lyase (PAL) pathways, of which IC is operative in chloroplast. IC is catalyzed by the chloroplast-localized IC synthase (ICS), and exported to cytosol by enhanced disease susceptibility 5 (EDS5) (Rekhter et al. 2019). IC is then catalyzed by avrPphB Susceptible 3 (PSB3) to form IC-9-glutamate, which is converted to SA

spontaneously or enhanced by pesudomonas susceptibility 1 (EPS1) (Torrens-Spence et al. 2019). Notably, rapid biosynthesis of SA caused by foliar pathogens infection is mainly through ICS pathway. (9S, 13S)-12-oxophytodienoic acid (OPDA), a precursor of JA is synthesized in chloroplast by 13-lipoxygenase (LOX), allene oxide synthase (AOS) and allene oxide cyclase (AOC) (Turner et al. 2002; Zhang et al. 2019). The OPDA is then transported to peroxisome to synthesize JA. It is well known that SA and JA are key components of plant defence against biotrophic and hemibiotrophic (SA-mediated), and necrotrophic (JA-mediated) pathogens, respectively (Bari and Jones 2009). As a consequence, the loss of photosynthetic tissue by the foliar fungal pathogen activity compromises SA- and JA-mediated plant immunity, which further increases plant susceptibility.

To combat foliar fungal infection, the prioritization of carbohydrates synthesized by non-infected of leaves towards production of defense compounds rather than plant growth. As defense compounds biosynthesis imposes a substantial demand for resources, the diversion of plant resources from growth to defense is detrimental to plant growth and reproduction under a fixed total resource budget (Huot et al. 2014; He et al. 2022). This phenomenon is commonly known as "growth-defense tradeoff", which is one of most fundamental principles of "plant economics" (Monson et al. 2022). Consequently, foliar pathogens deter plant health by directly compromising photosynthesis and plant immunity due to the loss of photosynthetic tissue, and indirectly modulating plant resources distribution.

7.1.2 Phyllosphere Fungi as Bio-control Agents that against Pathogens and Herbivores

Besides being pathogens, some fungi inhabiting leaves act as bio-control agents that are beneficial to plant health. Foliar fungi, especially fungal endophytes reduce disease by directly killing pathogenic microbes or insects through the production of toxins, or indirectly activating plant immunity (Jia et al. 2020). The extracts of 5 foliar fungal endophytes (*Diaporthe terebinthifolii* CMRP1430, *D. terebinthifolii* CMRP1436, *D. foliorum* CMRP1321 and *D. malorum* CMRP1438) isolated from *Schinus terebinthifolius* showed the anti-microbial activity in agar diffusion assays, and three key classes of chemical compounds, including ferric chloride, potassium hydroxide, and vanillin-sulfuric acid, were identified (dos Santos et al. 2021). Other studies have shown that the plants infected by endophytic fungi emit volatile organic compounds (VOCs) to inhibit pathogenic fungal growth. For example, the volatile oil extracted from *Epichloë gansuensis*-infected drunken horse grass effectively inhibited the growth of 6 fungal pathogens, including *Alternaria alternata*, *Bipolaris sorokiniana, Curvularia lunata*, *F. avenaceum*, *F. solani* and *Trichoderma viride* (Zhang et al. 2015). Moreover, some foliar fungi can produce anti-fungal proteins. For example, *Epichloë* endophytes, can produce an anti-fungal protein, Efe-Afp, which directly impedes the growth of plant pathogen *Sclerotinia homoeocarpa* (Tian et al. 2017).

There is a bit of literature showed that some phyllosphere fungi can function as entomopathogenic fungi that restrict insect activity by producing toxins. Sumarah et al. screened the toxicity of extracts from 150 foliar fungal endophytes from *Picea rubens* (red spruce) needles to the forest pest *Choristoneura fumiferana* (eastern spruce budworm) in dietary bioassays and found that 3 of these strains are toxic to *C. fumiferana* larvae (Sumarah et al. 2010). LC-MS and spectroscopic analyses showed that the extracts of 3 strains contained 9 major metabolites, all of which showed toxicity to *C. fumiferana.* When feeding on *Epichloë*-infected plants, insects begin to metabolize alkaloids into non-toxic compounds. If the energetic cost of such detoxification over other physiological processes, such as growth and reproduction, the fitness of insects can be compromised (Bastias et al. 2017). Moreover, *Epichloë* endophytes-derived alkaloids are harmful to animal herbivores by influencing their gut metabolome and microbiome. Mote et al. investigated the metabolomic features of plasma and urine from steers grazing *Epichloë*-infected tall fescue, and provided evidence that *Epichloë* infection perturbs tryptophan and lipid metabolism (Mote et al. 2017).

Some phyllosphere fungi cannot directly inhibit pathogens and insect growth, but their colonization reduces pathogen and pest disease severity, suggesting that plant immunity is activated by foliar fungi under pathogen and pest challenges. For example, foliar application of leaf-colonizing yeast *Pseudozyma churashimaensis* strain RGJ1 confers pepper's resistance to bacterial and virus pathogens through inducing the expression of resistance marker genes *Capsium annuum Pathogenesis-Related* (*CaPR*)*4* and *CaPR5* (Lee et al. 2017). Although more and more foliar fungi and their metabolites with anti-microbial or anti-insect activities have been isolated and identified, their anti-microbial or anti-insect capacities were determined under controlled conditions, which is far away from the natural situation *in planta*. Future works are required to confirm their pathogens and pest diseases suppression in agricultural and natural ecosystems, which will greatly facilitate their practical use. Moreover, recent studies have reported that dysbiosis in phyllosphere microbiome led to disease symptoms (leaf chlorosis and necrosis) (Chen et al. 2020a), and leaves can recruit beneficial microbes to combat pathogenic diseases (Li et al. 2022b). Although these studies focus on the functions of foliar bacterial community, they promote us to test whether phyllosphere fungi possess the similar functions at community level.

7.2 Effects on Plant Growth and Biomass

7.2.1 Phyllosphere Fungi Promote Plant Growth and Biomass through Producing Phytohormones

Phyllosphere fungi promote plant growth and biomass by producing phytohormones, including indole-3-acetic acid (IAA, a major auxin) and cytokinins (Liu et al. 2020). Auxin is one of the main regulators in plant developmental and

physiological processes, including embryogenesis, vascular differentiation, organogenesis, top growth, and root and shoot architecture (Quint and Gray 2006; Zhang et al. 2018c). Khan et al. isolated 17 endophytic fungal strains from leaves and stems of Frankincense tree (*Boswellia sacra*)*;* among them, *Aureobasidium* sp. BSS6 and *Preussia* sp. BSL10 showed high IAA production capacity (Khan et al. 2016). The root inoculation of *Preussia* sp. BSL10 significantly increased plant growth and biomass of *B. sacra* trees. Hoffman et al. reported that the presence of endohyphal bacteria (*Luteibacter* sp., *Xanthomonadales*) enhanced the IAA production of a foliar fungal endophyte (*Pestalotiopsis aff. Neglecta, Xylariales*), suggesting that the production of IAA in foliar fungi can be induced by their interactions with other microorganisms (Hoffman et al. 2013). Recently, several studies have indicated that the microbes-derived auxin plays crucial roles during the infection process by counteracting the plant immunity responses and alleviating ROS toxicity, but the knowledge comes from root-microbe interactions (Tzipilevich et al. 2021). Given that phyllosphere is a nutrient-limited, high ultraviolent radiation and low water availability environment (Vorholt 2012), the auxin production by fungi may contribute to their adaptability in phyllosphere.

7.2.2 Phyllosphere Fungi Promote Plant Growth and Biomass through Increasing Nutrient Uptake

It is well known that root-associated beneficial fungi, such as arbuscular mycorrhizal (AM) fungi, ectomycorrhizal (EcM) fungi, and fungal endophytes promote plant nutrient and water uptake. Emerging evidences show that foliar fungal endophytes can also enhance plant capability to absorb minerals, such as nitrogen (N), phosphorus (P) and potassium (K) (Malinowski et al. 2000). Christian et al. traced the N uptake and distribution of *Theobroma cacao* with or without foliar fungal endophyte (*Colletotrichum tropicale*) inoculation with ^{15}N isotope labeling methods (Christian et al. 2019). The results showed that endophyte-inoculated plants exhibited a greater ^{15}N uptake efficiency than endophyte-free plants. The inoculation of *Epichloë* endophytes improved the survival and biomass of *Lolium perenne* in low fertility soils by increasing N, P and Mn content in leaves, as well as K content in leaves and roots (Chen et al. 2020b). Here, we suggest the two mechanisms that explain the roles of foliar fungal colonization in root nutrients uptake. (1) Foliar fungal colonization upregulates the genes that are associated with plant nutrient uptake (Wang et al. 2018). (2) Foliar fungal colonization alters rhizosphere microbiome by modulating the composition of root exudates (Casas et al. 2011). Previously, Novas et al. reported that the root exudates of *Bromus setifolius* infected by *Neotyphodium* significantly increased AM fungal hyphal branches and length, and thus promote plant nutrient uptake (Novas et al. 2011). However, the internal signals and pathways that mediate the effects of leaf-inhabiting fungi on root exudates or rhizosphere microbiome are largely unknown.

7.2.3 Phyllosphere Fungi Increase Plant Tolerance to Environmental Stresses

The colonization of phyllosphere fungi (in particular endophytes) can confer protection for the host plants against various environmental stressors, such as drought, salinity, heavy metals, cold and flood (Lee et al. 2021). Foliar fungal endophytes increase plant tolerance to drought by increasing root biomass, regulating stomatal closure and accumulating solutes for osmotic stress. For example, Xu et al. investigated the effects of *E. sinensis* endophyte on physiology of *Festuca sinensis* under different soil water conditions, finding that *E. sinensis* infection improved the growth of *F. sinensis* under drought conditions by increasing root and shoot growth, improving photosynthetic rate, accumulating K^+ and Ca^{2+}, and promoting nutrient absorption (Xu et al. 2021). In particular, the inoculation of *E. sinensis* significantly modulated the content of abscisic acid (ABA). Similarly, fungal endophytes *Acremonium strictum* conferred drought tolerance to *Atractylodes lancea* plantlets by increasing the ABA level and root:shoot ratio of host plants (Yang et al. 2014). ABA plays a crucial role in triggering stomatal closure to avoid excessive water loss under drought (Gupta et al. 2020). In addition, foliar fungal infection increased the contents of osmo-protective compounds, such as sugars, proline, glutamic acid and mannitol (Yang et al. 2014). Higher levels of anti-oxidative enzymes, such as superoxide dismutase (SOD), ascorbate peroxidase (APX) and catalase (CAT) are found in foliar fungi-infected plants under drought, which contributes to the migration of damages by scavenging excessive ROS (Zhang and Nan 2007).

Foliar fungal infection also increases plant tolerance to salinity by increasing net photosynthesis, regulating ion transport and improving anti-oxidative system. For example, *Neotyphodium* colonization reduced Na^+ and Cl^- contents in tall and meadow fescues, but increased K^+ contents in the shoots under salinity stress (Sabzalian and Mirlohi 2010). Higher levels of K^+ can balance Na^+, which is crucial for the growth of plants under salinity conditions (Hussain et al. 2021). Pan et al. found that the infection of *E. coenophiala* promoted tall fescue salinity tolerance through lowering Na^{2+} accumulation and decreasing lipid peroxidation, and thus maintained higher plant growth and photochemcial efficiency (Pan et al. 2021). Enzymatic and non-enzymatic anti-oxidants are also induced by foliar fungal infection, which contribute to salinity tolerance of plants by counteracting ROS accumulation. For example, *E. gansuensis* infection increase growth and grass yield of *Achnatherum inebrians* under salinity by enhancing the activity of glucose-6-phosphate dehydrogenase (G6PDH) and plasma membrane (PM) H^+-ATPase activity to reduce ROS content (Wang et al. 2021). Interestingly, foliar fungal infection can regulate plant anatomical structures to acquire salinity tolerance. For example, the presence of *E. bromicola* increased the area of conducting tissues and the thickness of leaf veins, epodermis in stems, cortex and endodermis in roots of wild barley (*Hordeum brevisublatum*) under salinity stress (Chen et al. 2021b). In that way, foliar fungi help wild barley to reduce water loss and inhibit the decrease of transport capacity, and ultimately enhance the salinity tolerance.

Similar to drought and salinity stresses, foliar fungal infection can relieve the symptoms of plants to heavy metal toxicity by promoting plant growth and inducing anti-oxidant systems. For example, the *E. gansuensis*-infected drunken horse grass (*Achnatherum inebrians*) had more biomass and higher values for plant height and tillers compared to non-infected plants under cadmium stress (Zhang et al. 2010). More plant biomass can dilute heavy metal concentrations, and induced anti-oxidant systems can prevent plants from ROS injury under heavy metal stress (Zhang et al. 2010).

7.3 Effects on Plant Population and Community

It has been established that the associations between root and microbial symbionts, such as AM fungi, EcM fungi and rhizobia, largely influence plant population and community (van der Heijden et al. 2016; Keller and Lau 2018; Tedersoo et al. 2020). Mycorrhizal networks connect the conspecific and heterospecific plant individuals belowground, mediating nutrient flow and phytochemcial signals transmission, and ultimately influencing plant population and community (Genre et al. 2020). Given that plant leaves are associated with a large number of fungal species, phyllosphere fungi are also supposed to drive the structure of plant population and community. On one hand, phyllosphere fungi may affect plant population and community by influencing growth and biomass of individual plants. On the other hand, more importantly, phyllosphere fungi drive plant population and community by controlling the degradation rate of leaf litter and the occurrence of plant diseases.

As we described above, foliar fungal infection can influence the health, growth and biomass of individual plant, which depends on the fungal taxa. If the leaves of individual plant infected by pathogens, the health of neighboring plant community will be threatened, as fungal spores can be transported by rainfall, wind and insects (Roper et al. 2010; Kim et al. 2019). In an interesting study, the researchers investigated the dispersal of spores of leaf rust fungus *Puccinia triticina* on the infected wheat plants following a raindrop hits with high-speed photography (Kim et al. 2019). They found the raindrop-induced vortex ring carried the spores beyond the laminar boundary layer of leaves and lead to the long-distance transport of pathogens through the atmosphere. If the phyllosphere fungi are beneficial to health of plants, they will have the positive impacts on plant community establishment and persistence under stressful conditions.

Phyllosphere fungi can indirectly influence plant population and community by acting as pioneer decomposers and regulating the subsequent soil nutrient cycling (Saikkonen et al. 2015; Sun et al. 2020). For example, accumulations of leaf litter create a physical barrier that interferes the arrival of seeds to soil and the emergence of sprouts and seedlings. Vellend et al. reported that the germination of forest sedges (*Carex,* Cyperaceae) is lower for seeds beneath the leaf litter than those on the top of the litter layer (Vellend et al. 2000). In addition, plant litter can

intercept light, shading seeds and seedlings, reduce soil water evaporations, and control soil thermal amplitude. As such, the effects of litter on seedling emergency depend to some extent on the litter amount and quality, which can be adjusted by phyllosphere fungi. Additionally, plant litter is the major organic carbon source in ecosystems, especially in forest and grassland ecosystems. During the early stage of leaf litter decay, *Ascomycota* is dominate phylum that involves the decomposition of easily degradable and nutrient-rich compounds, such as oligosaccharides, organic acid, hemicellulose and cellulose (Ma et al. 2013). With the process of degradation, Ascomycota is gradually replaced by the saprotrophs in Basidiomycota, which can degrade highly recalcitrant compounds, such as lignin and suberin (Voriskova and Baldrian 2013). The cooperation of phyllosphere fungi and later decomposer releases nutrients from leaf litter to soil, which increases soil nutrient availability and promotes root nutrient uptake, and ultimately influences plant community.

In addition, based on the Janzen-Connell hypothesis, the researchers reported that pathogenic fungi significantly increased plant diversity, while insect herbivores changed plant community composition in rainforest (Bagchi et al. 2014). Plant diseases caused by fungal pathogens, from some perspectives, are regarded as the modulator of plant diversity and community structure. The occurrence of plant diseases constrains the population density of dominate species and increases the advantage of rare species, maintaining multiple species co-existence. Usually, we name the pattern as conspecific negative density dependence (CNDD). By a long-term monitoring on seedling demographic data in a subtropical forest, Chen et al. found the tree species with higher pathogenic fungal accumulation more suffered from CNDD, whereas the tree species with higher ectomycorrhizal fungal accumulation less suffered from CNDD (Chen et al. 2019). Nevertheless, how diverse phyllosphere fungi regulate plant communities by affecting CNDD is still unknown. In future, the related studies will definitely expand our knowledge on effects of phyllosphere fungi on plant population and community.

8 Interactions of Phyllosphere Mycobiome with Global Change Factors

The Earth and its ecosystems are undergoing radical global changes such as climate change (e.g., global warming, extreme drought and precipitation) and land-use change (e.g., habitat loss, urbanization, and fertilization) (Perreault and Laforest-Lapointe 2022; Zhu et al. 2022). Emerging studies have suggested that these global change factors had an important impact on multiple facets of the phyllosphere mycobiome (Table 3). A better understanding of how the phyllosphere mycobiome and plant-mycobiome interactions response to global change will be a crucial step for harnessing the plant mycobiome to improve plant fitness and productivity.

Table 3 Recent studies showing the impacts of multiple global change factors on the phyllosphere mycobiome

Plant species	Leaf Compartment	Factors	Impacts	References
Quercus robur	Episphere and endosphere	Warming	Decrease fungal species richness and evenness; decrease the relative abundance of putative fungal pathogens	Faticov et al. (2021)
Eucalyptus	Episphere and endosphere	Precipitation	Increase fungal species richness and abundance; increase the relative abundance of putative fungal pathogens	Chen et al. (2021a)
Sorghum bicolor	Episphere and endosphere	Drought	Significantly affect fungal community structure	Gao et al. (2020)
Zea mays, *Triticum aestivum*, and *Hordeum vulgare*	Endosphere	Fertilization	Chemical N fertilizer increased the relative abundance of potential plant pathogen	Xiong et al. (2021a)
Schefflera octophylla	Episphere	Nitrogen deposition	2-week NH3 exposure increased the relative abundance of *Alternaria*, *Cladosporium*, and *Sampaiozyma*.	Song et al. (2022a)
Betula pendula	Episphere	Urbanization	Decrease fungal diversity, DNA amount, and activity; increase microbial respiration	Ivashchenko et al. (2022)
Populus nigra	Episphere and endosphere	Acid rain	Simulated sulfuric and nitric acid rain significantly decreased fungal biomass in the phyllosphere	Du et al. (2020)

8.1 Warming, Precipitation, and Drought

It is unequivocal that human activities result in rapid changes in global climate, and global mean surface temperature is estimated to be increased by 2–3 °C within the next decades (Zhu et al. 2022; Allen et al. 2014). Global warming caused by the "Greenhouse effect" attracts great attention from the general publics and could strongly affect the assembly and function of microbiome (Zhu et al. 2022; Faticov et al. 2021). A lot of efforts have been made to explore impact of warming on diversity, composition, and function of microbial community but mainly focused on bacteria and soil samples (Yuan et al. 2021; Feng et al. 2019; Tao et al. 2020). In

addition to affecting bacterial community, growing evidence has suggested that warming significantly influences diversity and structure of the fungal community living in the phyllosphere (Faticov et al. 2021; Zhu et al. 2022; Liu et al. 2019). For example, it was recently showed that warming had a significant effect on fungal community composition of the oak phyllosphere and decreased fungal species richness and evenness (Faticov et al. 2021). Moreover, warming decreased the relative abundance of putative fungal pathogens in the early and late growing seasons (Faticov et al. 2021). Using the common-garden experiment, Balint and colleagues also found that warming significantly decreased fungal diversity in the phyllosphere of *Populus balsamifera*; warming changed the phyllosphere fungal community with the increase of plausible pathogens (Balint et al. 2015).

Liu and colleagues investigated effects of global change on foliar fungal diseases using a 6-year factorial experiment in a natural Tibetan alpine meadow ecosystem, and revealed that warming significantly increased fungal diseases for nine plant species and increased pathogen load of entire host communities (Liu et al. 2019). In contrast, altered precipitation had no significant effect on community pathogen load, indicating that warming has a more important role than precipitation in affecting plant health (Liu et al. 2019). Inconsistent with this finding, it was reported that changes in precipitation can largely influence plant pathogens and plant fitness by altering humidity and water availability (Xin et al. 2016; Romero et al. 2022). For instance, humidity and high temperature are identified as key factors invoking actual fungal plant-disease outbreaks, and *Puccinia* and *Fusarium* are frequently reported as causative agents of plant disease in phyllosphere (Romero et al. 2022). Similarly, a recent study on the phyllosphere of *Eucalyptus* in Australia suggested that precipitation was the most important factor predicting fungal taxonomic diversity and abundance (Chen et al. 2021a). Random forest analysis and structural equation models (SEM) further indicated that precipitation was the best predictor for putative fungal pathogens and can increase its abundance in the phyllosphere (Chen et al. 2021a).

In addition to warming and precipitation, there is a global increase in drought frequency and duration, as well as in extreme weather events including flood and drought (Zhu et al. 2022; Sardans et al. 2008). Increasing researches have showed that drought has important impacts on plant production and health by affecting plant-associated microbiomes and plant-microbiome interactions (Zhu et al. 2022; Santos-Medellin et al. 2021; Gao et al. 2020; Xu et al. 2018; de Vries et al. 2020). Gao and colleagues examined fungal communities associated with soil, root, and leaf compartments of the sorghum under drought stress, and demonstrated that stochastic processes (e.g., drift or stochastic dispersal) dominated mycobiome assembly at the early stage of host development (Gao et al. 2020). Although drought treatment had a significant effect on fungal community structure, there was no signal for stochasticity was observed when drought stress was relieved, indicating that host selection rather than drought plays a more important role in shaping fungal assembly (Gao et al. 2020). All these observations highlighted the importance of improving our understanding of how the phyllosphere mycobiome responses to

climate change factors and harnessing the plant mycobiome to improve host fitness under warming, precipitation, and drought stresses.

8.2 Fertilization, Nitrogen Deposition, Acid Rain, and Urbanization

Chemical fertilizers like nitrogen, phosphorus, and potassium are essential for plant growth and health and play a vital role in modern agricultural production. The use of chemical fertilizers, especially for nitrogen fertilizer, is likely to increase significantly in future agricultural production to feed the growing human population (Zhu et al. 2022; Singh et al. 2021). It has been well documented that the overuse of the fertilizers can negatively influence ecosystem function and agricultural production by increasing environmental pollution and soil degradation, such as nitrogen deposition, acid rain, and soil acidification (Carrara et al. 2018; Zhu et al. 2022; Raza et al. 2020). Moreover, increasing evidence showed that excessive chemical fertilization will threaten the diversity, composition, and functioning of soil and plant microbiomes (Fan et al. 2019; Xiong et al. 2021a; Sun et al. 2021a). For example, a recent work on the soil-plant continuum of maize, wheat, and barley has suggested that the excessive application of chemical N fertilizer increased the relative abundance of potential fungal pathogen in the leaf endosphere (Xiong et al. 2021a). Sun and colleagues examined fungal communities associated soil and plant compartments of the sorghum and suggested that the mycobiome in phyllosphere was more resistant than those in soils to fertilization treatments including inorganic, organic, and mixed fertilizations (Sun et al. 2021a). Among the treatments, the NPKM fertilization regime (mineral fertilizers NPK plus organic manure) had a positive effect on fungal alpha diversity in phyllosphere (Sun et al. 2021a). In addition to fertilization regime, agronomic managements (e.g., organic and conventional management) were found to significantly affect microbial diversity and function in soil and plant compartments (Karlsson et al. 2017; Wittwer et al. 2021; Chowdhury et al. 2019). Karlsson and colleagues sampled the wheat leaves from 22 organically and conventionally cultivated fields and found that organic farming increased fungal alpha diversity in the wheat phyllosphere, compared with conventional management (Karlsson et al. 2017).

It has been well documented that nitrogen deposition and acid rain caused by agricultural intensification, industrial pollution, and rapid urbanization are major environmental problems that adversely influence food production, environmental quality, and biogeochemical cycling (Yu et al. 2019; Guo et al. 2010; Zhang et al. 2018b). Previously, numerous studies have explored the impact of nitrogen deposition and acid rain on microbial diversity and composition but still focused on soil and rhizosphere samples (Li et al. 2019; Moore et al. 2021; Zhao et al. 2020). A few recent studies reported that microbial communities living in leaves can take up pollutant nitrogen including wet, dry and gaseous N, and nitrogen deposition and acid

rain could drive the assembly changes of the phyllosphere mycobiome (Zhu et al. 2022; Song et al. 2022a, b; Vacher et al. 2016). For example, 2-week NH_3 exposure increased the relative abundance of most fungal genera in phyllosphere, including *Alternaria*, *Cladosporium*, *Sampaiozyma*, *Cystobasidium*, *Gibellulopsis*, and *Cercospora* (Song et al. 2022a). Song and colleagues explored the impact of continuous NO_x exposure on the phyllosphere microbiome and found that NO_x exposure intensify the phyllosphere fungal interactions in co-occurrence networks (Song et al. 2022b). Helander and colleagues tested the influence of simulated acid rain on the occurrence of endophytes and found that the acid rain treatment (pH = 3) decreased approximately 25% of the number of isolated endophytes in the birch phyllosphere (Helander et al. 1993).

In addition, growing evidence has demonstrated a role of rapid urbanization in structuring plant-associated microbial communities (Jumpponen and Jones 2010; Berg and Cernava 2022; Perreault and Laforest-Lapointe 2022). For instance, it was reported that seasonal dynamics of the fungal communities in the *Quercus macrocarpa* phyllosphere differed between urban and nonurban environments, indicating the role of urbanization in the assembly of the phyllosphere mycobiome (Jumpponen and Jones 2010). Imperato and colleagues observed the higher fungal diversity and richness in the phyllosphere of urban environment (Imperato et al. 2019), while Jumpponen et al. found the lower diversity values of that within cities (Jumpponen and Jones 2010). Recently, the researchers investigated the leaves of *Betula pendula* in Moscow at increasing distances from the road; they found that microbial diversity and activity significantly declined with road vicinity, indicating the negative impact of urbanization on phyllosphere fungal diversity and function (Ivashchenko et al. 2022). Taken together, the results demonstrate that multiple global change factors exert the strong effects on many traits of the phyllosphere mycobiome, including fungal diversity, community composition, assembly processes, and biotic interactions. A systematic understanding of ecological and biological mechanisms that govern mycobiome assembly and phyllosphere-mycobiome interactions in the context of global change will provide the pivotal basis for the future plant mycobiome engineering.

9 Future Prospects

Phyllosphere mycobiome owns the extremely high species diversity, and thus should be protected as a hotspot in the global diversity conservation boom. In particular, considering the pressures from deforestation, grassland degradation, irrational use of agricultural fertilizers and pesticides, and urban pollution, it is timely to draw the monitoring of phyllosphere mycobiome into the global biodiversity monitoring network (Guerra et al. 2021). Compared with the phyllosphere fungal studies in natural ecosystems, greater research efforts are needed in agricultural and urban ecosystems. It is because they are more closely correlated with our lives and benefits. Rhizosphere microbiome optimization and synthetic colony techniques has been considered as an important way to solve the

future food crisis (Zhang et al. 2017). Obviously, a better understanding of the mechanism of community assembly of phyllosphere fungi will further help us to develop climate-smart agriculture and maintain the crop health (Trivedi et al. 2020). In addition, monitoring the phyllosphere fungal community dynamics in urban greenery will provide new ideas and approaches for monitoring and altering urban environmental pollution.

As phyllosphere fungi are accessible, replicated and easily manipulated, they are well suited for theoretical studies in ecology and biogeography (Andrews and Harris 2000). Several factors that drive the variation in phyllosphere fungal communities have been identified, however, it is more difficult for us to generalize about their distribution patterns and succession dynamics. Currently, we still lack the global-scale and standardized research paradigm for biogeography of phyllosphere fungi. Fungal taxonomic diversity may not be always correlated with their functional diversity. How much is the functional redundancy of phyllosphere mycobiome at the global scale? Trait-based approaches, as an important direction for the phyllosphere mycobiome studies, will hopefully give us some clues (Zanne et al. 2020).

In terms of technology, drone mounted robotic arms will boost the sampling work for phyllosphere fungal researches. Compared with the traditional sampling methods, such as using pruning shears, professional tree climbers and shotgun collection, drone sampling will help us acquire the leaf samples at the high-height canopy more effectively and safely. For example, we may survey the phyllosphere mycobiome of *Sequoia sempervirens* along its whole trunk, which is one of the tallest trees in the world. In addition, the in-depth integration of remote sensing and omics will correlate the fungal taxonomic and functional diversity to the entire ecosystem functioning (e.g., Liu et al. 2022). As Albert Einstein said, the more we see, the less we know. For phyllosphere mycobiome, we only begin to scratch the surface of such important microorganisms. More and more researches and reviews in these areas will be helpful in evaluating and predicting the variation in diversity and function of phyllosphere mycobiome, and providing the new theoretical guide for agricultural application and ecological protection in the context of global change.

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References

Agan A, Solheim H, Adamson K, Hietala AM, Tedersoo L et al (2021) Seasonal dynamics of fungi associated with healthy and diseased pinus sylvestris needles in Northern Europe. Microorganisms 9(8):1757. https://doi.org/10.3390/microorganisms9081757

Aguiar-Pulido V, Huang W, Suarez-Ulloa V, Cickovski T, Mathee K et al (2016) Metagenomics, metatranscriptomics, and metabolomics approaches for microbiome analysis: supplementary issue: bioinformatics methods and applications for big metagenomics data. Evolution Bioinformat 12s1:EBO.S36436. https://doi.org/10.4137/ebo.S36436

Allen SK, Plattner GK, Nauels A, Xia Y, Stocker TF (2014) Climate change 2013: the physical science basis. An overview of the working group 1 contribution to the fifth assessment report of the intergovernmental panel on climate change (IPCC). May 01, 2014

Almario J, Mahmoudi M, Kroll S, Agler M, Placzek A et al (2022) The leaf microbiome of arabidopsis displays reproducible dynamics and patterns throughout the growing season. MBIO 13(3): e02825-21. https://doi.org/10.1128/mbio.02825-21

Andrews JH, Harris RF (2000) The ecology and biogeography of microorganisms of plant surfaces. Annu Rev Phytopathol 38:145–180. https://doi.org/10.1146/annurev.phyto.38.1.145

Andrews JH, Kinkel LL, Berbee FM, Nordheim EV (1987) Fungi, leaves, and the theory of Island biogeography. Microb Ecol 14(3):277–290. https://doi.org/10.1007/Bf02012947

Apigo A, Oono R (2022) Plant abundance, but not plant evolutionary history, shapes patterns of host specificity in foliar fungal endophytes. Ecosphere 13(1):e03879. https://doi.org/10.1002/ecs2.3879

Arfi Y, Buee M, Marchand C, Levasseur A, Record E (2012) Multiple markers pyrosequencing reveals highly diverse and host-specific fungal communities on the mangrove trees Avicennia marina and Rhizophora stylosa. Fems Microbiol Ecol 79(2):433–444. https://doi.org/10.1111/j.1574-6941.2011.01236.x

Arnold AE (2007) Understanding the diversity of foliar endophytic fungi: progress, challenges, and frontiers. Fungal Biol Rev 21(2-3):51–66. https://doi.org/10.1016/j.fbr.2007.05.003

Arnold AE, Lutzoni F (2007) Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? Ecology 88(3):541–549. https://doi.org/10.1890/05-1459

Arnold AE, Maynard Z, Gilbert GS, Coley PD, Kursar TA (2000) Are tropical fungal endophytes hyperdiverse? Ecol Lett 3(4):267–274. https://doi.org/10.1046/j.1461-0248.2000.00159.x

Arnold AE, Miadlikowska J, Higgins KL, Sarvate SD, Gugger P et al (2009) A phylogenetic estimation of trophic transition networks for ascomycetous fungi: are lichens cradles of symbiotrophic fungal diversification? Syst Biol 58(3):283–297. https://doi.org/10.1093/sysbio/syp001

Bagchi R, Gallery RE, Gripenberg S, Gurr SJ, Narayan L et al (2014) Pathogens and insect herbivores drive rainforest plant diversity and composition. Nature 506(7486):85–88. https://doi.org/10.1038/nature12911

Bailey BA, Strem MD, Wood D (2009) Trichoderma species form endophytic associations within Theobroma cacao trichomes. Mycol Res 113:1365–1376. https://doi.org/10.1016/j.mycres.2009.09.004

Baldrian P (2017) Forest microbiome: diversity, complexity and dynamics. Fems Microbiol Rev 41(2):109–130. https://doi.org/10.1093/femsre/fuw040

Baldrian P, Větrovský T, Lepinay C, Kohout P (2021) High-throughput sequencing view on the magnitude of global fungal diversity. Fungal Divers 114(1):539–547. https://doi.org/10.1007/s13225-021-00472-y

Balint M, Tiffin P, Hallstrom B, O'Hara RB, Olson MS et al (2013) Host genotype shapes the foliar fungal microbiome of balsam poplar (Populus balsamifera). Plos One 8(1):e53987. https://doi.org/10.1371/journal.pone.0053987

Balint M, Bartha L, O'Hara RB, Olson MS, Otte J et al (2015) Relocation, high-latitude warming and host genetic identity shape the foliar fungal microbiome of poplars. Mol Ecol 24(1):235–248. https://doi.org/10.1111/Mec.13018

Banerjee S, Schlaeppi K, van der Heijden MGA (2018) Keystone taxa as drivers of microbiome structure and functioning. Nat Rev Microbiol 16(9):567–576. https://doi.org/10.1038/s41579-018-0024-1

Bao LJ, Sun B, Liu JY, Zhang SW, Xu N et al (2022) Leaf-associated epiphytic fungi of Gingko biloba, Pinus bungeana and Sabina chinensis exhibit delicate seasonal variations. J Fungi 8(6):631. https://doi.org/10.3390/jof8060631

Barberan A, Fernandez-Guerra A, Bohannan BJM, Casamayor EO (2012) Exploration of community traits as ecological markers in microbial metagenomes. Mol Ecol 21(8):1909–1917. https://doi.org/10.1111/j.1365-294X.2011.05383.x

Barge EG, Leopold DR, Peay KG, Newcombe G, Busby PE (2019) Differentiating spatial from environmental effects on foliar fungal communities of Populus trichocarpa. J Biogeogr 46(9):2001–2011. https://doi.org/10.1111/jbi.13641

Bari R, Jones J (2009) Role of plant hormones in plant defence responses. Plant mol biol 69(4):473–488. https://doi.org/10.1007/s11103-008-9435-0

Bashir I, War AF, Rafiq I, Reshi ZA, Rashid I et al (2022) Phyllosphere microbiome: diversity and functions. Microbiol Res 254:126888. https://doi.org/10.1016/j.micres.2021.126888

Bastias DA, Martínez-Ghersa MA, Ballaré CL, Gundel PE (2017) Epichloë fungal endophytes and plant defenses: not just Alkaloids. Trends Plant Sci 22(11):939–948. https://doi.org/10.1016/j.tplants.2017.08.005

Behnke-Borowczyk J, Kwasna H, Kulawinek B (2019) Fungi associated with Cyclaneusma needle cast in Scots pine in the west of Poland. Forest Pathol 49(2):e12487. https://doi.org/10.1111/efp.12487

Berg G, Cernava T (2022) The plant microbiota signature of the Anthropocene as a challenge for microbiome research. Microbiome 10(1):54. https://doi.org/10.1186/s40168-021-01224-5

Bowman EA, Arnold AE (2021) Drivers and implications of distance decay differ for ectomycorrhizal and foliar endophytic fungi across an anciently fragmented landscape. Isme J 15(12):3437–3454. https://doi.org/10.1038/s41396-021-01006-9

Bowsher AW, Benucci GMN, Bonito G, Shade A (2021) Seasonal dynamics of core fungi in the switchgrass phyllosphere, and co-occurrence with leaf bacteria. Phytobiomes J 5(1):60–68. https://doi.org/10.1094/Pbiomes-07-20-0051-R

Brestic M, Yang XH, Li XN, Allakhverdiev SI (2021) Crop photosynthesis for the twenty-first century. Photosynth Res 150(1-3):1–3. https://doi.org/10.1007/s11120-021-00869-5

Bright M, Bulgheresi S (2010) A complex journey: transmission of microbial symbionts. Nat Rev Microbiol 8(3):218–230. https://doi.org/10.1038/nrmicro2262

Busby PE, Ridout M, Newcombe G (2016) Fungal endophytes: modifiers of plant disease. Plant Mol Biol 90(6):645–655. https://doi.org/10.1007/s11103-015-0412-0

Busby PE, Newcombe G, Neat AS, Averill C (2022) Facilitating reforestation through the plant microbiome: perspectives from the phyllosphere. Annu Rev Phytopathol 60:337–356. https://doi.org/10.1146/annurev-phyto-021320-010717

Camargos Fonseca PL, Skaltsas D, da Silva FF, Kato RB, de Castro GM et al (2022) An integrative view of the phyllosphere mycobiome of native rubber trees in the Brazilian Amazon. J Fungi 8(4):373–373. https://doi.org/10.3390/jof8040373

Carrara JE, Walter CA, Hawkins JS, Peterjohn WT, Averill C et al (2018) Interactions among plants, bacteria, and fungi reduce extracellular enzyme activities under long-term N fertilization. Glob Chang Biol 24(6):2721–2734. https://doi.org/10.1111/gcb.14081

Casas C, Omacini M, Montecchia MS, Correa OS (2011) Soil microbial community responses to the fungal endophyte Neotyphodium in Italian ryegrass. Plant Soil 340(1-2):347–355. https://doi.org/10.1007/s11104-010-0607-8

Castaneda LE, Miura T, Sanchez R, Barbosa O (2018) Effects of agricultural management on phyllosphere fungal diversity in vineyards and the association with adjacent native forests. Peerj 6:e5715. https://doi.org/10.7717/peerj.5715

Chase JM (2003) Community assembly: when should history matter? Oecologia 136(4):489–498. https://doi.org/10.1007/s00442-003-1311-7

Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. Philos T R Soc B 366(1576):2351–2363. https://doi.org/10.1098/rstb.2011.0063

Chen L, Swenson NG, Ji N, Mi X, Ren H et al (2019) Differential soil fungus accumulation and density dependence of trees in a subtropical forest. Science 366(6461):124–128. https://doi.org/10.1126/science.aau1361

Chen T, Nomura K, Wang XL, Sohrabi R, Xu J et al (2020a) A plant genetic network for preventing dysbiosis in the phyllosphere. Nature 580(7805):653. https://doi.org/10.1038/s41586-020-2185-0

Chen ZJ, Jin YY, Yao X, Chen TX, Wei XK et al (2020b) Fungal endophyte improves survival of Lolium perenne in low fertility soils by increasing root growth, metabolic activity and absorption of nutrients. Plant Soil 452(1-2):185–206. https://doi.org/10.1007/s11104-020-04556-7

Chen QL, Hu HW, Yan ZZ, Li CY, Nguyen BAT et al (2021a) Precipitation increases the abundance of fungal plant pathogens in Eucalyptus phyllosphere. Environ Microbiol 23(12):7688–7700. https://doi.org/10.1111/1462-2920.15728

Chen TX, White JF, Li CJ (2021b) Fungal endophyte Epichloe bromicola infection regulates anatomical changes to account for salt stress tolerance in wild barley (Hordeum brevisubulatum). Plant Soil 461(1-2):533–546. https://doi.org/10.1007/s11104-021-04828-w

Chen KH, Liao HL, Arnold AE, Korotkin HB, Wu SH et al (2022) Comparative transcriptomics of fungal endophytes in co-culture with their moss host Dicranum scoparium reveals fungal trophic lability and moss unchanged to slightly increased growth rates. New Phytol 234(5):1832–1847. https://doi.org/10.1111/nph.18078

Chowdhury SP, Babin D, Sandmann M, Jacquiod S, Sommermann L et al (2019) Effect of long-term organic and mineral fertilization strategies on rhizosphere microbiota assemblage and performance of lettuce. Environ Microbiol 21(7):2426–2439. https://doi.org/10.1111/1462-2920.14631

Christian N, Herre EA, Clay K (2019) Foliar endophytic fungi alter patterns of nitrogen uptake and distribution in Theobroma cacao. New Phytol 222(3):1573–1583. https://doi.org/10.1111/nph.15693

Chu H, Gao GF, Ma Y, Fan K, Delgado-Baquerizo M (2020) Soil microbial biogeography in a changing world: recent advances and future perspectives. Msystems 5(2):e00803–e00819. https://doi.org/10.1128/mSystems.00803-19

Ciuffetti LM, Manning VA, Pandelova I, Betts MF, Martinez JP (2010) Host-selective toxins, Ptr ToxA and Ptr ToxB, as necrotrophic effectors in the Pyrenophora tritici-repentis-wheat interaction. New Phytol 187(4):911–919. https://doi.org/10.1111/j.1469-8137.2010.03362.x

Coleine C, Stajich JE, Selbmann L (2022) Fungi are key players in extreme ecosystems. Trends Ecol Evol 37(6):517–528. https://doi.org/10.1016/j.tree.2022.02.002

Cordier T, Robin C, Capdevielle X, Desprez-Loustau ML, Vacher C (2012a) Spatial variability of phyllosphere fungal assemblages: genetic distance predominates over geographic distance in a European beech stand (Fagus syluatica). Fungal Ecol 5(5):509–520. https://doi.org/10.1016/j.funeco.2011.12.004

Cordier T, Robin C, Capdevielle X, Fabreguettes O, Desprez-Loustau ML et al (2012b) The composition of phyllosphere fungal assemblages of European beech (Fagus sylvatica) varies significantly along an elevation gradient. New Phytol 196(2):510–519. https://doi.org/10.1111/j.1469-8137.2012.04284.x

Costa Pinto LSR, Azevedo JL, Pereira JO, Carneiro Vieira ML, Labate CA (2000) Symptomless infection of banana and maize by endophytic fungi impairs photosynthetic efficiency. New Phytol 147(3):609–615. https://doi.org/10.1046/j.1469-8137.2000.00722.x

Cross H, Sonstebo JH, Nagy NE, Timmermann V, Solheim H et al (2017) Fungal diversity and seasonal succession in ash leaves infected by the invasive ascomycete Hymenoscyphus fraxineus. New Phytol 213(3):1405–1417. https://doi.org/10.1111/nph.14204

David AS, Seabloom EW, May G (2016) Plant host species and geographic distance affect the structure of aboveground fungal symbiont communities, and environmental filtering affects belowground communities in a coastal dune ecosystem. Microb Ecol 71(4):912–926. https://doi.org/10.1007/s00248-015-0712-6

De Bellis T, Laforest-Lapointe I, Solarik KA, Gravel D, Kembel SW (2022) Regional variation drives differences in microbial communities associated with sugar maple across a latitudinal range. Ecology 103(8):e3727. https://doi.org/10.1002/ecy.3727

De Vries FT, Griffiths RI, Knight CG, Nicolitch O, Williams A (2020) Harnessing rhizosphere microbiomes for drought-resilient crop production. Science 368(6488):270. https://doi.org/10.1126/science.aaz5192

Dean R, Van Kan JAL, Pretorius ZA, Hammond-Kosack KE, Di Pietro A et al (2012) The top 10 fungal pathogens in molecular plant pathology. Mol Plant Pathol 13(7):804. https://doi.org/10.1111/j.1364-3703.2012.00822.x

Delhomme N, Sundstrom G, Zamani N, Lantz H, Lin YC et al (2015) Serendipitous metatranscriptomics: the fungal community of Norway Spruce (Picea abies). Plos One 10(9):e0139080. https://doi.org/10.1371/journal.pone.0139080

Dhayanithy G, Subban K, Chelliah J (2019) Diversity and biological activities of endophytic fungi associated with Catharanthus roseus. BMC Microbiol 19(1):22. https://doi.org/10.1186/s12866-019-1386-x

dos Santos GD, Gomes RR, Goncalves R, Fornari G, Maia BHLNS et al (2021) Molecular identification and antimicrobial activity of foliar endophytic fungi on the Brazilian pepper tree (Schinus terebinthifolius) reveal new species of diaporthe. Curr Microbiol 78(8):3218–3229. https://doi.org/10.1007/s00284-021-02582-x

Dove NC, Klingeman DM, Carrell AA, Cregger MA, Schadt CW (2021) Fire alters plant microbiome assembly patterns: integrating the plant and soil microbial response to disturbance. New Phytol 230(6):2433–2446. https://doi.org/10.1111/nph.17248

Du J, Qv M, Zhang Y, Cui M, Zhang H (2020) Simulated sulfuric and nitric acid rain inhibits leaf breakdown in streams: a microcosm study with artificial reconstituted fresh water. Ecotox Environ Safe 196:110535. https://doi.org/10.1016/j.ecoenv.2020.110535

Escalas A, Hale L, Voordeckers JW, Yang YF, Firestone MK, Alvarez-Cohen L et al (2019) Microbial functional diversity: from concepts to applications. Ecol Evol 9(20):12000–12016. https://doi.org/10.1002/ece3.5670

Eschen R, Hunt S, Mykura C, Gange AC, Sutton BC (2010) The foliar endophytic fungal community composition in Cirsium arvense is affected by mycorrhizal colonization and soil nutrient content. Fungal Biol-Uk 114(11–12):991–998. https://doi.org/10.1016/j.funbio.2010.09.009

Eusemann P, Schnittler M, Nilsson RH, Jumpponen A, Dahl MB et al (2016) Habitat conditions and phenological tree traits overrule the influence of tree genotype in the needle mycobiome-Picea glauca system at an arctic treeline ecotone. New Phytol 211(4):1221–1231. https://doi.org/10.1111/nph.13988

Fan K, Delgado-Baquerizo M, Guo X, Wang D, Wu Y et al (2019) Suppressed N fixation and diazotrophs after four decades of fertilization. Microbiome 7(1):143. https://doi.org/10.1186/s40168-019-0757-8

Faticov M, Abdelfattah A, Roslin T, Vacher C, Hamback P et al (2021) Climate warming dominates over plant genotype in shaping the seasonal trajectory of foliar fungal communities on oak. New Phytol 231(5):1770–1783. https://doi.org/10.1111/nph.17434

Faust K, Raes J (2012) Microbial interactions: from networks to models. Nat Rev Microbiol 10(8):538–550. https://doi.org/10.1038/nrmicro2832

Feng J, Penton CR, He Z, Van Nostrand JD, Yuan MM et al (2019) Long-term warming in Alaska enlarges the diazotrophic community in deep soils. mbio 10(1):e02521–18. https://doi.org/10.1128/mBio.02521-18

Fernandes MLP, Bastida F, Jehmlich N, Martinovic T, Vetrovsky T et al (2021) Functional soil mycobiome across ecosystems. J Proteomics 252:104428. https://doi.org/10.1016/j.jprot.2021.104428

Fiehn O (2002) Metabolomics – the link between genotypes and phenotypes. Plant mol biol 48(1-2):155–171. https://doi.org/10.1023/A:1013713905833

Franic I, Prospero S, Adamson K, Allan E, Attorre F et al (2022) Worldwide diversity of endophytic fungi and insects associated with dormant tree twigs. Sci Data 9(1):62. https://doi.org/10.1038/s41597-022-01162-3

Friesen ML, Porter SS, Stark SC, von Wettberg EJ, Sachs JL et al (2011) Microbially mediated plant functional traits. Annu Rev Ecol Evol S 42(42):23–46. https://doi.org/10.1146/annurev-ecolsys-102710-145039

Gao C, Montoya L, Xu L, Madera M, Hollingsworth J et al (2020) Fungal community assembly in drought-stressed sorghum shows stochasticity, selection, and universal ecological dynamics. Nat Commun 11(1):34. https://doi.org/10.1038/s41467-019-13913-9

Gao MJ, He Y, Yin X, Zhong XB, Yan BX et al (2021) Ca2+ sensor-mediated ROS scavenging suppresses rice immunity and is exploited by a fungal effector. Cell, 184(21):5391. https://doi.org/10.1016/j.cell.2021.09.009

Garcia E, Alonso A, Platas G, Sacristan S (2013) The endophytic mycobiota of Arabidopsis thaliana. Fungal Divers 60(1):71–89. https://doi.org/10.1007/s13225-012-0219-0

Genre A, Lanfranco L, Perotto S, Bonfante P (2020) Unique and common traits in mycorrhizal symbioses. Nat Rev Microbiol 18(11):649–660. https://doi.org/10.1038/s41579-020-0402-3

Giauque H, Hawkes CV (2016) Historical and current climate drive spatial and temporal patterns in fungal endophyte diversity. Fungal Ecol 20:108–114. https://doi.org/10.1016/j.funeco.2015.12.005

Glushakova AM, Chernov IY (2004) Seasonal dynamics in a yeast population on leaves of the common wood sorrel Oxalis acetosella L. Microbiology 73(2):184–188. https://doi.org/10.1023/B:MICI.0000023987.40253.2d

Glushakova AM, Yurkov AM, Chernov IY (2007) Massive isolation of anamorphous ascomycete yeasts Candida oleophila from plant phyllosphere. Microbiology 76(6):799–803. https://doi.org/10.1134/S0026261707060215

Gomes T, Pereira JA, Benhadi J, Lino-Neto T, Baptista P (2018) Endophytic and epiphytic phyllosphere fungal communities are shaped by different environmental factors in a mediterranean ecosystem. Microb Ecol 76(3):668–679. https://doi.org/10.1007/s00248-018-1161-9

Gouka L, Raaijmakers JM, Cordovez V (2022) Ecology and functional potential of phyllosphere yeasts. Trends Plant Sci. https://doi.org/10.1016/j.tplants.2022.06.007

Grossart HP, Van den Wyngaert S, Kagami M, Wurzbacher C, Cunliffe M et al (2019) Fungi in aquatic ecosystems. Nat Rev Microbiol 17(6):339–354. https://doi.org/10.1038/s41579-019-0175-8

Guerra CA, Bardgett RD, Caon L, Crowther TW, Delgado-Baquerizo M et al (2021) Tracking, targeting, and conserving soil biodiversity. Science 371(6526):239–241. https://doi.org/10.1126/science.abd7926

Guo JH, Liu XJ, Zhang Y, Shen JL, Han WX et al (2010) Significant acidification in major Chinese croplands. Science 327(5968):1008–1010. https://doi.org/10.1126/science.1182570

Gupta A, Rico-Medina A, Cano-Delgado AI (2020) The physiology of plant responses to drought. Science 368(6488):266–269. https://doi.org/10.1126/science.aaz7614

Hanson CA, Fuhrman JA, Horner-Devine MC, Martiny JBH (2012) Beyond biogeographic patterns: processes shaping the microbial landscape. Nat Rev Microbiol 10(7):497–506. https://doi.org/10.1038/nrmicro2795

Harrison JG, Forister ML, Parchman TL, Koch GW (2016) Vertical stratification of the foliar fungal community in the world's tallest trees. Am J Bot 103(12):2087–2095. https://doi.org/10.3732/ajb.1600277

Hawkes CV, Kivlin SN, Rocca JD, Huguet V, Thomsen MA et al (2011) Fungal community responses to precipitation. Glob Chang Biol 17(4):1637–1645. https://doi.org/10.1111/j.1365-2486.2010.02327.x

Hawkes CV, Kjoller R, Raaijmakers JM, Riber L, Christensen S et al (2021) Extension of plant phenotypes by the Foliar microbiome. Annu Rev Plant Biol 72:823–846. https://doi.org/10.1146/annurev-arplant-080620-114342

He ZH, Webster S, He SY (2022) Growth-defense trade-offs in plants. Curr Biol 32(12):R634–R639

Helander ML, Neuvonen S, Sieber T, Petrini O (1993) Simulated acid-rain affects birch leaf endophyte populations. Microb Ecol 26(3):227–234. https://doi.org/10.1007/BF00176955

Helander M, Ahlholm J, Sieber TN, Hinneri S, Saikkonen K (2007) Fragmented environment affects birch leaf endophytes. New Phytol 175(3):547–553. https://doi.org/10.1111/j.1469-8137.2007.02110.x

Higgins KL, Coley PD, Kursar TA, Arnold AE (2011) Culturing and direct PCR suggest prevalent host generalism among diverse fungal endophytes of tropical forest grasses. Mycologia 103(2):247–260. https://doi.org/10.3852/09-158

Higgins KL, Arnold AE, Coley PD, Kursar TA (2014) Communities of fungal endophytes in tropical forest grasses: highly diverse host- and habitat generalists characterized by strong spatial structure. Fungal Ecol 8:1–11. https://doi.org/10.1016/J.Funeco.2013.12.005

Hoffman MT, Arnold AE (2008) Geographic locality and host identity shape fungal endophyte communities in cupressaceous trees. Mycol Res 112:331–344. https://doi.org/10.1016/j.mycres.2007.10.014

Hoffman MT, Gunatilaka MK, Wijeratne K, Gunatilaka L, Arnold AE (2013) Endohyphal bacterium enhances production of indole-3-acetic acid by a foliar fungal endophyte. Plos One 8(9):e73132. https://doi.org/10.1371/journal.pone.0073132

Hunter PJ, Pink DAC, Bending GD (2015) Cultivar-level genotype differences influence diversity and composition of lettuce (Lactuca sp.) phyllosphere fungal communities. Fungal Ecol 17:183–186. https://doi.org/10.1016/j.funeco.2015.05.007

Huot B, Yao J, Montgomery BL, He SY (2014) Growth-defense tradeoffs in plants: a balancing act to optimize fitness. Mol Plant 7(8):1267–1287. https://doi.org/10.1093/mp/ssu049

Hussain S, Hussain S, Ali B, Ren XL, Chen XL et al (2021) Recent progress in understanding salinity tolerance in plants: story of Na+/K+ balance and beyond. Plant Physiol Bioch 160:239–256. https://doi.org/10.1016/j.plaphy.2021.01.029

Imperato V, Kowalkowski L, Portillo-Estrada M, Gawronski SW, Vangronsveld J et al (2019) Characterisation of the Carpinus betulus L. Phyllomicrobiome in urban and forest areas. Front Microbiol 10:1110. https://doi.org/10.3389/fmicb.2019.01110

Inacio J, Pereira P, de Carvalho M, Fonseca A, Amaral-Collaco MT et al (2002) Estimation and diversity of phylloplane mycobiota on selected plants in a Mediterranean-type ecosystem in Portugal. Microb Ecol 44(4):344–353. https://doi.org/10.1007/s00248-002-2022-z

Ivashchenko KV, Korneykova MV, Sazonova OI, Vetrova AA, Ermakova AO et al (2022) Phylloplane biodiversity and activity in the city at different distances from the traffic pollution source. Plants-Basel 11(3):402. https://doi.org/10.3390/plants11030402

Jia Q, Qu JW, Mu HN, Sun HG, Wu C (2020) Foliar endophytic fungi: diversity in species and functions in forest ecosystems. Symbiosis 80(2):103–132. https://doi.org/10.1007/s13199-019-00663-x

Jumpponen A, Jones KL (2009) Massively parallel 454 sequencing indicates hyperdiverse fungal communities in temperate Quercus macrocarpa phyllosphere. New Phytol 184(2):438–448. https://doi.org/10.1111/j.1469-8137.2009.02990.x

Jumpponen A, Jones KL (2010) Seasonally dynamic fungal communities in the Quercus macrocarpa phyllosphere differ between urban and nonurban environments. New Phytol 186(2):496–513. https://doi.org/10.1111/j.1469-8137.2010.03197.x

Karlsson I, Friberg H, Steinberg C, Persson P (2014) Fungicide effects on fungal community composition in the wheat phyllosphere. Plos One 9(11):e111786. https://doi.org/10.1371/journal.pone.0111786

Karlsson I, Friberg H, Kolseth AK, Steinberg C, Persson P (2017) Organic farming increases richness of fungal taxa in the wheat phyllosphere. Mol Ecol 26(13):3424–3436. https://doi.org/10.1111/mec.14132

Kay GM, Tulloch A, Barton PS, Cunningham SA, Driscoll DA et al (2018) Species co-occurrence networks show reptile community reorganization under agricultural transformation. Ecography 41(1):113–125. https://doi.org/10.1111/ecog.03079

Keller KR, Lau JA (2018) When mutualisms matter: rhizobia effects on plant communities depend on host plant population and soil nitrogen availability. J Ecol 106(3):1046–1056. https://doi.org/10.1111/1365-2745.12938

Kembel SW, Mueller RC (2014) Plant traits and taxonomy drive host associations in tropical phyllosphere fungal communities. Botany 92(4):303–311. https://doi.org/10.1139/cjb-2013-0194

Kernaghan G, Mayerhofer M, Griffin A (2017) Fungal endophytes of wild and hybrid Vitis leaves and their potential for vineyard biocontrol. Can J Microbiol 63(7):583–595. https://doi.org/10.1139/cjm-2016-0740

Khan AL, Hussain J, Al-Harrasi A, Al-Rawahi A, Lee IJ (2015) Endophytic fungi: resource for gibberellins and crop abiotic stress resistance. Crit Rev Biotechnol 35(1):62–74. https://doi.org/10.3109/07388551.2013.800018

Khan AL, Al-Harrasi A, Al-Rawahi A, Al-Farsi Z, Al-Mamari A et al (2016) Endophytic fungi from frankincense tree improves host growth and produces extracellular enzymes and indole acetic acid. Plos One 11(6):e0158207. https://doi.org/10.1371/journal.pone.0158207

Kharwar RN, Gond SK, Kumar A, Mishra A (2010) A comparative study of endophytic and epiphytic fungal association with leaf of Eucalyptus citriodora Hook., and their antimicrobial activity. World J Microb Biot 26(11):1941–1948. https://doi.org/10.1007/s11274-010-0374-y

Khoiri AN, Cheevadhanarak S, Jirakkakul J, Dulsawat S, Prommeenate P et al (2021) Comparative metagenomics reveals microbial signatures of sugarcane phyllosphere in organic management. Front Microbiol 12:623799. https://doi.org/10.3389/fmicb.2021.623799

Kim MS, Park EJ (2021) Postharvest-induced microbiota remodeling increases fungal diversity in the phyllosphere mycobiota of broccoli florets. Postharvest Biol Tec 181:111693. https://doi.org/10.1016/j.postharvbio.2021.111693

Kim S, Park H, Gruszewski HA, Schmale DG, Jung S (2019) Vortex-induced dispersal of a plant pathogen by raindrop impact. P Natl Acad Sci USA 116(11):4917–4922. https://doi.org/10.1073/pnas.1820318116

Kivlin SN, Kazenel MR, Lynn JS, Taylor DL, Rudgers JA (2019) Plant identity influences foliar fungal symbionts more than elevation in the Colorado Rocky mountains. Microb Ecol 78(3):688–698. https://doi.org/10.1007/s00248-019-01336-4

Knief C, Delmotte N, Chaffron S, Stark M, Innerebner G et al (2012) Metaproteogenomic analysis of microbial communities in the phyllosphere and rhizosphere of rice. Isme J 6(7):1378–1390. https://doi.org/10.1038/ismej.2011.192

Knights D, Kuczynski J, Charlson ES, Zaneveld J, Mozer MC et al (2011) Bayesian community-wide culture-independent microbial source tracking. Nat Methods 8(9):761–U107. https://doi.org/10.1038/nmeth.1650

Kretschmer M, Damoo D, Djamei A, Kronstad J (2019) Chloroplasts and plant immunity: where are the fungal effectors? Pathogens 9(1):19. https://doi.org/10.3390/pathogens9010019

Kusari S, Hertweck C, Spitellert M (2012) Chemical ecology of endophytic fungi: origins of secondary metabolites. Chem Biol 19(7):792–798. https://doi.org/10.1016/j.chembiol.2012.06.004

Lahlali R, Hijri M (2010) Screening, identification and evaluation of potential biocontrol fungal endophytes against Rhizoctonia solani AG3 on potato plants. Fems Microbiol Lett 311(2):152–159. https://doi.org/10.1111/j.1574-6968.2010.02084.x

Lambais MR, Barrera SE, Santos EC, Crowley DE, Jumpponen A (2017) Phyllosphere metaproteomes of trees from the Brazilian Atlantic forest show high levels of functional redundancy. Microb Ecol 73(1):123–134. https://doi.org/10.1007/s00248-016-0878-6

Lankadurai BP, Nagato EG, Simpson MJ (2013) Environmental metabolomics: an emerging approach to study organism responses to environmental stressors. Environ Rev 21(3):180–205. https://doi.org/10.1139/er-2013-0011

Larkin BG, Hunt LS, Ramsey PW (2012) Foliar nutrients shape fungal endophyte communities in Western white pine (Pinus monticola) with implications for white-tailed deer herbivory. Fungal Ecol 5(2):252–260. https://doi.org/10.1016/j.funeco.2011.11.002

Larran S, Perello A, Simon MR, Moreno V (2007) The endophytic fungi from wheat (Triticum aestivum L.). World J Microb Biot 23(4):565–572. https://doi.org/10.1007/s11274-006-9266-6

Lau MK, Arnold AE, Johnson NC (2013) Factors influencing communities of foliar fungal endophytes in riparian woody plants. Fungal Ecol 6(5):365–378. https://doi.org/10.1016/j.funeco.2013.06.003

Lazarevic J, Menkis A (2020) Fungal diversity in the phyllosphere of pinus heldreichii H. christ – an endemic and high-altitude pine of the mediterranean region. Diversity-Basel 12(5):172. https://doi.org/10.3390/d12050172

Lee G, Lee SH, Kim KM, Ryu CM (2017) Foliar application of the leaf-colonizing yeast Pseudozyma churashimaensis elicits systemic defense of pepper against bacterial and viral pathogens. Sci Rep-Uk 7. https://doi.org/10.1038/srep39432

Lee K, Missaoui A, Mahmud K, Presley H, Lonnee M (2021) Interaction between grasses and epichloe endophytes and its significance to biotic and abiotic stress tolerance and the rhizosphere. Microorganisms 9(11):2186. https://doi.org/10.3390/microorganisms9112186

Levy A, Conway JM, Dangl JL, Woyke T (2018) Elucidating bacterial gene functions in the plant microbiome. Cell Host Microbe 24(4):475–485. https://doi.org/10.1016/j.chom.2018.09.005

Li Y, Chen Z, He JZ, Wang Q, Shen C, Ge Y (2019) Ectomycorrhizal fungi inoculation alleviates simulated acid rain effects on soil ammonia oxidizers and denitrifiers in Masson pine forest. Environ Microbiol 21(1):299–313. https://doi.org/10.1111/1462-2920.14457

Li M, Hong L, Ye W, Wang Z, Shen H (2022a) Phyllosphere bacterial and fungal communities vary with host species identity, plant traits and seasonality in a subtropical forest. Environ Microbiome 17(1):29. https://doi.org/10.1186/s40793-022-00423-3

Li PD, Zhu ZR, Zhang YZ, Xu JP, Wang HK et al (2022b) The phyllosphere microbiome shifts toward combating melanose pathogen. Microbiome 10(1). https://doi.org/10.1186/s40168-022-01234-x

Lin HY, Li WH, Lin CF, Wu HR, Zhao YP (2022) International biological flora: Ginkgo biloba. J Ecol 110(4):951–982. https://doi.org/10.1111/1365-2745.13856

Lindow SE, Brandl MT (2003) Microbiology of the phyllosphere. Appl Environ Microb 69(4):1875–1883. https://doi.org/10.1128/AEM.69.4.1875-1883.2003

Lindow SE, Leveau JH (2002) Phyllosphere microbiology. Curr Opin Biotech 13(3):238–243. https://doi.org/10.1016/s0958-1669(02)00313-0

Liu X, Ma ZY, Cadotte MW, Chen F, He JS, Zhou SR (2019) Warming affects foliar fungal diseases more than precipitation in a Tibetan alpine meadow. New Phytol 221(3):1574–1584. https://doi.org/10.1111/nph.15460

Liu HW, Brettell LE, Singh B (2020) Linking the phyllosphere microbiome to plant health. Trends in Plant Sci 25(9):841–844. https://doi.org/10.1016/j.tplants.2020.06.003

Liu S, Garcia-Palacios P, Tedersoo L, Guirado E, van der Heijden MGA et al (2022) Phylotype diversity within soil fungal functional groups drives ecosystem stability. Nat Ecol Evol 6(7):900–909. https://doi.org/10.1038/s41559-022-01756-5

Lloyd KG, Steen AD, Ladau J, Yin J, Crosby L (2018) Phylogenetically novel uncultured microbial cells dominate Earth microbiomes. Msystems 3(5):e00055–e00018. https://doi.org/10.1128/mSystems.00055-18

Luo CW, Tsementzi D, Kyrpides NC, Konstantinidis KT (2012) Individual genome assembly from complex community short-read metagenomic datasets. Isme J 6(4):898–901. https://doi.org/10.1038/ismej.2011.147

Lynikiene J, Marciulyniene D, Marciulynas A, Gedminas A, Vaiciukyne M et al (2020) Managed and unmanaged pinus sylvestris forest stands harbour similar diversity and composition of the phyllosphere and soil fungi. Microorganisms 8(2):259. https://doi.org/10.3390/microorganisms8020259

Ma A, Zhuang X, Wu J, Cui M, Lv D, Liu C, Zhuang G (2013) Ascomycota members dominate fungal communities during straw residue decomposition in arable soil. Plos One 8(6):e66146. https://doi.org/10.1371/journal.pone.0066146

Malinowski DP, Alloush GA, Belesky DP (2000) Leaf endophyte Neotyphodium coenophialum modifies mineral uptake in tall fescue. Plant Soil 227(1-2):115–126. https://doi.org/10.1023/A:1026518828237

Manning VA, Chu AL, Scofield SR, Ciuffetti LM (2010) Intracellular expression of a host-selective toxin, ToxA, in diverse plants phenocopies silencing of a ToxA-interacting protein, ToxABP1. New Phytol 187(4):1034–1047. https://doi.org/10.1111/j.1469-8137.2010.03363.x

Martiny JBH, Bohannan BJM, Brown JH, Colwell RK, Fuhrman JA et al (2006) Microbial biogeography: putting microorganisms on the map. Nat Rev Microbiol 4(2):102–112. https://doi.org/10.1038/nrmicro1341

Martiny JB, Jones SE, Lennon JT, Martiny AC (2015) Microbiomes in light of traits: a phylogenetic perspective. Science 350(6261):aac9323. https://doi.org/10.1126/science.aac9323

Materatski P, Varanda C, Carvalho T, Dias AB, Campos MD et al (2019) Spatial and temporal variation of fungal endophytic richness and diversity associated to the phyllosphere of olive cultivars. Fungal Biol-Uk 123(1):66–76. https://doi.org/10.1016/j.funbio.2018.11.004

Matsumura E, Fukuda K (2013) A comparison of fungal endophytic community diversity in tree leaves of rural and urban temperate forests of Kanto district, Eastern Japan. Fungal Biol-Uk 117(3):191–201. https://doi.org/10.1016/j.funbio.2013.01.007

Meiser A, Balint M, Schmitt I (2014) Meta-analysis of deep-sequenced fungal communities indicates limited taxon sharing between studies and the presence of biogeographic patterns. New Phytol 201(2):623–635. https://doi.org/10.1111/Nph.12532

Mendgen K, Hahn M (2002) Plant infection and the establishment of fungal biotrophy. Trends Plant Sci 7(8):352–356. https://doi.org/10.1016/S1360-1385(02)02297-5

Millberg H, Boberg J, Stenlid J (2015) Changes in fungal community of Scots pine (Pinus sylvestris) needles along a latitudinal gradient in Sweden. Fungal Ecol 17:126–139. https://doi.org/10.1016/j.funeco.2015.05.012

Mogouong J, Constant P, Legendre P, Guertin C (2021) The phyllosphere microbiome of host trees contributes more than leaf phytochemicals to variation in the Agrilus planipennis Fairmaire gut microbiome structure. Sci Rep-Uk 11(1). https://doi.org/10.1038/s41598-021-95146-9

Monson RK, Trowbridge AM, Lindroth RL, Lerdau MT (2022) Coordinated resource allocation to plant growth-defense tradeoffs. New Phytol 233(3):1051–1066. https://doi.org/10.1111/nph.17773

Moore JAM, Anthony MA, Pec GJ, Trocha LK, Trzebny A et al (2021) Fungal community structure and function shifts with atmospheric nitrogen deposition. Glob Chang Biol 27(7):1349–1364. https://doi.org/10.1111/gcb.15444

Mote RS, Hill NS, Uppal K, Tran VT, Jones DP et al (2017) Metabolomics of fescue toxicosis in grazing beef steers. Food Chem Toxicol 105:285–299. https://doi.org/10.1016/j.fct.2017.04.020

Mwajita MR, Murage H, Tani A, Kahangi EM (2013) Evaluation of rhizosphere, rhizoplane and phyllosphere bacteria and fungi isolated from rice in Kenya for plant growth promoters. Springerplus 2:606. https://doi.org/10.1186/2193-1801-2-606

Nasanit R, Krataithong K, Tantirungkij M, Limtong S (2015) Assessment of epiphytic yeast diversity in rice (Oryza sativa) phyllosphere in Thailand by a culture-independent approach. Anton Leeuw Int J G 107(6):1475–1490. https://doi.org/10.1007/s10482-015-0442-2

Newman MEJ (2006) Modularity and community structure in networks. P Natl Acad Sci USA 103(23):8577–8582. https://doi.org/10.1073/pnas.0601602103

Nguyen D, Boberg J, Ihrmark K, Stenstrom E, Stenlid J (2016a) Do foliar fungal communities of Norway spruce shift along a tree species diversity gradient in mature European forests? Fungal Ecol 23:97–108. https://doi.org/10.1016/j.funeco.2016.07.003

Nguyen NH, Song ZW, Bates ST, Branco S, Tedersoo L et al (2016b) FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecol 20:241–248. https://doi.org/10.1016/j.funeco.2015.06.006

Nguyen D, Boberg J, Cleary M, Bruelheide H, Honig L et al (2017) Foliar fungi of Betula pendula: impact of tree species mixtures and assessment methods. Sci Rep 7:41801. https://doi.org/10.1038/srep41801

Nilsson RH, Anslan S, Bahram M, Wurzbacher C, Baldrian P et al (2019) Mycobiome diversity: high-throughput sequencing and identification of fungi. Nat Rev Microbiol 17:95–109. https://doi.org/10.1038/s41579-018-0116-y

Novas MV, Iannone LJ, Godeas AM, Scervino JM (2011) Evidence for leaf endophyte regulation of root symbionts: effect of Neotyphodium endophytes on the pre-infective state of mycorrhizal fungi. Symbiosis 55(1):19–28. https://doi.org/10.1007/s13199-011-0140-4

Ohm RA, Feau N, Henrissat B, Schoch CL, Horwitz BA et al (2012) Diverse lifestyles and strategies of plant pathogenesis encoded in the genomes of eighteen Dothideomycetes fungi. Plos Pathog 8(12):e1003037. https://doi.org/10.1371/journal.ppat.1003037

Oono R, Lefevre E, Simha A, Lutzoni F (2015) A comparison of the community diversity of foliar fungal endophytes between seedling and adult loblolly pines (Pinus taeda). Fungal Biol-Uk 119(10):917–928. https://doi.org/10.1016/j.funbio.2015.07.003

Oono R, Rasmussen A, Lefevre E (2017) Distance decay relationships in foliar fungal endophytes are driven by rare taxa. Environ Microbiol 19(7):2794–2805. https://doi.org/10.1111/1462-2920.13799

Oono R, Black D, Slessarev E, Sickler B, Strom A et al (2020) Species diversity of fungal endophytes across a stress gradient for plants. New Phytol 228(1):210–225. https://doi.org/10.1111/nph.16709

Osono T (2006) Role of phyllosphere fungi of forest trees in the development of decomposer fungal communities and decomposition processes of leaf litter. Can J Microbiol 52(8):701–716. https://doi.org/10.1139/W06-023

Osono T (2008) Endophytic and epiphytic phyllosphere fungi of Camellia japonica: seasonal and leaf age-dependent variations. Mycologia 100(3):387–391. https://doi.org/10.3852/07-110r1

Osono T, Mori A (2005) Seasonal and leaf age-dependent changes in occurrence of phyllosphere fungi of giant dogwood. Mycoscience 46(5):273–279. https://doi.org/10.1007/S10267-005-0246-8

Ottesen AR, Gonzalez Pena A, White JR, Pettengill JB, Li C et al (2013) Baseline survey of the anatomical microbial ecology of an important food plant: solanum lycopersicum (tomato). Bmc Microbiol 13:114. https://doi.org/10.1186/1471-2180-13-114

Pan JJ, May G (2009) Fungal-fungal associations affect the assembly of endophyte communities in maize (zea mays). Microb Ecol 58(3):668–678. https://doi.org/10.1007/s00248-009-9543-7

Pan YD, Birdsey RA, Fang JY, Houghton R, Kauppi PE et al (2011) A large and persistent carbon sink in the world's forests. Science 333(6045):988–993. https://doi.org/10.1126/science.1201609

Pan L, Cui SM, Dinkins RD, Jiang YW (2021) Plant growth, ion accumulation, and antioxidant enzymes of endophyte-infected and endophyte-free tall fescue to salinity stress. Acta Physiol Plant 43(6):95. https://doi.org/10.1007/s11738-021-03268-4

Peay KG, Kennedy PG, Talbot JM (2016) Dimensions of biodiversity in the Earth mycobiome. Nat Rev Microbiol 14(7):434–447. https://doi.org/10.1038/nrmicro.2016.59

Perreault R, Laforest-Lapointe I (2022) Plant-microbe interactions in the phyllosphere: facing challenges of the anthropocene. Isme J 16(2):339–345. https://doi.org/10.1038/s41396-021-01109-3

Pinto LSRC, Azevedo JL, Pereira JO, Vieira MLC, Labate CA (2000) Symptomless infection of banana and maize by endophytic fungi impairs photosynthetic efficiency. New Phytol 147(3):609–615

Põlme S, Abarenkov K, Henrik Nilsson R, Lindahl BD, Clemmensen KE et al (2021) FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. Fungal Divers 105(1):1–16. https://doi.org/10.1007/s13225-020-00466-2

Qi YZ, Li YP, Xie WW, Lu R, Mu FF et al (2020) Temporal-spatial variations of fungal composition in PM2.5 and source tracking of airborne fungi in mountainous and urban regions. Sci Total Environ 708:135027. https://doi.org/10.1016/j.scitotenv.2019.135027

Qian X, Chen L, Guo X, He D, Shi M et al (2018a) Shifts in community composition and co-occurrence patterns of phyllosphere fungi inhabiting Mussaenda shikokiana along an elevation gradient. Peerj 6:e5767. https://doi.org/10.7717/peerj.5767

Qian X, Duan TT, Sun X, Zheng Y, Wang YL et al (2018b) Host genotype strongly influences phyllosphere fungal communities associated with Mussaenda pubescens var. alba (Rubiaceae). Fungal Ecol 36:141–151. https://doi.org/10.1016/j.funeco.2018.10.001

Qian X, Li HZ, Wang YL, Wu BW, Wu MS et al (2019) Leaf and root endospheres harbor lower fungal diversity and less complex fungal co-occurrence patterns than rhizosphere. Front Microbiol 10:1015. https://doi.org/10.3389/fmicb.2019.01015

Qian X, Li S, Wu B, Wang Y, Ji N et al (2020) Mainland and island populations of Mussaenda kwangtungensis differ in their phyllosphere fungal community composition and network structure. Sci Rep 10(1):952. https://doi.org/10.1038/s41598-020-57622-6

Quince C, Walker AW, Simpson JT, Loman NJ, Segata N (2017) Shotgun metagenomics, from sampling to analysis. Nat Biotechnol 35(9):833–844

Quint M, Gray WM (2006) Auxin signaling. Curr Opin in Plant Biol 9(5):448–453. https://doi.org/10.1016/j.pbi.2006.07.006

Raza S, Miao N, Wang PZ, Ju XT, Chen ZJ et al (2020) Dramatic loss of inorganic carbon by nitrogen-induced soil acidification in Chinese croplands. Glob Chang Biol 26(6):3738–3751. https://doi.org/10.1111/gcb.15101

Redondo MA, Oliva J, Elfstrand M, Boberg J, Capador-Barreto HD et al (2022) Host genotype interacts with aerial spore communities and influences the needle mycobiome of Norway spruce. Environ Microbiol 24(8):3640–3654. https://doi.org/10.1111/1462-2920.15974

Rekhter D, Ludke D, Ding YL, Feussner K, Zienkiewicz K et al (2019) Isochorismate-derived biosynthesis of the plant stress hormone salicylic acid. Science 365(6452):498. https://doi.org/10.1126/science.aaw1720

Remus-Emsermann MNP, Schlechter RO (2018) Phyllosphere microbiology: at the interface between microbial individuals and the plant host. New Phytol 218(4):1327–1333. https://doi.org/10.1111/nph.15054

Rodrigues KF (1994) The foliar fungal endophytes of the amazonian palm euterpe-oleracea. Mycologia 86(3):376–385. https://doi.org/10.2307/3760568

Rodriguez RJ, White JF, Arnold AE, Redman RS (2009) Fungal endophytes: diversity and functional roles. New Phytol 182(2):314–330. https://doi.org/10.1111/j.1469-8137.2009.02773.x

Rojas EI, Rehner SA, Samuels GJ, Van Bael SA, Herre EA et al (2010) Colletotrichum gloeosporioides s.l. associated with Theobroma cacao and other plants in Panama: multilocus phylogenies distinguish host-associated pathogens from asymptomatic endophytes. Mycologia 102(6):1318–1338. https://doi.org/10.3852/09-244

Romero F, Cazzato S, Walder F, Vogelgsang S, Bender SF et al (2022) Humidity and high temperature are important for predicting fungal disease outbreaks worldwide. New Phytol 234(5):1553–1556. https://doi.org/10.1111/nph.17340

Roper M, Seminara A, Bandi MM, Cobb A, Dillard HR et al (2010) Dispersal of fungal spores on a cooperatively generated wind. P Natl Acad Sci USA 107(41):17474–17479. https://doi.org/10.1073/pnas.1003577107

Rudgers JA, Fischer S, Clay K (2010) Managing plant symbiosis: fungal endophyte genotype alters plant community composition. J Appl Ecol 47(2):468–477. https://doi.org/10.1111/j.1365-2664.2010.01788.x

Russell JR, Huang J, Anand P, Kucera K, Sandoval AG et al (2011) Biodegradation of polyester polyurethane by endophytic fungi. Appl Environ Microb 77(17):6076–6084. https://doi.org/10.1128/aem.00521-11

Sabzalian MR, Mirlohi A (2010) Neotyphodium endophytes trigger salt resistance in tall and meadow fescues. J Plant Nutr Soil Sc 173(6):952–957. https://doi.org/10.1002/jpln.200900345

Saikkonen K, Mikola J, Helander M (2015) Endophytic phyllosphere fungi and nutrient cycling in terrestrial ecosystems. Curr Sci India 109(1):121–126

Santos-Medellin C, Liechty Z, Edwards J, Nguyen B, Huang BH et al (2021) Prolonged drought imparts lasting compositional changes to the rice root microbiome. Nat Plants 7(8):1065. https://doi.org/10.1038/s41477-021-00967-1

Sapkota R, Knorr K, Jorgensen LN, O'Hanlon KA, Nicolaisen M (2015) Host genotype is an important determinant of the cereal phyllosphere mycobiome. New Phytol 207(4):1134–1144. https://doi.org/10.1111/nph.13418

Sapkota R, Jorgensen LN, Boeglin L, Nicolaisen M (2022) Fungal communities of spring barley from seedling emergence to harvest during a severe puccinia hordei epidemic. Microb Ecol. https://doi.org/10.1007/s00248-022-01985-y

Sardans J, Penuelas J, Estiarte M, Prieto P (2008) Warming and drought alter C and N concentration, allocation and accumulation in a Mediterranean shrubland. Glob Chang Biol 14(10):2304–2316. https://doi.org/10.1111/j.1365-2486.2008.01656.x

Sarver J, Schultz E, Apigo A, Gernandt DS, Salas-Lizana R et al (2022) Deep sequencing across multiple host species tests pine-endophyte specificity. Am J Bot 109(1):83–98. https://doi.org/10.1002/ajb2.1792

Saunders M, Kohn LM (2009) Evidence for alteration of fungal endophyte community assembly by host defense compounds. New Phytol 182(1):229–238. https://doi.org/10.1111/j.1469-8137.2008.02746.x

Schlechter RO, Miebach M, Remus-Emsermann MNP (2019) Driving factors of epiphytic bacterial communities: a review. J Adv Res 19:57–65. https://doi.org/10.1016/j.jare.2019.03.003

Schloss PD, Handelsman J (2003) Biotechnological prospects from metagenomics. Curr Opin Biotech 14(3):303–310. https://doi.org/10.1016/S0958-1669(03)00067-3

Schneider T, Riedel K (2010) Environmental proteomics: analysis of structure and function of microbial communities. Proteomics 10(4):785–798. https://doi.org/10.1002/pmic.200900450

Schonrogge K, Gibbs M, Oliver A, Cavers S, Gweon HS et al (2022) Environmental factors and host genetic variation shape the fungal endophyte communities within needles of Scots pine (Pinus sylvestris). Fungal Ecol 57:101162. https://doi.org/10.1016/j.funeco.2022.101162

Schulz B, Boyle C (2005) The endophytic continuum. Mycol Res 109:661–686. https://doi.org/10.1017/S095375620500273x

Serrano I, Audran C, Rivas S (2016) Chloroplasts at work during plant innate immunity. J Exp Bot 67(13):3845–3854. https://doi.org/10.1093/jxb/erw088

Shenhav L, Thompson M, Joseph TA, Briscoe L, Furman O et al (2019) FEAST: fast expectation-maximization for microbial source tracking. Nat Methods 16(7):627–632. https://doi.org/10.1038/s41592-019-0431-x

Siddique AB, Unterseher M (2016) A cost-effective and efficient strategy for Illumina sequencing of fungal communities: a case study of beech endophytes identified elevation as main explanatory factor for diversity and community composition. Fungal Ecol 20:175–185. https://doi.org/10.1016/j.funeco.2015.12.009

Singh P, Santoni S, Weber A, This P, Peros JP (2019) Understanding the phyllosphere microbiome assemblage in grape species (Vitaceae) with amplicon sequence data structures. Sci Rep 9(1):14294. https://doi.org/10.1038/s41598-019-50839-0

Singh BK, Trivedi P, Egidi E, Macdonald CA, Delgado-Baquerizo M (2021) Crop microbiome and sustainable agriculture. Nat Rev Microbiol 19(1):72–72. https://doi.org/10.1038/s41579-020-00483-7

Song M, Sun B, Li R, Qian Z, Bai Z et al (2022a) Successions and interactions of phyllospheric microbiome in response to NH3 exposure. Sci Total Environ 837:155805. https://doi.org/10.1016/j.scitotenv.2022.155805

Song M, Sun B, Li R, Zhang Z, Bai Z et al (2022b) Dynamic succession patterns and interactions of phyllospheric microorganisms during NOx exposure. J Hazard Mater 430:128371. https://doi.org/10.1016/j.jhazmat.2022.128371

Spanu PD, Abbott JC, Amselem J, Burgis TA, Soanes DM et al (2010) Genome expansion and gene loss in powdery mildew fungi reveal tradeoffs in extreme parasitism. Science 330(6010):1543–1546. https://doi.org/10.1126/science.1194573

Stone BWG, Weingarten EA, Jackson CR (2018) The role of the phyllosphere microbiome in plant health and function. Annu Plant Rev Online:533–556. https://doi.org/10.1002/9781119312994.apr0614

Sumarah MW, Puniani E, Sorensen D, Blackwell BA, Miller JD (2010) Secondary metabolites from anti-insect extracts of endophytic fungi isolated from Picea rubens. Phytochemistry 71(7):760–765. https://doi.org/10.1016/j.phytochem.2010.01.015

Sun SQ, Weng YT, Di XY, Liu ZH, Yang G (2020) Screening of cellulose-degrading fungi in forest litter and fungal effects on litter decomposition. Bioresources 15(2):2937–2946. https://doi.org/10.15376/biores.15.2.2937-2946

Sun AQ, Jiao XY, Chen QL, Trivedi P, Li ZX et al (2021a) Fertilization alters protistan consumers and parasites in crop-associated microbiomes. Environ Microbiol 23(4):2169–2183. https://doi.org/10.1111/1462-2920.15385

Sun X, Zheng Y, Xu G, Guo Q, Tan J et al (2021b) Fungal diversity within the phyllosphere of Pinus massoniana and the possible involvement of phyllospheric fungi in litter decomposition. Fungal Biol 125(10):785–795. https://doi.org/10.1016/j.funbio.2021.05.001

Suryanarayanan TS (2013) Endophyte research: going beyond isolation and metabolite documentation. Fungal Ecol 6(6):561–568. https://doi.org/10.1016/j.funeco.2013.09.007

Tan H, Liu X, Yin S, Zhao C, Su L et al (2022) Immune-mediated disease associated microbial community responded to PAH stress in phyllosphere of roadside greenspaces in Shanghai. Environ Pollut 292(Pt B):118379. https://doi.org/10.1016/j.envpol.2021.118379

Tao X, Feng J, Yang Y, Wang G, Tian R et al (2020) Winter warming in Alaska accelerates lignin decomposition contributed by Proteobacteria. Microbiome 8(1):84. https://doi.org/10.1186/s40168-020-00838-5

Tedersoo L, Bahram M (2019) Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. Biol Rev Camb Philos Soc 94(5):1857–1880. https://doi.org/10.1111/brv.12538

Tedersoo L, Bahram M, Polme S, Koljalg U, Yorou NS et al (2014) Fungal biogeography. Global diversity and geography of soil fungi. Science 346(6213):1256688. https://doi.org/10.1126/science.1256688

Tedersoo L, Anslan S, Bahram M, Polme S, Riit T et al (2015) Shotgun metagenomes and multiple primer pair-barcode combinations of amplicons reveal biases in metabarcoding analyses of fungi. Mycokeys 10:1–43. https://doi.org/10.3897/mycokeys.10.4852

Tedersoo L, Bahram M, Zobel M (2020) How mycorrhizal associations drive plant population and community biology. Science 367(6480):eaba1223. https://doi.org/10.1126/science.aba1223

Tedersoo L, Mikryukov V, Anslan S, Bahram M, Khalid AN et al (2021) The global soil mycobiome consortium dataset for boosting fungal diversity research. Fungal Divers 111(1):573–588. https://doi.org/10.1007/s13225-021-00493-7

Tedersoo L, Bahram M, Zinger L, Nilsson RH, Kennedy PG et al (2022) Best practices in metabarcoding of fungi: from experimental design to results. Mol Ecol 31(10):2769–2795. https://doi.org/10.1111/mec.16460

Tellez PH, Arnold AE, Leo AB, Kitajima K, Van Bael SA (2022) Traits along the leaf economics spectrum are associated with communities of foliar endophytic symbionts. Front Microbiol:13:927780. https://doi.org/10.3389/fmicb.2022.927780

Tian Z, Wang R, Ambrose KV, Clarke BB, Belanger FC (2017) The Epichloe festucae antifungal protein has activity against the plant pathogen Sclerotinia homoeocarpa, the causal agent of dollar spot disease. Sci Rep 7(1):5643. https://doi.org/10.1038/s41598-017-06068-4

Tiwari P, Bae H (2020) Horizontal gene transfer and endophytes: an implication for the acquisition of novel traits. Plants Basel 9(3):305. https://doi.org/10.3390/plants9030305

Toju H, Okayasu K, Notaguchi M (2019) Leaf-associated microbiomes of grafted tomato plants. Sci Rep 9(1):1787. https://doi.org/10.1038/s41598-018-38344-2

Torrens-Spence MP, Bobokalonova A, Carballo V, Glinkerman CM, Pluskal T et al (2019) PBS3 and EPS1 complete salicylic acid biosynthesis from isochorismate in arabidopsis. Mol Plant 12(12):1577–1586. https://doi.org/10.1016/j.molp.2019.11.005

Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK (2020) Plant-microbiome interactions: from community assembly to plant health. Nat Rev Microbiol 18(11):607–621. https://doi.org/10.1038/s41579-020-0412-1

Turner JG, Ellis C, Devoto A (2002) The jasmonate signal pathway. Plant Cell 14:S153–S164. https://doi.org/10.1105/tpc.000679

Tylianakis JM, Morris RJ (2017) Ecological networks across environmental gradients. Annu Rev Ecol Evol S 48:25–48. https://doi.org/10.1146/annurev-ecolsys-110316-022821

Tzipilevich E, Russ D, Dangl JL, Benfey PN (2021) Plant immune system activation is necessary for efficient root colonization by auxin-secreting beneficial bacteria. Cell Host Microbe 29(10):1507. https://doi.org/10.1016/j.chom.2021.09.005

U'ren JM, Lutzoni F, Miadlikowska J, Laetsch AD, Arnold AE (2012) Host and geographic structure of endophytic and endolichenic fungi at a continental scale. Am J Bot 99(5):898–914. https://doi.org/10.3732/Ajb.1100459

U'Ren JM, Lutzoni F, Miadlikowska J, Zimmerman NB, Carbone I et al (2019) Host availability drives distributions of fungal endophytes in the imperilled boreal realm. Nat Ecol Evol 3(10):1430–1437. https://doi.org/10.1038/s41559-019-0975-2

Undugoda LJS, Kannangara S, Sirisena DM (2016) Aromatic hydrocarbon degrading fungi inhabiting the phyllosphere of ornamental plants on roadsides of urban areas in Sri Lanka. J Bioremed Biodegr 07(01):328. https://doi.org/10.4172/2155-6199.1000328

Unterseher M, Persoh D, Schnittler M (2013) Leaf-inhabiting endophytic fungi of European Beech (Fagus sylvatica L.) co-occur in leaf litter but are rare on decaying wood of the same host. Fungal Divers 60(1):43–54. https://doi.org/10.1007/S13225-013-0222-0

Unterseher M, Siddique AB, Brachmann A, Persoh D (2016) Diversity and composition of the leaf mycobiome of beech (Fagus sylvatica) are affected by local habitat conditions and leaf biochemistry. Plos One 11(4):e0152878. https://doi.org/10.1371/journal.pone.0152878

Vacher C, Hampe A, Porte AJ, Sauer U, Compant S et al (2016) The phyllosphere: microbial jungle at the plant-climate interface. Annu Rev Ecol Evol S:1–24. https://doi.org/10.1146/annurev-ecolsys-121415-032238

van der Heijden MGA, de Bruin S, Luckerhoff L, van Logtestijn RSP, Schlaeppi K (2016) A widespread plant-fungal-bacterial symbiosis promotes plant biodiversity, plant nutrition and seedling recruitment. Isme J 10(2):389–399. https://doi.org/10.1038/ismej.2015.120

van der Linde S, Suz LM, Orme CDL, Cox F, Andreae H et al (2018) Environment and host as large-scale controls of ectomycorrhizal fungi. Nature 558(7709):243–248. https://doi.org/10.1038/s41586-018-0189-9

Vaz ABM, Da Costa AGFC, Raad LVV, Goes-Netoa A (2014a) Fungal endophytes associated with three South American Myrtae (Myrtaceae) exhibit preferences in the colonization at leaf level. Fungal Biol-Uk 118(3):277–286. https://doi.org/10.1016/J.Funbio.2013.11.010

Vaz ABM, Fontenla S, Rocha FS, Brandao LR, Vieira MLA et al (2014b) Fungal endophyte beta-diversity associated with Myrtaceae species in an Andean Patagonian forest (Argentina) and an Atlantic forest (Brazil). Fungal Ecol 8:28–36. https://doi.org/10.1016/j.funeco.2013.12.008

Vellend M (2010) Conceptual synthesis in community ecology. Q Rev Biol 85(2):183–206. https://doi.org/10.1086/652373

Vellend M, Lechowicz MJ, Waterway MJ (2000) Germination and establishment of forest sedges (Carex, Cyperaceae): tests for home-site advantage and effects of leaf litter. Am J Bot 87(10):1517–1525. https://doi.org/10.2307/2656878

Venkatachalam S, Ranjan K, Prasanna R, Ramakrishnan B, Thapa S et al (2016) Diversity and functional traits of culturable microbiome members, including cyanobacteria in the rice phyllosphere. Plant Biology 18(4):627–637. https://doi.org/10.1111/plb.12441

VerBerkmoes NC, Denef VJ, Hettich RL, Banfield JF (2009) Systems biology: functional analysis of natural microbial consortia using community proteomics. Nat Rev Microbiol 7(3):196–205. https://doi.org/10.1038/nrmicro2080

Vieira MLA, Hughes AFS, Gil VB, Vaz ABM, Alves TMA et al (2012) Diversity and antimicrobial activities of the fungal endophyte community associated with the traditional Brazilian medicinal plant Solanum cernuum Vell. (Solanaceae). Can J Microbiol 58(1):54–66. https://doi.org/10.1139/W11-105

Vincent JB, Weiblen GD, May G (2016) Host associations and beta diversity of fungal endophyte communities in New Guinea rainforest trees. Mol Ecol 25(3):825–841. https://doi.org/10.1111/mec.13510

Vorholt JA (2012) Microbial life in the phyllosphere. Nat Rev Microbiol 10(12):828–840. https://doi.org/10.1038/nrmicro2910

Voriskova J, Baldrian P (2013) Fungal community on decomposing leaf litter undergoes rapid successional changes. Isme J 7(3):477–486. https://doi.org/10.1038/ismej.2012.116

Wagner MR, Lundberg DS, Del Rio TG, Tringe SG, Dangl JL et al (2016) Host genotype and age shape the leaf and root microbiomes of a wild perennial plant. Nat Commun 7:12151. https://doi.org/10.1038/ncomms12151

Wang JF, Nan ZB, Christensen MJ, Zhang XX, Tian P et al (2018) Effect of epichloe gansuensis endophyte on the nitrogen metabolism, nitrogen use efficiency, and stoichiometry of achnatherum inebrians under nitrogen limitation. J Agr Food Chem 66(16):4022–4031. https://doi.org/10.1021/acs.jafc.7b06158

Wang JF, Hou WP, Christensen MJ, Xia C, Chen T et al (2021) The fungal endophyte Epichloe gansuensis increases NaCl-tolerance in Achnatherum inebrians through enhancing the activity of plasma membrane H+-ATPase and glucose-6-phosphate dehydrogenase. Sci China Life Sci 64(3):452–465. https://doi.org/10.1007/s11427-020-1674-y

Wei Y, Lan G, Wu Z, Chen B, Quan F et al (2022) Phyllosphere fungal communities of rubber trees exhibited biogeographical patterns, but not bacteria. Environ Microbiol 24(8):3777–3790. https://doi.org/10.1111/1462-2920.15894

Whipps JM, Hand P, Pink D, Bending GD (2008) Phyllosphere microbiology with special reference to diversity and plant genotype. J Appl Microbiol 105(6):1744–1755. https://doi.org/10.1111/j.1365-2672.2008.03906.x

Whitaker BK, Reynolds HL, Clay K (2018) Foliar fungal endophyte communities are structured by environment but not host ecotype in Panicum virgatum (switchgrass). Ecology 99(12):2703–2711. https://doi.org/10.1002/ecy.2543

Wilmes P, Bond PL (2004) The application of two-dimensional polyacrylamide gel electrophoresis and downstream analyses to a mixed community of prokaryotic microorganisms. Environ Microbiol 6(9):911–920. https://doi.org/10.1111/j.1462-2920.2004.00687.x

Wittwer RA, Bender SF, Hartman K, Hydbom S, Lima RAA et al (2021) Organic and conservation agriculture promote ecosystem multifunctionality. Sci Adv 7(34):eabg6995. https://doi.org/10.1126/sciadv.abg6995

Xiang Q, Chen QL, Zhu D, Yang XR, Qiao M et al (2020) Microbial functional traits in phyllosphere are more sensitive to anthropogenic disturbance than in soil. Environ Pollut 265(Pt A):114954. https://doi.org/10.1016/j.envpol.2020.114954

Xiao Y, Li HX, Li C, Wang JX, Li J et al (2013) Antifungal screening of endophytic fungi from Ginkgo biloba for discovery of potent anti-phytopathogenic fungicides. Fems Microbiol Lett 339(2):130–136. https://doi.org/10.1111/1574-6968.12065

Xin X-F, Nomura K, Aung K, Velasquez AC, Yao J et al (2016) Bacteria establish an aqueous living space in plants crucial for virulence. Nature 539(7630):524. https://doi.org/10.1038/nature20166

Xiong C, He JZ, Singh BK, Zhu YG, Wang JT et al (2021a) Rare taxa maintain the stability of crop mycobiomes and ecosystem functions. Environ Microbiol 23(4):1907–1924. https://doi.org/10.1111/1462-2920.15262

Xiong C, Singh BK, He JZ, Han YL, Li PP et al (2021b) Plant developmental stage drives the differentiation in ecological role of the maize microbiome. Microbiome 9(1):171. https://doi.org/10.1186/s40168-021-01118-6

Xu L, Naylor D, Dong ZB, Simmons T, Pierroz G et al (2018) Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria. P Natl Acad Sci USA 115(21):E4952. https://doi.org/10.1073/pnas.1807275115

Xu Q, Tang C, Wang X, Sun S, Zhao J et al (2019) An effector protein of the wheat stripe rust fungus targets chloroplasts and suppresses chloroplast function. Nat Commun 10(1):5571. https://doi.org/10.1038/s41467-019-13487-6

Xu W, Li M, Lin W, Nan Z, Tian P (2021) Effects of epichloe sinensis endophyte and host ecotype on physiology of festuca sinensis under different soil moisture conditions. Plants-Basel 10(8):1649. https://doi.org/10.3390/plants10081649

Xu NH, Zhao QQ, Zhang ZY, Zhang Q, Wang Y et al (2022a) Phyllosphere microorganisms: sources, drivers, and their interactions with plant hosts. J Agr Food Chem 70(16):4860–4870. https://doi.org/10.1021/acs.jafc.2c01113

Xu P, Fan X, Mao Y, Cheng H, Xu A et al (2022b) Temporal metabolite responsiveness of microbiota in the tea plant phyllosphere promotes continuous suppression of fungal pathogens. J Adv Res 39:49–60. https://doi.org/10.1016/j.jare.2021.10.003

Yang YF (2021) Emerging patterns of microbial functional traits. Trends Microbiol 29(10):874–882. https://doi.org/10.1016/j.tim.2021.04.004

Yang T, Dai CC (2013) Interactions of two endophytic fungi colonizing Atractylodes lancea and effects on the host's essential oils. Acta Ecologica Sinica 33(2):87–93. https://doi.org/10.1016/j.chnaes.2013.01.004

Yang T, Chen Y, Wang XX, Dai CC (2013a) Plant symbionts: keys to the phytosphere. Symbiosis 59(1):1–14. https://doi.org/10.1007/s13199-012-0190-2

Yang T, Du W, Zhou J, Wang XX, Dai CC (2013b) Effects of the symbiosis between fungal endophytes and Atractylodes lancea on rhizosphere and phyllosphere microbial communities. Symbiosis 61(1):23–36. https://doi.org/10.1007/s13199-013-0254-y

Yang T, Ma S, Dai CC (2014) Drought degree constrains the beneficial effects of a fungal endophyte on Atractylodes lancea. J Appl Microbiol 117(5):1435–1449. https://doi.org/10.1111/jam.12615

Yang T, Sun HB, Shen CC, Chu HY (2016a) Fungal assemblages in different habitats in an Erman's Birch forest. Front Microbiol 7:1368. https://doi.org/10.3389/Fmich.2016.01368

Yang T, Weisenhorn P, Gilbert JA, Ni Y, Sun R et al (2016b) Carbon constrains fungal endophyte assemblages along the timberline. Environ Microbiol 18(8):2455–2469. https://doi.org/10.1111/1462-2920.13153

Yang T, Shi Y, Zhu J, Zhao C, Wang J et al (2021) The spatial variation of soil bacterial community assembly processes affects the accuracy of source tracking in ten major Chinese cities. Sci China Life Sci 64(9):1546–1559. https://doi.org/10.1007/s11427-020-1843-6

Yang T, Tedersoo L, Soltis PS, Soltis DE, Sun M et al (2022) Plant and fungal species interactions differ between aboveground and belowground habitats in mountain forests of eastern China. Sci China Life Sci https://doi.org/10.1007/s11427-022-2174-3

Yang T, Tedersoo L, Liu X, Gao GF, Dong K et al (2022) Fungi stabilize multi-kingdom community in a high elevation timberline ecosystem. iMeta n/a(n/a):e49. https://doi.org/10.1002/imt2.49

Yao H, Sun X, He C, Maitra P, Li XC et al (2019) Phyllosphere epiphytic and endophytic fungal community and network structures differ in a tropical mangrove ecosystem. Microbiome 7(1):57. https://doi.org/10.1186/s40168-019-0671-0

Yu GR, Jia YL, He NP, Zhu JX, Chen Z et al (2019) Stabilization of atmospheric nitrogen deposition in China over the past decade. Nat Geosci 12(6):424. https://doi.org/10.1038/s41561-019-0352-4

Yuan MM, Guo X, Wu LW, Zhang Y, Xiao NJ et al (2021) Climate warming enhances microbial network complexity and stability. Nat Clim Change 11(4):343–U100. https://doi.org/10.1038/s41558-021-00989-9

Zanne AE, Abarenkov K, Afkhami ME, Aguilar-Trigueros CA, Bates S et al (2020) Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. Biol Rev Camb Philos Soc 95(2):409–433. https://doi.org/10.1111/brv.12570

Zhang J, Elser JJ (2017) Carbon: nitrogen: phosphorus stoichiometry in fungi: a meta-analysis. Front Microbiol 8:1281. https://doi.org/10.3389/fmicb.2017.01281

Zhang YP, Nan ZB (2007) Growth and anti-oxidative systems changes in Elymus dahuricus is affected by Neotyphodium endophyte under contrasting water availability. J Agron Crop Sci 193(6):377–386. https://doi.org/10.1111/j.1439-037X.2007.00279.x

Zhang T, Yao YF (2015) Endophytic fungal communities associated with vascular plants in the high arctic zone are highly diverse and host-plant specific. Plos One 10(6):e0130051. https://doi.org/10.1371/journal.pone.0130051

Zhang XX, Li CJ, Nan ZB (2010) Effects of cadmium stress on growth and anti-oxidative systems in Achnatherum inebrians symbiotic with Neotyphodium gansuense. J Hazard Mater 175(1–3):703–709. https://doi.org/10.1016/j.jhazmat.2009.10.066

Zhang XX, Xia C, Li CJ, Nan ZB (2015) Chemical composition and antifungal activity of the volatile oil from Epichloë gansuensis, endophyte-infected and non-infected Achnatherum inebrians. Sci China Life Sci 58(5):512–514. https://doi.org/10.1007/s11427-015-4837-0

Zhang RF, Vivanco JM, Shen QR (2017) The unseen rhizosphere root-soil-microbe interactions for crop production. Curr Opin Microbiol 37:8–14. https://doi.org/10.1016/j.mib.2017.03.008

Zhang BG, Zhang J, Liu Y, Shi P, Wei GH (2018a) Co-occurrence patterns of soybean rhizosphere microbiome at a continental scale. Soil Biol Biochem 118:178–186. https://doi.org/10.1016/j.soilbio.2017.12.011

Zhang TA, Chen HYH, Ruan HH (2018b) Global negative effects of nitrogen deposition on soil microbes. Isme J 12(7):1817–1825. https://doi.org/10.1038/s41396-018-0096-y

Zhang W, Sun K, Shi R-H, Yuan J, Wang X-J et al (2018c) Auxin signalling of Arachis hypogaea activated by colonization of mutualistic fungus Phomopsis liquidambari enhances nodulation and N-2-fixation. Plant Cell Environ 41(9):2093–2108. https://doi.org/10.1111/pce.13170

Zhang Z, Luo L, Tan X, Kong X, Yang J et al (2018d) Pumpkin powdery mildew disease severity influences the fungal diversity of the phyllosphere. Peerj 6:e4559. https://doi.org/10.7717/peerj.4559

Zhang W, Yuan J, Cheng T, Tang MJ, Sun K et al (2019) Flowering-mediated root-fungus symbiosis loss is related to jasmonate-dependent root soluble sugar deprivation. Plant Cell Environ 42(12):3208–3226. https://doi.org/10.1111/pce.13636

Zhang S, Li Z, Shu J, Xue H, Guo K, Zhou X (2022) Soil-derived bacteria endow Camellia weevil with more ability to resist plant chemical defense. Microbiome 10(1):97. https://doi.org/10.1186/s40168-022-01290-3

Zhao A, Liu L, Chen B, Fu W, Xie W et al (2020) Soil fungal community is more sensitive to nitrogen deposition than increased rainfall in a mixed deciduous forest of China. Soil Ecol Lett 2(1):20–32. https://doi.org/10.1007/s42832-020-0026-6

Zhou J, Ning D (2017) Stochastic community assembly: does it matter in microbial ecology? Microbiol Mol Biol Rev 81(4):e00002–e00017. https://doi.org/10.1128/MMBR.00002-17

Zhou JY, Liu ZL, Wang SF, Li J, Li YK et al (2020) Fungal endophytes promote the accumulation of Amaryllidaceae alkaloids in Lycoris radiata. Environ Microbiol 22(4):1421–1434. https://doi.org/10.1111/1462-2920.14958

Zhu YG, Xiong C, Wei Z, Chen QL, Ma B et al (2022) Impacts of global change on the phyllosphere microbiome. New Phytol 234(6):1977–1986. https://doi.org/10.1111/nph.17928

Zimmerman NB, Vitousek PM (2012) Fungal endophyte communities reflect environmental structuring across a Hawaiian landscape. P Natl Acad Sci USA 109(32):13022–13027. https://doi.org/10.1073/pnas.1209872109

Plant Mycobiome in Sustainable Agriculture

Mohamed Idbella, Stefano Mazzoleni, and Giuliano Bonanomi

1 Introduction

Interactions between plants and their inhabiting microbiota play a central role in maintaining biodiversity, community stability, and ecosystem functioning (Sanchez-Cañizares et al. 2017; Xiong et al. 2021). The plant microbiota comprises highly diverse species communities that can be transmitted horizontally through the environment or vertically through seeds (Trivedi et al. 2020).

Fungi are one of the most important components of the plant microbiota and they mediate vital ecological functions such as soil carbon cycling (Yang et al. 2022). Indeed, plants have been shown to be reservoirs of fungal diversity (Unterseher 2011).The plant mycobiota represents the plant-associated fungal community that has multiple functional roles in response to plant type and environmental indications (Pagano et al. 2017). However, the importance of plant mycobiota has often been neglected in microbiome research. Plants and associated fungi are often described as co-evolving entities based on plant-fungal relationships, where microbial diversity and interaction are fundamental to keeping host plants healthy and productive (Vandenkoornhuyse et al. 2015; Schiro et al. 2019). Several factors such as plant host and density, environmental conditions, nutrient availability, and interactions with other external microbiota contribute to maintaining the composition of the plant mycobiome (Bahram et al. 2015; Nilsson et al. 2018). For many technical reasons, such as the complexity of life cycles, the presence of different somatic structures such as spores and hyphae, genome size, lack of reference genomes, and limited capacity for genetic transformation, the mycobiota is less well studied than

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the bacteriota. Evidence suggests that different plant compartments provide specifically different ecological niches inhabited by various microbial communities (Wei et al. 2021). However, microbial diversity, community composition, and assemblages in different plant compartment niches are even less documented. In particular, above- and belowground plant compartments are widely recognized as important determinants of fungal communities in agricultural ecosystems.

Mycobiota are known to play a key role in plant fitness and functioning through complex life strategies (Baldrian 2016) that include a continuum of mutualism, commensalism, and parasitism that can change over the life of the same fungal organism (Robinson et al. 2004). There are cases where commensal or mutualistic fungal endophytes become pathogenic under certain conditions, such as changes in nutrient availability and other abiotic stresses (Schulz and Boyle 2005; Rai and Agarkar 2016). On the other hand, interactions among different fungal guilds, i.e., pathogens, saprotrophs, and symbiotrophs, alter soil carbon dynamics and nutrient availability through both priming and Gadgil effects (Yin et al. 2014; Gadgil and Gadgil 1971). Moreover, fungi harbour their own microbiota that may adhere to the hyphal surface, develop in the pseudo-tissues formed by hyphal aggregation, or colonize the fungal cytoplasm (Bonfante et al. 2019). Therefore, deciphering the maintenance of fungal biodiversity, community formation, and interactions with other microbiota is critical for a better mechanistic understanding of fungal ecological functioning (Fernandez and Kennedy 2016; Zhao et al. 2018).

Most of our knowledge of plant mycobiota comes from molecular analyses using the internal transcribed spacer (ITS) of the nuclear rRNA operon as the official taxonomic barcode for fungi (Schoch et al. 2012), which allows taxonomic delineation of most groups at a low taxonomic level, i.e., species level. Advances in such sequencing technologies and bioinformatics tools have helped to better explore the diversity of fungi, their functionality, and their complex interactions within the plant microbiota (Bharti and Grimm 2019; Wagg et al. 2019). Here, we discussed the extent to which different plant compartments, i.e., rhizosphere, phyllosphere, and endosphere, are diverse in their mycobiota and how such fungal communities can influence both crop production and plant diseases to enable more sustainable agriculture. Most importantly, we discuss how plant mycobiota interact with other microbiota such as soil bacterial and fungal communities for plant health and production.

2 Mycobiota Diversity and Composition Differ Among Plant Compartments

The main plant compartments that harbour mycobiota are the rhizosphere, phyllosphere, and endosphere (Fig. 1, Trivedi et al. 2020). Mycobiota are not randomly assembled, but their diversity and composition are influenced by various biotic and abiotic factors such as plant species, phylogeny, and functional traits (Burns et al.

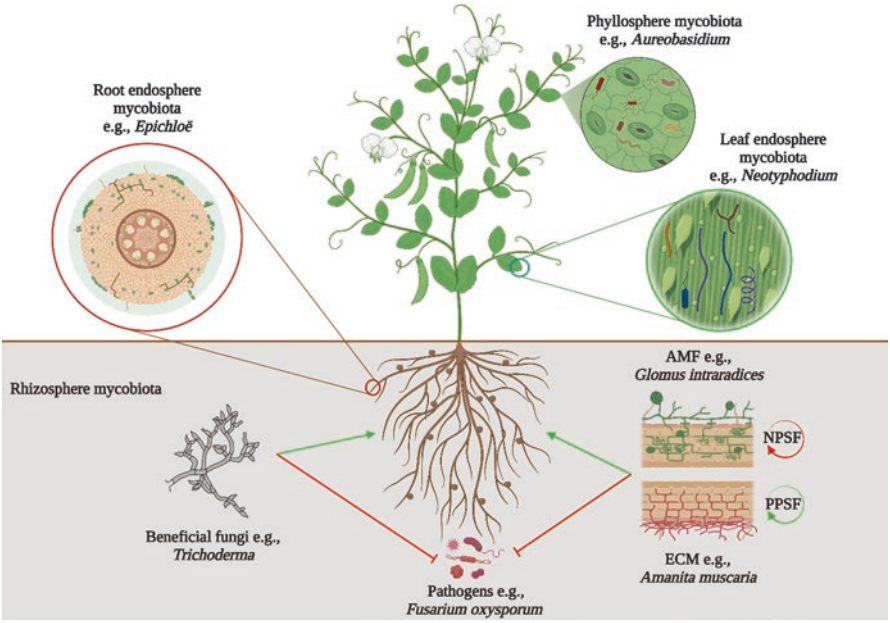

Fig. 1 Mycobiota associated with different plant compartments play an indispensable role in plant growth, health, tolerance to abiotic stress and resistance against pathogens and pests

2015; Barberán et al. 2015; Leff et al. 2018). Indeed, host plant specificity of fungi is well documented in the literature (Zhou and Hyde 2001; Dickie 2007; Prober et al. 2015; Leff et al. 2018), suggesting that variation in fungal community composition could be explained by the pattern of host plant preferences. However, the importance of host specificity on mycobiota composition continues to be debated. For example, Tedersoo et al. (2016) showed that the effects of plants on fungi are context-dependent and depend on environmental or edaphic conditions. On the other hand, the researchers concluded that the phylogenetic relatedness of plants could have an impact on the composition of mycobiota. Basically, this was an interesting area of research that began with the question of the extent to which host specificity, and thus fungal preferences, might be maintained between phylogenetically related plant species. This could be because phylogenetically related species emit phylogenetically similar signals and thus can recruit the same fungal species (Flores et al. 2014; Valverde-Barrantes et al. 2015). However, many studies have also noted the opposite trend regarding the importance of plant phylogeny in explaining fungal community composition (Leff et al. 2018). Finally, plant functional traits are also likely to mediate plant-fungal interactions. Many studies have shown that the abundance of different fungal groups, such as saprotrophic, pathotrophic, and symbiotic fungi, are related to plant traits (Eissenstat et al. 2015; Semchenko et al. 2018; Francioli et al. 2020). For example, a recent study by Sweeney et al. (2020) showed that root traits are strong determinants of fungal

community composition in the rhizosphere. Specifically, the authors showed that root diameter, root nitrogen content, specific root length, and specific root area are the most important determinants of the relative abundance or richness of trophic fungal guilds. Despite numerous plant-fungal interactions known in the literature, such as the "collaboration gradient" (Bergmann et al. 2020), which defines how plant tissue assembly strategies influence nutrient foraging via associations with fungal symbionts, and the increasing understanding of the importance of root exudates in shaping fungal communities (Hu et al. 2018), many studies have not found a significant link between plant traits and fungal community composition (Barberán et al. 2015; Leff et al. 2018).

2.1 Rhizosphere Mycobiota

The rhizosphere is defined as the volume of soil around living roots that is influenced by their activity (Hartmann et al. 2008). The rhizosphere is a hot spot for numerous organisms and is considered one of the most complex ecosystems on Earth (Raaijmakers et al. 2009). The rhizosphere harbours a rich diversity of microorganisms, many of which benefit plants by suppressing pathogenic invasions and helping to extract nutrients from the soil (Bulgarelli et al. 2013). Plant roots have co-evolved with soil as they play an important role in soil formation through a series of physical, chemical, and biological processes (Lambers et al. 2009). Through their interactions with plant roots, fungi support nutrient acquisition (Averill et al. 2019), resistance to pathogens (Marx 1972) and drought (Jayne and Quigley 2014), and play a key role in shaping plant productivity and community dynamics (Mommer et al. 2018; Liang et al. 2020). Therefore, understanding the taxonomic and functional components of the rhizosphere mycobiome is critical to manipulating them for sustainable ecosystem functioning.

Beneficial mycobiota inhabiting the rhizosphere play an important role in plant growth and fitness by providing nutrients to plants through decomposition of plant debris and mineral cycling in the soil (Ehrmann and Ritz 2014). In addition, rhizospheric mycobiota are important for plant health as they have been shown to play an effective role in controlling pathogens. Nevertheless, plants control rhizospheric fungi mainly through the production of carbon and its derivatives and bioactive metabolites (Ellouze et al. 2014). Mycobiota in the rhizosphere include both non-symbiotic and symbiotic beneficial fungi. Some examples of non-symbiotic beneficial fungi in the rhizosphere include *Penicillium* sp. (Babu et al. 2015), some endophytic fungi such as *Fusarium* spp., *Colletotrichum* spp., and *Cladosporium* spp. (Chadha et al. 2015; Shah et al. 2019), and *Trichoderma* strains (Kotasthane et al. 2015; Li et al. 2015). *Trichoderma*, an indispensable component of agroecosystems, is a genus of filamentous fungi that can feed on other fungi (mycotrophy) and is ubiquitous in almost all environments (Woo et al. 2022). *Trichoderma* controls fungal pathogens by acting as an antagonist based on competition, antibiosis,

and mycoparasitism, as well as by triggering local and systemic defence responses in the plant (Shoresh et al. 2010; Druzhinin et al. 2011). In contrast, symbiotic beneficial fungi in the rhizosphere include arbuscular mycorrhizal fungi (AMF), which form mutualistic associations with most vascular plants in which both partners exchange nutrients and energy (Smith and Read 2008). Mycorrhizal symbioses are found in almost all ecosystems worldwide and improve plant fitness and soil quality through important ecological processes. On the other hand, many mycobiota in the rhizosphere can negatively affect plant productivity by causing diseases, e.g., *Fusarium* species, *Verticillium* spp., *Pythium* spp., *Sclerotium* spp., *Botrytis cinerea*, and *Macrophomina* spp. (Tetali et al. 2015).

2.2 Phyllosphere Mycobiota

The phyllosphere is defined as the surface of aboveground plant organs and represents the largest microbial habitat on Earth (Dong et al. 2019). In this plant compartment, bacteria are the most abundant colonizing microbes, while fungi are comparatively less abundant. The leaf surface is highly heterogeneous in terms of nutrient concentrations (Mercier and Lindow 2000) and likely provides numerous potential niches for fungal colonization. Several studies of leaf-associated fungi have focused primarily on endophytic fungi that colonize the internal structures of plants (Arnold et al. 2003). In addition, studies have also documented the wide diversity of epiphytes, defined as fungi that colonize the surface of leaves (Lindow and Brandl 2003). Unlike the mycobiome of the rhizosphere, which is surrounded by a buffering soil that provides a relatively stable environment, the fungi of the phyllosphere are exposed to ephemeral and stressful environmental conditions, such as climate, low water and nutrient availability, high UV radiation, heat and cold stress including frost, osmotic stress, plant defence activities, and anthropogenic factors such as pesticide use (Karlsson et al. 2014; Glenn et al. 2015; Sousa et al. 2018).

Most fungi observed in the phyllosphere have been assigned to taxonomic groups known to be saprotrophic, pathogenic, and lichenogenic (Jumpponen and Jones 2009). In general, the interaction of phyllosphere mycobiota with the host plant is often beneficial. While leaf-inhabiting fungi obtain protection, habitat, and nutrient sources from the host plant, members of the phyllosphere help increase plant productivity and/or improve overall protective capacity against plant pathogens (Finkel et al. 2017). Several reports showed that phyllosphere fungi can stimulate plant growth and protect against pathogens. For example, Epichloë species, the most studied aboveground endophytes, produce various types of alkaloids that protect the host from vertebrates and invertebrate herbivores (Schardl et al. 2013), and they can also improve plant performance in the face of disease or abiotic stress (Bastias et al. 2017; Fuchs and Krauss 2019; Pérez et al. 2020). Like fungal endophytes, fungal epiphytes can also protect host plants from disease (Saikkonen

2007). Epiphytic fungi can also act as decomposers of plant exudates on living leaves (Jumpponen and Jones 2009), and as initial colonizers, they likely play an important role in the initial decomposition of leaves after senescence (Osono et al. 2004; Voříšková and Baldrian 2013). Although the phyllosphere is a heterogeneous habitat for fungi, the drivers of fungal associations with different plant hosts are still poorly understood.

2.3 Endosphere Mycobiota

Fungal endophytes are defined as fungi that periodically or continuously colonise the internal parts of plant tissues without manifesting disease in their host (Hyde and Soytong 2008). Several studies have distinguished two types of endophytes, obligate and opportunistic. Obligate endophytes require plant tissue to complete their life cycle; some examples can be found in mycorrhizal fungi and members of the fungal genera *Balansia*, *Epichloë*, and *Neotyphodium* (Schardl et al. 2004; Parniske 2008). Opportunistic endophytes, on the other hand, are endophytes that thrive primarily outside plant tissue and sporadically invade the plant endosphere (Hardoim et al. 2015). However, there is evidence for another intermediate group of endophytes, termed facultative, which includes most endophytic fungi (Saikkonen et al. 2010). In principle, all types of plants harbour endophytes, and all microbes have adopted an endophytic lifestyle and can have a positive impact on plant growth and enhance the ability of plants to adapt to biotic and abiotic stresses (Hardoim et al. 2015; Grabka et al. 2022). However, the major dilemma is that a given microorganism can be pathogenic under certain conditions and commensal or perhaps even mutualistic under other conditions (Freeman and Rodriguez 1993). For example, *Fusarium graminearum* has been shown to cause head blight disease in many cereals (Hao et al. 2020) but is harmless in carrots (Louarn et al. 2013). Indeed, advances in next-generation sequencing have contributed to the understanding of endophytic lifestyle, as several studies identifying fungal endophyte communities by amplicon sequencing have found potentially known pathogens without their sequelae on the host plant, suggesting that some pathogens may be silenced in their endophytic lifestyle by the other microorganisms present. This suggests that a balanced microbiome is key to a healthy plant.

3 Management of Native Mycobiota for Sustainable Agriculture

Plant-inhabiting fungal communities can be directed by various means in a specific direction where they exert their maximum ability to positively influence plant growth and health by promoting/increasing the abundance of some selected

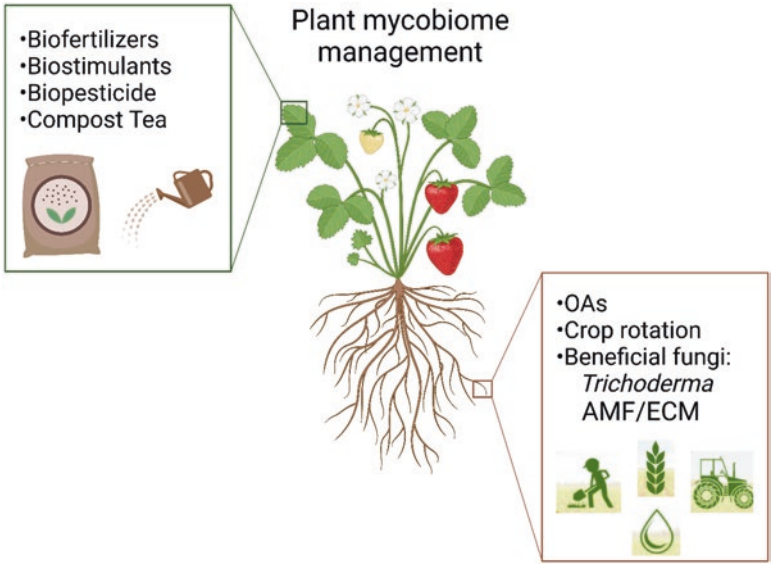

Fig. 2 Management of plant mycobiota differ among compartments and imply different strategies for a sustainable agriculture

mycobiota. In fact, many strategies have been proposed for good management of plant native mycobiota (Fig. 2).

3.1 Crop Rotation

Crop rotation is an ancient agricultural management tool (Howard 1996) based on growing different crops in succession on a given area to effectively maintain soil microbial diversity and protective capacity against disease (Fiers et al. 2012). Crop rotation promotes soil structure and organic matter conservation and reduces soil erosion that often accompanies continuous row crop production (Peters et al. 2003). However, one of the most important benefits of crop rotation is the reduction of plant diseases caused by soilborne pathogens, especially fungi (Pedersen and Hughes 1992). The effects of crop rotation on mycobiota vary and depend on many factors, such as crop genotypes (Garbeva et al. 2004), cropping sequence (Gan et al. 2003), length of rotation (Bennett et al. 2012), and soil properties (Bernard et al. 2012). Diversification of crops used in rotation provides various organic residues, both from litter decomposition and root exudates, which can result in a diverse food base that promotes fungal diversity, activity, and biomass (Swer et al. 2011). In addition, crop rotation also reduces disease pressure in agroecosystems by disrupting the life cycle of pathogens associated with a particular crop (Ellouze et al. 2014). Therefore, it is important to select crops in rotation that are not alternative hosts for pathogenic fungi to reduce disease-related yield losses.

Indeed, crop rotation is evident in the concept of plant-soil feedback (PSF). When growing in soil, plants may change its microbiome depending on their genotype, their functional traits and environment; these changes affect the performance of plants grown successively in that soil (Van der Putten et al. 2013). Negative PSF occurs when a plant grows better in a soil that was previously inhibited by the same plant species, while positive PSF is when a plant grows better in a soil that was previously conditioned by the same plant species. Accumulation of host-specific pathogenic fungi in plant rhizospheres has been identified as an important driver of negative PSF (Semchenko et al. 2018). Evidence suggests that positive PSF is the result of improved plant growth and resistance to pathogens (Pineda et al. 2020). The direction of PSF and thus the net outcome for plant growth depends on antagonistic and synergistic interactions within the soil microbiome (Bever et al. 2012). Therefore, targeting positive PSF would open new opportunities for crop management.

3.2 Organic Amendments Application

Organic amendments (OAs) such as compost, biochar, green manure, and animal manure have been shown to improve soil fertility, enhance soil structure, increase soil organic matter, increase microbial activity and biomass, and control soilborne pathogens (Ros et al. 2006; Janvier et al. 2007; Li et al. 2012; Iacomino et al. 2022). Previous studies have also reported the effects of OAs application on the development of rhizosphere microbial community richness and diversity in the long term (Hiddink et al. 2005; Hartmann et al. 2015). However, medium- or long-term responses to OAs remain controversial, as previous work has reported both limited and no effects on microbial diversity (Renella et al. 2008; Bastida et al. 2013). There is evidence that OAs can increase soil suppressiveness to numerous fungal plant pathogens such as *Botrytis cinerea*, *Fusarium oxysporum*, *Verticillium dahliae*, *Sclerotinia minor*, and *Rhizoctonia solani* by altering the soil microbiota (Jaiswal et al. 2017; Bonanomi et al. 2020, 2022). Application of OAs can control fungal pathogens directly by releasing fungitoxic compounds (Blok et al. 2000) or indirectly by promoting the development of a suppressive mycobiota such as plant growth promoting fungi (PGPF) like arbuscular mycorrhizal fungi (Bonanomi et al. 2018). Previous studies have shown that PGPF not only promote plant growth, but also play a critical role in protecting against pathogens (Artursson et al. 2006; Mendes et al. 2013). Competition for nutrients and space (Hoitink and Boehm 1999), direct parasitism (Bellini et al. 2023), and antagonism through the production of secondary metabolites are the main mechanisms that beneficial fungi use to combat pathogens. However, they can also act indirectly by inducing a systemic resistance response in host plants (Vallad et al. 2003).

3.3 Arbuscular Mycorrhizal Fungi (AMF)

AMF penetrate the plant's root tissue and form mycorrhizae, a secure relationship in which they extract carbon from plant roots and in return provide important nutrients that are useful to the plant. Mycorrhizal fungi form symbiotic relationships with 70–90% of terrestrial plant roots (Parniske 2008), and their global presence in forest and agroecosystems accounts for 50% of microbial biomass (Olsson et al. 1999). While AMF are dependent on their host plant for carbon nutrition, they provide a greater surface area for the acquisition of nutrients, particularly phosphorus, via their external mycelium that spreads in the soil beyond the rhizosphere (Roth and Paszkowski 2017). The effects of AM fungi on pathogens are most likely indirect, resulting from improved host tolerance by enhancing root growth and function or improved host resistance by stimulating a defence response or altering root exudations used by pathogens (Graham and Menge 1982; Smith 1988; Morandi 1996). However, AMF are also thought to suppress pathogen growth by competing with pathogens for space and resources (Smith 1988; Traquair 1995) or by promoting other soil microbiota antagonistic to pathogens (Thomas et al. 1994). On the other hand, the large surface area of the extra-radical mycelium of AMF provides nutrient-rich niches for colonisation and growth of other soil microbiota, especially bacteria (Larsen et al. 2009). Such associated bacteria with suppressive effects have also been identified. Nevertheless, scattered evidence suggests that some soils either suppress or favour external mycelium activity since they can suppress AMF colonisation and plant growth response (Wilson et al. 1988). For example, Leigh et al. (2011) showed that the addition of a bacterial soil filtrate reduced the length of extra-radical mycelium of AMF. However, soil-induced suppression of AMF is still uncommon, and the mechanisms are not yet known.

AMF and fungal endophytes are considered as the common root symbionts and perform vital functions in the host microbiome (Zhong et al. 2018). However, we know little about whether the net effects are more beneficial or detrimental to the plant when these two mutualists co-occur. Previous studies have shown that co-colonization of fungal endophytes and AMF leads to competitive or synergistic interactions (Liu et al. 2020; Idbella et al. 2021). Apart from competition for resources offered by the host, the association of endophytic fungi and AMF may also be influenced by the exudates of the endophytic fungi and the root of the host (Alzarhani et al. 2019). In fact, there is evidence that the same endophytic fungus can have opposite effects on colonization of different AMFs (Liu et al. 2020). However, little is known about the interaction between endophytic fungi and AMF on host resistance and pathogen defence.

It has been repeatedly demonstrated that the direction and strength of PSF is strongly related to host plant mycorrhizal fungi type/guild (Dickie et al. 2014; Bennett et al. 2017). In general, negative PSFs are restricted to AMF-associated plant species, and positive PSFs are typically observed in ectomycorrhizal (EMF) plant species (Bennett et al. 2017). This effect may be due to the greater access and

transfer of nitrogen through EMF to their hosts, making them more useful than AMFs in nitrogen-limited systems (Corrales et al. 2016). Moreover, AMF have been shown to increase the abundance of soil biota that make the soil less suitable for conspecific seedlings compared to heterospecifics, thus promoting the coexistence of different AMF-associated plant species at the community level (Bever 2002; Kytoviita et al. 2003; Mangan et al. 2010). EMF, instead, increase the abundance of soil biota favouring conspecific seedlings over heterospecific ones, thus promoting the dominance of EMF associated plant species at the community level (Booth 2004; McGuire 2007). In addition, EMF form a physical sheath around young feeder roots that can prevent pathogen infection and therefore develop less negative PSFs (Marx 1972). However, we still do not know exactly how the different AMF species associated with different crop varieties determine the direction and magnitude of PSF.

4 Conclusions & Perspectives

Contrary to previous assumptions, recent advances in molecular technologies, high-throughput omics, functional genomics, and computational tools have revealed the greater diversity and complexity of the plant mycobiome. Although we are aware of the importance of the plant mycobiome, most of the studies conducted still focus on the bacterial communities rather than the entire microbiota, leaving us far from fathoming the complexity of the interplay between plants and the mycobiome. Indeed, more functional and long-term experimental field studies are needed to manipulate the plant microbiota, and especially experiments that consider the mycobiota in the context of the entire microbiota to unlock the full potential of the mycobiome. In addition, deciphering the driving forces that modulate the composition and functioning of the mycobiota is critical to maximizing the benefits of the mycobiome for sustainable agriculture and understanding plant-fungal interactions. Such research advances would provide more opportunities for optimizing mycobiome applications in crop production.

References

Alzarhani AK, Clark DR, Underwood GJ, Ford H, Cotton TA, Dumbrell AJ (2019) Are drivers of root-associated fungal community structure context specific? ISME J 13:1330–1344

Arnold AE, Mejía LC, Kyllo D, Rojas EI, Maynard Z, Robbins N, Herre EA (2003) Fungal endophytes limit pathogen damage in a tropical tree. Proc Natl Acad Sci U S A 100:15649–15654

Artursson V, Finlay RD, Jansson JK (2006) Interactions between arbuscular mycorrhizal fungi and bacteria and their potential for stimulating plant growth. Environ Microbiol 8:1–10

Averill C, Bhatnagar JM, Dietze MC, Pearse WD, Kivlin SN (2019) Global imprint of mycorrhizal fungi on whole-plant nutrient economics. Proc Natl Acad Sci U S A 116:23163–23168

Babu AG, Kim SW, Yadav DR, Hyum U, Adhikari M, Lee YS (2015) *Penicillium menonorum*: a novel fungus to promote growth and nutrient management in cucumber plants. Microbiology 43:49–56

Bahram M, Peay KG, Tedersoo L (2015) Local-scale biogeography and spatiotemporal variability in communities of mycorrhizal fungi. New Phytol 205:1454–1463

Baldrian P (2016) Forest microbiome: diversity, complexity and dynamics. FEMS Microbiol Rev 41(2):fuw040

Barberán A, Mcguire KL, Wolf JA, Jones FA, Wright SJ, Turner BL, Essene A, Hubbell SP, Faircloth BC, Fierer N (2015) Relating belowground microbial composition to the taxonomic, phylogenetic, and functional trait distributions of trees in a tropical forest. Ecol Lett 18:1397–1405

Bastias DA, Martínez-Ghersa MA, Ballaré CL, Gundel PE (2017) Epichloë fungal endophytes and plant defenses: not just alkaloids. Trends Plant Sci 22:939–948

Bastida F, Hernández T, Albaladejo J, García C (2013) Phylogenetic and functional changes in the microbial community of long-term restored soils under semiarid climate. Soil Biol Biochem 65:12–21

Bellini A, Gilardi G, Idbella M, Zotti M, Pugliese M, Bonanomi G, Gullino ML (2023) Trichoderma enriched compost BCAs and potassium phosphite control Fusarium wilt of lettuce without affecting soil microbiome at genus level. Appl Soil Ecol 182:104678

Bennett AJ, Bending GD, Chandler D, Hilton S, Mills P (2012) Meeting the demand for crop production: the challenge of yield decline in crops grown in short rotations. Biol Rev 87:52–71

Bennett JA et al (2017) Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. Science 355:181–184

Bergmann J, Weigelt A, van der Plas F, Laughlin DC, Kuyper TW, Guerrero-Ramirez N, Valverde-Barrantes OJ, Bruelheide H, Freschet GT, Iversen CM et al (2020) The fungal collaboration gradient dominates the root economics space in plants. Science. Advances 6:eaba3756

Bernard E, Larkin RP, Tavantzis S et al (2012) Compost, rapeseed rotation, and biocontrol agents significantly impact soil microbial communities in organic and conventional potato production systems. Appl Soil Ecol 52:29–41

Bever JD (2002) Negative feedback within a mutualism: host–specific growth of mycorrhizal fungi reduces plant benefit. Proc R Soc B 269:2595–2601

Bever JD, Platt TG, Morton ER (2012) Microbial population and community dynamics on plant roots and their feedbacks on plant communities. Annu Rev Microbiol 66:265–283

Bharti R, Grimm DG (2019) Current challenges and best-practice protocols for microbiome analysis. Brief Bioinform 22:178–193

Blok WJ, Lamers JG, Termorshuizen AJ, Bollen GJ (2000) Control of soilborne plant pathogens by incorporating fresh organic amendments followed by tarping. Phytopathology 90:253–259

Bonanomi G, Lorito M, Vinale F, Woo SL (2018) Organic amendments, beneficial microbes, and soil microbiota: toward a unified framework for disease suppression. Annu Rev Phytopathol 56:1–20

Bonanomi G, Zotti M, Idbella M, Di Silverio N, Carrino L et al (2020) Decomposition and organic amendments chemistry explain contrasting effects on plant growth promotion and suppression of Rhizoctonia solani damping off. PLoS One 15(4):e0230925

Bonanomi G, Zotti M, Idbella M, Cesarano G, Al-Rowaily SL, Abd-ElGawad AM (2022) Mixtures of organic amendments and biochar promote beneficial soil microbiota and affect *Fusarium oxysporum* f. sp. lactucae, *Rhizoctonia solani* and *Sclerotinia minor* disease suppression. Plant Pathol 71:818–829

Bonfante P, Venice F, Lanfranco L (2019) The mycobiota: fungi take their place between plants and bacteria. Curr Opin Microbiol 49:18–25

Booth MG (2004) Mycorrhizal networks mediate overstorey-understorey competition in a temperate forest. Ecol Lett 7:538–546

Bulgarelli D, Schlaeppi K, Spaepen S, Loren V, van Themaat E, Schulze-Lefert P (2013) Structure and functions of the bacterial microbiota of plants. Annu Rev Plant Biol 64:807–838

Burns JH, Anacker BL, Strauss SY, Burke DJ (2015) Soil microbial community variation correlates most strongly with plant species identity, followed by soil chemistry, spatial location and plant genus. AoB Plants 7:plv030

Chadha N, Mishra M, Rajpal K, Bajaj R, Choudhary DK, Varma A (2015) An ecological role of fungal endophytes to ameliorate plants under biotic stress. Arch Microbiol 197:869–881

Corrales A, Mangan SA, Turner BL, Dalling JW (2016) An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. Ecol Lett 19:383–392

Dickie IA (2007) Host preference, niches and fungal diversity. New Phytol 174:225–228

Dickie IA, Koele N, Blum JD, Gleason JD, McGlone MS (2014) Mycorrhizas in changing ecosystems. Botany 92:149–162

Dong CJ, Wang LL, Li Q, Shang QM (2019) Bacterial communities in the rhizosphere, phyllosphere and endosphere of tomato plants. PLoS One 14(11):e0223847

Ehrmann J, Ritz K (2014) Plant: soil interactions in temperate multi-cropping production systems. Plant Soil 376:1–29

Eissenstat DM, Kucharski JM, Zadworny M, Adams TS, Koide RT (2015) Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. New Phytol 208:114–124

Ellouze W, Taheri AE, Bainard LD, Yang C, Bazghaleh N, Navarro-Borrell A, Hanson K, Hamel C (2014) Soil fungal resources in annual cropping systems and their potential for management. Biomed Res Int 2014:531824

Fernandez C, Kennedy P (2016) Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils? New Phytol 209:1382–1394

Fiers M, Edel-Hermann V, Chatot C, Le Hingrat Y, Alabouvette C, Steinberg C (2012) Potato soilborne diseases. A Rev Agron Sustain Dev 32(1):93–132

Finkel OM, Castrillo G, Herrera Paredes S, Salas Gonzalez I, Dangl JL (2017) Understanding and exploiting plant beneficial microbes. Curr Opin Plant Biol 38:155–163

Flores O, Garnier E, Wright IJ, Reich PB, Pierce S, Dìaz S, Pakeman RJ, Rusch GM, Bernard-Verdier M, Testi B et al (2014) An evolutionary perspective on leaf economics: phylogenetics of leaf mass per area in vascular plants. Ecol Evol 4:2799–2811

Francioli D, van Rijssel SQ, van Ruijven J, Termorshuizen AJ, Cotton TEA, Dumbrell AJ, Raaijmakers JM, Weigelt A, Mommer L (2020) Plant functional group drives the community structure of saprophytic fungi in a grassland biodiversity experiment. Plant Soil 461:91–105

Freeman S, Rodriguez RJ (1993) Genetic conversion of a fungal plant pathogen to a nonpathogenic, endophytic mutualist. Science 260:75–78

Fuchs B, Krauss J (2019) Can Epichloë endophytes enhance direct and indirect plant defence? Fungal Ecol 38:98–103

Gadgil RL, Gadgil PD (1971) Mycorrhiza and litter decomposition. Nature 233:133

Gan YT, Miller PR, McConkey BG, Zentner RP, Stevenson FC, McDonald CL (2003) Influence of diverse cropping sequences on durum wheat yield and protein in the semiarid northern Great Plains. Agron J 95:245–252

Garbeva P, van Veen PJA, van Elsas JD (2004) Microbial diversity in soil: selection of microbial populations by plant and soil type and implications for disease suppressiveness. Annu Rev Phytopathol 42:243–270

Glenn DM, Bassett C, Dowd SE (2015) Effect of pest management system on 'Empire' apple leaf phyllosphere populations. Sci Hortic 183:58–65

Grabka R, d'Entremont TW, Adams SJ, Walker AK, Tanney JB, Abbasi PA, Ali S (2022) Fungal endophytes and their role in agricultural plant protection against pests and pathogens. Plan Theory 11:384

Graham JH, Menge JA (1982) Influence of vesicular–arbuscular mycorrhizae and soil phosphorus on take-all disease of wheat. Phytopathology 72:95–98

Hao G, McCormick S, Usgaard T, Tiley H, Vaughan MM (2020) Characterization of three Fusarium graminearum effectors and their roles during Fusarium head blight. Front Plant Sci 11:579553

Hardoim PR, van Overbeek LS, Berg G, Pirttiläd AM, Compante S, Campisanof A, Döringg M, Sessitsche A (2015) The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. Microbiol Mol Biol Rev 79:293–320

Hartmann A, Rothballer M, Schmid M (2008) Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. Plant Soil 312:7–14

Hartmann M, Frey B, Mayer J, Mader P, Widmer F (2015) Distinct soil microbial diversity under long-term organic and conventional farming. ISME J 9:1177–1194

Hiddink GA, Van Bruggen AHC, Termorshuizen AJ, Raaijmakers JM, Semenov AV (2005) Effect of organic management of soils on suppressiveness to *Gaeumannomyces graminis* var. Tritici and its antagonist, *Pseudomonas fluorescens*. Eur J Plant Pathol 113:417–435

Hoitink H, Boehm M (1999) Biocontrol within the context of soil microbial communities: a substrate-dependent phenomenon. Annu Rev Phytopathol 37:427–446

Howard RJ (1996) Cultural control of plant diseases: a historical perspective. Can J Plant Pathol 18:145–150

Hu L, Robert CAM, Cadot S, Zhang X, Ye M, Li B, Manzo D, Chervet N, Steinger T, Van Der Heijden MGA et al (2018) Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. Nat Commun 9:2738

Hyde KD, Soytong K (2008) The fungal endophyte dilemma. Fungal Divers 33:163–173

Iacomino G, Sarker TC, Ippolito F, Bonanomi G, Vinale F, Staropoli A, Idbella M (2022) Biochar and compost application either alone or in combination affects vegetable yield in a volcanic mediterranean soil. Agronomy 12(9):1996

Idbella M, Bonanomi G, De Filippis F, Amor G, Chouyia FE, Fechtali T, Mazzoleni S (2021) Contrasting effects of *Rhizophagus irregularis* versus bacterial and fungal seed endophytes on *Trifolium repens* plant-soil feedback. Mycorrhiza 31:103–115

Jaiswal AK, Elad Y, Paudel I, Graber ER, Cytryn E, Frenkel O (2017) Linking the belowground microbial composition, diversity and activity to soilborne disease suppression and growth promotion of tomato amended with biochar. Sci Rep 7:44382

Janvier C, Villeneuve F, Alabouvette C, Edel-Hermann V, Mateille T, Steinberg C (2007) Soil health through soil disease suppression: which strategy from descriptors to indicators? Soil Biol Biochem 39:1–23

Jayne B, Quigley M (2014) Influence of arbuscular mycorrhiza on growth and reproductive response of plants under water deficit: a meta-analysis. Mycorrhiza 24:109–119

Jumpponen A, Jones KL (2009) Massively parallel 454 sequencing indicates hyperdiverse fungal communities in temperate Quercus macrocarpa phyllosphere. New Phytol 184:438–448

Karlsson I, Friberg H, Steinberg C, Persson P (2014) Fungicide effects on fungal community composition in the wheat phyllosphere. PLoS One 9:e111786

Kotasthane A, Agrawal T, Kushwah R, Rahatkar OV (2015) In-vitro antagonism of Trichoderma spp. against Sclerotium rolfsii and Rhizoctonia solani and their response towards growth of cucumber, bottle gourd and bitter gourd. Eur J Plant Pathol 141:523–543

Kytoviita MM, Vestberg M, Tuomi JA (2003) Test of mutual aid in common fungal networks: established vegetation negates benefit in seedling. Ecology 84:898–906

Lambers H, Mougel C, Jaillard B, Hinsinger P (2009) Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective. Plant Soil 321:83–115

Larsen J, Cornejo P, Barea JM (2009) Interactions between the arbuscular mycorrhizal fungus *Glomus intraradices* and the plant growth promoting rhizobacteria *Paenibacillus polymyxa* and *P. macerans* in the mycorrhizosphere of Cucumis sativus. Soil Biol Biochem 41:286–292

Leff JW, Bardgett RD, Wilkinson A, Jackson BG, Pritchard WJ, De Long JR, Oakley S, Mason KE, Ostle NJ, Johnson D et al (2018) Predicting the structure of soil communities from plant community taxonomy, phylogeny, and traits. ISME J 12:1794–1805

Leigh J, Fitter AH, Hodge A (2011) Growth and symbiotic effectiveness of an arbuscular mycorrhizal fungus in organic matter in competition with soil bacteria. FEMS Microbiol Ecol 76:428–438

Li R, Khafipour E, Krause DO, Entz MH, de Kievit TR, Fernando WGD (2012) Pyrosequencing reveals the influence of organic and conventional farming systems on bacterial communities. PLoS One 7:e51897

Li RX, Cai F, Pang G, Shen QR, Li R, Chen W (2015) Solubilisation of phosphate and micronutrients by *Trichoderma harzianum* and its relationship with the promotion of tomato plant growth. PLoS One 10:e0130081

Liang M, Johnson D, Burslem DFRP, Yu S, Fang M, Taylor JD, Taylor AFS, Helgason T, Liu X (2020) Soil fungal networks maintain local dominance of ectomycorrhizal trees. Nat Commun 11:1–7

Lindow SE, Brandl MT (2003) Microbiology of the phyllosphere. Appl Environ Microbiol 69:1875–1883

Liu H, Wu M, Liu J, Qu Y, Gao Y, Ren A (2020) Tripartite interactions between endophytic fungi, arbuscular mycorrhizal fungi, and *Leymus chinensis*. Microb Ecol 79:98–109

Louarn S, Nawrocki A, Thorup-Kristensen K, Lund OS, Jensen ON, Collinge DB, Jensen B (2013) Proteomic changes and endophytic micromycota during storage of organically and conventionally grown carrots. Postharvest Biol Technol 76:26–33

Mangan SA et al (2010) Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. Nature 466:752–755

Marx DH (1972) Ectomycorrhizae as biological deterrents to pathogenic root infections. Annu Rev Phytopathol 10:429–454

McGuir K (2007) Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology 88:567–574

Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiol Rev 37:634–663

Mercier J, Lindow SE (2000) Role of leaf surface sugars in colonization of plants by bacterial epiphytes. Appl Environ Microbiol 66:369–374

Mommer L, Cotton TEA, Raaijmakers JM, Termorshuizen AJ, van Ruijven J, Hendriks M, van Rijssel SQ, van de Mortel JE, van der Paauw JW, Schijlen EGWM et al (2018) Lost in diversity: the interactions between soil-borne fungi, biodiversity and plant productivity. New Phytol 218:542–553

Morandi D (1996) Occurrence of phytoalexins and phenolic compounds in endomycorrhizal interactions, and their potential role in biological control. Plant Soil 185:241–251

Nilsson RH, Anslan S, Bahram M, Wurzbacher C, Baldrian P, Tedersoo L (2018) Mycobiome diversity: high-throughput sequencing and identification of fungi. Nat Rev Microbiol 17(2):95–109

Olsson PA, Thingstrup I, Jakobsen I et al (1999) Estimation of the biomass of arbuscular mycorrhizal fungi in a linseed field. Soil Biol Biochem 31:1879–1887

Osono T, Bhatta BK, Takeda H (2004) Phyllosphere fungi on living and decomposing leaves of giant dogwood. Mycoscience 45:35–41

Pagano MC, Correa EJA, Duarte NF, Yelikbayev B, O'Donovan A, Gupta VK (2017) Advances in eco-efficient agriculture: the plant-soil mycobiome. Agriculture 7:14

Parniske M (2008) Arbuscular mycorrhiza: the mother of plant root endosymbioses. Nat Rev Microbiol 6:763–775

Pedersen EA, Hughes GR (1992) The effect of crop rotation on development of the septoria disease complex on spring wheat in Saskatchewan. Can J Plant Pathol 14:152–158

Pérez LI, Gundel PE, Zabalgogeazcoa I, Omacini M (2020) An ecological framework for understanding the roles of Epichloë endophytes on plant defenses against fungal diseases. Fungal Biol Rev 34:115–125

Peters RD, Sturz AV, Carter MR, Sanderson JB (2003) Developing disease-suppressive soils through crop rotation and tillage management practices. Soil Tillage Res 72:181–192

Pineda A, Kaplan I, Hannula SE, Ghanem W, Bezemer TM (2020) Conditioning the soil microbiome through plant–soil feedbacks suppresses an aboveground insect pest. New Phytol 226:595–608

Prober SM, Leff JW, Bates ST, Borer ET, Firn J, Harpole WS, Lind EM, Seabloom EW, Adler PB, Bakker JD et al (2015) Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. Ecol Lett 18:85–95

Raaijmakers JM, Paulitz TC, Steinberg C, Alabouvette C, Moënne-Loccoz Y (2009) The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. Plant Soil 321:341–361

Rai M, Agarkar G (2016) Plant-fungal interactions: what triggers the fungi to switch among lifestyles? Crit Rev Microbiol 42(3):428–438

Renella G, Landi L, Ascher J, Ceccherini MT, Pietramellara G, Mench M, Nannipieri P (2008) Long-term effects of aided phytostabilisation of trace elements on microbial biomass and activity, enzyme activities, and composition of microbial community in the Jales contaminated mine spoils. Environ Pollut 152:702–712

Robinson RM, Morrison DJ, Jensen GD (2004) Necrophylactic periderm formation in the roots of western larch and Douglas-fir trees infected with *Armillaria ostoyae*. II. The response to the pathogen. For Pathol 34(2):119–129

Ros M, Pascual JA, Garcia C, Hernandez MT, Insam H (2006) Hydrolase activities, microbial biomass and bacterial community in a soil after long-term amendment with different composts. Soil Biol Biochem 38:3443–3452

Roth R, Paszkowski U (2017) Plant carbon nourishment of arbuscular mycorrhizal fungi. Curr Opin Plant Biol 39:50–56

Saikkonen K (2007) Forest structure and fungal endophytes. Fungal Biol Rev 21:67–74

Saikkonen K, Wali PR, Helander M (2010) Genetic compatibility determines endophyte-grass combinations. PLoS One 5:e11395

Sanchez-Cañizares C, Jorrin B, Poole P, Tkacz A (2017) Understanding the holobiont: the interdependence of plants and their microbiome. Curr Opin Microbiol 38:188–196

Schardl CL, Leuchtmann A, Spiering MJ (2004) Symbioses of grasses with seedborne fungal endophytes. Annu Rev Plant Biol 55:315–340

Schardl CL, Florea S, Pan J, Nagabhyru P, Bec S, Calie PJ (2013) The epichloae: alkaloid diversity and roles in symbiosis with grasses. Curr Opin Plant Biol 16:480–488

Schiro G, Colangeli P, Müller MEH (2019) A metabarcoding analysis of the mycobiome of wheat ears across a topographically heterogeneous field. Front Microbiol 10:2095

Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Levesque CA, Chen W, Consortium FB (2012) Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for fungi. PNAS 109:6241–6246

Schulz B, Boyle C (2005) The endophytic continuum. Mycol Res 109(6):661–686

Semchenko M, Leff JW, Lozano YM, Saar S, Davison J, Wilkinson A, Jackson BG, Pritchard WJ, De Long JR, Oakley S et al (2018) Fungal diversity regulates plant-soil feedbacks in temperate grassland. Sci Adv 4:eaau4578

Shah N, Meisel JS, Pop M (2019) Embracing ambiguity in the taxonomic classification of microbiome sequencing data. Front Genet 10:1022

Shoresh M, Mastouri F, Harman GE (2010) Induced systemic resistance and plant responses to fungal biocontrol agents. Annu Rev Phytopathol 48:21–43

Smith GS (1988) The role of phosphorus nutrition in interactions of vesicular–arbuscular mycorrhizal fungi with soilborne nematodes and fungi. Phytopathology 78:371–374

Smith SE, Read DJ (2008) Mycorrhizal Symbiosis, 3rd edn. Elsevier/Academic, New York

Sousa LP, Da Silva MJ, Mondego JMC (2018) Leaf-associated bacterial microbiota of coffee and its correlation with manganese and calcium levels on leaves. Genet Mol Biol 41:455–465

Sweeney CJ, de Vries FT, van Dongen BE, Bardgett DR (2020) Root traits explain rhizosphere fungal community composition among temperate grassland plant species. New Phytol 229:1492–1507

Swer H, Dkhar MS, Kayang H (2011) Fungal population and diversity in organically amended agricultural soils of Meghalaya, India. J Org Syst 6:3–12

Tedersoo L, Bahram M, Cajthaml T, Põlme S, Hiiesalu I, Anslan S, Harend H, Buegger F, Pritsch K, Koricheva J et al (2016) Tree diversity and species identity effects on soil fungi, protists and animals are context dependent. ISME J 10:346–362

Tetali S, Karpagavalli S, Pavani SL (2015) Management of dry root rot of black gram caused by *Macrophomina phaseolina* (Tassi) Goid. using bio agent. Plant Arch 15(2):647–650

Thomas L, Mallesha BC, Bagyaraj DJ (1994) Biological control of damping-off of cardamom by the VA mycorrhizal fungus, *Glomus fasciculatum*. Microbiol Res 149:413–417

Traquair JA (1995) Fungal biocontrol of root diseases: endomycorrhizal suppression of cylindrocarpon root rot. Can J Bot 73:S89–S95

Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK (2020) Plant–microbiome interactions: from community assembly to plant health. Nat Rev Microbiol 18:607–621

Unterseher M (2011) Diversity of fungal endophytes in temperate forest trees. In: Pirttilä AM, Frank AC (eds) Endophytes of forest trees: biology and applications, vol 80. Springer, Dordrecht, pp 31–46

Vallad GE, Cooperband L, Goodman RM (2003) Plant foliar disease suppression mediated by composted forms of paper mill residuals exhibits molecular features of induced resistance. Physiol Mol Plant Pathol 63:65–77

Valverde-Barrantes OJ, Smemo KA, Blackwood CB (2015) Fine root morphology is phylogenetically structured, but nitrogen is related to the plant economics spectrum in temperate trees. Funct Ecol 29:796–807

Van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T et al (2013) Plant–soil feedbacks: the past, the present and future challenges. J Ecol 101(2):265–276

Vandenkoornhuyse P, Quaiser A, Duhamel M, le Van A, Dufresne A (2015) The importance of the microbiome of the plant holobiont. New Phytol 206(4):1196–1206

Voříšková J, Baldrian P (2013) Fungal community on decomposing leaf litter undergoes rapid successional changes. ISME J 7:477–486

Wagg C, Schlaeppi K, Banerjee S, Kuramae EE, van der Heijden MGA (2019) Fungal bacterial diversity and microbiome complexity predict ecosystem functioning. Nat Commun 10:1–10

Wei G, Ning K, Zhang G, Yu H, Yang S, Dai F, Dong L, Chen S (2021) Compartment niche shapes the assembly and network of Cannabis sativa associated microbiome. Front Microbiol 12:714993

Wilson GWT, Hetrick BAD, Kitt DG (1988) Suppression of mycorrhizal growth response of big bluestem by non-sterile soil. Mycologia 80:338–343

Woo SL, Hermosa R, Lorito M et al (2022) Trichoderma: a multipurpose, plant-beneficial microorganism for eco-sustainable agriculture. Nat Rev Microbiol. https://doi.org/10.1038/s41579-022-00819-5

Xiong C, Zhu YG, Wang JT, Singh B, Han LL, Shen JP, Li PP, Wang GB, Wu CF, Ge AH, Zhang LM, He JZ (2021) Host selection shapes crop microbiome assembly and network complexity. New Phytol 229:1091–1104

Yang H, Yang Z, Wang QC, Wang YL, Hu HW, He JZ et al (2022) Compartment and plant identity shape tree mycobiome in a subtropical forest. Microbiol Spectr 10(4):e01347–e01322

Yin H, Wheeler E, Phillips R (2014) Root-induced changes in nutrient cycling in forests depend on exudation rates. Soil Biol Biochem 78:213–221

Zhao PY, Li C, Chai BF (2018) Environmental filters drive the assembly of the soil fungal community in the Larix principis-rupprechtii forests of the Guandi Mountains. Huan Jing Ke Xue 39:3876–3884

Zhong R, Xia C, Ju YW, Li NN, Zhang XX, Nan ZB, Christensen MJ (2018) Effects of epichloë gansuensis on root-associated fungal communities of achnatherum inebrians under different growth conditions. Fungal Ecol 31:29–36

Zhou D, Hyde KD (2001) Host-specificity, host-exclusivity, and host-recurrence in saprobic fungi. Mycol Res 105:1449–1457

Plant-Fungus Interactions in Rust Diseases

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1 Introduction

The region of host cell plasmalemma, which becomes invaginated and encloses a haustorium as it develops, has been the subject of much investigation as a major site of interactions between biotrophic fungal pathogens and host plant cells. Gay and Woods (1987) have discussed the nature and functioning of such interfaces comprehensively. In the wider context of biotrophic symbioses, including specialized pathogens, Smith and Smith (1990) have reviewed mechanisms of nutrient transfer, the role of ATPases, and discrepancies between different reports of enzymic activity on extrahaustorial (host) membranes and haustorial (fungal) membranes. Although the distribution of ATPase activity has been examined in several different types of biotrophic systems, mutualistic and parasitic, with varying durations of association of heterotroph and autotroph, the generalizations arrived at frequently rest on single examples of each group. Gay and co-workers have demonstrated cytochemically the distribution of ATPase in fungal infections involving different groups of fungi and different higher plants (Gay 1984; Gay and Woods 1987; Spencer-Phillips and Gay 1981; Woods and Gay 1983, 1987; Woods et al. 1988). The detection system (Bentwood and Cronshaw 1978, Woods and Gay 1987) corresponded to the specific

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features of plasmalemmal ATPases (Bowman and Bowman 1986), including Mg^{2+} requirement, insensitivity to NO_3^+ and inhibition by vanadate.

An ATPase domain hypothesis has been proposed (Gay and Woods 1987; Spencer-Phillips and Gay 1981) to account for the polarized transport of nutrients across the interface between the host cell and haustorium and has been supported by dynamic evidence from experiments by Gay et al. (1987) with powdery mildew infections of barley. Manipulation of leaf or coleoptile epidermal strips allowed the exposure of living haustoria to specific inhibitors and promoters of ATPase activity. Observations of fluorescence of fluorescein within haustoria and host cytoplasm under these treatments confirmed the previously postulated tight coupling of the host cell and haustorium and demonstrated that proton extrusion via the wall-lining plasmalemma of infected cells is accompanied by a compensating flow of protons through the extrahaustorial region and the haustorial plasma membrane.

In the case of rust infections, investigations of ATPase activity have so far been limited to the D-haustoria of dikaryotic infections of *Uromyces appendiculatus* (Spencer-Phillips and Gay 1981) and filamentous haustoria of monokaryotic stages of *Puccinia poarum* (Woods and Gay 1987) and *P. lagenophorae* (Baka 1989). In these, the host plasmalemma lining the cell wall showed a high level of ATPase activity but haustoria of monokaryotic and dikaryotic infections differed strikingly in the cytochemically detected distribution of the enzyme: ATPase activity was absent from the extrahaustorial membrane EHM of the D-haustorium but present on the equivalent membrane enclosing the M-haustoria. In *P. poarum*, however, it was of interest that ATPase activity and the deposition of wall material, staining specifically as polysaccharide, were lower in younger than older regions and were absent from the tip of the filamentous haustorium (Woods and Gay 1987).

The consistent differences between monokaryotic and dikaryotic phases of rust infections in the morphological specialization of haustoria and their distribution within host tissues (Al-Khesraji and Losel 1980, 1981; Al-Khesraji et al. 1980; Baka 1989; Baka and Losel 1992a, b; Harder 1978; Larous 1990; Larous and Losel 1993a; Bushnell 1972; Littlefield and Heath 1979), are likely to be associated with important physiological differences. The following study therefore examines the plasmalemmal ATPase activity of host and fungal cells in spermogonial-aecial and uredinial-tetial phases of further species of rust fungi. Autoecious rusts were included in order to allow comparisons between monokaryon and dikaryon in tissues of the same host species rather than those growing in alternate hosts. To check the comparability of our application of the ATPase detection technique with that of Woods and Gay (1987), a short investigation of the monokaryotic haustoria of *P. poarum* was also made.

The invasion of host vascular tissue by rust fungi has been relatively infrequently recorded (Al-Khesraj and Losel 1980; Andreev et al. 1982; Colley 1918; Harder 1978; Jakson and Parker 1958; Krebill 1968; Larous 1990; Pady 1935; Van der Kamp 1969, 1970; Woo and Martin 1988; Zimmer 1965).

During the spermogonial-aecial stages of the life cycle of *Puccinia poarum*, monokaryotic intercellular and intracellular hyphae can be readily observed in the vascular tissue of *Tussilago farfara*, in the phloem region, xylem parenchyma and

bundle sheath. However, in the dikaryotic, uredinial-telial stages of the same pathogen on the alternate host *Poa pratensis*, only the mesophyll and bundle sheath cells contain haustoria. The question of whether similar differences occur also in autoecious rusts, infecting only a single host species, was investigated in the following study.

Melampsora euphorbiae (C. Schub.) Castagne is an autoecious macrocyclic rust pathogenic on various *Euphorbia* species and shows particular virulence against *E. helioscopia* and *E. peplus* (Wilson and Henderson 1966; Baka and Gjærum1996), which are among the most serious agricultural weeds. Because of the severity of its effects on these two species, *M. euphorbiae* may be considered a potential biological agent for their control. Other *Melampsora* species, e.g. *M. lini* (Coffey et al. 1972), *M. laricipopulina* (Siwecki 1990), *M. medusae, M. coleosporoides* and *M. epitea* (Spiers and Hopcroft 1985) have been studied at EM level but no ultrastructural or cytochemical investigation of *M. euphorbiae* appears to have been reported. From fine structural studies, a general picture has emerged of the close biotrophic relationship of rust fungi with their host plants (Littlefield and Heath 1979; Harder and Chong 1984; Baka 1992; Baka and Losel 1992a; Larous and Losel 1993a, b). Monokaryotic and dikaryotic phases of rust infections commonly develop on different hosts, producing up to five types of spore within the life cycle, and differ in haustorium morphology as well as physiologically (Littlefield and Heath 1979; Baka et al. 1995). Early evidence of differences in wall composition in a single phase of a rust life cycle was provided by the light microscope study of Kaminskyj and Heath (1983) with differential staining of *Uromyces phaseoli* urediniospore germlings, during the development of germ-tubes, infection structures and intercellular hyphae. The importance of understanding the organization and composition of interfaces between such specialized pathogens and their host plants has often been emphasized (Littlefield and Heath 1979; Harder et al. 1986). Investigations of fungal cell wall chemistry, often in relation to taxonomy, (Bartnicki-Garcia 1968; Gooday 1977; Wessels and Sietsma 1979; Farkas 1979), indicate that carbohydrates usually constitute 80–90% of wall dry weight. The distribution of different polysaccharides within and on the surface of fungal walls and their significance in recognition reactions, host penetration, pathogen development and morphology have been discussed (Farkas 1979; Wessels and Sietsma 1979; Freytag and Mendgen 1991a, b). In this connection, Mendgen et al. (1985), and Mendgen and Deising (1993) have drawn attention to the special interest in the different types of infection structures formed by rust fungi during their life cycle. The use of lectins, labelled with colloidal gold (Benhamou 1989) or fluorochromes (Mendgen et al. 1985; O'Connell 1991), for identifying and quantifying specific compounds at the ultrastructural level, has permitted the localization of sugar residues and carbohydrate fractions in various pathogens and host tissues (Benhamou and Ouellette 1986a; Benhamou 1988; Mendgen and Deising 1993; Bourett et al. 1993). The Thiery silver proteinate method (Thiery 1967) is more limited since it reacts positively with a wide range of carbohydrates (Joseleau and Ruel 1985).

This study reports the first ultrastructural investigation of the cytochemical localization of different sugar residues within fungal structures and host tissues, using

the lectin-gold complex method. The present observations may contribute to a better understanding of the structural and physiological interactions of rust fungi with their host plants.

2 ATPase Activity at the Host-Pathogen Interfaces of Rust Infection

2.1 Spermognial-Aecial Stages

In leaf tissue of *Cirsium arvense* infected by *Puccinia punctiformis* and of *Mentha piperata* infected by *P. menthae* a dense precipitate of lead phosphate, indicating the location of ATPase activity, was visible on the host plasmalemma, both lining the host cell wall and enclosing each filamentous haustorium (Figs. 1, 2 and 3). The intensity of the reaction varied in different regions of blocks, according to the degree of penetration of reagents into tissue. However, in some sections of the filamentous haustorium of *P. menthae*, as shown in Fig. 3, lead precipitation varied within one extrahaustorial membrane, decreasing towards the distal region. The distal region

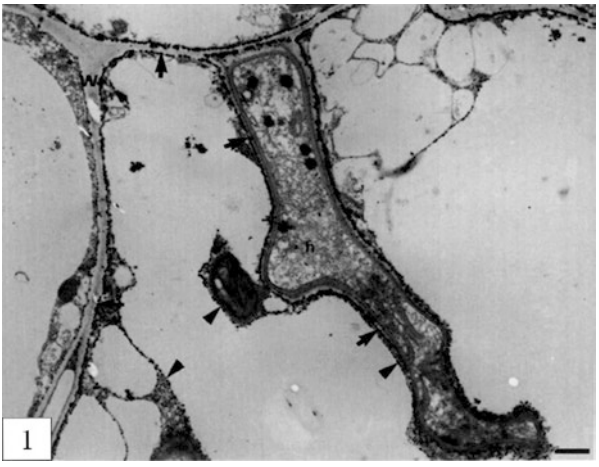


Fig. 1 Section of infected leaf tissue of *Cirsium arvense* after incubation in media containing ATP, magnesium ions, and nitrate, observed without further staining. Filamentous haustorium of *Puccinia punctiformis* in mesophyll cell. Lead precipitate indicates ATPase activity (arrows) on the host plasma membrane lining cell wall (W) and enclosing haustorium (h) but not on the fungal plasma membrane. Note activity is shown on some regions of the host tonoplast (arrowheads). The reaction product on the host wall adjacent to the haustorium probably lies over a trapped portion of the host plasma membrane. Bar = 1.0 μm

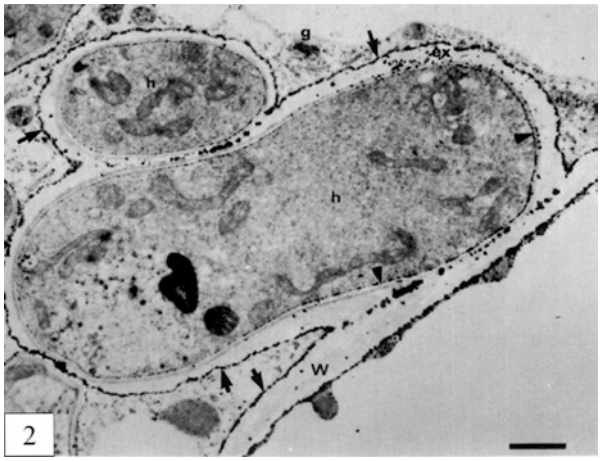


Fig. 2 Section of infected leaf tissue of *Cirsium arvense* after incubation in media containing ATP, magnesium ions, and nitrate, observed without further staining. Filamentous haustorium (h) of *Puccinia punctiformis* in bundle sheath cell, showing ATPase activity on both invaginated and uninvaginated host plasma membrane (arrow) and Golgi body (g). Enzyme activity is also indicated on the fungal plasma membrane (arrowheads) and in the extrahaustorial matrix (ex). Bar = 1.0 μm

also lacked the host wall-like material, characteristic of the extrahaustorial matrix of older regions of such haustoria (Al-Khesraji and Losel 1981; Littlefield and Heath 1979).

Control preparations, exposed to vanadate (Fig. 4) or without substrate (Figs. 7b and 8b), showed markedly less lead precipitate, in all the regions examined. Scattered precipitates of fine, electron-dense particles were sometimes observed in the host or fungal cytoplasm; both in tissue incubated with ATP and in substrate-deficient treatments but were not associated with membranes. With β-glycerophosphate as substrate instead of ATP, the location of lead phosphate deposits indicated that the distribution of general phosphatase activity was similar to that of ATPase (Fig. 5), except that only ATPase activity was present at the tonoplast.

In some preparations of *P. punctiformis*, the fungal plasmalemma of filamentous haustoria showed evidence of enzymic activity when either ATP (Fig. 2) or ß-glycerophosphate (Fig. 5) was used as substrate. However, no precipitates were observed on the haustorial plasmalemma of *P. menthae*. The results of the preliminary investigation of monokaryotic infections of *Tussilago farfara* by *P. Poarum*, using the same ATPase detection procedure as Woods and Gay (1987), differed from the previous observations only in showing ATPase and β-glycerophosphatase activity on the fungal plasmalemma (Fig. 6).

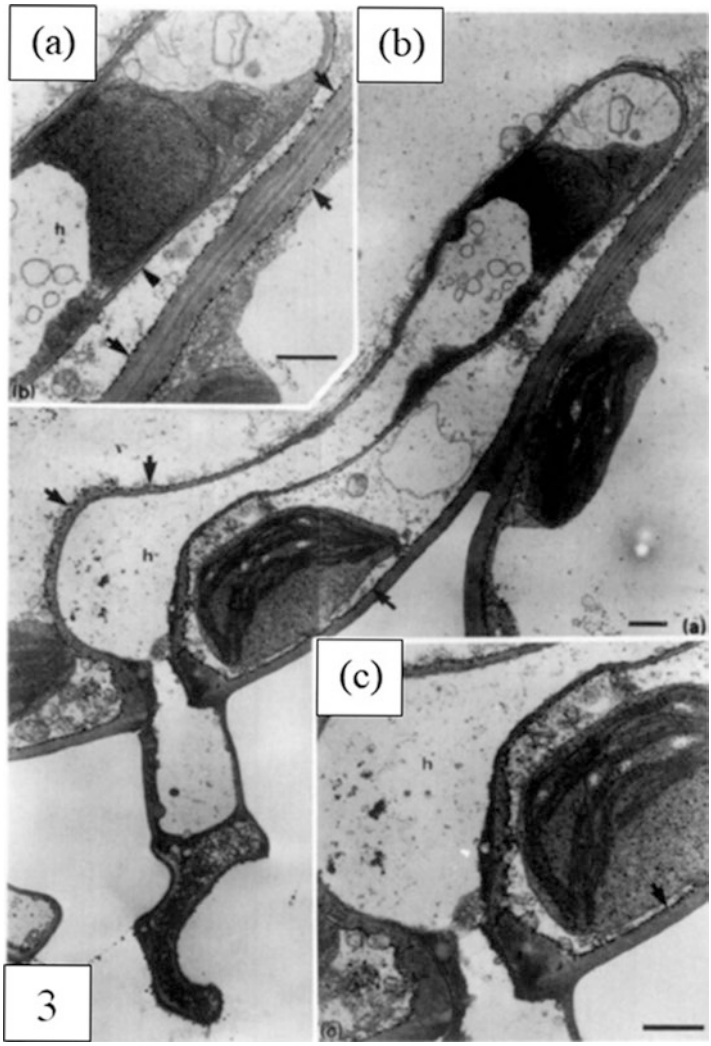


Fig. 3 (**a**) Filamentous haustorium (h) of the monokaryotic stage of *Puccinia menthae* incubated with ATP, as for Figs. 1 and 2, then stained with uranyl acetate /lead citrate. Lead deposition. Indicative ATPase activity (arrows), is seen on the wall-lining region of host plasmalemma and on regions of invaginated plasmalemma proximal to point of entry into the host cell, but decreases towards the distal end of the haustorium. Bar = 1.0 µm. (**b**) Apical region of haustorium at higher magnification, to compare the lack of lead precipitation on the extrahaustorial membrane (arrowhead) with the ATPase reaction of the wall-lining region of the host plasmalemma (arrows). Bar = 1.0 µm. (**c**) Haustorium close to the entry point enlarged to show the similarity of ATPase reaction (arrows) and deposition of wall material (w) on wall-lining and invaginated domains of host plasmalemma. Bar = 1.0 µm

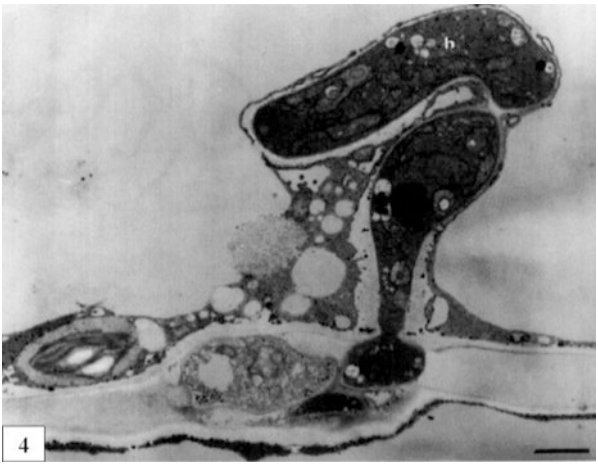


Fig. 4 Filamentous haustorium (h) of *Puccinia menthae*, after incubation with ATP in the presence of sodium orthovanadate, showing lead precipitation, compared with Fig. 3. Bar = 1.0 μm

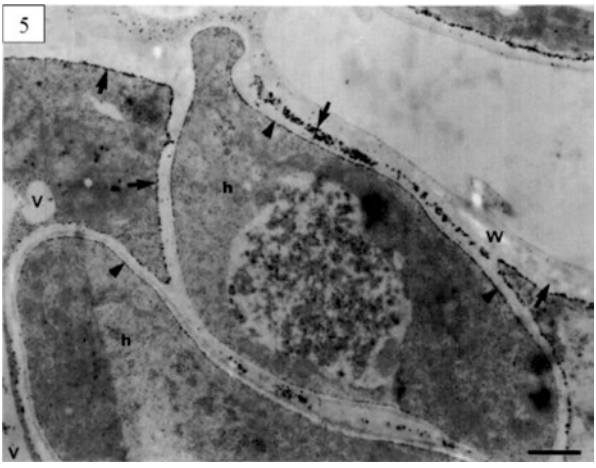


Fig. 5 Filamentous haustoria (h) of *P. punctiformis* in mesophyll cell after incubation in the presence of β-glycerophosphate and Mg^{++} and without further staining. Precipitates indicating general phosphatase activity (arrows) lie on both wall-lining and invaginated regions of host plasmalemma but not on membranes of vacuoles (v). Some activity is also indicated on haustorial plasmalemma (arrowheads). Bar = 1.0 μm

2.2 Uredinial Stages

No ATPase activity was detected on the invaginated host plasmalemma forming the extrahaustorial membrane of D-haustoria of the dikaryotic, uredinial stages of *P. Punctiformis* (Fig. 7a) and *U. vicia-fabae* (Fig. 8a).

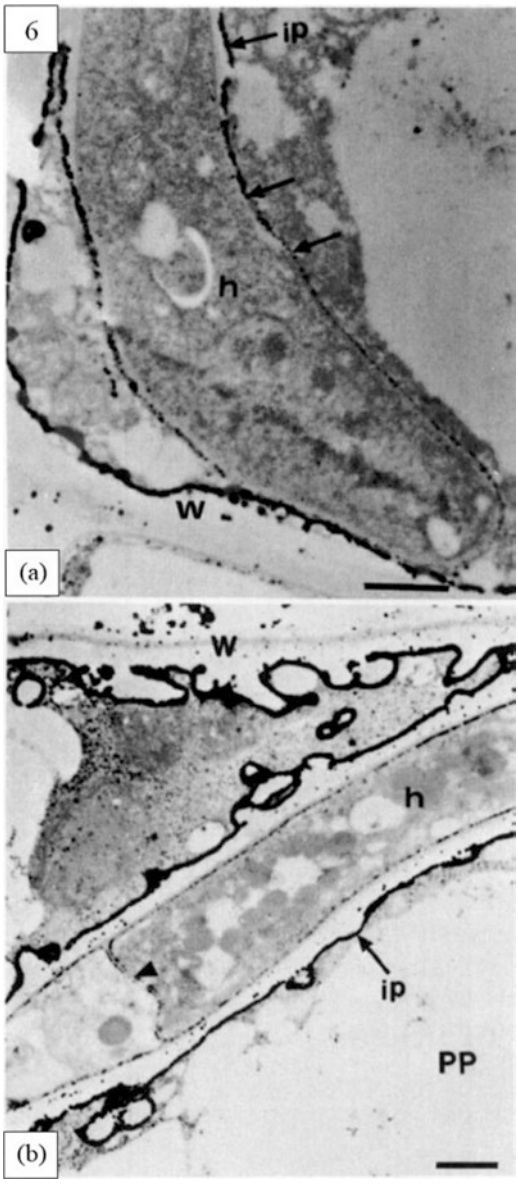


Fig. 6 Filamentous haustoria of *P. poarum* in phloem parenchyma of *Tussilago farfara* after incubation in ATPase detection medium. (**a**) Young M-haustorium showing ATPase reaction (arrows) on the invaginated plasmalemma (ip) near penetration point, similar to that of uninvaginated plasmalemma adjacent to host wall (w) but decreasing distally, where the extrahaustorial matrix is very thin. Bar = 1.0 µm. (**b**) Older M-haustorium with strong ATPase reaction throughout the invaginated (ip) and wall-lining domains of host plasmalemma, surrounding the transfer cell type of projections of the wall (w) and extrahaustorial matrix enclosing the haustorium (h). ATPase activity is indicated on the fungal plasmalemma, including the septum region (arrowhead). Bar = 1.0 µm

These haustoria showed the specialized morphology of D-haustoria with a very constricted point of entry, narrow neck region bearing an electron-dense neckband and expanded clavate body. In both infections, ATPase activity was indicated on the host plasmalemma lining the cell wall. Lead deposits were also associated with the endoplasmic reticulum, chloroplasts and nuclear membrane. ATPase (Fig. 9) but not

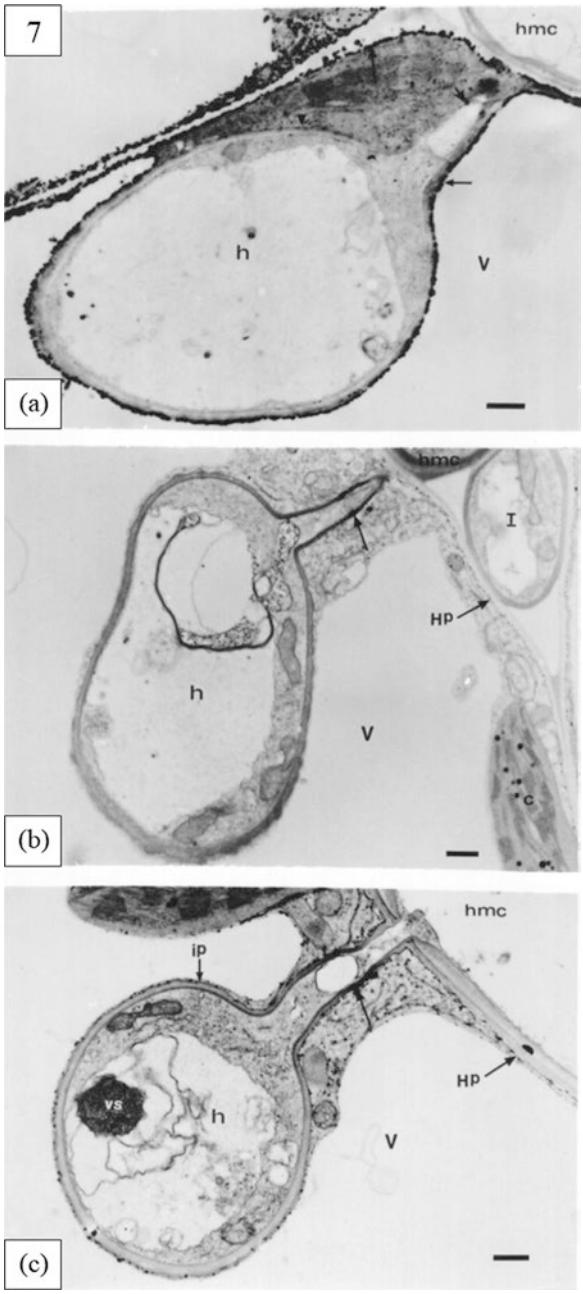


Fig. 7 D-haustoria of *P. punctiformis* in the mesophyll of *C. arvense* during the dikaryon phase of infection, after incubation in ATPase detection medium or control media, observed without further staining. (**a**) In the presence of ATP, a dense precipitate is seen on the host plasmalemma lining the host cell wall (w) and on the tonoplast (arrows) but neither the invaginated region of plasmalemma (arrowhead) surrounding the haustorium (h) nor the fungal plasmalemma shows evidence of ATPase activity. Bar = 0.5 µm. (**b**) Section incubated in medium without ATP substrate lacks the precipitates seen in (**a**). Bar = 1.0 µm. (**c**) Section incubated in the presence of ATP and Mg^{++}, with the addition of sodium orthovanadate as an inhibitor, shows a marked reduction in lead precipitation, compared with (**a**). Bar = 1.0 µm

ß-glycerophosphatase (Fig. 10) activity was indicated on the plasmalemma of *P. Punctiformis*. However, no enzymic reactions were detected on the plasmalemma of *P. menthae*.

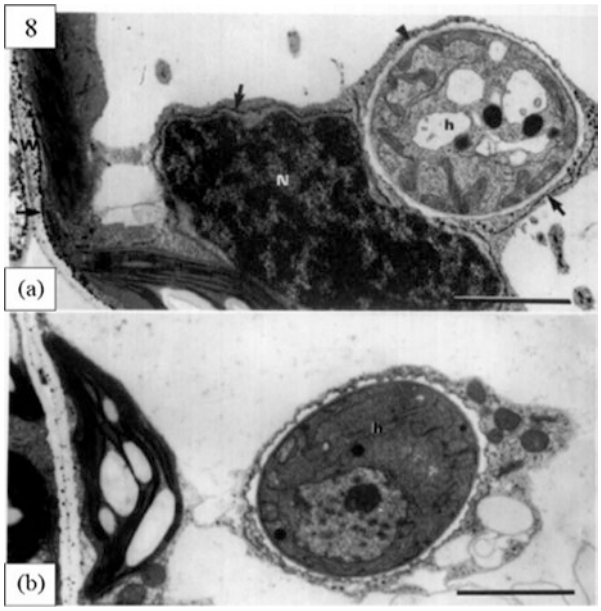


Fig. 8 D-haustoria (h) of *U. vicia-fabae* in mesophyll cells of *Vicia faba*. (**a**) Tissue incubated in the presence of ATP and observed without further staining. Lead precipitates indicate ATPase activity (arrows) on host plasmalemma lining the host cell wall (w) and within-host cytoplasm, particularly over ER cisternae and the membrane of the host nucleus (N), but no activity is detected on the extrahaustorial membrane (arrowhead). Bar = 1.0 μm. (**b**) ATPase control without substrate lacks the precipitates seen in Fig. (a). Bar = 1.0 μm

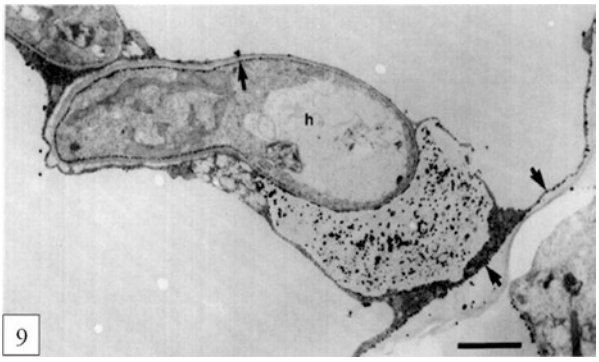


Fig. 9 D-haustorium of *P. punctiformis* (h), after incubation in the presence of ATP. Precipitates indicating ATPase activity (arrows) lie over the fungal plasmalemma, wall-lining host plasmalemma, and on obliquely sectioned collar (C) of wall-like material but not on the tonoplast or extrahaustorial membrane. Bar = 0.5 μm

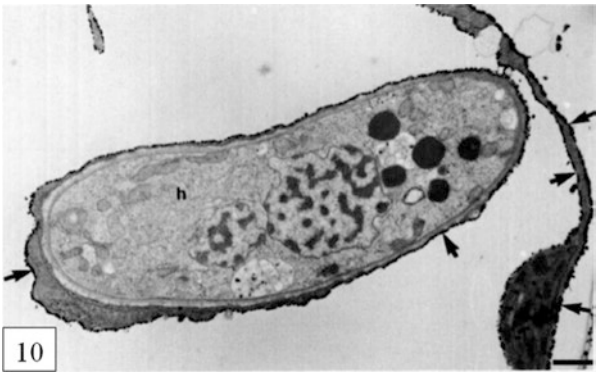


Fig. 10 D-haustorium of *P. punctiformis* (h) in a mesophyll cell, after incubation in the presence of β-glycerophosphate. Precipitates provide evidence of phosphatase activity on uninvaginated host plasmalemma and tonoplast (arrows) but not on the extrahaustorial membrane or fungal plasmalemma. Bar = 1.0 μm

Control treatments without substrate or with sodium orthovanadate as a specific inhibitor of ATPase activity showed markedly less, or a complete absence of lead precipitation (Figs. 7b, c and 8b).

As in the cells containing filamentous haustoria, incubation in β-glycerophosphate gave rise to a similar distribution of lead phosphate precipitates to that resulting from ATP in the incubation mixture. The distribution of enzymic reactions observed in tissues examined here and in previous studies is summarized in Table 1.

The different distribution of activity of phosphatases associated with the membranes enclosing M- and D-haustoria of *P. punctiformis* in tissues of *C. arvense*, like the contrasting morphology of the two types of haustoria (Baka and Losel 1992a), clearly relate to genomic differences between the mono- and dikaryotic phases of the fungal life cycle and are not simply due to interactions with alternate hosts. This physiological distinction between monokaryotic and dikaryotic phases of rust infections is consistently borne out by the observations in this and previous work on the various rust infections summarized in Table 1.

The present investigation of ATPase activity in *P. punctiformìs* infections appears to be the first to compare spermogonial-aecial and uredinial stages of single autoecious rust. Indeed, few EM studies of autoecious rusts, in both mono- and dikaryotic phases have been published (Gay and Woods 1987; Harder 1978; Larous and Losel 1993b; Littlefield and Heath 1979; Al-Khesraji 1981).

The interpretation of the observations of this and most previous studies on plant tissue depends on the reliability of the lead precipitation technique in the detection of ATPase, as distinct from phosphatase activity. From parallel cytochemical and *in vitro* investigations of ATPase activity in *Avena sativa* root tissue, Katz et al. (1988) reported a number of problems associated with the choice of fixatives and inhibitors and questioned whether the ATPase localized by the lead precipitation procedure, as commonly applied, identified the plasma membrane proton pump. These workers proposed a rigorous set of criteria for unambiguous cytochemical localization of the

Table 1 Presence (+) or absence (−) of ATPase and phosphatase reactions on host plasma membrane (HPM), proximal (pr) and distal (ds) regions of the invaginated host plasma membrane (extrahaustorial membrane, EHM), and fungal plasma membrane (FPM) of haustoria of studies of rust infections

	Pycnial-aecial				Uredial			Reference
	HPM	EHM		FPM	HPM	EHM	FPM	
Rust fungus		pr	ds					
Puccinia punctiformis								Baka et al. (1995)
ATP-ase	+	+	+	+	+	−	+	
Phosphatase	+	+	+	+	+	−	−	
P. menthae								Baka et al. (1995)
ATP-ase	+	+	−	−				
Phosphatase	+	+	−	−				
P. poarum								Baka et al. (1995)
ATP-ase	+	+	−	−				
Phosphatase	+	+	−	−				
P. lagenophorae								Baka (1989)
ATP-ase	+	+	+	+				
Phosphatase	+	+	+	+				
Uromyces viciae-fabae								Baka et al. (1995)
ATP-ase					+	−	−	
Phosphatase					+	−	−	
Uromyces appendiculatus								Spencer-Phillips and Gay (1981)
ATP-ase					+	−	−	
Phosphatase					+	−	−	

proton pump, recommending formaldehyde at 0 °C for fixation, a low concentration of lead or the use of other phosphate-precipitating agents, and the employment of 0.1 mM molybdate to reduce background deposition from soluble phosphatase activity (Hail and Williams 1991). In subsequent work, Chauhan et al. (1991) repeated and extended many of the experiments of Katz et al. (1988) and compared cerium-based and lead-based methods for localization of ATPase activity in maize root cells. With either lead- or cerium-based capture methods, precipitates occurred over both faces of the plasma membrane, a finer and more consistent deposition with less general cytoplasmic staining being found with cerium. The strongest cytochemical staining was obtained in tissue fixed with a mixture of cold 3% paraformaldehyde and 0.25% glutaraldehyde (concentrations close to those employed in the present study). With paraformaldehyde alone, advocated but apparently not used in cytological experiments by Katz et al. (1988), there was clear ATPase staining but poor cytoplasmic preservation. Both methods of capture were considered specific for plasmalemma ATPase, since Mg^{2+} requirement and vanadate sensitivity were demonstrated; 50 rnM KNO_3 which specifically inhibits tonoplast ATPase had no effect on the cytochemical staining and omission of substrate or replacement with ß-glycerophosphate resulted in an absence of reaction product on the plasmalemma. Both lead and cerium interfered with the deposition of the reaction product, due to

non-enzymatic hydrolysis, this effect being greater with cerium. It was suggested that histochemical detection of ATPase might be more sensitive than biochemical assays even if the cytochemical staining represents only a small proportion of the plasma membrane activity.

Resolution of the question of whether the cytochemical reactions listed in Table 1 correspond to H^+-ATPase activity as well as similarly distributed non-specific phosphatase activity may have to await the isolation of specific immunocytochemical probes. However, the consistent observations in the present work that different parts of one plasma membrane, and even of one extrahaustorial membrane, react differently, providing strong evidence of physiological specialization at the parasitic interface. Recent progress in the employment of monoclonal antibodies in the cytochemical analysis of host-pathogen interfaces includes the recognition of specific glycoproteins of the fungal plasmalemma of isolated haustorial complexes of *Erysiphe pisi*. This differed from those of the plasmalemma of the surface mycelium (Mackie et al. 1991, 1993; Reberts et al. 1993) and the localization of glycoproteins, expressed in the intracellular hyphae of *Colletotrichum lindemuthianum* during the early biotrophic growth phase in leaf tissue of *Phaseolus vulgaris* but not present on conidia or appressoria (Pain et al. 1994).

In the rust infections examined here, the absence of ATPase activity from the extrahaustorial membrane of D-haustoria of *P. Punctiformis* and *U. vicia-fabae* is consistent with earlier findings for dikaryotic *U. appendiculatus* (Spencer-Phillips and Gay 1981). Likewise, the presence of ATPase reactions on the extrahaustorial domain of host plasmalemma in *P. punctiformis* and *P. menthae* infections corresponds to previous reports for *P. poarum* (Woods and Gay 1987) and *P. lagenophorae* (Baka 1989) in which the invaginated host plasmalemma surrounding M-haustoria appears similar to the rest of the host cell membrane. O'Connell (1987) detection of ATPase activity on the invaginated plasmalemma enclosing the unspecialized hemibiotroph *Colletotrichum lindemuthianum*, during its brief biotrophic phase in cells of *Phaseolus vulgaris*, is of interest in this connection.

The present evidence for parallel decreases in ATPase activity and in the associated deposition of wall material from proximal to distal regions of the invaginated plasmalemma of M-haustoria of *P. poarum* and *P. menthae* supports the very thorough previous study of *P. poarum* (Woods and Gay 1987), but these phenomena were not detected in *P. punctiformis* or *P. lagenophorae* (Baka 1989). Beale et al. (1990) provide an interesting parallel from a light microscope study of the downy mildew species *Peronospora viciae*, in which an adaptation of the ATPase detection reaction was employed to improve the visibility of intercellular hyphae and haustoria within pea leaf tissue. In *P. viciae* also, the staining showing ATPase activity decreased towards the tip of some of the simple, filamentous haustoria.

Where ATPase and phosphatase activities are absent from the membrane enclosing the distal region of M-haustoria, the physiology may resemble the situation in D-haustoria, where it was interpreted by Spencer-Phillips and Gay (1981) as indicating diminished control of the passage of solutes via the host plasmalemma. Similar interpretations were proposed for the Oomycetes *Albugo candida* (Woods and Gay 1983) and *Bremia lactucae* (Woods et al. 1988). In M-haustoria (Woods and Gay 1987) however, this is probably a transient condition, followed by

increasing ATPase activity and deposition of wall material, as successive regions of the filamentous structure mature. Woods and Gay 1987) suggested that the relative inefficiency of the apparently unspecialized M-haustoria could be compensated by the observed location of monokaryotic haustoria within the vascular tissues.

The only previous evidence for ATPase activity on the haustorial plasma membrane appears to be from EM cytochemical studies of *Erysiphe pisi* (Spencer-Phillips and Gay 1981), M-haustoria of *Puccinia lagenophorae* Baka 1989), and the light microscopic observations on *P. viciae* (Beale et al. 1990) mentioned above. ATPase activity has now been found in the plasmalemma of both types of haustoria of *P. Punctiformis* and in M-haustoria of *P. poarum*, although not detected in *P. poarum* previously (Woods and Gay (1987), in haustoria of *P. menthae* and *U. vicia-fabae* in the present study, nor in those of the downy mildew *Bremia lactucae* (Woods et al. 1988). These discrepancies may reflect differences in penetration of fixative and/or substrate into the fungal structures (e.g. Beale et al. (1990) noted that over-fixation inhibited the ATPase reaction) as well as specific features of fungal ATPases, such as a lower pH optimum than found in plasmalemma H^+-ATPases of plants (Bowman and Bowman 1986). Although ATP-ases from a number of plant sources (Serrano 1989, Sussman ad Harper 1989) and from several species of saprophytic fungi (Bowman and Bowman 1986), in which plasmalemma proton pumps are particularly active (Sussman ad Harper 1989), have been investigated at the molecular level, no ATPases of plant-pathogenic fungi appear to have been characterized so far.

The functioning of ATPases in nutrient transport across the plant plasmalemma has been studied most intensively in relation to transfer cells and phloem loading (Van Bel 1993), both cytochemically in *P. sativum* (Bentwood and Cronshaw 1978) and by combined cytochemical and biochemical studies (Williams and Hall 1987) of *Ricinus communis* cotyledons. Leaves of *Pisum sativum*, *Phaseolus vulgaris* (Spencer-Phillips and Gay 1981) and *T. farfara* (Woods and Gay 1987) showed stronger plasmalemmal ATPase reactions in epidermal, phloem transfer and companion cells, i.e. tissues importing photosynthate, than in cells of the mesophyll. Interactions between biotrophic fungal pathogens and host plant cells appear to induce a comparable differential distribution of ATPase activity (Gay 1984; Gay and Wood 1987) corresponding to the special source-sink relationships of infected tissues.

3 Infection of Vascular Tissues in Host-Rust Interaction

The taxonomically related, autoecious rusts, *Puccinia punctiformis* (Str.) Rohl and *P. lagenophorae* Cooke were selected, since their respective hosts *Cirsium arvense* L. and *Senecio vulgaris* L., are in the same family as *T. farfara*, the host of the monokaryon of *P. poarum*. The occurrence of infection in the leaf vascular system was investigated throughout the macrocyclic life cycle of *P. punctiformis* and in the aecial stage of *P. lagenophorae*.

P. punctiformis produces spermogonia on systemically infected shoots in late spring, followed by uredinoid aecia (Wilson and Henderson 1966), and termed primary uredinia (Buller 1950). The spores in these sori are morphologically identical

to urediniospores but the associated limited mycelium bears unspecialized, filamentous intracellular structures (Baka and Losel 1992a) of the type normally found in monokaryotic phases of the rust life cycle (Littlefield and Heath 1979). Infection of healthy thistles by primary urediniospores initiates a dikaryotic mycelium with typical D-haustoria and bearing secondary uredinia and telia (Baka and Losel 1992a). *P. lagenophorae*, native to Australia and found in Europe only since 1961 (Wilson and Henderson 1966), was investigated mainly in the aecial phase. Teliospores develop later among the aeciospores and in telia, which, in some cases (N. Paul, personal communication), even develop within the pith cavity.

3.1 Puccinia Punctiformis

Healthy leaves of *C. arvense* showed normal vascular tissue components (Fig. 11). In infected leaves of *C. arvense* bearing spermogonia, monokaryotic filamentous haustoria were common xylem parenchyma (Fig. 12) and bundle sheath cells (Fig. 13) but sparsely distributed within the vascular tissue. During the subsequent

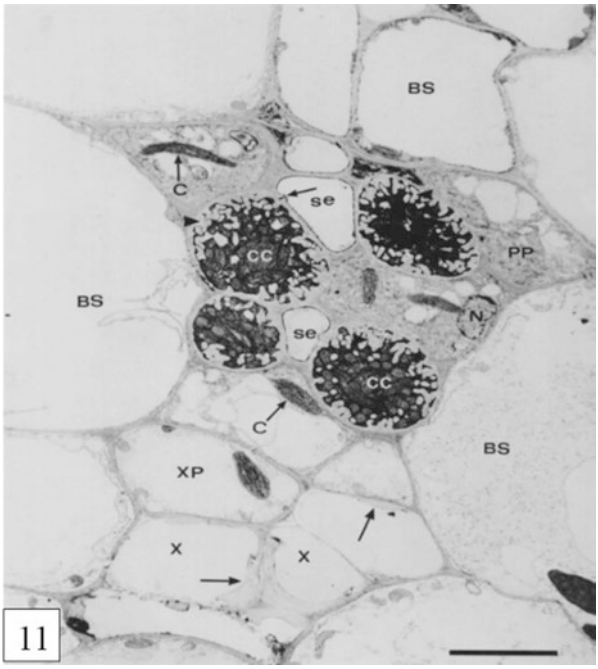


Fig. 11 TEM micrograph of a transverse section of a vascular bundle from healthy *C. arvense* leaf showing typical components of phloem and xylem. Note the plasmalemma (small arrow) between the sieve element (se) and the companion cell (cc). Note also the wall ingrowths (arrowheads) of both phloem parenchyma (pp) and companion cells. The thickening of xylem vessels (large arrows), bundle sheath (BS), xylem (x), xylem parenchyma (XP) chloroplasts (C), and nucleus (N) can also be seen. Bar = 0.5 μm

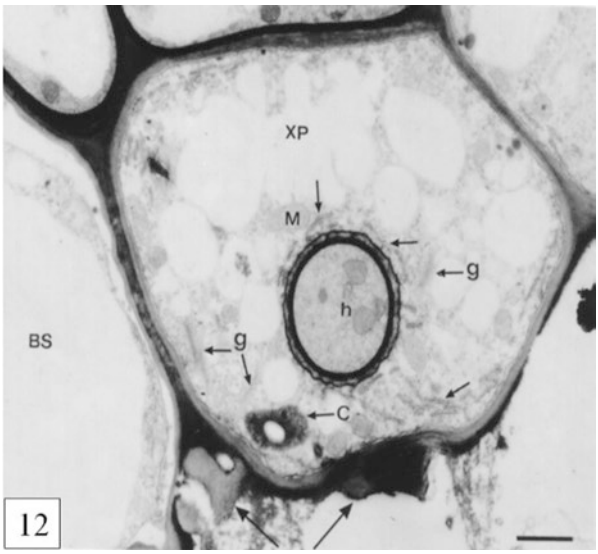
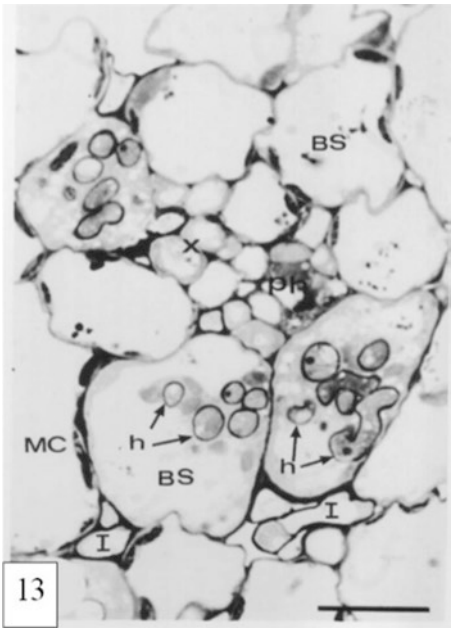


Fig. 12 Filamentous haustorium in xylem parenchyma of *Cirsium arvense* leaf, during spermogonial stage of *Puccinia punctiformis*. The host cell cytoplasm contains mitochondria and profiles of endoplasmic reticulum (arrows), closely associated with extrahaustorial membrane and plasmalemma. A large arrow indicates a secondary wall in the adjacent tracheary element. Bar = 1.0 µm

Fig. 13 Light micrograph of a semi-thin section of a small vascular bundle of *C. arvense* during aecial stage of *P. punctiformis* showing numerous sections of fungal structures in bundle sheath cells. Intercellular hyphae are present in vascular tissue as well as in mesophyll. Bar = 5.0 µm



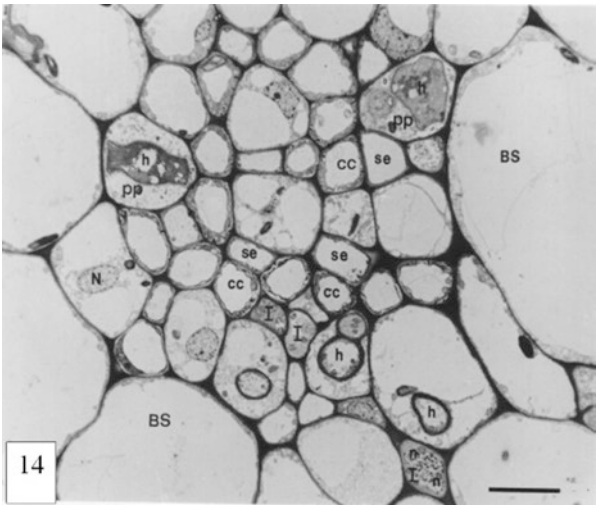


Fig. 14 Phloem region of larger vascular bundle showing the infection of phloem parenchyma cells. Note intercellular hyphae. Bar = 5.0 μm

development of aecia, bundle sheath cells often became densely infected and intercellular hyphae grew within the vascular region (Fig. 14). Filamentous haustoria were frequent in phloem parenchyma (Fig. 15), xylem parenchyma and even xylem elements where, in some instances, they were embedded in bands of lignified wall thickening (Fig. 16).

The cytoplasm of infected cells of the vascular region was of relatively healthy appearance with abundant profiles of endoplasmic reticulum and mitochondria. The hypha-like intracellular structures, like those previously described in the mesophyll (Baka and Losel 1992). were not observed to exit from the host cells. These structures grew mainly longitudinally in vascular elements, commonly presenting circular profiles in transverse sections of leaf veins. Later in aecial development, morphologically similar haustoria were seen in vascular tissue. These intracellular structures, like those previously noted in the mesophyll (Baka 1987; Baka and Losel 1992a), lacked the narrow neck and neckband typical of the specialized D-haustoria (Littlefield and Heath 1979) of uredinial-telial phases of rust life cycles. As in mesophyll cells of these and other (Harder 1978; Littlefield and Heath 1979; Woods and Gay 1987) rust species, a material resembling the host wall in its staining reactions tended to accumulate around older filamentous haustoria, in the extrahaustorial matrix between the invaginated regions of host plasmalemma and fungal walls (Fig. 14). This layer was absent in young haustoria, as in Fig. 11. In secondary uredinial and telial stages of infection by *P. punctiformis*, examination of many tissue blocks from different plants failed to reveal any penetration of the vascular system by the fungus, although the bundle sheath cells were infected by clavate, D-haustoria of the type familiar in dikaryotic infections by rust fungi.

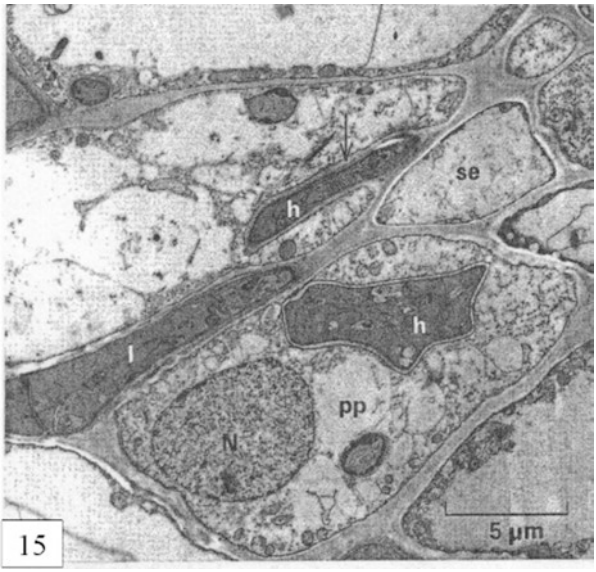
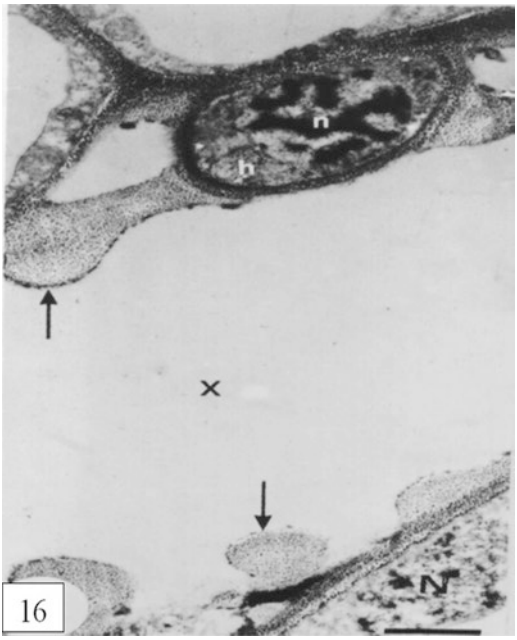


Fig. 15 Haustoria and intercellular hypha in phloem parenchyma. Compare the staining of host wall material and extrahaustorial matrix (arrow). Bar = 5.0 µm

Fig. 16 Section of fungal cell embedded in the band of lignified secondary thickening of xylem vessel (arrow). Note the healthy appearance of the fungal nucleus and cytoplasm. Bar = 1.0 µm



3.2 *Puccinia lagenophorae*

In leaves of *Senecio vulgaris*, the development of aecia of *P. lagenophorae*, was consistently associated with a vascular infection which light microscopy showed to be more densely concentrated in this region than in the mesophyll (Fig. 17). Filamentous haustoria were found in all types of cells of both phloem and xylem (Figs. 18, 19, 20 and 21). The cytoplasm of infected phloem parenchyma, transfer cells, and xylem parenchyma, remained relatively electron-dense, even after infection, with a well-developed membrane system and abundant mitochondria, giving the impression of a metabolically active condition (Figs. 17, 18, 19 and 20). In some older infections of transfer cells of the phloem of *Senecio*, host wall-like material was occasionally found to be deposited in the extrahaustorial matrix surrounding filamentous haustoria in a manner similar to the wall ingrowths projecting from the rest of the host cell wall (Fig. 19). As in *P. punctiformis*, where xylem vessels had been penetrated, fungal cells were sometimes embedded within the lignified bands of secondary wall thickening (Fig. 21).

The above observations appear to be the first ultrastructural investigation of the relationship of autoecious rusts with host vascular tissues. The intensive invasion of the vascular system of *Senecio vulgaris* by the aecial phase of *P. lagenophorae* contrasts strikingly with the more limited vascular infection by *P. punctiformis* in *C. arvense* and closely resembles the distribution of the monokaryon of *P. poarum* in leaves of *T. farfara* (Al-Khesraji et al. 1980). In the case of the heteroecious rusts,

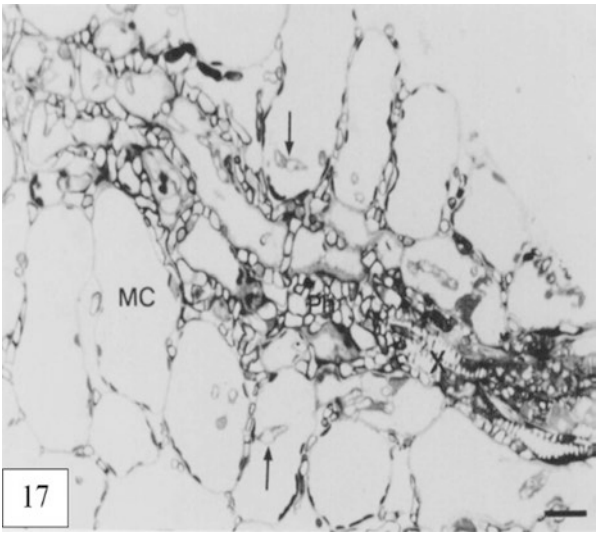


Fig. 17 Light micrograph of a longitudinal section of leaf veins of *Senecio vulgaris* during the aecial stage of *Puccinia lagenophorae*, showing inter- and intra-cellular infection of bundle sheath, phloem, and xylem. Compare the density of infection of the vascular strand and adjacent mesophyll. Bar = 10 μm

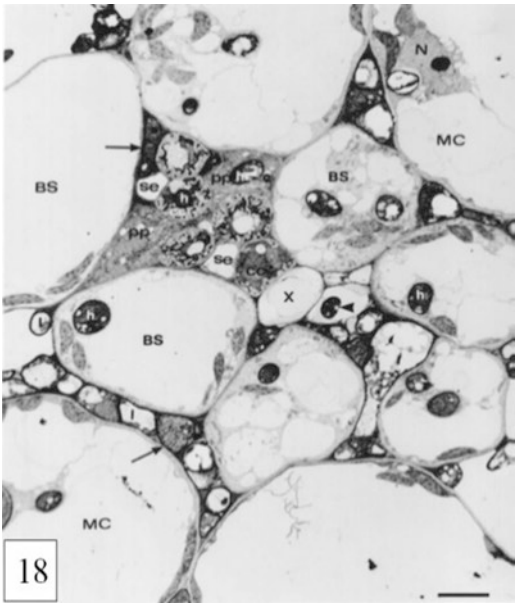


Fig. 18 Transverse section of small vascular bundle, showing fungal structures adjacent to and within cells of bundle sheath, phloem, and xylem (arrowhead). Note bi-nucleate cells of intercellular hyphae (arrow). Bar = 5 µm

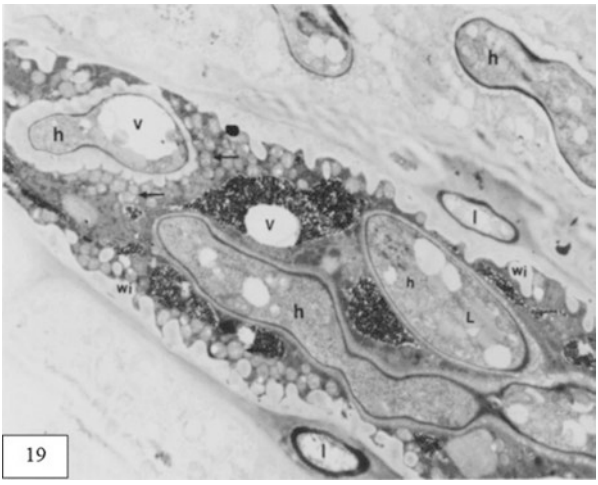


Fig. 19 Longitudinal section through heavily infected transfer cells of phloem. Note long, intracellular, fungal structures with a moderately electron-dense extracellular matrix, which, in the one on the right, resembles wall in-growths of transfer cell. The upper cell contains large numbers of mitochondria and deposits of electron-dense granules. The haustoria in the lower cell are probably younger, having no wall-like material visible in the matrix. Bar = 2.0 µm

P. coronata avenae (Harder 1978) and *P. poarum* (Al-Khesraji et al. 1980), the monokaryons which infect the vascular systems of *Rhamnus cathartica* and *T. farfara*, respectively, it could be argued that the exclusion of the dikaryon from

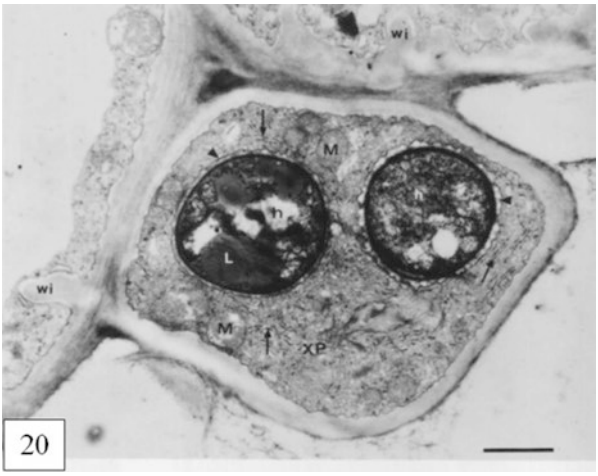


Fig. 20 Transverse sections of two filamentous haustoria in xylem parenchyma cell. The host cytoplasm is of healthy appearance, unvacuolated, containing mitochondria and numerous profiles of endoplasmic reticulum (arrows). The extrahaustorial matrix surrounding the haustorium on the left is moderately electron-dense but that on the right (arrow) shows no deposition of wall-like material. Bar = 1.0 μm

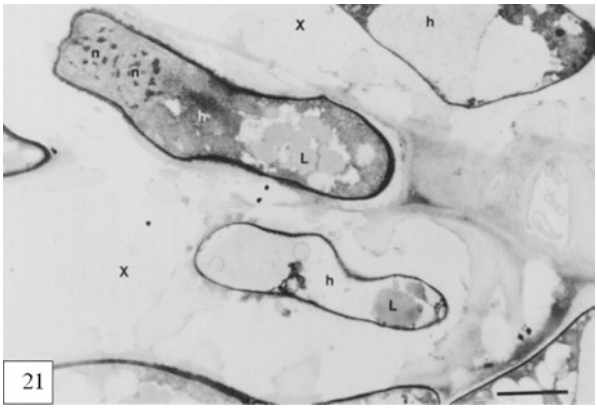


Fig. 21 Tracheary elements of xylem with intercellular hypha and intracellular fungal structures, partially embedded in secondary wall thickening. Note the breakdown of the primary wall (arrows). Bar = 0.5 μm

vascular tissues of the alternate hosts, *A. sativa* and *Poa pratensis*, might be determined by anatomical or physiological characteristics of these grasses, such as the lignified bundle sheath. The present study has shown this pattern persisting even where there is no difference in host species during the life cycle. The dikaryon initiated by the uredinoid aeciospores of *P. punctiformis* appears to be incapable of penetrating the vascular system of *C. arvense*. The situation is still unclear in

P. lagenophorae, which lacks uredinia and spermogonia, and where the limited amount of telial material examined proved too brittle to provide good sections. The only evidence so far for the occurrence of D-haustoria in host vascular tissue is from a study of wheat varieties infected by *P. graminis* where vascular penetration was recorded in the most susceptible of a range of varieties examined (Andreev et al. 1982). During the spermogonial and aecial stages of infection by *P. punctiformis* and *P. lagenophorae* the fungal structures within living cells of the vascular system, like those in the mesophyll (Baka 1987; Baka and Losel 1992b), correspond to descriptions of P-haustoria (Harder 1978), or M-haustoria (Littlefield and Heath 1979). Since, like those of *P. poarum* (Juniper et al. 1970; Woods and Gay 1987), they have not been observed to exit from a host cell, they fit Bushnell's definition of a haustorium (Baka and Losel 1992b), rather than intracellular hypha, as employed by Gold et al. (1979). These intracellular structures like those of the monokaryons of *P. poarum* (Al-Khesraji and Losel 1981; Woods and Gay 1987), *P. coronata* (Harder 1978), *P. menthae* (Larous 1990) and other rusts (Littlefield and Heath 1979), lack the strongly-constricted neck with osmiophilic neck-band, characteristic of the specialized D-haustoria of uredinial-telial dikaryon (Baka and Losel 1992a; Littlefield and Heath 1979). They share common features of a wider point of entry into the host cell and similar cytochemical reactions of the extrahaustorial matrix (Baka 1987; Baka and Losel 1992a; Larous 1990), elegantly demonstrated by Woods and Gay in monokaryotic infections of *P. poarum* (Woods and Gay 1987). The distinction between intracellular hyphae, as found in *P. recondita* (Gold et al. 1979), and *P. menthae* (Larous 1990), and filamentous haustoria are likely to be functionally less significant than their differences from D-haustoria. The encasement of the fungal wall in older regions of filamentous haustoria by host wall-like material has been studied cytochemically in *P. poarum* (Woods and Gay 1987), *P. punctiformis* and *P. lagenophorae* (Baka 1987; Baka and Losel 1992b) and other rust fungi (Larous 1990; Littlefield and Heath 1979). A more specialized reaction of this type has been noted here in some transfer cells of leaf veins of *S. vulgaris*, where transfer cell-like projections of wall material, have occasionally been observed around intracellular structures of *P. lagenophtrae*. The question arises whether the proliferation of the enclosing extrahaustorial membrane, associated with such wall deposition, may facilitate the movement of solutes from host cell to hypha, by a mechanism comparable to the loading of conducting elements adjacent to transfer cells. Such deposition of wall material, like the embedding of fungal cells within bands of lignified secondary wall thickening, in xylem elements of *C. arvense* and *S. vulgaris*, supports the cytochemical evidence (Baka 1987; Larous 1990; Woods and Gay 1987) that the invaginated region of plasmalemma, surrounding the fungal wall of older regions of filamentous haustoria, carries out similar wall-synthesizing reactions to those of the uninvaginated region lining the host cell wall. The hyphae found within non-living xylem elements may have developed initially as haustoria in young, undifferentiated cells. Following the maturation and death of the host cell, however, they become essentially apoplastic, lack the extrahaustorial matrix of functional haustoria, and frequently appear necrotic. As suggested in the

case of *P. poarum*, the ability of the spermogonial-aecial thallus of these rust fungi to gain access to host nutrients of the vascular system may compensate for the unspecialized nature of the associated filamentous haustoria (Al-Khesraji et al. 1980; Woods and Gay 1987), The lack of this characteristic in the uredinial-telial dikaryon points to fundamental physiological and morphogenetic differences in genome expression which merit further investigation.

4 Cytochemical Aspects of the Interaction Between the Rust Fungus *Melampsora euphorbiae* and Its Host, *Euphorbia peplus*

By use of the probes listed in Table 2, specific sugar residues were detected and localized in fungal (Table 3) and host cells (Table 4). Incubation of infected *Euphorbia* leaves with WGA/ovomucoid-gold complex, resulted in labelling of chitin (a β-1, 4-linked N-acetylglucosamine polymer) in hyphal walls, more intensively on septa than on longitudinal walls (Fig. 22a). Urediniospore walls were labelled (Figs. 22b), but the spines embedded in the outer wall of mature urediniospores gave no chitin reaction (Fig. 22c). The haustorium wall, extrahaustorial matrix and extrahaustorial membrane (Fig. 22d) were, however, almost free of labelling. Cytoplasm, mitochondria, oil drops and vacuoles of both fungus and host remained unlabelled (Fig. 22d). Surprisingly, however, this probe was also bound to the secondary wall of xylem vessels (Fig. 22e). The density of distribution of gold particles was greatly reduced over sections treated with WGA-gold complex preincubated with N-acetyl-chitotriose.

When ConA gold conjugate was used to detect α-D-mannose and/or α-D-glucose residues, heavy binding was observed to the glycogen-like granules in the hyphal cytoplasm (Figs. 23a, b), starch grains in the host cell (Fig. 23c), and to a myelin-like profile of concentric membranes (Fig. 23d), but not to host or fungal walls (Fig. 23c, d). Weak labelling was also observed in the cytoplasm of the fungus (Fig. 23d).

Table 2 Lectins and enzymes used for investigation of rust infected tissue, their sources and pH values of colloidal gold for complex formation

Probe[a]	Source[b]	Substrate specificity	pH
WGA	*Triticum vulgare*	Chitin	7.4
ConA	*Concanavalia ensiformis*	α-D-mannose, a-D-glucose	8.0
RcA_1	*Ricinus communis*	β-D-galactose	8.0
LTA	*Lotus tetragonolobus*	α-L-fucose	7.0
β-glucosidase	Almond	β-glucosides	9.3

[a]*WGA* wheat germ agglutinin, *ConA* concanavalin A, *RcA1 Ricinus communis* agglutinin, *LTA* Lotus tetragonolobus lectin
[b]All from Sigma, UK

Table 3 Occurrence, localization[a] and relative amounts[b] of carbohydrates detected in *Melampsora euphorbiae*

Probe[a]	Specificity	IHW	HW	UW	FCY	GP	LO	FL	Al
WGA	Chitin	+	–	+	–	–	–	–	–
ConA	α-D-mannose, α-D-glucose	–	–	–	+	++	–	–	–
RcA_1	β-D-galactose	++	+	–	–	–	++	–	–
LTA	α-L-fucose	++	t	–	+	–	–	–	+++
β-Glucosidase	β-Glucosides	–	–	–	–	–	–	–	–

[a]Abbreviations as in Table 1
[b]Location: *IHW* Intercellular hypha wall, *HW* Haustorium wall, *UW* Urediospore wall, *FCY* Fungal cytoplasm, *GP* Glycogen particles, *LO* Lomasomes, *FL* Fungal lipid drops, *AL* Amorphous layer between hyphae
[c]Relative amount, indicated by distribution density of gold particles: +++ = very high; ++ = high; + = moderate; t = trace; – = absent

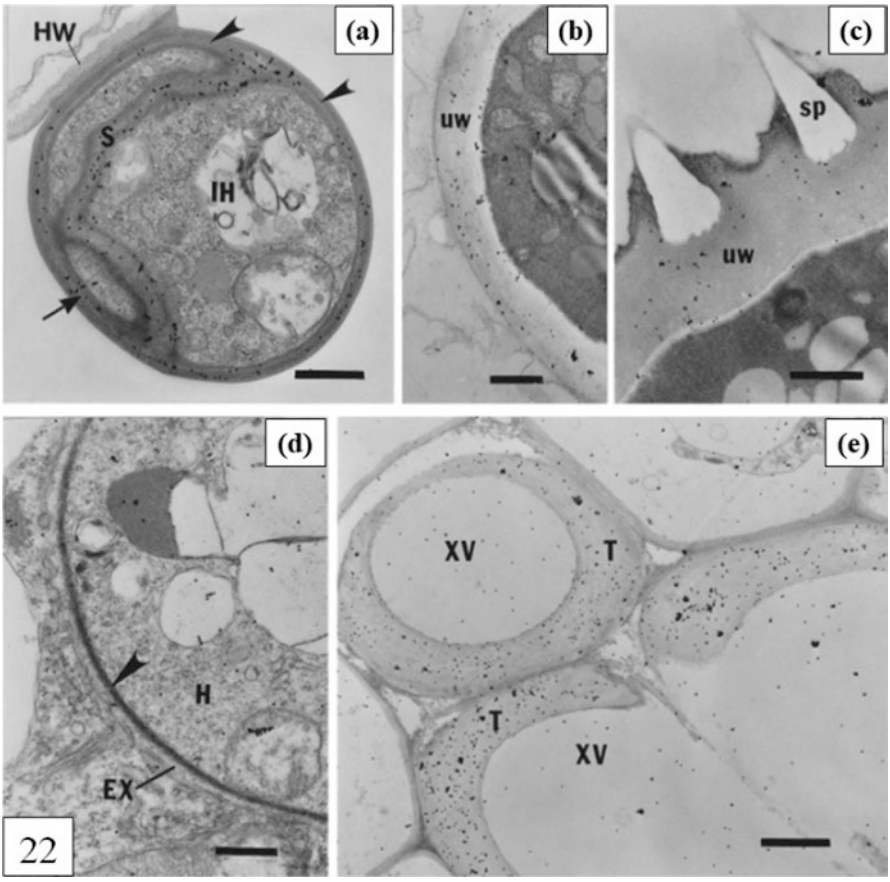
Table 4 Occurrence, localization[a] and relative amounts[b] of carbohydrates detected in tissue of host plant *Euphorbia peplus*

Probe[c]	Specificity	CW	XT	SG	MS	HN	HL	HCY	ELW	ILX
WGA	Chitin	–	++	–	–	–	–	–	–	–
-ConA	α-D-mannose, α-D-glucose	–	–	+++	++	–	–	–	–	–
RcA_1	β-D-galactose	++	–	–	–	–	–	–	–	–
LTA	α-L-fucose	–	–	–	–	–	–	–	–	–
β-Glucosidase	β-Glucosides	–	–	–	–	–	–	–	+++	+

[a]Location: *CW* Cell wall, *XT* Xylem thickening, *SG* Starch grain, *MS* myelin-like profile of concentric membranes, *HN* Nucleus, *HL* Lipid drops, *HCY* cytoplasm, *ELW* external layer of wall, *ILX* inner layer of xylem primary wall
[b]Relative amount, indicated by distribution density of gold particles: +++ = very high; ++ = high; + = moderate; t = trace; – = absent
[c]Abbreviations as in Table 1

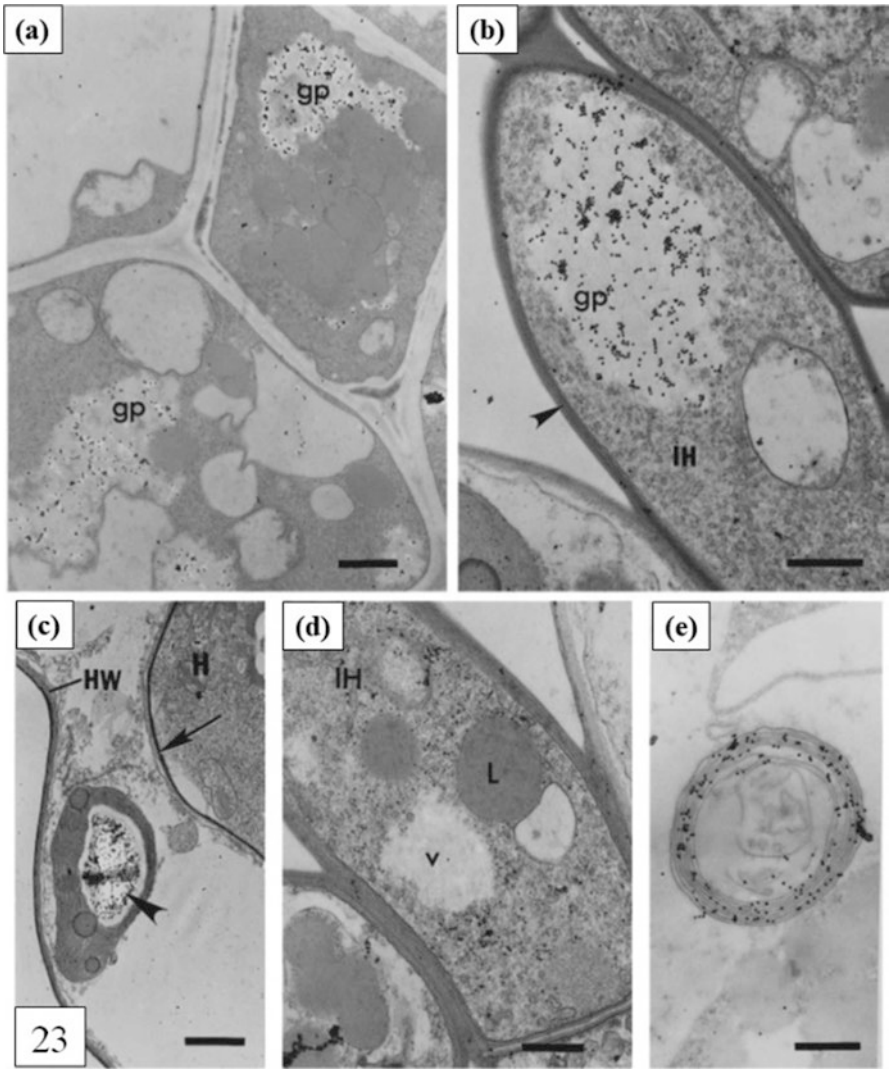
Treatment of the sections with ConA-gold complex, previously absorbed to α-D-mannose or α-D-glucose, gave negative results. After incubation with the *Ricinus communis* agglutinin I (RCA_1)-gold complex, to detect α-D-galactose, an increase in labelling was observed in the walls of intercellular hyphae (Fig. 24a, c), and in haustorial and host cell walls (Fig. 23c). The vesicular structures inside intercellular hyphae identified as lomasomes (Littlefield and Heath 1979) were heavily labelled (Fig. 24b) but other cytoplasmic components of both host and fungus were not significantly labelled (Figs. 24a–c). In a control test including the previous adsorption of the RcA_1-gold complex on D-galactose, no labelling was observed.

Incubation with *Lotus tetragonolobus* lectin-gold complex to detect L-fucose, revealed a regular deposition of gold particles over the walls of intercellular hyphae (Figs. 25a). In contrast, there was little labelling of haustorial walls (not shown) and none over either host cell walls or host and fungal organelles (Figs. 25a–d). Negative results were obtained when the sections were incubated with the lectin-gold



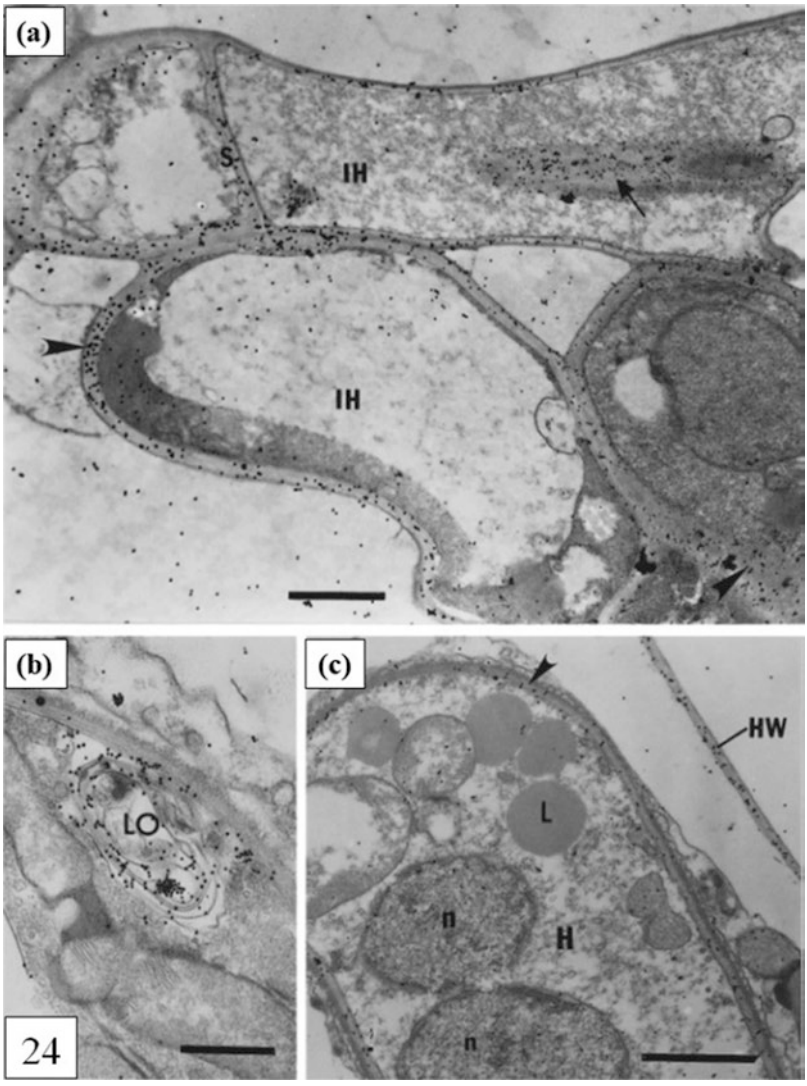
Figs. 22 Rust-infected leaf tissue of *E. peplus* labelled with WGA and ovomucoid-gold complex. (**a**). Obliquely sectioned intercellular hypha (IH) showing labelling over the wall (arrow) and septum (S) and absence of labelling in wall regions furthest from the septum (arrowheads). The host wall (HW) and adhesion matrix remain unlabelled. Bar = 0.5 μm. (**b**). Labelling over the wall (uw) of immature urediniospore. Bar = 1.0 μm. (**c**). Labelling is distributed over the secondary wall (uw) of mature urediniospore but absent from the spines (sp). Bar = 0.5 μm. (**d**). No significant labelling is observed over the haustorial body (H), haustorial wall (arrowhead), or extrahaustorial matrix (EX). Bar = 0.5 μm. (**e**). Labelling of wall thickening (T) of host xylem vessels (XV). Bar = 1.0 μm

complex, which had been previously adsorbed to L-fucose. Treatment with β-glucosidase-gold complex, to detect β-glucosides, resulted in intense labelling of the external layer of host cell walls. This labelling was concentrated at contact regions between host cells (Figs. 25c). Labelling also occurred over the primary wall of developing xylem vessels (Fig. 25e) and, to a lesser extent, associated with the outer surface of the plasmalemma, between deposits of wall thickening. In contrast, the fungal and host cytoplasm and the secondary thickening of young xylem elements were free of labelling (Fig. 25a–e).



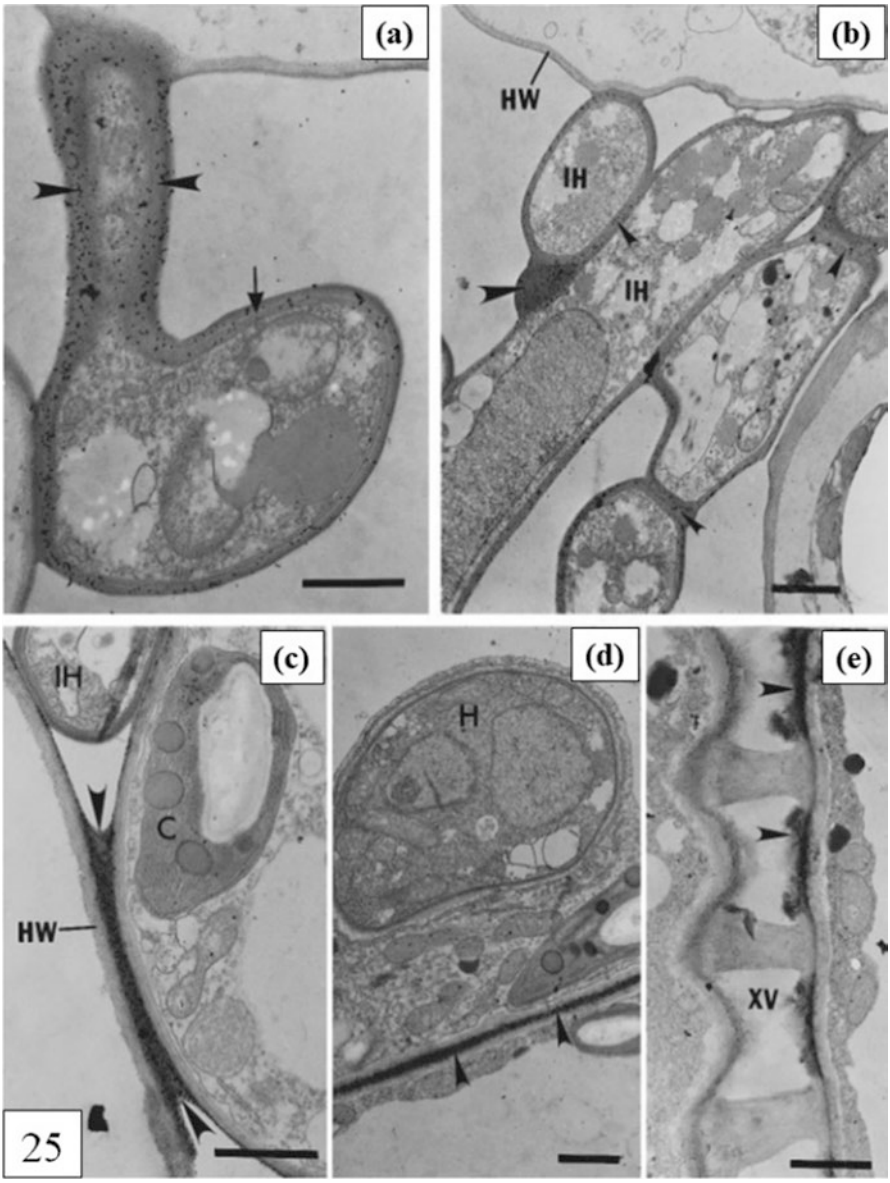
Figs. 23 Rust-infected leaf tissue of *E. peplus* following treatment with ConA-gold complex. (**a**). Glycogen particles (gp) of the hyphae under the uredinium are heavily labelled. Bar = 0.5 um. (**b**). Glycogen particles of intercellular hypha (IH) are also heavily labelled but no label occurs over the fungal wall (arrowhead). Bar = 1.0 μm. (**c**). A strong positive reaction of starch grain (arrowhead) in host chloroplast but not over walls (arrow) of haustorium (H) or host cell (HW). Bar = 0.5 μm. (**d**). Some labelling over cytoplasm of intercellular hypha (IH) but very little over the wall. Fungal vacuoles (v) and lipid droplets (L) are unlabelled. Bar = 0.5 μm. (**e**). Membranes of myelin-like structure in host cells are heavily labelled. Bar = 1.0 μm

Adsorption of the β-glucosidase-gold complex with the β-glucoside salicin, prior to incubation, gave negative results. These cytochemical observations are summarized in Tables 2 and 3.



Figs. 24 Rust-infected leaf tissue of *E. peplus* following treatment with RcA_1-gold complex. (**a**). Wall (arrowheads) and septum (S) of intercellular hyphae (IH) and an unidentified structure (arrow) are strongly labelled. Bar = 0,5 μm. (**b**). Heavily labelled fungal lomasome (LO). Bar = 0.5 μm. (**c**). A label is present on the haustorium (H) wall (arrowhead), more densely over the host cell wall (HW) but relatively sparse over fungal nuclei (n) and cytoplasm. No significantly labelling of oil drops (L). Bar = 1.0 μm

As described in other rust infections, a collar of wall-like material, usually interpreted as a host response to the fungal invasion, formed around the haustorium neck. The changes in appearance and the cytochemical reaction of this collar during haustorium development support previous reports (Table 4) that deposition of



Figs. 25 Rust-infected leaf tissue of *E. peplus* following treatment with LtA-gold complex. (**a**). The hyphal wall shows regions of strong (arrow) and weaker labelling (arrowheads). Fungal organelles are unlabelled. Bar = 1.0 µm. (**b**). The walls (small arrowheads) of intercellular hyphae (IH) and extramural matrix (large arrowheads) between hyphae are labelled but the host cell wall (HW) is unlabelled. Bar = 1.0 µm. (**c**). Rust-infected leaf tissue of *E. peplus* treated with β-glucosidase-gold complex. Gold particles restricted to the outermost layer (arrowheads) of the host cell wall (HW), absent from intercellular are hypha (IH), host chloroplast (C) and cytoplasm. Bar = 1.0 µm. (**d**). Rust-infected leaf tissue of E. peplus treated with β-glucosidase-gold complex. Haustorium (H) and host cytoplasm are almost free of labelling although the outermost layer (arrowheads) of the host wall is heavily labelled. Bar = 1.0 µm. (**e**). Rust-infected leaf tissue of E. peplus treated with β-glucosidase-gold complex. Labelling of the primary wall (arrowheads) in developing xylem vessel (XV), some gold particles opposite, on the outer surface of host plasmalemma, but bars of secondary wall thickening are unlabelled. Bar = 1.0 µm

callose (a β-1,3-linked glucose polymer) may occur between the plant plasma membrane and cell wall, in response to stress, wounding, or pathogen invasion (Littlefield and Heath 1979) (Table 5).

From the stereological analysis of electron micrographs of cowpea leaf tissue infected with *Uromyces vignae*, Skalamera and Heath (1995) concluded that both callose synthesis and fungal presence are associated with de novo synthesis of membranes and that callose deposition may require an increase in the smooth membrane, whereas the establishment of a haustorium may be dependent on the increased synthesis of the rough endoplasmic reticulum. The complex distribution of carbohydrates on cell walls of several rust fungi has been investigated both biochemically and histochemically (Courtory and Simar 1974; Kim et al. 1982; Kaminskyj and Heath 1983; Chong et al. 1985, 1986; Mendgen et al. 1985; Freytag and Mendgen 1991a, b; Mendgen and Deising 1993). The above evidence for the presence of chitin in hyphal and urediniospore walls of *M. euphorbiae* and its absence from haustorial walls agrees with studies on *Puccinia graminis* f. sp. *tritici* by Chong et al. (1985) and Harder et al. (1986) who presented evidence that urediniospore walls also contained large amounts of polysaccharides or glycoproteins with vicinal hydroxyl groups. Without better evidence for the occurrence of chitin in plant cell walls, the specificity of WGA-ovomucoid-gold labelling of secondary wall material in *E. peplus* xylem vessels requires further investigation. The density of gold particles at this site (Fig. 14) and their absence from the primary walls strikingly resemble the labelling of xylem elements in healthy roots of *Hevea brasiliensis* demonstrated by Nicole and Benhamou (1991). These observations and similar reports (Chamberland et al. 1985; Benhamou and Asselin 1989) have been interpreted as indicating N-acetylglucosamine residues in secondary walls. In this connection, the relatively high amounts of hexosamine-containing compounds found in healthy as well as fungal infected tissues, during chitin estimations (Ride and Drysdale 1971; Losel and Lewis 1974) are of interest. Whipps and Lewis (1980) demonstrated that acetone extraction of this fraction before KOH hydrolysis greatly improves the sensitivity of the assay. The absence of chitin from the haustorial walls of *M. euphorbiae* and *P. graminis* f. sp. *tritici* may be related to the accumulating evidence for the role of chitin as an elicitor of plant defence reactions against fungal pathogens (Barber et al. 1989). Infection structures lacking chitin on the wall surface may avoid triggering chitinase activity and the breakdown of wall polymers. Such hydrolytic activity has been detected in plants at the early stages of infection and is now considered to play a role in plant defence systems (Isaac 1992). During the development of Fusarium wilt disease in tomato, Ferraris et al. (1987) observed increased glycosidase activity (β-1,3-glucanase, chitianase, β1,4-glucosidase and N-acetylglucosaminadase), which could be correlated with disease severity and was greater in susceptible than in resistant plants. Sequential changes in fungal surface carbohydrate composition during germination of rust urediniospores, differentiation of infection structures and fungal development within the host mesophyll have been described by Freytag and Mendgen (1991a, b). Chitin, which covered germ tube walls, along with α- and β-glucans and hexose, decreased or was masked in appressoria, where glucans and hexoses were predominant together with smaller

Table 5 Presence (+) or absence (−) of sugar residues, previously reported from some phytopathogenic fungi

Pathogen	Disease	Chitin	Mannose and glucose	Galactose	Fucose	Pectin	Glucosides	References
Puccinia graminis f. sp. *tritici*	Wheat rust	++	++	N	−	N	N	Chong et al. (1985, 1986)
Ophistoma ulmi	Dutch elm	++	++	+	N	++	N	Benhamou (1988) and Benhamou et al. (1988)
Verticillum albo-atrum	Potato wilt	+	−	+++	N	+	−	Benhamou (1988) and Benhamou et al. (1988)
Ascocalyx abietina	Scleroderris canker of conifers	+	+	+	+	+	N	Benhamou and Quellette (1986a, b) and Bendayan and Benhamou (1987)
Magnaporthe grisea	Rice blast	N	−	N	N	N	N	Bourett et al. (1993)
Sphaerotheca pannosa	Powdery mildew of rose	+	N	N	N	−	N	Hajlaoui et al. (1992)
Fusarium oxysporum f. sp. *radices-lycopersici*	Tomato wilt	+	N	−	N	N	N	Benhamou et al. (1988) and Chamberland et al. (1985)
Colletotrichum lindemuthianum	Bean anthracnose	+	+	−	−	N	N	O'Connell (1991) and O'Connell and Ride (1990)
Fusarium oxysporum f. sp. *lycopersici*	Tomato wilt	++	++	+++	N		++	Al-Askar et al. (2015)

N = not investigated

amounts of N-acetylglucosamine, N-acetylgalactosamine, and galactose. Comparable changes in chitin distribution during plant penetration have been reported for *Colletotricum lindemuthianum* (Chamberland et al. 1985; O'Connell and Ride 1990). Mendgen and Deising (1993) commented on the significance of such alterations to the surface of infection structures and associated differences in exposure of chitin at successive developmental stages, for successful infection by various biotrophic pathogens. Chitin was identified in cell walls of both fungi in interactions between the mycopathogen *Trichoderma harzianum* and sclerotia of the soil-borne plant pathogen *Sclerotium rolfsii* (Benhamou and Chet 1996). ConA labelling of host starch and fungal glycogen, similar to that in *M. euphorbiae* infection of *E. peplus*, was reported in wheat leaves infected by *Puccinia graminis* f. sp. *tritici* (Chong et al. 1986) and uninfected leaves of maize (Bouchet et al. 1984). The absence of label from haustorial walls in the present study may be due to the relatively young haustoria examined, since Chong et al. (1986) noted that ConA bound only to older haustoria. Although not distinguishing between α-D-mannose and α-D-glucose, ConA has a much higher affinity for the former (Bouchet et al. 1984). The small amounts of hexose localized in the hyphal cytoplasm of *M. euphorbiae* may represent storage products, as suggested by Clay et al. (1991) in the case of ConA-gold labelling in sporangial cytoplasm of *Rhizidiomyces apophysatus*. Comparison of the present evidence for galactose residues in hyphal and haustorial walls of *M. euphorbiae* with the findings of Benhamou et al. (1988), who did not detect galactose in hyphal walls of *Fusarium oxysporum*, but found small amounts in *Ophiostoma ulmi*, supports their view that such variations may correspond to different types of pathogen-host interactions. The concentration of galactose residues in lomasome-like structures of *M. euphorbiae*, apparently the first report of this in fungi, may indicate synthesis of galactolipids or galactose-linked protein, which could be significant in fungus-host interactions. Furthermore, both galactose and mannose are common components of membrane sphingolipids in the relatively few species of fungi where sphingolipids have been investigated (Losel 1988). The association of L-fucose with walls of intercellular hyphae of *M. euphorbiae* corresponds with previous evidence from walls of urediniosporelings of *P. graminis tritici* (Kim et al. 1982) and hyphae of the ascomycete *Ascocalyx abietina* (Benhamou and Ouellette 1986b). L-fucose has been reported to occur at non-reducing termini of glycoproteins and some glycolipids (Flowers 1981). Benhamou and Ouellette (1986a) suggested that these molecules may act as chain-stoppers in biosynthetic processes controlling the extent of chain elongation. β-glucosides, which were here localized in the fibrillar outermost layer of mesophyll cell walls of rust-infected *E. peplus*, appeared also to occur on the inner wall layer of xylem vessels but not in fungal walls or intracellularly. Benhamou (1988) did not find these residues in ascomycetes, but Bendayan and Benhamou (1987) detected β-glucosides in fibrillar wall layers adjacent to intercellular spaces of tobacco leaf tissue as well as in endoplasmic reticulum, nucleus and chloroplast stroma. It is of interest that the sites showing β-glucoside reactions in rust-infected *E. peplus* leaves correspond to those associated with peroxidase activity in rusted flax, investigated by Coffey and Cassidy (1984), who noted enhanced peroxidase activity preceding lignification of walls of

incompatible host cells. In compatible host cells, evidence of peroxidase activity was found on the host tonoplast surrounding haustoria but on no other membranes. Polysaccharides associated with lignin may, however, also play other roles in host defence mechanisms. The present study has contributed further evidence that wall carbohydrate composition varies in different fungal pathogens and is affected by the age and location of the fungal structures. Using fluorescein isothiocyanate-labelled lectins and measuring fluorescence with a microscope photometer, Mendgen et al. (1985) demonstrated differences in surface carbohydrates of infection structures of Uromyces appendiculatus and Puccinia coronata with developmental and physiological stages. Mendgen and Deising (1993) have discussed corresponding changes in hydrolytic enzyme activity during infection by rusts and other biotrophic pathogens. Increasing sensitivity of methodology, e.g. combination with freeze substitution to improve cytochemical differentiation of intracellular processes, as in hyphal tip studies on *Magnaporthe grisea* by Bourett et al. (1993), changes in resins (Gruber 1987) and an extending range of probes with improved specificity (Sahai et al. 1993) have increased the power and reliability of cytochemical investigations. Quantitative analytical studies during successive phases of the complete life cycle of *M. euphorbiae* and other rust fungi within host plants may be expected to provide a better understanding of their physiological interactions and significance in pathogenesis (Baka and Losel 1998).

5 Conclusion

Phosphatase activities have been localized cytochemically at haustorial-host interfaces of spermogonial-aecial and uredinial stages of *Puccinia punctiformis*, the monokaryotic phase of *P. menthae* and dikaryotic infections of *Uromyces viciafabae*. ATPase activity, similar to that of the wall-lining plasmalemma of the host cell, was associated with the extrahaustorial membrane of the filamentous monokaryotic (M-) haustoria of the spermogonial-aecial infections but not with the dikaryotic (D-) haustoria of the uredinial infection. In *P. menthae*, ATPase activity associated with the extrahaustorial membrane decreased towards the distal region of M-haustoria, as previously reported for *P. poarum*. This supports the hypothesis that, in some cases, the membrane enclosing the apical portion of M-haustoria transiently resembles the extrahaustorial membrane of D-haustoria, whereas adjacent to older, proximal regions is functionally similar to the remainder of the host plasmalemma. ATPase activity was recorded at the fungal plasmalemma of both M- and D-haustoria of *P. punctiformis* but not in *P. menthae*. These results are in accord with the established view that the filamentous haustoria of the monokaryon are physiologically, as well as morphologically, less specialized than those of the dikaryon.

This investigation lends support to the evidence for structural and functional differences between haustoria of monokaryotic and dikaryotic phases of the rust life cycle, and for greater variability in the interfaces between monokaryotic structures and host cells than is found in the dikaryon. The increasing likelihood that such variation is a feature of the developmental stage indicates the need for time-course studies of haustorial differentiation in monokaryotic infections.

The distribution of two autoecious rust fungi within host leaves has been investigated with particular reference to the vascular system. Vascular infection by the thistle rust *Puccinia punctiformis* was low at the spermogonial stage but increased during the development of the uredinoid aecia. Aecial stages of *P. lagenophora* were accompanied by dense fungal growth in leaf veins of *Senecio vulgaris*. In both cases, host cells were penetrated by unspecialized, filamentous, fungal structures. No vascular infection by the dikaryon was found in the uredinial-telial phases of *P. punctiformis* on thistle leaves, although specialized D-haustoria were present with high frequency in mesophyll cells. These observations are consistent with the hypothesis that access to host translocates, afforded by vascular penetration, may compensate for the probably lower efficiency of the unspecialized filamentous haustoria found in spermogonial and aecial stages.

Cytochemical investigations of the interaction between *Melampsora euphorbiae* and its host *Euphorbia peplus* are described. Two types of the collar around the haustorial neck could be recognized, corresponding to the maturity of the haustorium. Using various lectin-gold complexes as probes, different glycoconjugates were revealed in the fungus and host. Chitin was found in walls of urediniospores and intercellular hyphae but not in haustoria. D-glucose and or D-mannose were strongly indicated in host starch grains and glycogen particles inside the intercellular hyphae, but only lightly in the fungal cytoplasm. Galactose residues and L-fucose were detected in fungal walls, more strongly in those of intercellular hyphae than haustoria. Galactose was also localized cytochemically in lomasome membranes of the fungus. β-glucosides were detected in the fibrillar wall material bordering intercellular spaces of host tissue (Baka and Losel 1998).

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– Baka ZAM, Losel DM (1998) Ultrastructure and lectin-gold cytochemistry of the interaction between the rust fungus *Melampsora euphorbiae* and its host Euphorbia peplus. Mycol Res 102: 1387–1398.
– Baka ZAM, Losel DM (1992) Infection of vascular tissues by autoecious rusts, *Puccinia punctiformis* and *P. lagenophorae*: a cytological study. Physiol Molec Plant Pathol 40: 411–421.
– Baka ZAM, Larous, Losel DM (1995) Distribution of ATPase activity at the host pathogen interfaces of rust infections. Physiol Molec Plant Pathol 47: 67–82.

References

Al-Askar AA, Baka ZA, Rashad YM, Ghoneem KM, Abdulkhair WM, Hafez EE, Shabana YM (2015) Evaluation of *Streptomyces griseorubens* E44G for the biocontrol of *Fusarium oxysporum* f. sp. *lycopersici:* ultrastructural and cytochemical investigations. Ann Microbiol 65:1815–1182

Al-Khesraji TO (1981) Comparative anatomy and histology of the association of *Puccinia poarum* with its alternate hosts. Ph.D. thesis, University of Sheffield, England

Andreev LN, Plotnihova YM, Serezhhina GV (1982) Haustoria of *Puccinia graminis* Pers. f. sp. *tritici* Eriks. & Henn. in the vascular system of wheat. Mikol I Fitopatol 16:335–338

Baka ZAM (1987) Responses of plant tissue to infection by rust fungi: fine structure, cytochemistry and autoradiography. PhD thesis, University of Sheffield, England

Baka ZAM (1989) Electron microscopical localization of ATP-ase activity in leaves of *Senecio vulgaris* infected with *Puccinia lagenophorae*. Egyp J Bot 32:161–171

Baka ZAM (1992) Observations on the ultrastructure of the uredinial stage of *Puccinia polypogonis* on *Polypogon monspeliensis*. Mycopathologia 120:103–111

Baka ZAM, Gjærum HB (1996) Egyptian Uredinales. I Rusts on wild plants from the Nile Delta. Mycotaxon 60:291–303

Baka ZAM, Lösel DM (1992a) Infection of vascular tissues by the autoecious rusts *Puccinia punctiformis* and *Puccinia lagenophorae*: a cytological study. Physiol Mol Plant Pathol 40:411–421

Baka ZAM, Lösel DM (1992b) Ultrastructure of the thistle rust *Puccinia poarum*. Mycol Res 96:81–88

Baka ZAM, Lösel DM (1998) Ultrastructure and lectin-gold cytochemistry of the interaction between the rust fungus *Melampsora euphorbiae* and its host, *Euphorbia peplus*. Mycol Res 102:1387–1398

Baka ZAM, Larous L, Lösel DM (1995) Distribution of ATPase activity at the host-pathogen interfaces of rust infections. Physiol Mol Plant Pathol 47:67–82

Barber MS, Bertram RE, Ride JP (1989) Chitin oligosaccharides elicit lignification in wounded leaves. Physiol Mol Plant Pathol 34:3–12

Bartnicki-Garcia S (1968) Cell wall chemistry, morphogenesis and taxonomy of fungi. Annu Rev Microbiol 22:87–108

Beale AJ, Clark JSC, Spencer-Phillips PTN (1990) Microscopy of endophytic hyphae facilitated by enzymic maceration and ATPase cytochemistry. In: Elder HY, Goodhew PJ (eds) EMAG-MİCRO 89: 2, Biological. Institute of Physics Publishing Ltd., Bristol, pp 711–714

Bendayan M, Benhamou N (1987) Ultrastructural localization of glucoside residues on tissue sections by applying the enzyme-gold approach. J Histochem Cytochem 35:1149–1155

Benhamou N (1988) Ultrastructural localization of carbohydrates in the cell walls of two pathogenic fungi: a comparative study. Mycologia 80:324–337

Benhamou N (1989) Preparation and application of lectin-gold complexes. In: Hayat MA (ed) colloidal gold: principles, methods and applications, vol 1. Academic Press, San Diego, pp 95–134

Benhamou N, Asselin A (1989) Attempted localization of a substrate for chitinases in plant cells reveals abundant N-acetyl-D-glucosamine residues in secondary walls. Biol Cell 67:341–350

Benhamou N, Chet I (1996) Parasitism of sclerotia of *Sclerotium rolfsii* by *Trichoderma harzianum*: ultrastructural and cytochemical aspects of the interaction. Phytopathology 86:405–416

Benhamou N, Ouellette GB (1986a) Ultrastructural localization of glycoconjugates in the fungus *Ascocalyx abietina*, the scleroderris canker agent of conifers, by means of lectin-gold complexes. J Histochem Cytochem 34:855–867

Benhamou N, Ouellette GB (1986b) Use of pectinases complexed to colloidal gold for the structural localization of polygalacturonic acids in the cell walls of the fungus *Ascocalyx abietina*. Histochem J 18:95–104

Benhamou N, Gilboa-Garber N, Trudel J, Asselin A (1988) A new lectin-gold complex for ultrastructural localization of galacturonic acids. J Histochem Cytochem 36:1403–1411

Bentwood BJ, Cronshaw J (1978) Cytochemical localization of adenosine triphosphatase in the phloem of *Pisum sativum* and its relation to the function of transfer cells. Planta 140: 111–120
Bouchet B, Ray L, Gallant DJ (1984) Use of colloidal gold labelled concanavalin A as marker for the starch granule. C R Acad Sci III 299:813–818
Bourett TM, Picollelli MA, Howard RJ (1993) Postembedment labelling of intracellular concanavalin A-binding sites in freeze-substituted fungal cells. Experim Mycol 17:223–235
Bowman BJ, Bowman EJ (1986) H^+-ATP-ases from mitochondria, plasma membranes, and vacuoles of fungal cells. J Membr Biol 94:83–97
Buller AHR (1950) Researches on fungi, vol 7. University of Toronto Press, Toronto
Bushnell WR (1972) Physiology of fungal haustoria. Annu Rev Phytopathol 10:151–176
Chamberland H, Charest PM, Ouellette GB, Pauze FJ (1985) Chitinase-gold complex used to localize chitin ultrastructurally in tomato root cells infected by *fusarium oxysporum* f. sp. *radicis-lycopersici*, compared with a chitin specific gold conjugated lectin. Histochem J 17:313–321
Chauhan E, Cowan DS, Hail JL (1991) Cytochemical localization of plasma membrane ATPase activity in plant cells. Protoplasma 165:27–36
Chong J, Harder DE, Rohringer R (1985) Cytochemical studies on *Puccinia graminis* f. sp. *tritici* in a compatible wheat host. I. Walls of intercellular hyphal cells and haustorium mother cells. Cana J Bot 63:1713–1724
Chong J, Harder DE, Rohringer R (1986) Cytochemical studies on *Puccinia graminis* f. sp. *tritici* in a compatible wheat host. II. Haustorium mother cell walls at the host cell penetration site, haustorial walls, and the extrahaustorial matrix. Can J Bot 64:2561–2575
Clay RP, Benhamou N, Fuller MS (1991) Ultrastructural detection of polysaccharides in the cell walls of two members of the Hyphochytriales. Mycol Res 95:1057–1064
Coffey MD, Cassidy DSM (1984) Peroxidase activity and induced lignification in rusted flax interactions varying in their degree of incompatibility. Can J Bot 62:134–141
Coffey MD, Palevitz BA, Allen PJ (1972) The fine structure of two rust fungi, *Puccinia helianthi* and *Melampsora lini*. Can J Bot 50:231–240
Colley RH (1918) Parasitism, morphology and cytology of *Cronartium ribicola*. J Agr Res 15:619–660
Courtory R, Simar LJ (1974) Importance of controls for the determination of carbohydrates in electron microscopy with the silver methenamine or the thiocarbohydrazide-silver proteinate methods. J Microsc 100:199–211
Farkas V (1979) Biosynthesis of cell walls in fungi. Microbiol Rev 43:117–144
Ferraris L, Abbatista Gentile I, Matta A (1987) Activation of glycosidases as a consequence of infection stress in fusarium wilt of tomato. J Phytopathol 118:317–325
Flowers HM (1981) Chemistry and biochemistry of D- and L-fucose. In: Tipson RS, Horton D (eds) Advances in carbohydrate chemistry and biochemistry, vol 39. London, Academic Press, pp 280–345
Freytag S, Mendgen K (1991a) Surface carbohydrates and cell wall structure of in vitro-induced uredospore infection structures. Protoplasma 161:94–103
Freytag S, Mendgen K (1991b) Carbohydrates on the surface of urediniospore-and basidiospore-derived infection structures of heteroecious and autoecious rust fungi. New Phytol 119:527–534
Gay JL (1984) Mechanisms of biotrophy in fungal pathogens. In: Wood RKS, Jellis GJ (eds) Plant diseases: infection, damage and loss. Oxford, Blackwell Scientific Publications, pp 49–59
Gay JL, Salzberg A, Woods AM (1987) Dynamic experimental evidence for the plasma membrane ATPase domain hypothesis of haustorial transport and for ionic coupling of the haustorium of *Erysiphe graminis* to the host cell *Hordeum vulgare*. New Phytol 107:541–548
Gay JL, Woods AM (1987) Induced modifications in the plasma membranes of infected cells. In: Pegg GF, Ayres PG (eds) Fungal infections of plants. Cambridge University Press, London, pp 79–91
Gold RE, Littleffeld LJ, Statler GD (1979) Ultrastructure of the pycnial and aecial stages of *Puccinia recondita*. Can J Bot 57:74–86

Gooday GW (1977) Biosynthesis of the fungal wall-mechanisms and applications. J Gen Microbiol 99:1–12
Gruber PJ (1987) Lectins. In: Vaughn KC (ed) CRC handbook of plant cytochemistry, vol 2. Boca Raton, CRC Press, pp 45–63
Hail JL, Williams L (1991) Properties and functions of proton pumps in higher plants. Pesticide Sci 32:339–351
Hajlaoui MR, Benhamou N, Belanger RR (1992) Cytochemical study of the antagonistic activity of *Sporothrix flocculosa* on rose powdery mildew, *Sphaerotheca pannosa* var *rosae*. Phytopathology 82:583–589
Harder DE (1978) Comparative ultrastructure of uredial and pycnial infections of *Puccinia coronata avenae*. Can J of Bot 56:214–224
Harder DE, Chong J (1984) Structure and physiology of haustoria. In: Bushnell WR, Roelfs AP (eds) The cereal rusts, vol 1. New York, Academic, pp 431–476
Harder DE, Chong J, Rohringer R, Kim WK (1986) Structure and cytochemistry of the walls of urediospores, germ tubes, and appressoria of *Puccinia graminis tritici*. Can J Bot 64:476–485
Isaac S (1992) Fungal-plant interactions. Chapman and Hall, London
Jackson LWR, Parker NN (1958) Anatomy of fusiform galls on loblolly pine. Phytopathology 48:637–640
Joseleau JP, Ruel K (1985) A new cytochemical method for ultrastructural localization of polysaccharides. Biol Cell 53:61–66
Juniper BE, Cox GC, Gilchrist AJ, Williams PK (1970) Techniques for plant electron microscopy. Blackwell Scientific Publications, Oxford
Kaminskyj SGW, Heath MC (1983) Histological responses of infection structures and intercellular mycelium of *Uromyces phaseoli* var. *typica* and *U. phaseoli* var. *vignae* to the HNO_2-MBTH-$FeCl_2$ and the IKIH-H_2SO_4 tests. Physiol Plant Pathol 22:173–179
Katz DB, Sussman MR, Mierzwa RJ, Evert RF (1988) Cytochemical localization of ATPase activity in oat roots localizes a plasma membrane-associated soluble phosphatase, not the proton pump. Plant Soil 86:841–847
Kim WK, Rohringer R, Chong J (1982) Sugar and amino acid composition of macromolecular constituents released from walls of uredosporelings of *Puccinia graminis tritici*. Can J Plant Pathol 4:317–327
Krebill RG (1968) Histology of canker rusts in pines. Phytopathology 53:155–164
Larous L (1990) Comparative ultrastructure and cytochemistry of rust infections with particular reference to *Puccinia menthae* and *Uromyces vicia-fabae*. Ph.D. thesis, University of Sheffield, England
Larous L, Lösel DM (1993a) Vascular infection by *Puccinia menthae* and other fungi. Mycol Res 97:409–414
Larous L, Lösel DM (1993b) Strategies of pathogenicity in monokaryotic and dikaryotic phases of rust fungi with special reference to vascular infection. Mycol Res 97:415–420
Littlefield LJ, Heath MC (1979) Ultrastructure rust fungi. Academic, New York
Losel DM (1988) Fungal lipids. In: Ratledge C, Wilkinson SG (eds) Microbial lipids, vol 1. London, Academic Press, pp 699–806
Losel DM, Lewis DH (1974) Lipid metabolism in leaves of *Tussilago farfara* during infection by *Puccinia poarum*. New Phytol 73:1157–1169
Mackie AJ, Roberts AM, Callow JA, Green JR (1991) Molecular differentiation in pea powdery mildew haustoria-identification of a 62 kDa N-linked glycoprotein unique to the haustorial plasma membrane. Planta 183:399–408
Mackie AJ, Roberts AM, Green JR, Callow JA (1993) Glycoproteins recognized by monoclonal antibodies UB7, UB8 and UBIO are expressed early in the development of pea powdery mildew haustoria. Physiol Mol Plant Pathol 43:135–146
Mendgen K, Deising H (1993) Infection structures of fungal plant pathogens – a cytological and physiological evaluation. New Phytol 124:193–213

Mendgen K, Lange M, Bretschneider K (1985) Quantitative estimation of the surface carbohydrates on the infection structures of rust fungi with enzymes and lectins. Archiv Microbiol 140:307–311

Nicole NR, Benhamou N (1991) Ultrastructural localization of chitin in cell walls of *Rigidoporus lignosus*, the white-rot fungus of rubber tree roots. Physiol Mol Plant Pathol 39:415–431

O'Connell RJ (1991) Cytochemical analysis of infection structures of *Colletotrichum lindemuthianum* using fluorochrome-labelled lectins. Physiol Mol Plant Pathol 39:189–200

O'Connell RJ, Ride JB (1990) Chemical detection and ultrastructural localization of chitin in cell walls of *Colletotrichum lindemuthianum*. Physiol Mol Plant Pathol 37:39–53

O'Connell RJ (1987) Absence of a specialized interface between intracellular hyphae of *Colletotrichum lindemuthianum* and cells of *Phaseolus vulgaris*. New Phytol 107:725–734

Pady SM (1935) The role of intracellular mycelium in systemic infections of *Rubus* with the orange rust. Mycologia 27:618–637

Pain NA, O'Connell RJ, Mendgen K, Green JR (1994) Identification of glycoproteins specific to biotrophic intracellular hyphae formed in the *Colletotrichum lindemuthianum*-bean interaction. New Phytol 127:233–242

Ride JP, Drysdale RB (1971) A rapid method for the chemical estimation of filamentous fungi in plant tissue. Physiol Plant Pathol 2:7–15

Roberts AM, Mackie AJ, Hathaway V, Callow JA, Green JR (1993) Molecular differentiation in the extrahaustorial membrane of pea powdery mildew haustoria at early and late stages of development. Physiol Mol Plant Pathol 43:147–160

Sahai AS, Balasubramanian R, Manocha S (1993) Immunofluorescence study of zygomycetous fungi with two chitin-binding probes. Exp Mycol 17:55–69

Serrano R (1989) Structure and function of plasmalemma ATPase. Annu Rev Plant Physiol Plant Molec Biol 40:61–94

Siwecki R (1990) Ultrastructure of *Melampsora larici-populina*. Report Tottori Mycol Instit 28:95–108

Skalamera D, Heath MC (1995) Changes in the plant endomembrane system associated with callose synthesis during the interaction between cowpea (*Vigna unguiculata)* and the cowpea rust fungus (*Uromyces vignae*). Can J Bot 73:1731–1738

Smith SE, Smith FA (1990) Structure and function of the interfaces in biotrophic symbioses as they relate to nutrient transport. New Phytol 114:1–38

Spencer-Phillips PTN, Gay JL (1981) Domains of ATPase in plasma membranes and transport through infected cells. New Phytol 89:393–400

Spiers AG, Hopcroft DH (1985) Ultrastructural studies of pathogenesis and uredinial development of *Melampsora larici-populina* and *Melampsora medusae* on poplar and *Melampsora coleosporioides* and *Melampsora epitea* on willow. New Zealand J Bot 23:117–134

Sussman MR, Harper JF (1989) Molecular biology of the plasma membrane of higher plants. Plant Cell 1:953–960

Thiery JP (1967) Mise en evidence des polysaccharides sur coupes fines en microscopie electronique. J Microsc 6:987–1018

TO AI-K, Lösel DM (1980) Intracellular structures of *Puccınia poarum* on its alternate hosts. Trans Br Mycol Soc 75:397–411

TO AI-K, Lösel DM (1981) The fine structure of haustoria, intracсllular hyphae and intercellular hyphae of *Puccinia poarum*. Physiol Plant Pathol 19:301–311

TO AI-K, Lösel DM, Gay JL (1980) The infection of vascular tissue in leaves of *Tussilago farfara* by the pycnial-aecial stages of *Puccinia poarum* Niel. Physiol Plant Pathol 17:193–197

Van Bel AJE (1993) Strategies of phloem loading. Annu Rev Plant Physiol Plant Molec Biol 44:253–281

Van der Kamp BJ (1969) *Peridermium pini* (Pers.) Lev. and the resin-top disease of Scots Pine. II. Lesion anatomy. Forestry 42:185–201

Van der Kamp BJ (1970) *Peridermium pini* (Pers.) Lev. and the resin-top disease of Scots Pine. III. Infection and lesion development. Forestry 43:73–88

Wessels JG, Sietsma JH (1979) Fungal cell walls. In: Tanner W, Loewus FH (eds) Encyclopedia of plant physiology, new series, plant carbohydrates, vol II. Heidelberg-Berlin, New York, Springer, pp 353–385

Whipps JM, Lewis DH (1980) Methodology of a chitin assay. Trans Br Mycol Soc 74:416–418

Williams L, Hall JL (1987) ATPase and proton pumping activities in cotyledons and other phloem containing tissues of *Ricinus communis*. J Exper Bot 38:185–202

Wilson IM, Henderson DM (1966) British rust fungi. Cambridge University Press, Cambridge, pp 67–70

Woo JY, Martin NE (1988) Hyphalike haustoria of the haploid stage of *Cronartium ribicola* in *Pinus monticola* as observed with the scanning electron microscope. Eur J Forest Patholo 4:193–l99

Woods AM, Gay JL (1983) Evidence for a neckband delimiting structural and physiological regions of the host plasma membrane associated with haustoria of *Albugo candida*. Physiol Plant Pathol 23:73–88

Woods AM, Gay JL (1987) The interface between haustoria of *Puccinia poarum* (monokaryon) and *Tussilago farfara*. Physiol Mol Plant Pathol 30:167–185

Woods AM, Didehvar F, Gay JL, Mansfield JW (1988) Modifications of the host plasmalemma in haustorial infections of *Lactuca sativa* by *Bremia lactucae*. Physiol Mol Plant Pathol 33:296–301

Zimmer DE (1965) Rust infection and histological response of susceptible and resistant safflower. Phytopathology 55:296–301

Rust Haustoria

Zakaria A. M. Baka

1 Introduction

Rust fungi are frequent names for members of the order Uredinales. All Uredinales are parasitic on plants, frequently resulting in catastrophic losses in a variety of significant crop species (Alexopoulos et al. 1996). Rust fungi, along with oomycetes that cause downy mildew and powdery mildew fungi, are members of the obligate biotrophs, a group of parasites that are incredibly successful. The phrase "obligate biotrophic" refers to a certain way of life in which the pathogen must have a living host in order to complete its life cycle (Silva et al. 2022; Faoro et al. 2022). In response, the host plant often sustains only minor harm over an extended period of time (Staples 2000). Rust fungi, which are among the most harmful pathogenic organisms of agriculturally significant crops and are widely spread, are responsible for major losses in quality and productivity.

However, due to their inability to reproduce and finish their life cycle on artificial medium, obligatory parasitic pathogenic microbes are still the subject of pathogenesis research (Mapuranga et al. 2022). Voegele et al. (2009) proposed the following criteria to characterize the obligatory biotrophs in order to distinguish them from hemibiotrophs and necrotrophs; (1) Obligate biotrophs lack the ability to be cultured *in vitro*, (2) generate highly differentiated infection structures, (3) have restricted secretory activity, (4) create a small contact zone between fungal and plant plasma membranes, (5) engage in long-term suppression of host defense responses, (6) form haustoria (specialized hyphae that penetrate host cells).

The rust fungi are obligate parasites of plants, which they rely on for food, reproduction, and the completion of their life cycles. Rust fungi, which parasitize a wide range of plants, including advanced monocots and dicots, number over 7000

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species. In economically significant, plant species like cereals, legumes, composites, and many trees, rust fungi cause diseases. The rust-colored masses of urediospores that are clonally formed on plant hosts are what give rust fungi their name. The rusts' life cycles, which can range from two to five distinct spore stages and encompass haploid, diploid, and dikaryotic nuclear states, make them scientifically fascinating. While some rust species only need one host to complete their life cycle, others need two hosts that are not related taxonomically. Rust species have evolved to be quite selective about the kinds of plants they can infect, inhabit, and reproduce on (Kolmer et al. 2009).

2 Rust Haustorium

Further differentiation signals are required to form infection structures. A topographical signal was demonstrated to be necessary for distinguishing of an appressorium from a number of rust species (Read et al. 1997). Urediospores with thick walls, black pigment, and ornamentation germinate with a germ tube, which upon coming into touch with a topographic signal of the right magnitude develops into a well-defined appressorium (Hoch et al. 1987; Staples and Hoch 1997). At the appressorium's base, a penetration hypha develops, and it enters the leaf through the stomatal hole (Boshoff et al. 2022). Within the stomatal cavity, a vesicle is created from which an infectious hypha arises. A haustorial mother cell, from which a haustorium is created, differentiates when it comes into touch with a mesophyll cell. Rust fungi create unique branches in their intercellular hyphae that pierce the host cell walls (Bushnell 1972; Harder and Chong 1991; Baka and Losel 1992a). In contrast to monokaryotic phases, these intracellular structures have been examined more thoroughly during dikaryotic stages. Harder (1978), Gold and Littlefield (1979), Al-Khesraji and Losel (1981), Glidewell and Mims (1979), and Borland and Mims (1980) all conducted light and electron microscopic studies of the intracellular structures of macrocyclic rusts in various phases (Al-Khesraji and Losel 1980). The monokaryotic phase typically appears to lack the typical dikaryotic infection haustoria (Rice 1927; Rijkenberg and Truter 1973; Losel and Lewis 1974; Harder 1978; Gold et al. 1979; Al-Khesraji and Losel 1981).

Numerous researchers have described the typical dikaryotic haustorium, which has an enlarged clavate or club-shaped body and a slender tubular neck (Littlefield and Heath 1979; Borland and Mims 1980; Al-Khesraji and Losel 1981; Coffey and Allen 1983; Heath and Bonde 1983; Harder 1984; Longo and Bruscaglioni 1986; Baka 1992, 1996a, b, 2002, 2014; Baka and Losel 1992b, 1998; Larous et al. 2008). A terminal cell of an intercellular hypha, the haustorium mother cell, which is connected to this haustorium, is a hypha. Numerous workers looked at the haustorium mother cell wall thickening at the penetration site (see reviews above). The haustorium's and its mother cell's cytoplasm is continuous and lacks a septum (Coffey et al. 1972). According to Heath and Heath (1975) and Mendgen (1975), the

cytoplasm is transferred from the haustorium mother cel1 to the haustorium. This is followed by vacuolation of the haustorium mother cell (Coffey 1976).

The majority of the rusts have a neckband on their dikaryotic haustorium (Rijkenberg and Truter 1973; Coffey 1976; Harder 1978; Borland and Mims 1980; Al-Khesraji and Losel 1981; Heath and Bonde 1983; Harder 1984; Longo and Bruscaglioni 1986; Baka 1992, 1996a, b, 2002, 2014; Baka and Losel 1992b, 1998). The neckband may serve as a seal to prevent an apoplastic flow of materials along the neck wall, according to theories put forth by Coffey et al. (1972) and Coffey (1976), or it may serve as a site of material exchange between the fungus and its host (Heath 1976; Baka and Losel 1998). There may be different haustorial morphologies (Rice 1927).

A somewhat electron-lucent layer, surrounded by the host plasma membrane, separates the haustorium's cytoplasm from the host cytoplasm. Ehrlich and Ehrlich (1963), Bracker (1967), Rijkenberg and Truter (1973), Coffey (1975), Fraymouth (1956), Ehrlich and Ehrlich (1963), Peyton and Bowen (1963), Hirata and Kojima (1962), and Ehrlich and Ehrlich (1971) all refer to this layer as a sheath, encapsulation, sac, and extrahaustorial matrix (Bushnell 1972; Coffey 1976; Hickey and Coffey 1978; Littlefield and Heath 1979; Al-Khesraji and Losel 1981; Harder 1984; Baka and Losel 1992b, 1998).

According to several researchers (Bushnell 1972; Coffey et al. 1972; Manocha 1975; Harder 1978; Baka 1992, 1996a, b, 2002, 2014; Baka and Losel 1992b, 1998), the extrahaustorial matrix contains more electron-dense materials as the haustorium ages. In other instances, a substantial extrahaustorial matrix surrounds the juvenile haustorium (Kajiwara 1971). According to Manocha (1966), a resistant host develops the extrahaustorial matrix around haustoria more quickly than a susceptible one. The extrahaustorial matrices of sensitive and resistant hosts, however, are similar in other situations (Zimmer 1970).

Materials may pass from the host to the haustoria or *vice versa* through the extrahaustorial membrane, which is the invaginated host plasma membrane surrounding the haustoria (Ehrlich and Ehrlich 1971; Littlefield and Heath 1979). There may be different amounts of nuclei in the haustorial body of dikaryotic infection (Table 1).

Littlefield and Bracker (1972); Coffey et al. (1972); Al-Khesraji and Losel (1981); Baka (1996a, b, 2014) found that haustoria contain mitochondria, ribosomes, endoplasmic reticulum, multivesicular bodies, vacuoles, lipid drops, and glycogen. Microbodies are infrequently discovered in the haustoria of rust fungus, according to Mendgen (1973) and Harder and Chong (1991) report.

2.1 Monokaryotic and Dikaryotic Haustoria

Plant infections called rust fungi can infect a variety of commercially significant crop species and make them diseased (Littlefield and Heath 1979). While the urediospore-derived dikaryotic stage penetrates plant tissue through stomata openings, grows between plant cells, and subsequently produces highly specialized

Table 1 Number of nuclei in D-haustoria of some rust fungi

Rust fungus	Number of nuclei	Author
Puccinia carthami	1	Zimmer (1970)
P. helianthi	2	Coffey et al. (1972)
P. poarum	1	Al-Khesraji and Losel (1981)
P. podphylli	2	Borland and Mims (1980)
P. polypogonis	2	Baka (1992)
P. tuyutensis	2	Baka (1996a, b)
P. punctiformis	2	Baka and Losel (1992b)
P. pimpinellae	2	Baka (2014)
Cronartium flaccidum	2	Longo and Bruscaglioni (1986)
C. quercuum f. sp. *fusiformae*	2	Khan et al. (1982)
Gymnospoangium juniper-virginiana	1	Mims and Glidewell (1978)
Hemileia vastatrix	2	Rijo and Sargent (1974)
Melampsora euphorbiae	2	Baka and Losel (1998)
M. lini	2	Coffey (1976)
Uromyces appendiculatus	1	Hardwick et al. (1971)
U. euphorbiae	2	Baka (2002)

D-haustoria inside mesophyll cells, the basidiospore-derived-monokaryotic stage typically directly penetrates plant epidermal cells, producing an intracellular hypha, which then branches out into an intercellular mycelium, which develops intracellular M-haustoria (Littlefield and Heath 1979). As a result, both growth phases result in the production of intracellular structures, or haustoria. The only plant structure that has been penetrated is the cell wall because the haustoria are still covered by the invaginated plant plasma membrane. Even so, because fungal structures are in close proximity to the plant protoplast, they have the ability to significantly rearrange organelles to be in close proximity to these structures for nutrient demands (Heath and Skalamera 1997).

2.2 *Case Study: Haustoria of* Puccinia punctiformis

2.2.1 Filamentous Haustoria (M-haustoria)

During the P-PU (pycnial and primary uredial) stages of *P. punctiformis*, the mesophyll cells of *C. arvense* are penetrated by relatively unmodified haustoria differing in structure from the haustoria of uredial-telial stages. These haustoria are filamentous with irregular shapes (Figs. 1 and 2). There are two types of filamentous haustoria. The first type, which is observed during the pycnial stage, has a septum between the haustorial mother cell and the rest of the haustorium (Fig. 1). A wide proximal part and a narrow, distal, tapering end inside the mesophyll cell characterize this type. The host plasma membrane completely surrounds this type of

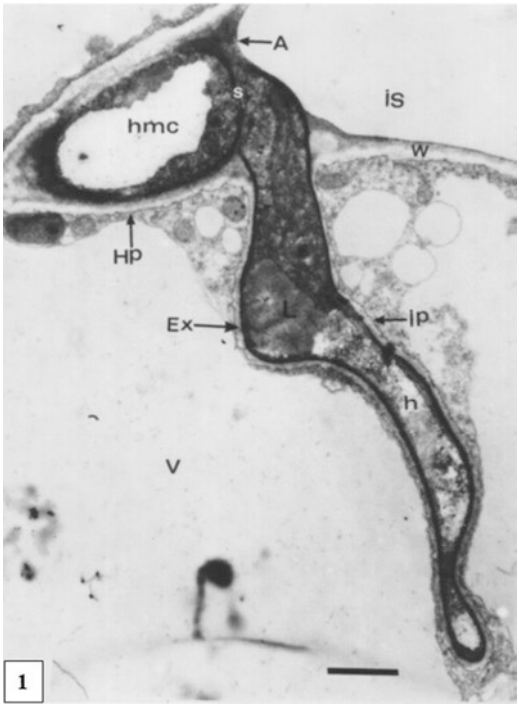

Fig. 1 TEM micrograph of a section through penetration point of filamentous haustorium during pycnial stage of *P. punctiformis*. A septum (s) is formed between the haustorial mother cell (hmc) and the penetrating haustorium (h). The haustorium is characterized by a wide proximal part and an apparently narrower tapering distal end. The host plasma membrane (Hp) is completely surrounding the haustorium to become an invaginated plasmalemma (ip). Note a thin extrahaustorial matrix (Ex) between the invaginated host plasma membrane and fungal wall. Note also lipid drops (L) inside the haustorium. Amorphous material (A) can also be seen between the mother cell and the host wall. *Is* intercellular space, *W* cell wall, *v* host cell vacuole. Scale bar = 1.0 μm

haustorium and separates the host cytoplasm from a relatively thin extrahaustorial matrix, this matrix seems to resemble host wall material. The second type of haustorium, found during the primary uredial stage when pycnia have completely disappeared, is characterized by having no septum formed between the haustorial mother cell and the rest of the haustorium and by a constriction at the penetration site (Fig. 2). This type is also completely enclosed by a host plasma membrane and an extrahaustorial matrix, which is relatively thicker than those of the first type of haustorium and is of a fibrillar appearance like host wall material. The haustorial mother cell is seen embedded in the middle lamellae of the host cell wall. It also differs from the first type in the formation of a small collar, which lie on one side of the neck. No neckband is detected in filamentous haustoria of *P. punctiformis* after normal UA/PbC staining. During the pycnial stage, the haustorium is characterized by having only one nucleus in its cytoplasm (Figs. 3 and 4) and confirmed by light microscope examination after nuclear staining, although in rare cases, two nuclei

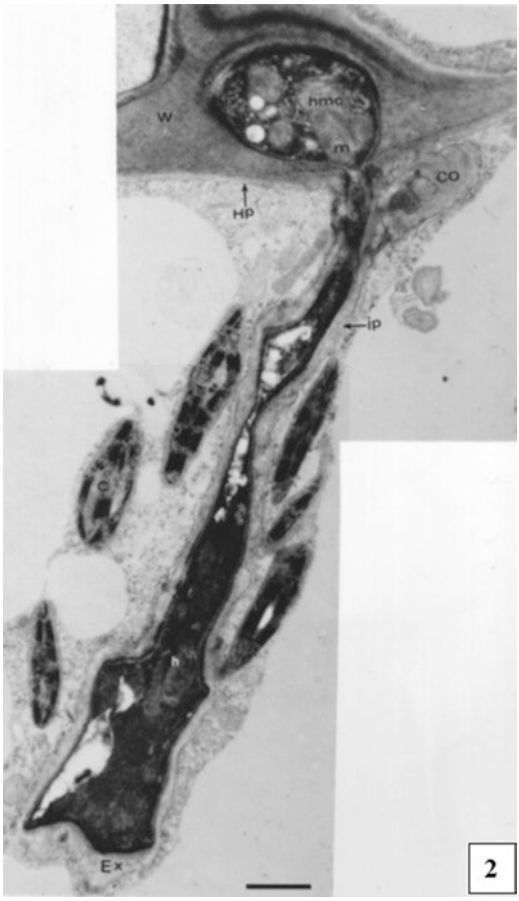

Fig. 2 TEM micrograph of a section through penetration site of filamentous haustorium of *P. punctiformis* in the mesophyll of *C. arvense* during primary uredial stage of infection. The haustorium mother cell (hmc) is embedded in the host cell wall (W) material. A constriction is formed between the mother cell and penetrating haustorium. The host plasma membrane (Hp) is completely enclosed the haustorium to become invaginated (ip). A relatively thick matrix, deposited on the fungal wall, is composed of fibrillar material. A smaller collar (CO) is formed at one side (probably the section is not completely median). Note a mitochondrion (M) begin to migrate from mother cell to the haustorium (h). Note also the host cytoplasm with its chloroplasts (C) around nearly the whole body of the haustorium. Scale bar = 1.0 μm

are found (Fig. 5). The haustoria during the primary uredial stage mostly have two nuclei. The nuclei are enclosed by a double membrane and contain variable amounts of heterochromatin and euchromatin. Nucleoli are not observed in the haustoria during the pycnial stage of infection but they are detected during the primary uredial stage. Figure 6 shows that the haustoria of the pycnial stage are completely enclosed by an extrahaustorial matrix, similar in its staining to the host cell wall, this matrix lying between the invaginated plasma membrane and the fungal wall.

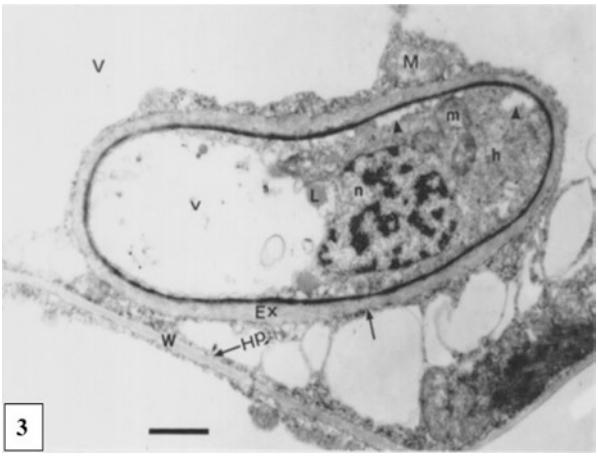

Fig. 3 TEM micrograph of a longitudinal section of filamentous haustorium (h) of *P. puncitformis* inside mesophyll cell of *C. arvense* during the pycnial stage of infection showing nucleus (n), mitochondria (m), oil drops (L), glycogen (arrowheads) and big vacuole (v). Note the haustorium is enclosed by a matrix (Ex) stained similar to host cell wall (W) material. Note also an invaginated host plasma membrane (arrow), host plasma membrane (Hp) and host cell vacuole (v). Host mitochondrion (M) can also be seen which ls closely associated with the haustorium. Scale bar = 1.0 μm

2.2.2 Clavate Haustoria (D-haustoria)

Secondary uredial and telial (SU-T) stages are characterized by the formation of specialized haustoria with a clavate shape (which is mainly dikaryotic). A peg formed from the haustorial mother cell penetrates the host cell wall. At this stage, the haustorial mother cell wall, which lies in close contact with the host cell walls usually, becomes thick, and an extension of host wall material develops (Fig. 7). The haustorial neck then penetrates this wall material and a smaller collar is formed. This fibrillar collar usually appears as a limited extension from the host cell wall around the proximal part of the haustorial neck. The haustorial neck is greatly constricted at the penetration site and shows an electron-dense area (after UA/PbC staining), the neckband, on the neck wall (Fig. 8). A smaller electron-dense and slightly raised area in the host cell wall on both sides of the haustorial neck are seen (Fig. 8).

The haustorial neck, which penetrates the host cell wall, is continuous with the inner layer of the presumably acts as an adhesive material between the mother cell and the host cell wall (Fig. 9). Figure 9 also shows a vacuolated haustorium mother cell after complete migration of the cytoplasm to the haustorium. The haustoria of SU-T stages are characterized by a long-constricted neck and swollen haustorial body (Figs. 9, 10 and 11). Electron micrographs of mature haustoria of SU-T stages show that their bodies contain one nucleus (Fig. 9). The nucleolus is not observed in the haustoria of SU-T stages.

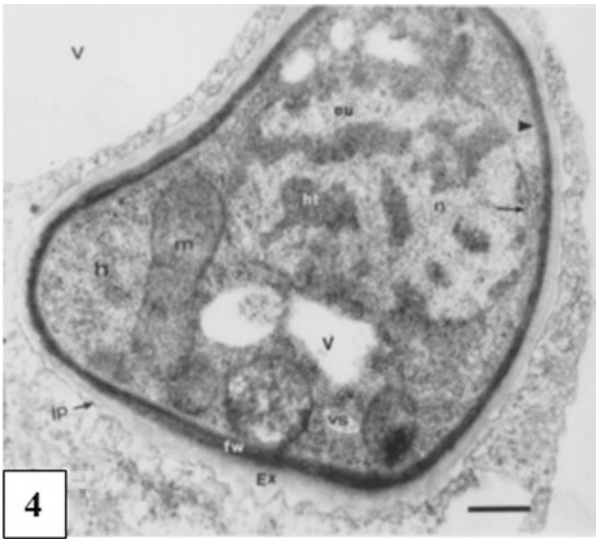

Fig. 4 TEM micrograph of a transverse section of filamentous haustorium (h) during pycnial stage of *P. punctiformis* showing nucleus (n) with heterochromatin (ht) and euchromatin (eu). The nucleus is enclosed by a nuclear membrane (arrow). The haustorium is surrounded by an extra-haustorial matrix (Ex) and invaginated host plasma membrane (ip). Note fungal mitochondria (m), vacuole (v), vesicle (vs) and fungal plasma membrane (arrowhead). Note also an electron-dense fungal wall (fw) and host cell vacuole (V). Scale bar = 0.5 μm

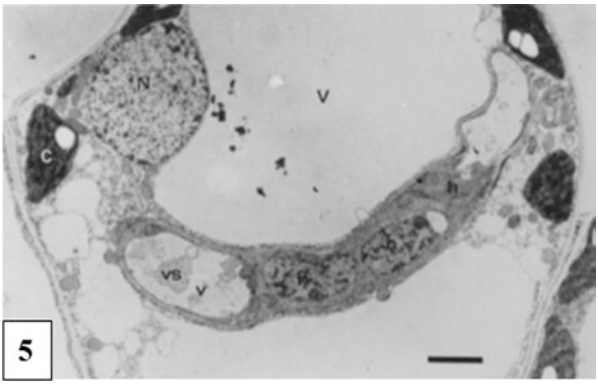

Fig. 5 TEM micrograph of a longitudinal section of filamentous haustorium (h) during pycnial stage of *P. punctiformis* showing two nuclei (n), vacuole (v) and vesicle (vs). Note host chloroplasts (C), nucleus (N), and vacuole (V). Scale bar = 2.0 μm

Electron-dense bodies, which frequently appear near to the haustorial neck, are characterized in transverse section by a solid core, surrounded by a single membrane (Fig. 12), and may appear as bead-like groups, particularly around telial haustorium (Figs. 13 and 14). The clavate haustorium has two nuclei during the flecking

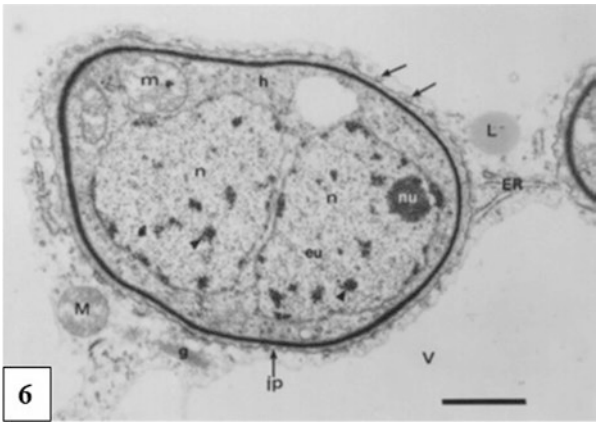

Fig. 6 TEM micrograph of a filamentous haustorium (h) during the primary uredial stage of *P. punctiformis* showing two nuclei (n) with nucleolus (nu). Note small patches of heterochromatin (arrowheads) and large amounts of euchromatins (eu). Note that vesicle-like structures (arrows) are associated with the invaginated host plasma membrane (ip). Note also fungal mitochondria (m). Host endoplasmic reticulum (ER), mitochondria (M), Golgi bodies (g), vacuole (V) and lipid bodies (L) can also be seen. Scale bar = 2.0 µm

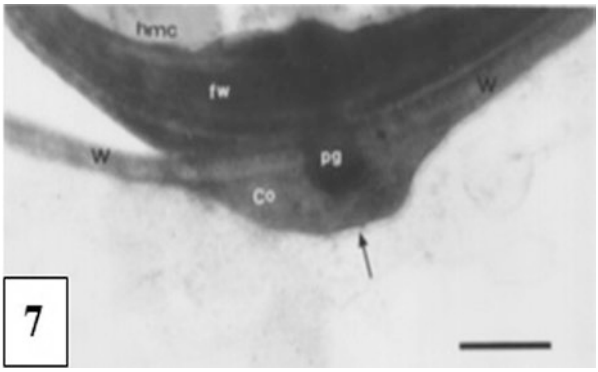

Fig. 7 TEM micrograph of a haustorial mother cell (hmc) of secondary uredial stage of *P. punctiformis* in the process of forming a penetration peg (pg). Note the thickening of the haustorial mother cell wall (fw) at the penetration site and the beginning of collar (co) formation from the host cell wall (W). Note also the host plasma membrane (arrow) around the collar. Scale bar = 0.5 µm

stage of secondary uredinia. The cytoplasm of filamentous and clavate haustoria of *P. punctiformis* contains mitochondria with plate-1ike cristae, endoplasmic reticulum, ribosomes, oil drops, vacuoles, and vesicles (Figs. 9, 12, 13, 15 and 16). Figure 15 shows an aggregation of big oil drops in a rosette arrangement and vesicles with electron-dense inclusions. All contents of filamentous and clavate haustoria are surrounded by the fungal plasma membrane. Both filamentous and clavate haustoria are enclosed by an extrahaustorial matrix, which is bounded by the

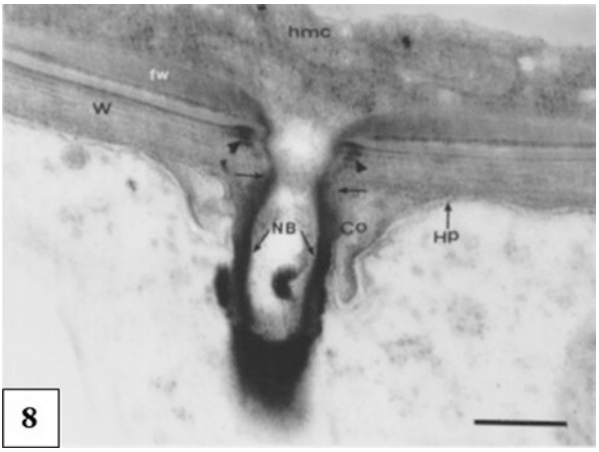

Fig. 8 TEM micrograph of a section during the secondary uredial stage of *P. punctiformis* showing a more advanced penetration site than Fig. 7. Note a localized thickening of the haustorium mother cell (hmc) wall (fw) at the point of entry and part of the neck region with the neckband (NB). Note also the continuity of the haustorial mother cell wall with the haustorial neck wall, a constriction of the neck at the point of entry (arrows), host cell wall (W) and a small collar (Co) enclosed by a host plasma membrane (Hp). Electron-dense areas (arrowheads) on the host cell wall to either side of the neck can also be seen. Scale bar = 0.05 μm

invaginated host plasma membrane and varies in thickness, depending on the age of haustoria. In filamentous haustoria, this matrix consists of the deposition of variable amounts of materials, closely resembling the host cell wall, directly deposited on the more electron-dense fungal wall (Fig. 16). This matrix appears fibrillar in nature, particularly around old haustoria (Figs. 17, 18 and 19). The matrix around the clavate haustorium is more electron-dense than that of the filamentous haustorium and tends to be accompanied by fibrillar materials of electron density similar to the fungal wall, although in some cases, the matrix leaves an electron-lucent zone containing electron-dense deposits (Fig. 16). The extrahaustorial membrane of the filamentous haustorium appears similar in electron density to the uninvaginated host plasma membrane. Figure 19 shows an association of circular structures, probably the endoplasmic reticulum, with the extrahaustorial membrane. The extrahaustorial membrane of clavate haustoria is more electron-dense than the uninvaginated host plasma membrane (Fig. 19). The host nuclei, Golgi bodies, and ER are generally associated with both filamentous and clavate haustoria. The primary phases of development of *P. punctiformis* are characterized by monokaryotic intercellular hyphae during the pycnial stage and dikaryotic intercellular hyphae during the primary uredial stage. Figure 20 shows a diagrammatic representation of the comparison between filamentous (M-haustorium and clavate haustorium of *P. punctiformis*. Table 2 summarize the comparison between the filamentous and clavate haustoria of *P. punctiformis*.

Buller (1950) in his light microscope studies on the same rust fungus claimed that the systemic intercellular hyphae derived from overwintering are dikaryotic,

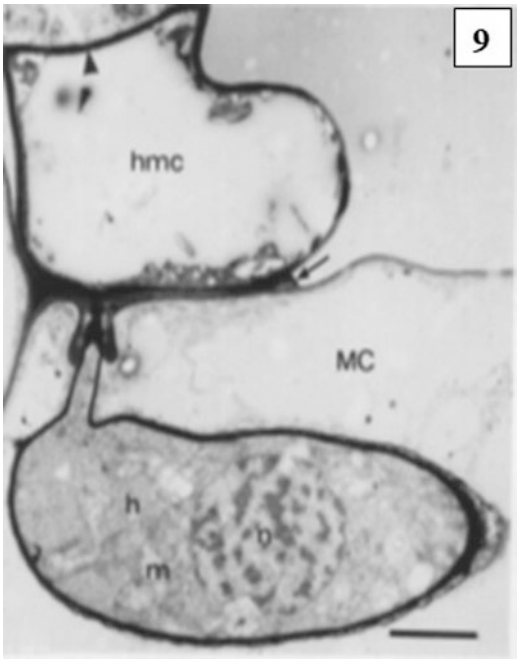

Fig. 9 TEM micrograph of penetration site of clavate haustorium (h) from secondary uredial stage of *P. punctiformis* showing a narrow neck with collar (Co). The haustorium body contains one nucleus (n) and mitochondria (m). The haustorium mother cell (hmc) become completely empty due to the migration of cytoplasm to the haustorium. Note a septum (arrowhead) between the mother cell and the rest of the intercellular hypha. Note also the host mesophyll cell (MC) and an amorphous material (arrow) deposited between the mother cell and host cell wall. Scale bar = 2.0 μm

but that by de-dikaryotization (Littlefield and Heath 1979), haploid intercellular hyphae were produced to give pycnia and protouredia. The mycelia later become dikaryotic giving rise to primary uredia. According to Allen (1934), anastomoses between hyphae of compatible mycelia may occur. Dikaryotization involving nuclear migration has been reported in *P. helianthi* (Craigie 1959) and *P. graminis* (Craigie and Green 1962). This is may be supported by the present investigation where a nucleus appears to be beginning to migrate from one cell to another via the septal pore of the intercellular hypha. This is consistent with the absence of flexuous hyphae from the pycnium of *P. Punctiformis.* Wilson and Henderson (1966) considered the primary uredial stage of *P. punctiformis* as a uredinoid aecial stage.

Generally, the morphology of filamentous haustoria of *P. punctiformis* is similar to that of pycnial and aecial haustoria described by other workers with light and electron microscopy (Baka and Losel 1992a). The haustoria of pycnial and primary uredial stages of *P. punctiformis* are referred to as filamentous haustoria and not intracellular hyphae because they do not emerge from one cell to another like those observed by Gold and Littlefield (1979), and Heath and Bonde (1983), which are

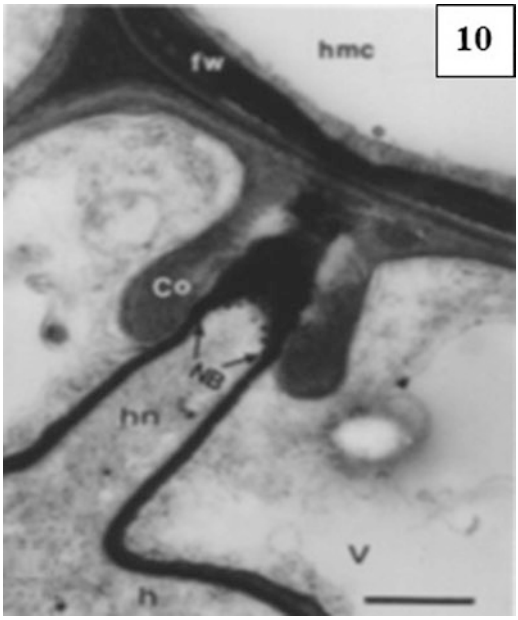

Fig. 10 TEM micrograph of a magnified part of Fig. 9 showing localized thickening of the haustorium mother cell (hmc) wall (fw) at the point of entry. The collar (Co) around the upper part of the haustorial neck (hn) and an electron opaque neckband (NB). Note host cell vacuole (V). Scale bar = 0.5 µm

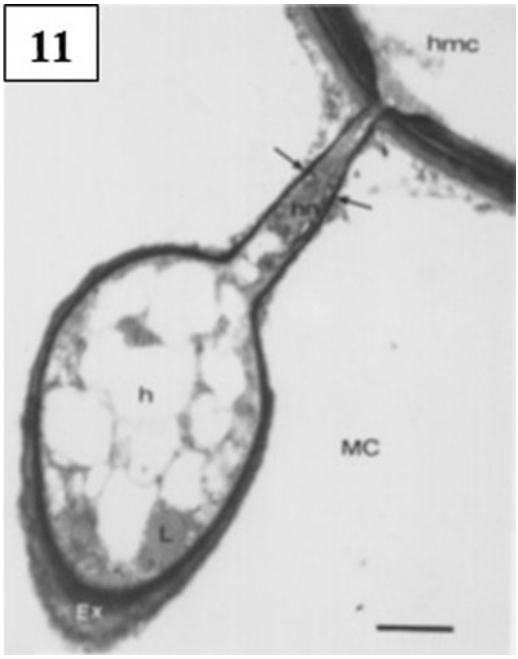

Fig. 11 TEM micrograph of a clavate haustorium (h) during the telial stage of *P. punctiformis*. The haustorium has a long neck (hn) with a neck-band (arrows) but no collar. The haustorial body contains vacuoles and lipid drops (L). Note haustorial mother cell (hmc), an electron-opaque extrahaustorial matrix (Ex), and host mesophyll cell (MC). Scale bar = 1.0 µm

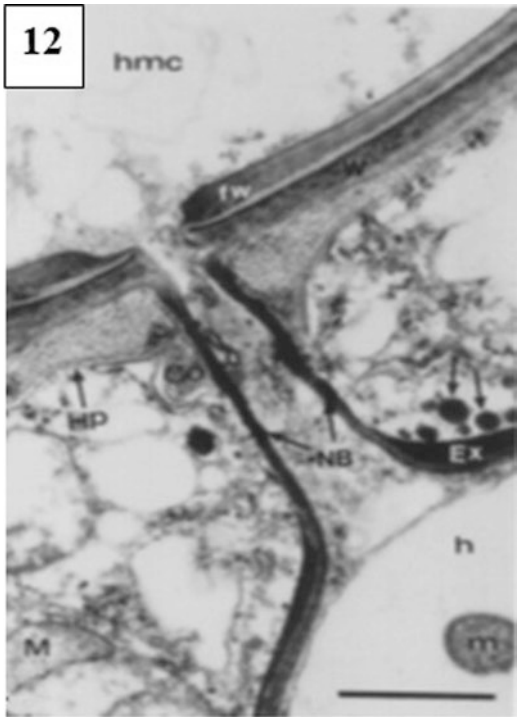

Fig. 12 TEM micrograph of penetration site of clavate haustorium (h) during telial stage of *P. punctiformis* showing a thick wall (fw) of the haustorial mother cell (hmc), haustorial neck with neckband (NB), and collar (Co) with fibrillar material. The part of the haustorial neck wall above the neckband, towards the haustorial mother cell, is more electron-dense than the part below the neckband toward the haustorial body. Note electron-dense bodies presumably tubules of ER with solid core bounded by a single membrane (arrows). Note also the continuity of the host plasma membrane around the collar. Electron-dense extrahaustorial matrix (Ex), host plasma membrane (Hp), and fungal mitochondria (m) can also be seen. Scale bar = 1.0 μm

generally termed intracellular hyphae. Moreover, since these haustoria may contain two nuclei at the primary uredial stage of *P. punctiformis*, the terms monokaryotic haustoria or P-haustoria (referring to their association with pycnial stage) are not suitable. This agrees with other observations on rust fungi (Allen 1934; Rijkenberg and Truter 1973; Robb et al. 1975a, b; Borland and Mims 1980). These types of dikaryotic haustoria differ from the dikaryotic haustoria of secondary uredial and telial stages of *P. punctiformis*, which are referred to in this account as clavate haustoria. In many ways, these differences are more or less similar to those summarized by Harder (1984). Generally, the ultrastructure of clavate haustoria of both secondary uredial and telial stages of *P. punctiformis* is similar to that of D-haustoria, described by other investigators.

Haustorial penetration seems to be both mechanical and enzymatic. This is clear during early stage of penetration from the presence of raised areas of the host wall and at the same time electron-dense areas of host wall at both sides of the penetration peg. The raised area may be attributed to mechanical force and electron-dense

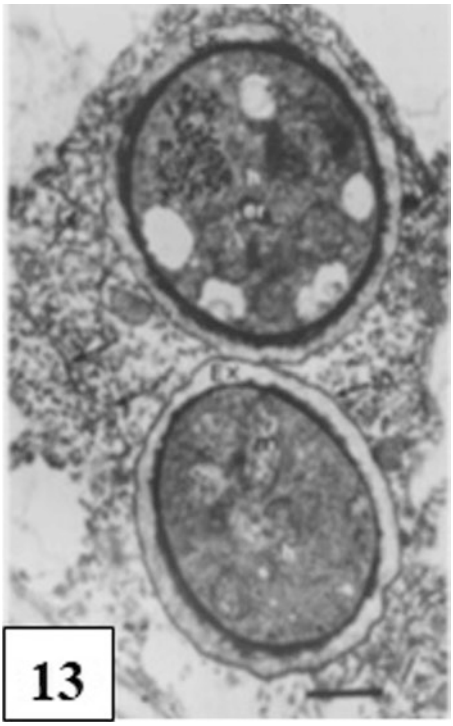

Fig. 13 TEM micrograph of two transverse sections of clavate haustoria (h) during telial stage of *P. punctiformis* showing fibrillar nature of extrahaustorial matrix (Ex). Note large amounts of bead-like structures (arrows) suggesting tubules of host ER around the haustoria. Note also fungal mitochondria (m), fungal endoplasmic reticulum (er), and host cell wall (W). Electron-dense extrahaustorial membrane (ip) can also be seen. Scale bar = 1.0 μm

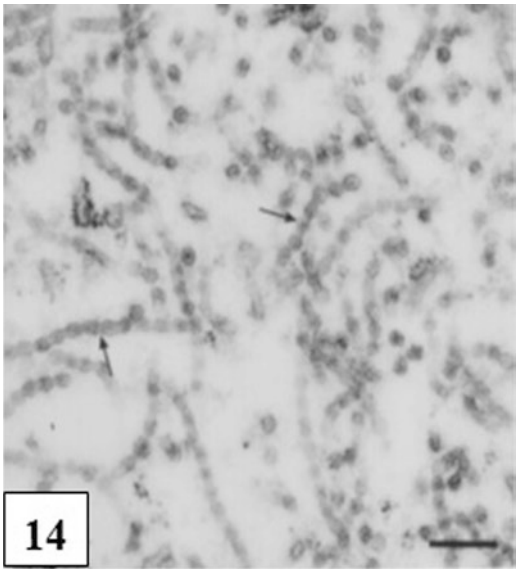

Fig. 14 EM micrograph of magnified part of Fig. 13 showing the bead-like structures (arrows) suggesting tubules of host ER. Each unit of the chain consists of a solid core surrounded by a single membrane. Scale bar = 0.25 μm

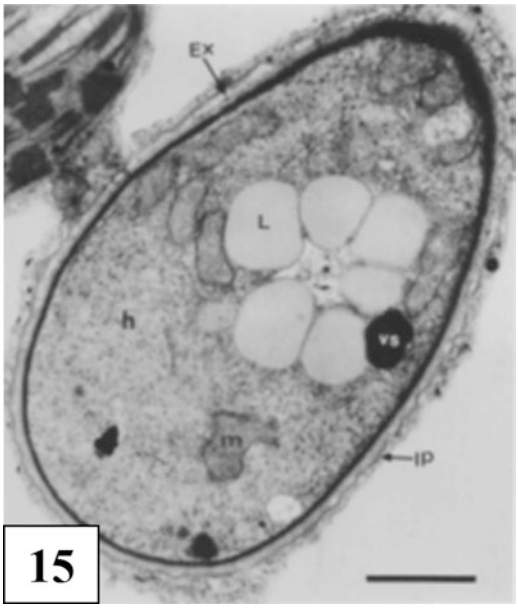

Fig. 15 TEM micrograph of a clavate haustorium (h) during the secondary uredial stage of *P. punctiformis* showing an aggregation of large lipid drops (L) as a rosette-shape, mitochondria, and electron-dense vesicle (vs). Note invaginated host plasma membrane (ip) enclosed a fibrillar extrahaustorial matrix (Ex). Scale bar = 1.0 μm

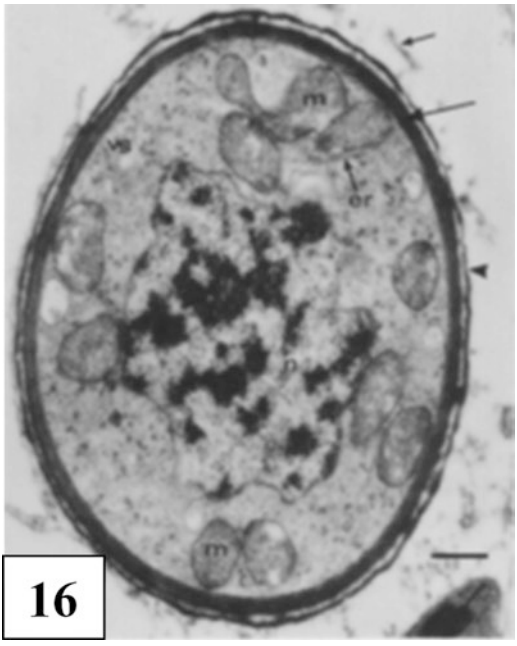

Fig. 16 TEM micrograph of a transverse section of clavate haustorium during the telial stage of *P. punctiformis* showing several mitochondria (m), nucleus (n), endoplasmic reticulum (er), and vesicle (vs). Note an electron-dense extrahaustorial matrix (long arrow) and invaginated host plasma membrane (arrowhead). Not also, the tubules of host ER (short arrow) are close to the haustorium. Scale bar = 1.0 μm

areas may be due to reaction between host wall and enzymes produced from the fungus. This corresponds with observations of other authors who referred to the haustorial penetration as enzymatic (Littlefield and Heath 1979; Al-Khesraji and Losel 1981; Chong et al. 1981; Longo and Bruscaglioni 1986). The clavate haustoria of secondary uredial and telial stages of *P. punctiformis*, unlike the filamentous

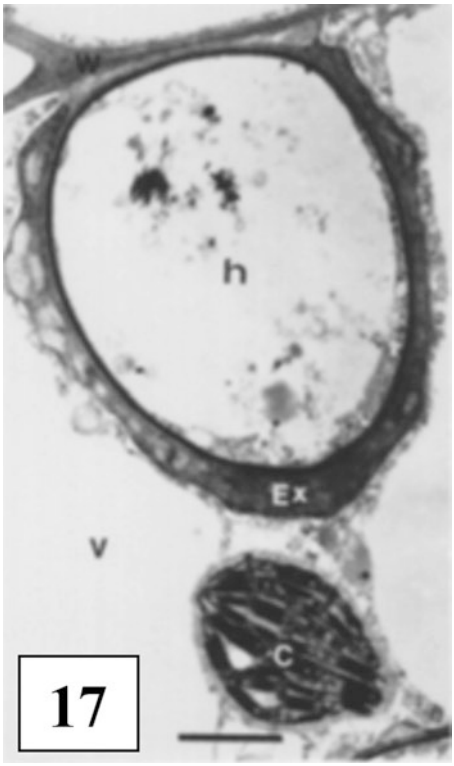

Fig. 17 TEM micrograph of a vacuolated filamentous haustorium (h) during P-PU stages of *P. punctiformis* showing an electron-dense extrahaustorial matrix (Ex) surrounding the haustorial body. The matrix is composed of a host wall-like material and shows a fibrillar appearance. The haustorium is highly vacuolated indicating that, it is old. Note host chloroplast (C) close to the haustorium. Note also the host cell vacuole (V). Scale bar = 1.0 μm

haustoria, are characterized by an electron-dense neckband on the haustorial neck, observed after lead staining, which acts as a seal to stop an apoplastic flow of materials along the neck wall (Heath 1976). The neckband becomes visible with the appearance of the penetration peg prior to the formation of the haustorial body. This is consistent with the observation of Littlefield (1972) on *Melampsora lini*. The mature clavate haustoria of *P. punctiformis* are characterized by having a single nucleus without a nucleolus while the young haustorium during the flecking secondary uredial stage contains two nuclei. Many workers reported that the number of nuclei may vary in D-haustoria. The absence of nucleoli from mature clavate haustoria corresponds to the interpretation of Harder and Chong (1984). They suggested that the reduced granular component of nucleoli in haustoria is possibly because the haustoria are not actively involved in the synthesis of new material. It is assumed by Littlefield and Heath (1979) that at maturity, the haustorial body contains two nuclei while the haustorial mother cell is vacuolated and devoid of nuclei although in the present study only one nucleus is observed in mature clavate haustorium and the haustorial mother cell is completely vacuolated.

The filamentous haustoria of *P. punctiformis* are completely enclosed by host wall-like material which is referred to in this study as an extrahaustorial matrix (Bushnell 1972). This matrix becomes more fibrillar around the old vacuolated

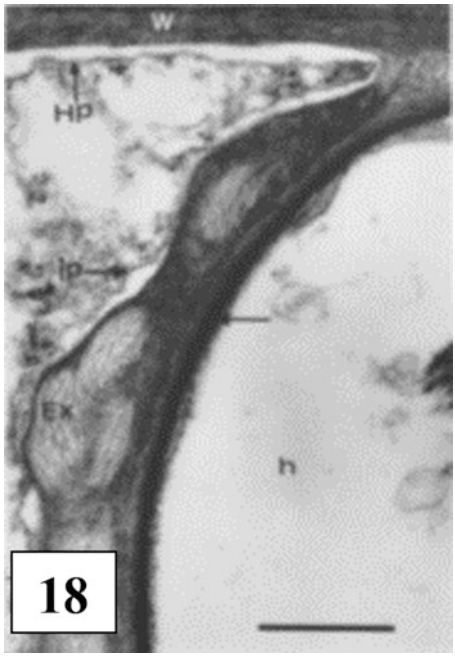

Fig. 18 TEM micrograph of a magnified part of Fig. 4:32 showing fibrillar extrahaustorial matrix (Ex) of the haustorium (h). Note that invaginated (ip) and uninvaginated (Hp) host plasma membranes. Note also an electron-dense fungal wall (arrow). And host cell wall (W). Scale bar = 0.5 μm

haustoria than around the young haustoria. The collar and matrix are not exactly the same as the host wall material. This change may be due to other products of the host fungus interaction, In some investigations of M-haustoria, the matrix has not been distinguished from the col1ar material (Littlefield and Heath 1979; Rijkenberg and Truter 1973). The exrahaustorial matrix around either mono- and dikaryotic filamentous haustoria of *P. punctiformis* appears similar to the matrix of other monokaryotic haustoria (Littlefield and Heath 1979; Al-Khesraji and Losel 1980, 1981). The matrix around clavate haustoria of *P. punctiformis* differs in appearance from those of filamentous haustoria of *P. punctiformis* in the presence of electron-dense deposits which may originate from the fungus. This agrees with the observations of Al-Khesraji and Losel (1981) on the dikaryotic haustoria of *P. poarum*. This matrix may be a product of host-parasite interaction (Ehrlich and Ehrlich 1963; Zimmer 1970) or could be of fungal origin (Mims and Glidewell 1978; Glidewell and Mims 1979).

High-resolution autoradiographic studies have indicated that the matrix is of host origin (Mendgen and Heitefuss 1975; Mendgen 1979). Harder (1978) suggested that the matrix might be of both host and fungal origin. The variability in the appearance of the extrahaustorial matrix may relate to the age of the haustoria or the degree of compatibility with the host (Harder and Chong 1991). Both filamentous and clavate haustoria are surrounded by an invaginated host plasma membrane or the extrahaustorial membrane as named by Bushnell (1972) which appears continuous with the uninvaginated host plasma membrane. The filamentous haustoria are completely enclosed by the exbrahaustorial membrane which is separated from the fungal wall

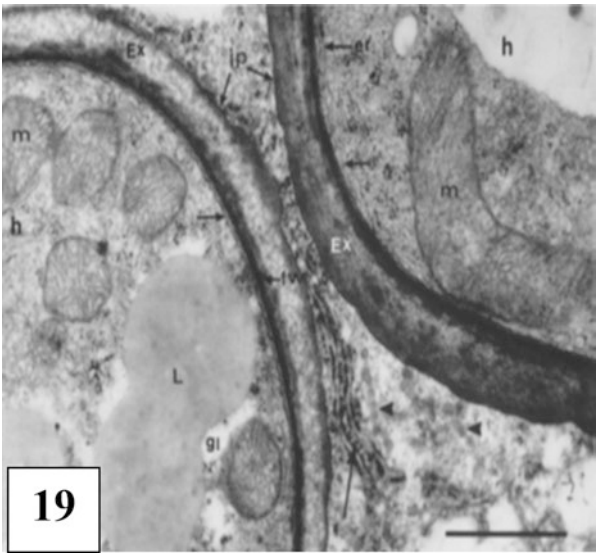

Fig. 19 TEM micrograph of two parts of haustorial bodies (h) during the telial stage of *P. punctiformis* showing fungal wall (fw) and extrahaustorial matrix (Ex) bounded by electron-dense extrahaustorial membranes (ip). Electron-dense fibrills are seen in the extrahaustorial matrix probably derived from the fungal wall. Note fungal mitochondria (M), oil drops associated with electron-lucent granules suggesting glycogen (gl), endoplasmic reticulum (er), and fungal plasma membrane (small arrows). Note also the close association of host endoplasmic reticulum (large arrow) and tubules of ER (arrowheads) with the extrahaustorial membrane. Scale bar = 0.5 μm

by an extrahaustorial matrix, while in the case of clavate haustoria, this membrane is appressed to the haustorial neck, particularly at the neckband. This corresponds to the observations of Littlefield and Bracker (1972) on *Melampsora lini* and Harder et al. (1978) on *P. graminis*. This is similar to the membrane-wal1 relationship shown for the Casparian strip in endodermal cells of higher plants by Bonnett (1968) as was confirmed by Heath (1976) when she pointed to the functional similarity of the haustorial neckband of rust fungi and the Casparian strip of vascular plants. The undulation of the extrahaustorial membrane observed in clavate haustoria of *P. punctiformis* is in agreement with the report of Chong et al. (1981).

Gunning (1977) suggested that the undulated nature of the extrahaustorial membrane around fungal haustoria increased the surface area to facilitate the transfer of substances. Some vesicles are observed in contact with the invaginated PM around the filamentous haustorium of *P. punctiformis*. These are presumably smooth ER, although in most cases proliferation of rough ER is observed close to the filamentous and clavate haustoria of the parasite in this study, and no direct contacts are detected. Some workers reported that the ER in close association with invaginated PM was consistently ribosome-free (Heath and Heath 1971; Littlefield and Bracker (1972). Moreover, Morre and Mollenhauer (1974) concluded that smooth ER might be a transitional element between membrane systems. One striking feature

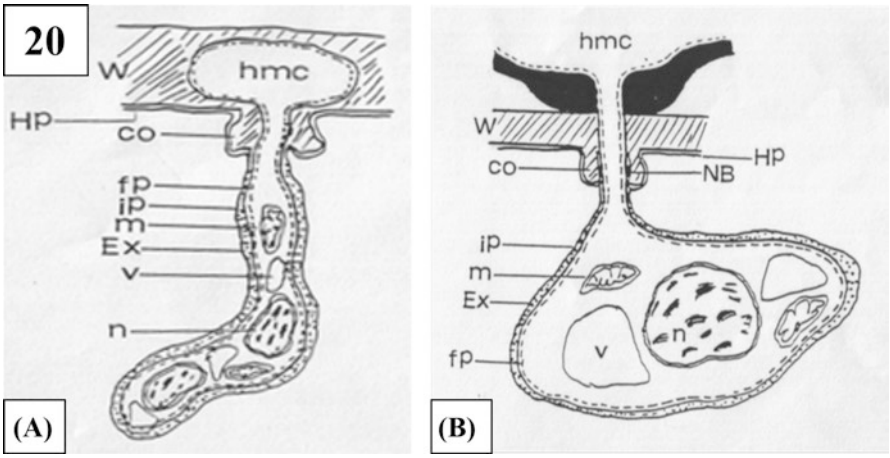

Fig. 20 Diagrammatic representation of filamentous (**a**) and clavate (**b**) haustoria of *P. punctiformis*. Hmc = haustorial mother cell; W = Host cell wall; Hp = Host plasma membrane; co = collar; NB = Neckband; ip = invaginated host plasma membrane; Ex = Extrahaustorial matrix; n = Haustorial nucleus; v = haustorial vacuole; m = haustorial mitochondria; fp = fungal plasma membrane

Table 2 Comparison between the filamentous and clavate (haustoria during the pycnial-primary uredial (P-PU) and secondary uredial-telial (SU-T) stages of *P. punctiformis*

Item	FH of P-PU stages	CH of SU-T stages
Number of nuclei per fungal cell	Two	One or two
Nucleolus visible	Present	Absent
Adhesive material between the fungal wall and host cell wall	Absent	Absent
Collar	Present	Present
Constricted neck and neckband	Absent	Present
Localized thickening at point of entry	Absent	Present
Septation	Absent	Absent
Crystal-containing microbodies	Absent	Absent
Growth within host vascular tissue	Present	Absent
Contents of extrahaustorial matrix	Resemble host cell wall	Electron-dense material
Association with host nucleus	Present	Absent
Lomasomes	Absent	Absent

FH filamentous haustorium, *CH* clavate haustorium
All fungal structures contain mitochondria, oil drops, endoplasmic reticulum, glycogen-like particles and vesicles with membranous structures

frequently noticed in mesophyll cells invaded by clavate haustoria of *P. punctiformis*, was the accumulation of vesicles and tubules around the haustoria. These vesicles and tubules resembled those reported in tissues infected by *P. coronate avenae* (Chong and Harder 1982), *Melampsora lini* (Coffey 1976), *Physopella zeae* (Heath

and Bonde 1983), *P. coronata* (Chong 1981). Similar vesicles, which were observed near the haustoria of *Physopella zeae* were suggested by Heath and Bonde (1983) to be of Golgi origin. Heath and Heath (1971) suggested that the vesicles attached to the host plasma membrane in cowpea infected with *Uromyces phaseoli* var. *vignae* possibly supplied the extra membrane needed to cover the developing extrahaustorial matrix. Harder (1978) noted that the vesicles and tubules associated with the haustoria of *P. coronata avenae* contained densely staining material similar to that in the extrahaustorial matrices of mature haustoria. This supports the idea that the extrahaustorial matrix is the host origin. It seems that the membrane complex found close to the haustoria is specific to the fungus and even to the infection stage. These types of vesicles and tubules were observed around clavate haustoria and not around filamentous haustoria although they invaded cells of the same host. These observations are in agreement with those of Harder and Chong (1984), who found similar membrane complexes in oat, induced by *P. graminis* f. sp. *tritici* and also in wheat, induced by *P. graminis* f. sp. *tritici* as distinct from the type induced in oat by *P. coronata*.

Harder and Chong (1984) concluded that the fungus is able to pass messages into host cell to alter specifically the metabolic processes in that cell. They added that these complexes are open directly to the extrahaustorial matrix and are themselves interconnected via the host ER system and suggested that these tubular complexes provide and facilitate the flow of metabolites. The contents of filamentous and clavate haustoria of *P. punctiformis* are basically the same. The vacuolation and oil drops are increased in old haustoria compared with young haustoria. Glycogen is detected in both filamentous and clavate haustoria. Some other workers have found glycogen in D-haustoria (Zimmer 1970; Coffey et al. 1972; Mares 1979). Generally, the growth of filamentous haustoria of *P. punctiformis* inside host cells is less than that of clavate haustoria.

Al-Khesraji and Losel (1980) presented quantitative data on the penetration of different stages of *P. poarum*. They found a lower frequency of penetration of host cells by intracellular structures in *Tussilag*o than in *Poa*, suggesting that the monokaryon of *P. poarum* may be less important in nutrition than the haustoria of the dikaryon. The high frequency of invaded vascular tissue may supply the fungus directly with nutrients rather than from mesophyll cells (Baka and Losel 1992a, b). The close association of host nuclei with filamentous and clavate haustoria is clearly evident except during pycnial stage and a greater degree of association is detected with filamentous haustoria during the primary uredial stage of *P. punctiformis*. Al-Khesraji and Losel (1980) pointed out that the pycnial and aecial stages of rust frequently elicit greater disturbance of normal host physiology than the uredial stages of rust fungi. Figure 20 shows a diagrammatic representation of both types of haustoria of *P. punctiformis*.

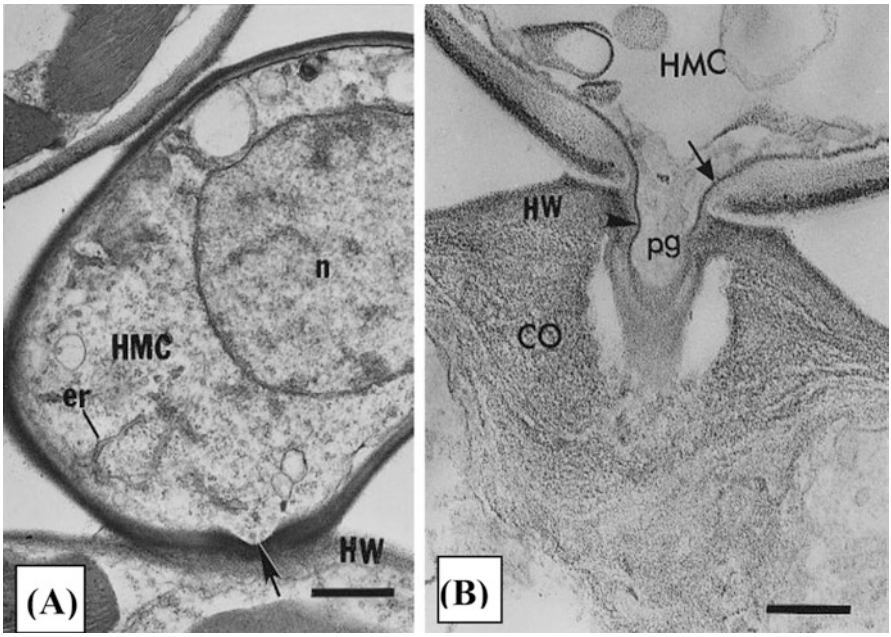

Fig. 21 Penetration of *E. peplus* mesophyll cells by *M. euphorbiae*. (**a**) Haustorium mother cell (HMC) in close attachment to the host cell wall (HW) at the penetration site, where a tiny peg (arrow) is starting to form. The HMC contains nucleus (n), endoplasmic reticulum (er) and ribosome-rich cytoplasm. Bar = 0.5 µm. (**b**) Point of entry of penetration peg (pg) from haustorium mother cell (HMC) through the host cell wall (HW). A collar (CO) as a response to penetration is formed. Note the continuity of plasmalemma (arrow) in HMC and inner layer of the penetration peg. Note also the constriction (arrowhead) of the penetration peg. Bar = 0.25 µm

2.2.3 Development of D-haustorium of *Melampsora euphorbiae*

Intercellular hyphae of the dikaryotic phase of *M. euphorbiae* in infected leaf tissue of *Euphorbia peplus* were septate and usually showed two nuclei per cell as well as the normal cytoplasmic organelles of eukaryotic cells (Baka and Losel 1998). Haustoria developed from specialized haustorium mother cells (HMC) which adhered to the host cell wall (Fig. 21a). A very slender penetration hypha emerged from the HMC at the point of contact with the host cell wall (Fig. 21b). Further development of the penetration hypha, the wall of which was continuous with the inner layer of the HMC wall, resulted in penetration of the host wall (Fig. 21b). Subsequent extension within the host cell formed the haustorium neck (sectioned obliquely in Fig. 22d), and expansion of the tip formed the haustorium body (Fig. 22d).

The penetration hypha was usually slightly constricted at the site of entry. Two types of collar deposits could be recognized surrounding the neck on the inside of the cell wall close to the penetration site. A small collar of microfibrillar material resembling the host cell wall in its intensity of reaction was associated with young haustoria (Fig. 22b), while a more extensive electron-lucent collar, appearing

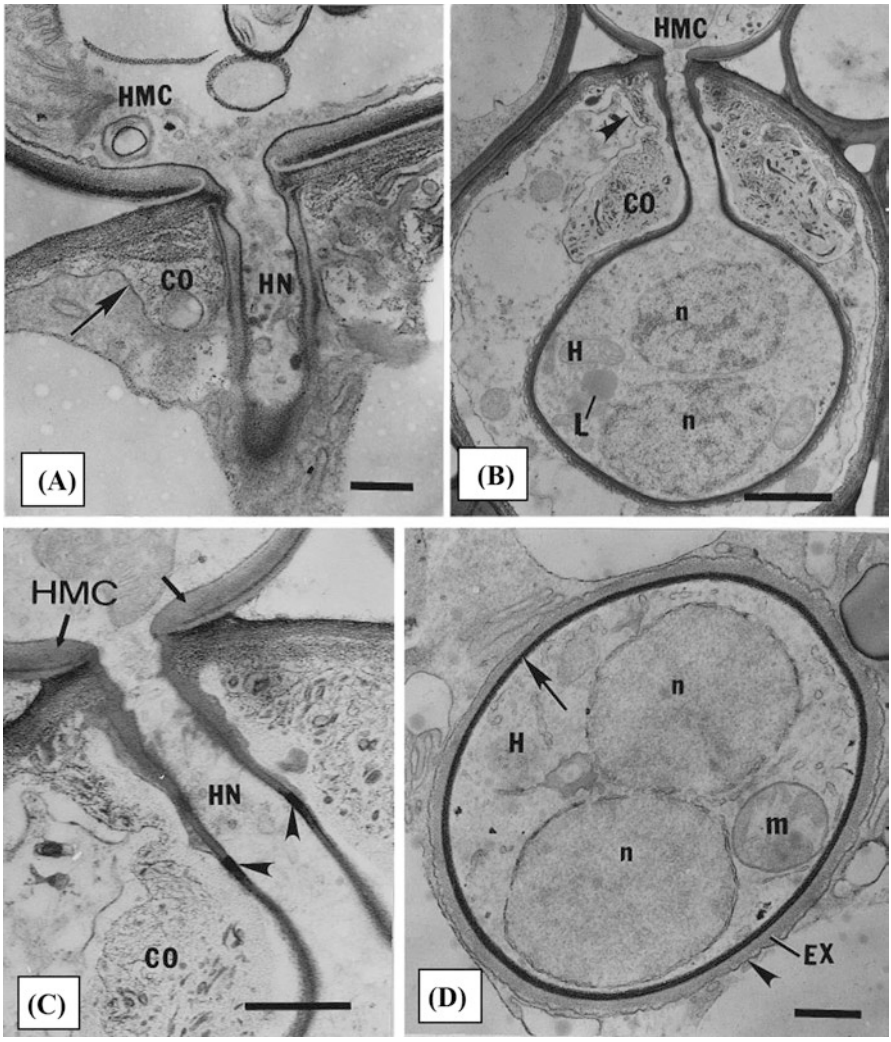

Fig. 22 Penetration of *E. peplus* mesophyll cells by *M. euphorbiae*. (**a**) A more advanced stage of penetration showing the haustorium neck (HN). Note the continuity of host plasmalemma (arrow) around the collar (CO). HMC = haustorium mother cell. (**b**) Median section through haustorium mother cell (HMC), neck, and mature haustorium (H), containing two nuclei (n) and lipid drop (L), inside the host cell. Note the extensive collar (CO) surrounding the neck and the continuity of the invaginated host plasmalemma (arrowhead) around the collar. Bar = 1 μm. (**c**) Magnified part of Fig. 6 showing haustorium neck (HN) with neckband (arrowheads). Note the thickening (arrows) of the haustorium mother cell (HMC) wall at the site of penetration and the collar (CO). Bar = 0.5 μm. (**d**) Transverse section through the body of a haustorium (H) with two nuclei (n) and mitochondrion (M). The haustorial wall (arrow) is more electron-dense than the extrahaustorial matrix (EX) or the extrahaustorial membrane (arrowhead). Bar = 0.5 μm

similar to callose, enclosed the neck of mature haustoria (Fig. 22a, b). Like D-haustoria of other rust fungi, the mature haustorium of *M. euphorbiae*, was clavate, having a narrow cylindrical neck with a distinct electron-opaque neckband in the wall midway along its length (Fig. 22a, b). The haustorium body usually contained two nuclei and oil drops (Fig. 22b, d). The host plasma membrane was invaginated around the collar and haustorium and also enfolded between the collar and haustorium (Fig. 22c).

2.2.4 The Function of Rust Haustorium

It appears that rust haustoria perform two primary functions: controlling the host-parasite relationship and nutrient intake (Harder and Chong 1991; Mendgen et al. 2000). The host range of rust fungus, which is often constrained to related host species, has been extensively described through experiments. Comparing haustoria from related rust species showed that each species has different structural alterations (Berndt 1999). Additionally, interactions between various rusts and the same host plant exhibit species-specific interactions: *Puccinia graminis* causes endoplasmic reticulum-derived membranes with tiny interconnected tubules to emerge in oat plants, whereas *P. coronata* causes the formation of very distinct long, thin tubular extensions (Harder and Chong 1991). These findings imply that in addition to the signals shared by the parasite and host during the growth of infection structures (Heath 1997), species- or even race-specific signals may also be involved in the establishment of the fine structure of the haustorial parasite-host interface. Suppressors may be present in such signals.

It has been hypothesized that suppressors play a role in preserving the fundamental compatibility between biotrophic fungi and their host plants (Bushnell and Rowell 1981). Induced susceptibility, a phenomenon, provides support for suppressors. *Uromyces vignae*-infected French bean tissue allowed for the growth of secondary infections by a number of non-host pathogens (Fernandez and Heath 1991). There is little direct evidence of rust haustoria consuming specific host metabolites like sugars and amino acids. Radioisotope studies have been conducted for more than three decades (Mendgen et al. 2000). They are limited by the fact that any tagged substrate provided to infected host plants is partially digested before reaching the fungus. Additionally, $^{14}CO_2$ or $^{3}H_2O$ may form as products, depending on the isotope utilized, and skew the results. While attempts to distinguish between uptakes by intercellular hyphae vs. haustoria revealed certain trends, they were unable to determine the exact destiny of individual chemicals from the plant cell into the haustorium (Mendgen 1981).

Because haustoria are the only fungal structures present within the host tissue in powdery mildews, their function in the nutrient acquisition is more obvious. Feeding studies using radiolabeled sugars appeared to show that the primary carbohydrate acquired from epidermal cells is glucose rather than sucrose (Sutton et al. 1999). Manners (1989) proposed that the extrahaustorial membrane loses control of solute export and that ATPase activity of the haustorial plasma membrane would sustain a

high efflux of solutes through the haustorial interface based on inhibitor studies with haustoria of *Erysiphe graminis*. However, contradictory findings have been obtained using the lead precipitation method to identify relevant membrane ATPase activity on either the host or the fungal side (Woods and Gay 1988; Baka et al. 1995).

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- Baka ZAM, Losel DM (1998) Ultrastructure and lectin-gold cytochemistry of the interaction between the rust fungus *Melampsora euphorbiae* and its host *Euphorbia peplus*. Mycol Res 102: 1387–1398.
- Baka ZAM, Losel DM (1992). Ultrastructure of the thistle rust, *Puccinia punctiformis*. Mycol Res 96: 81–88.

References

Abu-Zinada AAH, Cobb A, Boulter D (1975) An electron microscopic study of the effects of parasite interaction between *Vicia faba* L. and *Uromyces fabae*. Physiol Plant Pathol 5:113–118

Alexopoulos CJ, Mims CW, Blackwell M (1996) Introductory mycology. Wiley, New York

Al-Khesraji TO, Losel DM (1980) The infection of vascular tissue in leaves of *Tussilago farfara* L. by pycnial-aecial stages of *Puccinia poarum* Niel. Physiol Plant Pathol 17:193–197

Al-Khesraji TO, Losel DM (1981) The fine structure of haustoria, intracellular hyphae and intercellular hyphae of *Puccinia poarum*. Physiol Plant Pathol 19:301–311

Allen RF (1934) A cytological study of heterothalism in *Puccinia sorghi*. J Agric Res 49(1047):1068

Baka ZAM (1992) Observations on the ultrastructure of the uredinial stage of Puccinia polypogonis on Polypogon monspeliensis. Mycopathol 120:103–111

Baka ZAM (1996a) Observations on the ultrastrueture of the uredinial stage of *Puccinia polypogonis* on *Polypogon monspeliensis*. Mycopathologia 120:103–111

Baka ZAM (1996b) Comparative ultrastructure of aecial and telial infections of the autoecious rust fungus *Puccinia tuyutensis*. Mycopathologia 134:143–150

Baka ZAM (2002) Ultrastructure of intercellular hypha and haustorium of the rust fungus, *Uromyces euphorbiae*. Mycopathologia 156:215–221

Baka ZAM (2014) Ultrastructure of the dikaryotic stage of anise rust, *Puccinia pimpinellae* (F. Strauss) Link. Afr J Microbiol Res 8:888–894

Baka ZAM, Losel DM (1992a) Ultrastructure of the thistle rust, *Puccinia punctiformis*. Mycol Res 96:81–88

Baka ZAM, Losel DM (1992b) Infection of vascular tissues by autoecious rusts, *Puccinia punctiformis* and *P. lagenophorae*: a cytological study. Physiol Mol Plant Pathol 40:411–421

Baka ZAM, Losel DM (1998) Ultrastructure and lectin-gold cytochemistry of the interaction between the rust fungus *Melampsora euphorbiae* and its host *Euphorbia peplus*. Mycol Res 102:1387–1398

Baka ZAM, Larous L, Losel DM (1995) Distribution of ATPase activity at the host pathogen interfaces of rust infections. Physiol Mol Plant Pathol 47:67–82

Berndt R (1999) Neotropical rust fungi: new species and observations. Mycologia 91:1045–1059

Berndt R, Oberwinkler F (1997) Haustorial ultrastructure and morphology of *Melampsorella* and *Thekopsora areolata*. Mycologia 89:698–705

Bonnett HT (1968) The root endodermis: fine structure and function. J Cell Biol 37:199–205

Borland J, Mims CW (1980) An ultrastructural comparison of the aecial and telial haustoria of the autoecious rust *Puccinia podophylli*. Mycologia 72:767–774

Boshoff WHP, Visser B, Bender CM, Wood AR, Rothmann L, Wilson K, Hamilton-Attwell VL, Pretorius ZA (2022) Fig rust caused by *Phakopsora nishidana* in South Africa. Phytopathol Mediterr 61:283–298

Bracker (1967) Ultrastructure of fungi. Annu Rev Phytopathol 5:343–374

Bracker CW, Littlefield LJ (1973) Structural concepts of host-pathogen interfaces. In: Byrde RJW, Cutting CV (eds) Fungal pathogenicity and the plant's response. Academic, London, pp 159–318

Buller AHR (1950) *Puccinia suaveolens* and its sexual process. In: Buller AHR (ed) Researches on fungi. University of Toronto Press, Toronto, pp 344–388

Bushnell WR (1972) Physiology of fungal haustoria. Annu Rev Phytopathol l0:151–176

Bushnell WR, Gay JL (1978) Accumulation of solutes in relation to the structure and function of haustoria in powdery mildew. In: Spencer DM (ed) The powdery mildews. Academic, London, pp 183–235

Bushnell WR, Roelfs AP (eds) (1984) The cereal rusts, vol I. Academic, New York, p 431

Bushnell WR, Rowell JB (1981) Suppressors of defense reactions: a model for roles in specificity. Phytopathology 71:1012–1014

Chong JYN (1981) Ontogeny of mono- and dikaryotic haustoria of *Puccinia coronate avenae*: ultrastructure, cytochemistry and electron-probe X-ray analysis. PhD. dissertation, Department of Botany, University of Manitoba, Winnipeg

Chong J, Harder DE (1982) Ultrastructure of haustorium development in *Puccinia coronata avenae:* some host responses. Phytopathology 72:1527–1533

Chong J, Harder DE, Rohringer R (1981) Ontogeny of mono- and dikaryotic rust haustoria: cytochemical and ultrastructural studies. Phytopathology 71:975–983

Coffey MD (1975) Obligate parasites of higher plants particularly rust fungi. Symp Soc Exp Biol 29:297–323

Coffey MD (1976) Flax rust resistance involving the k-gene: an ultrastructural study. Can J Bot 54:1443–1457

Coffey MD, Allen FHE (1983) Quantitative histological and ultrastructural analysis of interactions between the flax rust near isogenic host lines varying in their degree of incompatibility. Can J Bot 61:1831–1850

Coffey MD, Palevitz BA, Allen PJ (1972) The fine structure of two rust fungi, *Puccinia helianthi* and *Melampsora lini*. Can J Bot 50:231–240

Craigie JH (1959) Nuclear behaviour in the diploidization of infections of *Puccinia helianthi*. Can J Bot 37:843–855

Craigie JH, Green GJ (1962) Nuclear behaviour leading to conjugate association in haploid infections of *Puccinia graminis*. Can J Bot 40:163–178

Ehrlich MA, Ehrlich HG (1963) Electron microscopy of the sheath surrounding the haustorium of *Erysiphe graminis*. Phytopathology 53:1378–1380

Ehrlich MA, Ehrlich HG (1971) Fine structure of the host-parasite interfaces in mycoparasitism. Annu Rev Phytopathol 9:155–184

Faoro F, Faccio A, Balestrini R (2022) Contributions of ultrastructural studies to the knowledge of filamentous fungi biology and fungi-plant interactions. Front Fungal Biol 2:805739

Fernandez MR, Heath MC (1991) Interactions of the nonhost French bean plant (*Phaseolus vulgaris*) with parasitic and saprophytic fungi. IV. Effect of preinoculation with the bean rust fungus on growth of parasitic fungi nonpathogenic on beans. Can J Bot 69:1642–1646

Fraymouth JF (1956) Haustoria of the Peronosporales. Trans Br Mycol Soc 39:79–107

Gay JL, Salzberg A, Woods AM (1987) Dynamic experimental evidence for the plasma membrane ATPase domain hypothesis of haustorial transport and for ionic coupling of the haustorium of *Erysiphe graminis* to the host cell (*Hordeum vulgare*). New Phytol 107:541–548

Glidewell DC, Mims CW (1979) Ultrastructure of the haustorial apparatus in the rust fungus *Kunkelia nitens*. Bot Gaz 140:148–152

Gold RE, Littlefield LJ (1979) Light and scanning electron microscopy of the telial, pycnial and aeciel stages of *Melampsora lini*. Can J Bot 57:629–638

Gold RE, Littlefield LJ, Statler GD (1979) Ultrastructure of the pycnial and aecial stages of *Puccinia recondita*. Can J Bot 57:74–86
Gunning BES (1977) Transfer cells and their roles in transport of solutes in plants. Sci Prog (Oxford) 64:539–568
Harder DE (1978) Comparative ultrastructure of the haustoria in uredial and pycnial infections of *Puccinia coronata avenae*. Can J Bot 56:214–224
Harder DE (1984) Developmental ultrastructure of hyphae and spores. In: Bushnell WR, Roelfs AP (eds) The cereal rusts. Academic, pp 333–373
Harder DE, Chong J (1984) Structure and physiology of haustoria. In: Roelfs AP (ed) Bushnell WR. The cereal rusts. Academic Press, Inc, pp 431–467
Harder DE, Chong J (1991) Rust haustoria. In: Mendgen K, Lesemann DE (eds) Electron microscopy of plant pathogens. Springer, Berlin, pp 235–248
Harder DE, Rohringer R, Samborski DJ, Kim WK, Chong J (1978) Electron microscopy of susceptible and resistant near isogenic (Sr616/Sr6) lines of wheat infected by Puccinia graminis tritici. I. The host-pathogen interface in the compatible (Sr6/P6) interaction. Can J Bot 56:2955–2966
Hardwick NV, Greenwood AD, Woods RKS (1971) The fine structure of the haustorium of Uromyces appendiculatus in Phaseolus vulgaris. Can J Bot 49:383–390
Heath MC (1971) Haustorial sheath formation in cowpea leaves immune to rust infection. Phytopathology 61:383–388
Heath MC (1976) Ultrastructural and functional similarity of the haustorial neckband of rust fungi and the Casparian strip of vascular plants. Can J Bot 54:2484–2489
Heath MC (1997) Signaling between pathogenic rust fungi and resistant or susceptible host plants. Ann Bot 80:713–720
Heath MC, Bonde MR (1983) Ultrastructural observations of the rust fungus *Physopella zeae* in *Zea mays*. Can J Bot 61:2231–2242
Heath MC, Heath IB (1975) Ultrastructural changes associated with the haustorial mother cell during haustorium formation in *Uromyces phaseoli* var. *vignae*. Protoplasma 84:297–314
Heath MC, Skalamera D (1997) Cellular interactions between plants and biotrophic fungal parasites. Adv Bot Res 24:195–225
Hickey EL, Coffey MD (1978) A cytochemical investigation of the host-parasite interface in *Pisum sativum* infected by the downy mildew fungus *Peronospora pisi*. Protoplasma 97:201–220
Hirata K, Kojima M (1962) On the structure of the sac of the haustorium of some powdery mildews, with some considerations on the significance of the sac. Trans Mycol Soc Jpn 3:43–46
Hoch HC, Staples RC, Whitehead B, Comeau J, Wolf ED (1987) Signaling for growth orientation and cell differentiation by surface topography in *Uromyces*. Science 235:1659–1662
Kajiwara T (1971) Structure and physiology of haustoria of various parasites. In: Adai S, Ouchi S (eds) Morphological and biochemical events in plant-parasite interaction. Mochiznki Publ Co, pp 255–277
Katz D, Sussman M, Mierzwa R, Evert R (1988) Cytochemical localization of ATPase activity in oat root localizes a plasma membrane-associated soluble phosphatase, not the proton pump. Plant Physiol 86:841–847
Khan SR, Kimbrough JW, Webb PG (1982) The fine structure of septa and haustoria of Cronartium quercuum formae speciales fusiforme on Quercus rubra. Mycologia 74:809–819
Kolmer JA, Ordonez ME, Groth JV (2009) The rust fungi. In: Encyclopedia of life sciences (ELS). Wiley, Chichester
Larous L, Kameli A, Lösel DM (2008) Ultrastructural observations on *Puccinia menthae* infections. J Plant Pathol 90:185–190
Littlefield LJ (1972) Development of haustoria of Melampsora lini. Can J Bot 50:1701–1703
Littlefield LJ, Bracker CE (1972) Ultrastructural specialization of the host-pathogen interface in rust-infected flax. Protoplasma 74:271–305
Littlefield LI, Heath MC (1979) Ultrastructure of rust fungi. Academic, New York

Longo N, Bruscaglioni L (1986) Ultrastructural observations of the dikaryotic haustorium of *Cronartium flaccidum* in *Vincetoxicum hirundinaria medicus*. Caryologia 39:51–64
Losel DM, Lewis DH (1974) Lipid metabolism in leaves of *Tussilago farfara* during infection by *Puccinia poarum*. New Phytol 73:1157–1169
Manners J (1989) The host-haustorium interface in powdery mildews. Aust J Plant Physiol 16:45–52
Manocha MS (1966) Fine structure of rust haustoria in susceptible and resistant wheat. Indian Phytopathol 19:159–161
Manocha MS (1975) Autoradiography and fine structure of host-parasite interface in temperature-sensitive combinations of stem rust. J Phytopathol 82:207–215
Mapuranga J, Zhang N, Zhang L, Chang J, Yang W (2022) Infection strategies and pathogenicity of biotrophic plant fungal pathogens. Front Microbiol 13:799396
Mares DJ (1979) A light and electron microscope study of the interaction of yellow rust *Puccinia striiformis* with a susceptible wheat cultivar. Ann Bot 43:183–190
Mendgen K (1973) Microbodies (glyoxysomes) in infection structures of *Uromyces phaseoli*. Protoplasma 78:477–482
Mendgen K (1975) Ultrastructural demonstration of different peroxidase activities during bean rust infection process. Physiol Plant Pathol 6:275–282
Mendgen K (1979) Microautoradiographic studies on host-parasite interactions. II. The exchange of ^{3}H-lysine between *Uromyces phaseoli* and *Phaseolus vulgaris*. Arch Microbiol 123:129–135
Mendgen K (1981) Nutrient uptake in rust fungi. Phytopathology 71:983–989
Mendgen K, Heitefuss R (1975) Micro-autoradiographic studies on host-parasite interactions. I. The infection of *Phaseolus vulgaris* with tritium labeled uredospores of *Uromyces phaseoli*. Arch Microbiol 105:193–199
Mendgen K, Struck C, Voegele RT, Hahn M (2000) Biotrophy and rust haustoria. Physiol Mol Plant Pathol 4:141–145
Mims CW, Glidewell DC (1978) Some ultrastructural observations on the host-pathogen relationship within the telial gall of the rust fungus *Gymnosporangium juniperi-virginianae*. Bot Gaz 139:11–17
Morre DJ, Mollenhauer HH (1974) The endomembrane concept: a functional integration of endoplasmic reticulum and Golgi apparatus. In: Robards AB (ed) Dynamic aspects of plant ultrastructure. McGraw-Hill, New York, pp 84–137
Peyton GA, Bowen CC (1963) The host-parasite interface of *Peronospora manshurica* on *Glycine max*. Am J Bot 50:787–797
Read ND, Kellock LJ, Collins TJ, Gundlach AM (1997) Role of topography sensing for infection structure differentiation in cereal rust fungi. Planta 202:163–170
Rice MA (1927) The haustoria of certain rusts and the relation between host and pathogen. Bull Torrey Bot Club 54:63–153
Rijkenberg FHJ (1975) The uredial stage of maize rust. Proc Electron Microsc Soc S Afr 5:35–36
Rijkenberg FHJ, Truter S (1973) Haustoria and intracellular hyphae in the rusts. Phytopathology 63:281–286
Rijo L, Sargent JA (1974) The fine structure of the coffee leaf rust. Hemileia vastatrix. Can J Bot 52:1363–1367
Robb J, Harvey AE, Shaw M (1975a) Ultrastructure of tissue cultures of *Pinus monticola* infected by *Cronartium ribicola* I. Pre-penetration host changes. Physiol Plant Pathol 5:1–8
Robb J, Harvey AE, Shaw M (1975b) Ultrastructure of tissue cultures of *Pinus monticola* infected by *Cronartium ribicola* II. Penetration and post-penetration. Physiol Plant Pathol 5:9–18
Silva MDC, Guerra-Guimarães L, Diniz I, Loureiro A, Azinheira H, Pereira AP, Tavares S, Batista D, Várzea V (2022) An overview of the mechanisms involved in Coffee-*Hemileia vastatrix* interactions: plant and pathogen perspectives. Agronomy 12:326
Staples RC (2000) Research on the rust fungi during the twentieth century. Annu Rev Phytopathol 38:49–69

Staples RC, Hoch HC (1997) Physical and chemical cues for spore germination and appressorium formation by fungal pathogens. In: Carroll GC, Tudzynski P (eds) Plant relationships. Part A. The Mycota, vol V. Springer, Berlin, pp 27–40

Sutton PN, Henry MJ, Hall JL (1999) Glucose, and not sucrose, is transported from wheat to wheat powdery mildew. Planta 208:426–430

Voegele RT, Hahn M, Mendgen K (2009) The uredinales: cytology, biochemistry, and molecular biology. In: Esser K (ed) The Mycota. A comprehensive treatise on fungi as experimental systems for basic and applied research. Springer, Berlin/Heidelberg, pp 69–98

Wilson IM, Henderson DM (1966) British rust fungi. Cambridge University Press, London

Woods AM, Gay IL (1988) The interface between haustoria of *Puccinia poarum* (monokaryon) and *Tussilago farfara*. Physiol Mol Plant Pathol 33:296–301

Zimmer DE (1970) Fine structure of *Puccinia carthami* and the ultrastructural nature of exclusionary seedling-rust resistance of safflower. Phytopathology 60:1157–1163

Recent Advancement in Fungal Biocontrol Agents

Najam-ul-Sehar Afshan

1 Introduction

Globally, food production is at risk due to different plant diseases and pests, especially crops having increased yield are more frequently attacked by the pathogens and pests making them more vulnerable to diseases. Many living organisms including fungi, viruses, bacteria, and nematodes attack on plants and obtain nutrients from them. The use of synthetic pesticides (insecticides, fungicides, and herbicides) has become an important part of agriculture as pest management approaches mostly rely on them. Besides the prevalence of chemical approach on other control ways, the usage of man-made pesticides/fungicides in management of plant diseases/pests is gradually decreasing due to rising global concerns on hazards owing to the food and environmental residues (Juntarawijit and Juntarawijit 2018; Ons et al. 2020; Palmieri et al. 2022). Due to negligible harmful impacts on the environment and increased safety, usage of biological control agents to counter plant diseases and pests is becoming a more feasible and reliable alternative to synthetic pesticides and is accepted for use in organic cultivation (Thambugala et al. 2020; Collinge et al. 2022; Palmieri et al. 2022).

2 Fungal Biocontrol Agents (FBCAs)

Currently, usage of microbial antagonists against many plant diseases and pests is gaining importance as many commercial bioproducts comprising microbial BCAs have been effectively introduced in modernized agriculture (Thambugala et al. 2020). Recently, exploratory research work on naturally existing microorganisms,

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like fungi, for the prevention of crop diseases as biocontrol agents has become more intense. As biocontrol agents, the fungi can help against different pests like microbial pathogens and nematodes infecting different plant parts and provide shield against diseases by the support of biocontrol strategies like mycoparasitism, antibiosis, competition, conferring induced systemic resistance to the host plant, and mycovirus treated cross-protection. Hence, the utilization of a fungal biocontrol agent (FBCA) is now acknowledged as an increasingly developing natural process in the area of agriculture for improved yield of plants and increased food production (Singh and Giri 2017; Thambugala et al. 2020; Lahlali et al. 2022).

There is rapid increase in the application of FBCAs against plant pathogens because fungi are target specific and have a relatively high sexual and asexual reproductive frequency with a small generation time. Further, they are highly sustainable in the environment as they can persist easily in the absence of the host, living as a saprotroph instead of parasite (Thambugala et al. 2020). For improvement in biocontrol ability, advanced biotechnological and genetic techniques could be used for introducing desired beneficial fungal genes into the host plants genomes as well as these genes may be interrupted or overexpressed (Ghorbanpour et al. 2018).

Extensive research work has done to develop different fungal strains as the biocontrol means against plant diseases including *Trichoderma* spp., arbuscular mycorrhizas (AMF), ectomycorrhizas, yeasts, rust fungi and endophytes. Among these, the genus *Trichoderma* Pers. is the most prevalent one (Abdullah et al. 2021) including other fungi, such as *Alternaria* Nees, *Botrytis* P. Micheli ex Pers., *Aspergillus* P. Micheli ex Haller, *Fusarium* Link, *Gaeumannomyces* Arx & D.L. Olivier, *Phytophthora* de Bary, *Pyricularia* (Sacc.) Sacc., *Pythium* Pringsh., *Rhizoctonia* DC. (Pal and Gardener 2006; Adebola and Amadi 2010), *Penicillium* Link (Alam et al. 2011), *Gliocladium* Corda (Agarwal et al. 2011) and *Saccharomyces* Meyen (Nally et al. 2012).

Selected strains of nematophagous fungi can be employed as biological control agents to counter root-knot nematode, *Meloidogyne enterolobii* Yang & Eisenback under certain circumstances (Silva et al. 2017). Similarly, Arbuscular mycorrhizal fungi (AMF) can also provide resistance to plants against numerous soil-borne pathogens including root-knot nematodes, however, their mode of action is still obscure (Vos et al. 2012; Tariq et al. 2020).

Different fungal antagonists are significant for the regulation of plant pathogens and are being utilized as Biocontrol Agents (BCAs) globally. Thambugala et al. (2020) provided an inclusive list of different FBCAs used against fungal plant pathogens, clarifying their phylogenetic relationships following modern taxonomic concepts. Their review included details of about 300 fungal antagonists with their target pathogens and plant diseases. Among these, genus *Trichoderma* was found dominant having 25 BCAs against different plant diseases proliferated by fungi.

Trichoderma is a noteworthy mycoparasite and used as biopesticide against numerous aeronautical and soil-borne plant pathogens in field or greenhouse experiments. Many fungal cell wall-degrading enzymes like chitinases, hydrolases, 1,3- proteases, glucanases, and mannanases are produced by different members of this genus and are used in commercial agriculture including greenhouse industry (Thambugala et al. 2020). For determination of biocontrol process of different *Trichoderma* spp. against

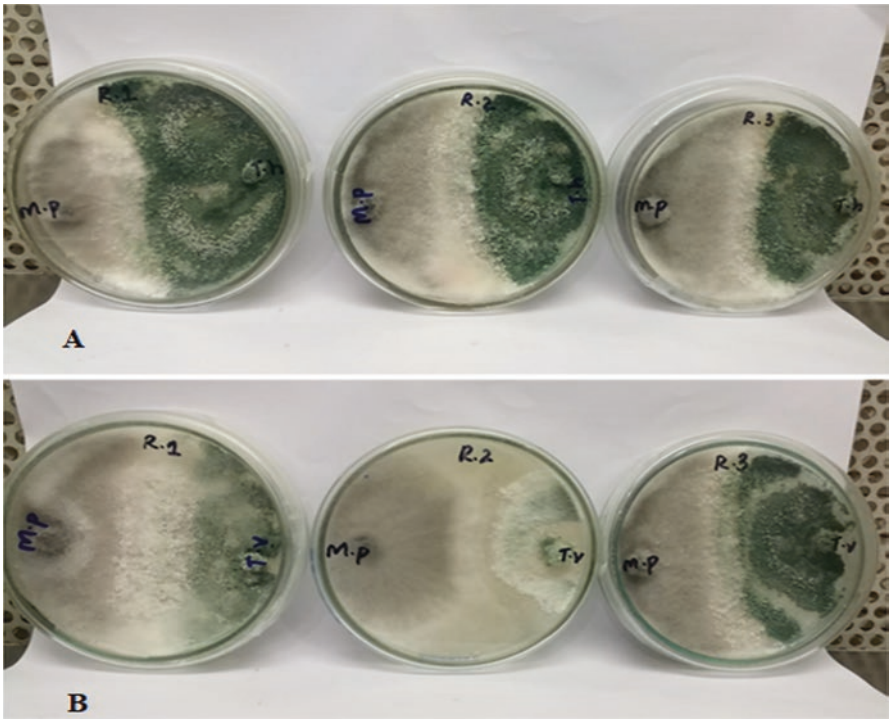

Fig. 1 (**A**) Interaction of *Trichoderma harzianum* and *Macrophomina phaseolina* (**B**) Interaction of *Trichoderma viride* and *Macrophomina phaseolina*

fungal pathogen *Macrophomina phaseolina* (Tassi) Goid., *in-vitro* interaction of *M. phaseolina* with *T. harzianum* Rifai and *T. viride* Pers. was performed in Fungal Biotechnology and systematics Research Laboratory, Institute of Botany, University of the Punjab, Lahore, Pakistan by the author and her team. Zones of inhibition appeared indicating inhibitory effects of both antagonists against pathogen (Fig. 1).

Different filamentous fungi are also found very potential BCAs against different olive tree pathogens including fungi, bacteria and nematodes. A complete review was provided about all the experiments conducted to control Olive pathogens using FBCAs including mycorrhizal and endophytic filamentous fungi. They adopted various modes of action like activation of the plant's defensive responses, antibiosis, competition and parasitism etc. (Poveda and Baptista 2021).

3 Modes of Action of Fungal Biocontrol Agents (FBCAs)

The complexity in biocontrol mechanisms of FBCAs are primarily due to proteins and different molecules secreted by fungi working as effectors, antibiotics, elicitors as well as degrading enzymes (Srivastava et al. 2021). Different modes of action used by FBCAs have been identified and categorized as (Fig. 2):

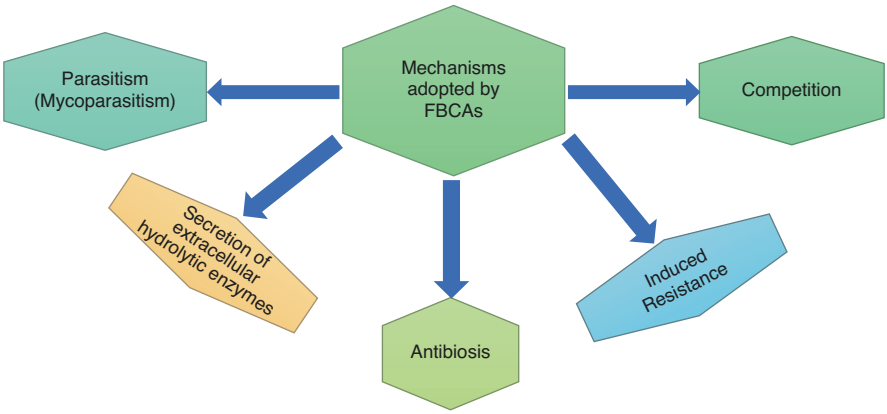

Fig. 2 Different mechanisms adopted by FBCAs

(i) Direct antagonism (antibiosis, mycoparasitism and competition)
(ii) Indirect antagonism (induced resistance etc.) (Raymaekers et al. 2020)

A single BCA depends on different mechanisms and its ability to adopt a specific mode of action against a plant pathogen varies according to the pathogen category, specific host plant and prevalent ecological conditions including temperature, pH and nutrient availability etc. (Vinale et al. 2008; Palmieri et al. 2022). So, there are four basic mechanisms adopted by fungal biocontrol agents against plant pathogens including (a) exploitation competition for resources i.e. carbon, nitrogen, oxygen etc. (b) antibiosis i.e. interference competition for space secreting toxic secondary metabolites (c) mycoparasitism and (d) induced resistance. Further, stimulation of plant growth due to improved nutrient absorption or through variations in plant hormonal pathways could be considered a fifth mechanism of biocontrol by rhizosphere bacteria and fungi. However, it is not recognized as a biocontrol strategy by some researchers (Jensen et al. 2017; Stenberg et al. 2021).

Comprehensive study on different fungal plant pathogens is required to understand plant pathogens, their diseases, modes of actions, disease cycles and pathogen/pest regulator strategies (Wang and Coleman 2019). Only scanty data is available on systematic research related to defense-response activation processes and signaling identification to understand key interactions between fungi and their hosts as well as disease-resistance peculiarities and mechanisms for major crop plants (Peng et al. 2021). Initiation of recent biotechnological methods will lead to increase the usage of fungal biocontrol agents (FBCAs) against different plant diseases. During past several years, numerous experiments have been carried out to identify and characterize novel FBCAs and assess their effectiveness against different plant pathogens under diverse environmental conditions. Here we provide details about some rapidly developing FBCAs and their modes of actions using recent advanced technologies.

4 Modern Biotechnological Approaches

Recent development in biotechnological research has opened ways to the development of fungal BCAs that can be used against a wide range of plant diseases. The development and application of genomics, genetic engineering, and recombinant DNA techniques for the improvement of fungal strains for biocontrol mechanisms have brought a revolution. An acceptable and possibly long-term biocontrol option is the production of resistant crop varieties or clones in addition to identify fungal antagonists, their genetic traits and to evaluate their potential for enhanced biocontrol action (Janisiewicz and Korsten 2002; Droby 2006; O'Brien 2017; Thambugala et al. 2020).

The several lytic enzyme-encoding genes introduced into *Trichoderma virens* genome has emerged in a fungal strain showing significantly improved inhibition of the fungal plant pathogens including *Globisporangium ultimum* (Trow) Uzuhashi (= *Pythium ultimum* Trow), *Rhizoctonia solani* J.G. Kühn and *Rhizopus arrhizus* A. Fisch. (= *Rhizopus oryzae* Went & Prins.) by secreting a mixture of glucanases (Djonovic et al. 2007).

Genetic transformation of *Cyclaneusma minus* (Butin) DiCosmo, Peredo & Minter was done by using protoplasts produced through incubation with Glucanex™ enzyme. It was varied with a gene coding green fluorescent protein (GFP), allowing to recognize numerous *Trichoderma* strains having biocontrol capabilities against the disease (McDougal et al. 2012).

The usage of endophytic fungi as biocontrol agents have been studied in detail by different researchers indicating their biocontrol strategies as parasite causing direct inhibition of the pathogen, lytic enzymes and secondary metabolites formation and competition for nutrients and/or space (Chadha et al. 2015; Deshmukh et al. 2015; Card et al. 2016; Larran et al. 2016; De Vries et al. 2018; De Silva et al. 2019; Rabiey et al. 2019). It was also found that endophytes can activate systematic resistance through signaling pathways that are either salicylic-acid (SA) or JA/ET-dependent and may act as BCA by inducing host resistance (Li et al. 2018; Bastías et al. 2018; Vahabi et al. 2018; Poveda and Baptista 2021).

5 Microbial Consortia

Biocontrol research is primarily relied on the use of single microorganism, however, complicated interactions inside the soil microbial community and the environment have strong impact on the inoculant's functionality and persistence (Trivedi et al. 2020; Pozo et al. 2021). The biocontrol mechanisms using single microorganism that may be a fungus or a bacterium, sometime become useless due to the heterogeneity of the soil types, their characters and the variations in fungal pathogens (Niu et al. 2020; Trivedi et al. 2020). The reason behind this ineffectiveness is insufficient host colonization by useful microorganisms as well as their reduced effect on growth

and virulence of soil-borne pathogens. The major limitation for commercial exploitation of individual biocontrol agents is the comparatively narrow spectrum of their biocontrol activity against plant pathogens. A recent biological control approach to solve this problem is to develop mixture of microorganisms covering many target organisms and conditions inclusively (Kannan and Sureendar 2009; Faust 2019; Mitter et al. 2019).

In order to improve the efficacy and stability of microorganisms introduced in the soil and rhizosphere, a combination of BCAs comprising of two or more than two microbial strains, known as microbial consortia is developed (Niu et al. 2020). The layout of microbial consortia for the improvement of the recent biological control strategies is being considered a main process in biotechnology, and is also used in the sustainable agricultural practices (Minchev et al. 2021) for the prevention of soil-borne diseases. Different microbiota comprising of discrete application of fungi (Vargas-Inciarte et al. 2019) or prokaryotes (Liu et al. 2017; Palmieri et al. 2017) or use of a combination of bacteria and fungi (Minchev et al. 2021; Win et al. 2021) are available, for example, the insect pathogen *Metarhizium brunneum* Petch jointly with the FBCA *Clonostachys rosea* (Link) Schroers against fungal pathogen *Fusarium culmorum* (Wm.G. Sm.) Sacc. and root-feeding insects of wheat (Keyser et al. 2016; Collinge et al. 2022).

6 Myconanotechnology

The development of sustainable techniques and tools for biocontrol strategies circumventing traditional agriculture practices is the foremost requirement against virulent microbial pathogens of plants. Nanotechnology provides an explication to the rising challenges in plant disease management as the engineered nanoparticles (NPs) possess the desired shape and size having specific optical properties enabling them to be used for various agricultural applications especially as novel pesticide formulations with enhanced pathogen and pest control efficacies. Hence nanotechnology provides a good management alternative to tackle different plant diseases produced by bacteria, fungi, viruses and pests (Alghuthaymi et al. 2021; Mansoor et al. 2021).

A comprehensive review about the practice of different nanoparticles to prevent phytopathogenic fungi is provided by Cruz-Luna et al. (2021). For the regulation of plant diseases, silica, carbon, silver, and non-metal oxides or alumino-silicates are the most commonly used nanoparticles (Alghuthaymi et al. 2021), while silver nanoparticles (AgNPs) have excellent antimicrobial properties, followed by Cu nanoparticles (Thakkar et al. 2010; Ghosh et al. 2012; Mansoor et al. 2021). The formation of nanoparticles using microorganisms especially fungi is an emerging green nanotechnology and has recently developed as a novel way for nanoparticle synthesis as it is harmless in terms of toxicity while NPs developed through chemical and physical methods may cause environmental hazards by imparting toxicity (Bhattacharya et al. 2022).

Fungi have prodigious prospects in nanotechnology and are gaining more consideration due to their environment friendly nature of metabolite-mediated nanoparticles and have found properties in plant disease management practices by producing environment friendly, non-toxic fungicides and insecticides to improve agricultural productions (Elijah et al. 2021).

Myconanotechnology, an ally between mycology and nanotechnology (Hanafy 2018; Sousa et al. 2020) is of extreme importance due to presence of diverse fungal species (Khande and Shahi 2018) while mycofabrication is a term used for the formation and designing of metal nanoparticles by the use of fungi (Guilger-Casagrande and Lima 2019). For biological systems, many fungal extracts have been employed in the synthesis of silver (Ag) nanoparticles and are applied in agriculture sector, exhibiting good biocontrol potential against plant-pathogenic bacteria, fungi, insects and viruses because of their high bioactivity and antimicrobial properties (Tomah et al. 2020). Hence, the usage of AgNPs against plant pathogens can reduce the biocides and pesticides usage, improve the efficacy of agrochemicals (Ahmed and Dutta 2019; Ramírez-Valdespino and Orrantia-Borunda 2021) and show effectiveness against a broader range of microbes at very minute concentrations with almost slight intrinsic toxicity towards other life forms (Singh et al. 2016; Mohanta et al. 2018; Moradi et al. 2021). Myconanotechnology is an eco-friendly and economical choice and the use of fungi in this strategy is appealing due to production of different enzymes and their easy handling in the laboratory (Gade et al. 2010; Youssef et al. 2017; Adebayo et al. 2021; Bahrulolum et al. 2021; Zaki et al. 2022).

6.1 Filamentous Fungi

Filamentous fungi including *Penicillium*, *Fusarium*, *Aspergillus*, and *Trichoderma* are the microorganisms having greatest potential for NP biosynthesis due to extracellular protein production, easy and extensive cultivation, biomass collection, greater tolerance to metals and resistance to high pressure (Narayanan and Sakthivel 2010; Vahabi et al. 2011; Salvadori et al. 2014; Guilger-Casagrande and Lima 2019; Rai et al. 2021).

Ramírez-Valdespino and Orrantia-Borunda (2021) reported that *Trichoderma* is the potential fungus used for the mycosynthesis of NPs and development of products useful in the improvement of crop weight and control of phytopathogens. The main NPs synthesized by *Trichoderma* include copper (CuNPs) and CuONPs, gold (AuNPs), ZnONPs, AgNPs, and selenium (SeNPs) showing antimicrobial activities.

A wider range of MtNPs such as gold, iron oxide, silver, and even bimetallic nanoparticles can be produced by filamentous fungi (Molnár et al. 2018) such as *Phoma* sp., *Pestalotiopsis* sp., *Humicola* sp., *Trichoderma* sp., *Fusarium oxysporum* Schltdl., *Aspergillus niger* Tiegh., *Amorphotheca resinae* Parbery (= *Hormoconis resinae* (Lindau) Arx & G.A. de Vries), *Phanerodontia chrysosporium* (Burds.) Hjortstam & Ryvarden (= *Phanerochaete chrysosporium* Burds.) and *Penicillium* spp. (Mittal et al. 2020; Rai et al. 2021).

Trichoderma harzianum is one of the utmost significant fungal species in agriculture serving as a biological control agent against phytopathogens. Different enzymes (N-acetyl-β-D-glucosamine deacetyl transferase, chitinases, and proteases) released by this fungus are critical to mycoparasitism (Guilger-Casagrande et al. 2019; Konappa et al. 2021; Zaki et al. 2022). Due to its potential for the control of phytopathogens and ease to handle, *T. harzianum* has been greatly studied in the area of nanotechnology and biotechnology, offering new possibilities for the production of novel products (Fraceto et al. 2018; Zaki et al. 2021, 2022). Several novel fungal proteins are obtained from different fungal species having exceptional capping and reducing properties that may be utilized in the biological formation of different metallic nanoparticles (Li et al. 2012; Mohanta et al. 2018) and applied in agriculture sector as biocontrol agents.

6.2 Mushrooms

The use of mushroom and their extracts in biological synthesis of AgNPs is a simple, novel, rapid, economical and eco-friendly approach. However, due to seasonal appearance of mushrooms along with their critical location of growth, very few reports exist about the applications of mushrooms in metallic nanoparticles synthesis (Owaid and Ibraheem 2017).

Numata et al. (2004) examined the role of mushrooms in myconanotechnology by producing nano-fibers from the purified polysaccharides (β-1,3-glucan) of *Schizophyllum commune* Fr. Then, proteins extracted from the substrate of *Pleurotus ostreatus* (Jacq.) P. Kumm., were used against microbes *in vitro* as nano-drugs (Vigneshwaran et al. 2007). Mohanta et al. (2016) reported mycosynthesis of AgNPs utilizing *Ganoderma lucidum* (Curtis) P. Karst. and *G. applanatum* (Pers.) Pat. extracts having higher antimicrobial activities. Inbakani and Siva (2017) described the biological synthesis of AgNPs from edible mushrooms extracts including *Agaricus bisporus*, *Calocybe indica* Purkay. & A. Chandra, *Pleurotus floridanus* Singer, and *P. ostreatus* as a bioreductant and biocontrol agent against various bacteria.

The wild mushroom *Ganoderma sessiliforme* Murrill was also used for the production of silver nanoparticles (AgNPs) and their antimicrobial activity was evaluated opposed to common food-borne bacteria. The synthesized AgNPs were found efficient biocontrol agents against food-borne pathogens, having promising application in the food packaging industry (Mohanta et al. 2018). The oyster mushroom was used in the production and application of nanoparticles especially AgNPs that showed repressive effects against many plant pathogens including bacteria, fungi, and yeasts etc. (Owaid 2019).

Production of mycosynthesized AgNPs from different mushrooms including *Agaricus bisporus* (J.E. Lange) Imbach (Owaid et al. 2020), and *Pleurotus* spp., having biocontrol potential against pathogenic fungi, yeasts, bacteria, and tumors

etc. have achieved recently (Owaid 2019; Jaloot et al. 2020). Similarly, Silver nanoparticles mycosynthesized from Shaggy Bracket fungus, *Inonotus hispidus* (Bull.) P. Karst. have been reported to have antimicrobial peculiarities against bacteria and fungi (Jaloot et al. 2020).

Silver nanoparticles were also prepared from crude polysaccharide extracts of *A. brasiliensis* Fr., *Agaricus bisporus*, and *Tropicoporus linteus* (Berk. & M.A. Curtis) L.W. Zhou & Y.C. Dai (= *Phellinus linteus* (Berk. & M.A. Curtis) Teng) and tested against many pathogens showing 100 times more effectivity than antibiotics. The nanoparticles synthesized from these mushrooms were found very effective against *Pseudomonas aeruginosa* and *Candida albicans* (Klaus et al. 2020).

Powdery Mildews caused by *Golovinomyces ambrosiae* (Schwein.) U. Braun & R.T.A. Cook on Sunflower (*Helianthus annuus* L.) is an important disease worldwide including Pakistan. In an experiment conducted by our team at Fungal Biotechnology and Systematics Research Laboratory, University of the Punjab, Lahore, Pakistan, the silver nanoparticles synthesized from *Pleurotus cystidiosus* O.K. Mill. were outspread to the Sunflower plants infected with powdery mildew fungus and found suitable in the control of this disease. Biochemical analysis was also done to observe the physiological changes in plants after treatments. The suppression in further growth of mycelia of the pathogen was observed after application of the silver nanoparticles (Fig. 3).

During green synthesis of MtNPs, it is important to identify most suitable fungus for making nanoparticles with the required characteristics, the suitable fundamentals for its growth, maintenance of sterile conditions and proper time needed for the fungus growth. However, more studies are required to unveil this important aspect of biocontrol research, as use of fungi for the green production of MtNPs has many possible applications especially in agriculture sciences for the regulations of plant pathogens, weeds and pests.

7 Arbuscular Mycorrhizal Fungi (AMF)

Arbuscular mycorrhizal fungi (AMF) are the most ordinary and important group of fungi having definite inhibitory or antagonistic effect on soil-borne pathogens (Allsup et al. 2021). AMF plays significant role as biocontrol agent by regulating the production of secondary bioproducts in host plants by making changes in the morphological or microscopical structure of plant roots, improves the chemical and physical characteristics of the rhizosphere environment and competes with different pathogens for photosynthates and space as well as activates disease resistance and defense systems in plants (Aseel et al. 2019; Pozo et al. 2013; Singh et al. 2019). These different mechanisms/processes operate frequently and simultaneously making mycorrhizal fungi effective BCAs to counter fungal pathogens (Hilbig and Allen 2019), oomycetes (Hou et al. 2019), nematodes (Poveda et al. 2020) and/or bacteria (Poveda et al. 2021; Poveda and Baptista 2021).

Fig. 3 (**A**–**H**) Application of AgNPs from *Pleurotus cystidiosus* on sunflower plants infected with powdery mildew showing disease suppression

AMF has been extensively employed as an advanced biological control way against different phytopathogenic fungi. The role of AMF in biological control process is a recent pest control technology, as about 30 AMF species have found productive against plant soil-borne diseases (Weng et al. 2022). Therefore, detailed

analysis of the biological control mechanism of AMF against plant diseases is of great theoretical and practical concern (Lin et al. 2021).

AMF provides improved resistance against plant diseases caused by *Phytophthora parasitica* Dastur (Vigo et al. 2000; Liu et al. 2018), *Fusarium oxysporum* Schltdl. (Wang et al. 2012), and *Rhizoctonia solani* J.G. Kühn (Huang et al. 2020), and boosts mineral nutrient attainment, especially phosphorus (Smith and Read 2008). Mishra et al. (2018) reported a reduction in the occurrence of nematode attacks and fungal diseases on host plants by 44–57% and 30–42% respectively due to biocontrol potential of Arbuscular mycorrhizal fungi (AMF).

AMF may reduce disease severity as studies on inoculation of *Glomus mosseae* (T.H. Nicolson & Gerd.) Gerd. & Trappe on *Pisum sativum* showed reduction in the prevalence of powdery mildews (*Erysiphe pisi* DC.) indicating a decrease in the disease index (DI) from 55.2% to 28.7% (Liu et al. 2018). AMF also modify different defense mechanisms in plants such as stimulation of different plant biochemicals, damage compensation, increase in plant nutrients acquisition, and induction of disease-resistance genes capability to compete with plant pathogens for food products (Liu et al. 2018; Varma and Choudhary 2019).

Arbuscular mycorrhizal fungi are also known to increase plants protection against different biotrophic fungal pathogens including rusts and powdery mildews. To investigate the root colonization frequency of mycorrhizae of plants relative to powdery mildew disease, experiments were conducted on powdery mildew infected plants of *Helianthus annuus*. Results showed that plants affected with powdery mildew fungus *Golovinomyces ambrosiae* (Schwein.) U. Braun & R.T.A. Cook produce more arbuscules as the percentage of supply and exchange of nutrients increase with enhanced intensity of powdery mildew disease (Afshan et al. 2022).

AMF may lessen the utilization of pesticides by minimizing the destruction caused by fungi, bacteria, nematodes and other pathogens of different plants (Li et al. 2018; Weng et al. 2022). Moreover, the biocontrol peculiarities of AMF are wide-ranging and more distinct against fungal root pathogens than shoot ones. AMF is more effective biocontrol agent against a number of fungal pathogens including *Alternaria*, *Botrytis, Colletotrichum*, *Cylindrocladium*, *Erysiphe, Fusarium*, *Gaeumannomyces*, *Macrophomina*, *Rhizoctonia* and *Verticillium* etc. but is not much effective against many bacterial and viral pathogens (Pandit et al. 2022).

The limitations of AMF cultivation methods also restrict their application as their mass production through fermentation and industrialization is currently not possible. Therefore, rapid cultivation of AMF and assessment of microbial biocontrol including effect of biocontrol microorganisms on other microorganisms' diversity in the soil are future research priorities. The biocontrol mechanism of AMF is influenced by various biotic and abiotic factors. There is need for the monitoring factors to enhance the plant benefits including optimal inoculation period and dose, environmental conditions, farming methods and fertilization amount, should be considered in detail to launch a scientific and successful AMF biocontrol program (Weng et al. 2022).

8 Rust Fungi

The plant rust fungi are considered important biocontrol agents because they are highly host specific, virulent, may cause infections directly through stomata or the host epidermis, and are wind dispersed (Gardner 2006; Morin et al. 2011; Barton 2012). Their high mobility within and between plant populations helps in long distance dispersal required for the prevention of invasive alien weed varieties occupying broad areas (Morin et al. 2012; Tanner et al. 2015). Globally, they are ever more recognized as being great potent and harmless biocontrol sources in classical weed biological control strategies.

The rust fungi are being employed for classical biological control (CBC) of weeds after the declaration of *Puccinia chondrillina* (Bubák & Syd.) Arthur & Mains against *Chondrilla juncea* (skeleton weed), in Australia in 1971 (Hasan & Wapshere 1973). After this, several rust fungi are reported and being employed as biological control agents against various noxious and invasive weeds that are a continuous threat to agricultural productivity and cause considerable reduction in the quantity and quality of crop production (Yandoc-Ables et al. 2006). Morley and Morin (2008) reported that *Endophyllum osteospermi* (Doidge) (boneseed rust) is a potential biocontrol source for boneseed *Chrysanthemoides monilifera* subsp. *monilifera* (L.) Norlindh, because it decreases reproduction and development of the plants, causing 'witches' brooms.

In Pakistan, parthenium weed (*Parthenium hysterophorus*) infected with rust fungus from different areas of Punjab and Khyber Pakhtunkhwa was taken and rust fungus was characterized and identified as *Puccinia abrupta* var. *partheniicola* (H.S. Jacks.) Parmelee. In order to investigate biological control potential of *P. abrupta* var. *partheniicola* against parthenium weed, post-infection biochemical analysis of healthy and infected plants was also performed. It was observed that chlorophyll, carotenoid, flavonoid and phenolic contents were higher in healthy plants as compared to infected ones. This work was a first attempt to describe the biological control potential of *Puccinia abrupta* var. *partheniicola* against *Parthenium* weed in Pakistan (Fig. 4). Recently, *Puccinia rapipes* Berndt & E. Uhlmann against *Lycium ferocissimum* Erkelenz, (African boxthorn) in Australia (Ireland et al. 2019); *P. spegazzinii* De Toni against *Mikania micrantha* Kunth in Australia (Anonymous 2020); *P. abrupta* var. *partheniicola* (H.S. Jacks.) Parmelee against *Parthenium hysterophorus* L. (Maharjan et al. 2020); *Phragmidium violaceum* against blackberries (Hennecke et al. 2021) and *P. komarovii* var. *glandulifera* against an exotic weed *Impatiens glandulifera* Royle (Pollard et al. 2022) have been introduced as fungal biocontrol agents.

Recently, the employment of advanced molecular and omic tools in the processes of biocontrol potential of certain FBCAs is a major research tool. Studies based on these tools help in the selection of a suitable criterion for the choice and use of new FBCAs. Furthermore, recognition and regularization of FBCAs on plant body as well as in the environment, are being done using molecular tools, that is necessary for gaining information about the persistence of these agents (Palmieri et al. 2022). In order to take benefit of the antagonistic activity, knowledge of the particular

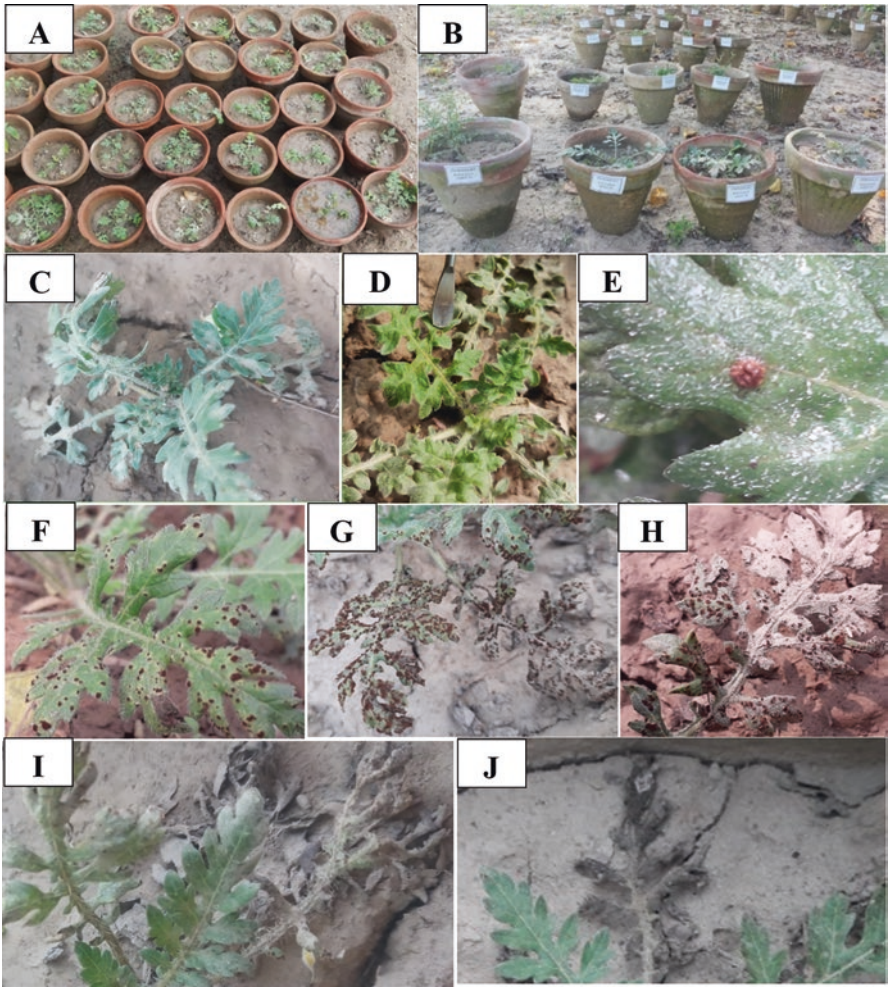

Fig. 4 (**A**–**J**) *Parthenium* plants showing development of rust infection & death of plant tissues

mechanism of biocontrol directed by FBCAs to counter plant pathogens at a molecular level is a fundamental requirement. Currently, the availability and development of next-generation sequencing (NGS) tools have brought revolution in the biocontrol field making it a functional approach (Collinge et al. 2022).

9 Recent Molecular Approaches

The production of whole genome sequencing, comparative genome and gene/protein expression studies for identification of molecular pathways have a tremendous impact in biocontrol techniques. Further, transcriptomics (RNAseq) and proteomics

data, and leading genes are potentially contributing a significant role in facilitation of fungal biocontrol mechanisms. The molecular and omic tools can provide a better, effective and quicker election of microbial antagonists, a comprehensive knowledge regarding their modes of act, a critical inspection to improve FBCAs activity, thus simplifying their registration procedures (Palmieri et al. 2022). Previously, research on the interactions of Microbial biological control agents and targeted pathogen with the resident microflora have been hindered due to limitations of available molecular methods. The usage of Next Generation Sequencing (NGS) techniques entailing metatranscriptomics and metagenomics have allowed identification of the composition and roles of the microbiome (Massart et al. 2015a, b). Different studies on signalomics and metametabolomics (Mhlongo et al. 2018) provided comprehensive information on developed MBCAs and resident microbes interactions. Finally, a complete understanding of MBCA-microbiota interactions following recent molecular and omic approaches in the mechanisms of biocontrol activity will provide better formulation and timely application of MBCAs avoiding any further failure (Köhl et al. 2019).

To understand biocontrol and plant-growth promoting ways of filamentous fungi, many molecular techniques are applied alone or in combination. For example, gene expression changes and utilization of omics approaches in the well-known biocontrol and plant-growth fostering agent *Trichoderma hamatum* (Bonord.) Bainier and *Trichoderma* sp. during antagonistic interactions (Shaw et al. 2016; Sharma et al. 2017), comparative study of genomics and transcriptomics to explain the biocontrol mechanisms employed by different mycoparasites *Paraphaeosphaeria minitans* (W.A. Campb.) Verkley, Göker & Stielow (= *Coniothyrium minitans* W.A. Campb.) against *S. sclerotiorum* (Zhao et al. 2020), *Chaetomium globosum* Kunze against *Bipolaris sorokiniana* (Darshan et al. 2020), and *Clonostachys rosea* against *Fusarium graminearum* Schwabe (Demissie et al. 2020) were studied describing excess production of fungal cell-wall-degrading enzymes (FCWDs) during process of parasitism. Lysøe et al. (2017) reported an advanced method of course-based transcriptomic way to recognize genes manifested in a three-way relation between the Biocontrol agent, *C. rosea*, the pathogen *Helminthosporium solani* Durieu & Mont., and the host *Solanum tuberosum*.

The function of drug efflux transporters in the biocontrol process of *Clonostachy rosea* against *Fusarium graminearum* was also demonstrated using comparative genomics (Broberg et al. 2021) following classical RNAseq protocol, while dual RNAseq analysis was performed in other studies (Palmieri et al. 2022). The manipulation of the omics approach in biocontrol processes of FBCAs against plant pathogens not only provides an inclusive knowledge of the fundamental molecular processes related to this method but also helps in further experimentation using different functional genetics techniques including targeted mutagenesis or overexpression analyses etc. for the confirmation of a particular gene/pathway included in the proposed biocontrol phenotype. The genus *Trichoderma,* a filamentous mycoparasitic fungus is extensively studies using recent molecular mechanisms of biocontrol.

References

Abdullah NS, Doni F, Mispan MS, Saiman MZ, Yusuf YM, Oke MA, Suhaimi NSM (2021) Harnessing *Trichoderma* in agriculture for productivity and sustainability. Agronomy 11:2559

Adebayo EA, Azeez MA, Alao MB, Oke AM, Aina DA (2021) Fungi as veritable tool in current advances in nanobiotechnology. Heliyon 7(11):e08480

Adebola MO, Amadi JE (2010) Antagonistic activities of *Paecilomyces* and *Rhizopus* species against the cocoa black pod pathogen (*Phytophthora palmivora*). Sci Afr 4:235–239

Afshan NS, Yaseen A, Niazi AR, Zulfiqar A, Riaz A, Qurra-tul-Ain RM, Fiza I (2022) Morphological and molecular characterization of *Golovinomyces ambrosiae* on sunflower (*Helianthus annuus*) in Pakistan, with its impact on plant metabolites and relative mycorrhizal status. J Plant Dis Prot 129:253–260

Agarwal T, Malhotra A, Trivedi PC, Biyani M (2011) Biocontrol potential of *Gliocladium virens* against fungal pathogens isolated from chickpea, lentil and black gram seeds. J Agric Technol 7(6):1833–1839

Ahmed AA, Dutta P (2019) *Trichoderma asperellum* mediated synthesis of silver nanoparticles: characterization and its physiological effects on tea [*Camellia sinensis* (L.) Kuntze var. assamica (J. Masters) Kitam.]. Int J Curr Microbiol App Sci 8(4):1215–1229

Alam SS, Sakamoto K, Inubushi K (2011) Biocontrol efficiency of Fusarium wilt diseases by a root-colonizing fungus *Penicillium* sp. Soil Sci Plant Nutr 57(2):204–212

Alghuthaymi MA, Rajkuberan C, Rajiv P, Kalia A, Bhardwaj K, Bhardwaj P, Abd-Elsalam KA, Valis M, Kuca K (2021) Nanohybrid antifungals for control of plant diseases: current status and future perspectives. J Fungi (Basel) 7(1):48

Allsup CM, Lankau RA, Paige KN (2021) Herbivory and soil water availability induce changes in arbuscular mycorrhizal fungal abundance and composition. Microb Ecol 84(1):141–152

Anonymous (2020) Rust pathogen for the biological control of the mile-a-minute weed. The Department of Agriculture, Fisheries and Forestry. media@agriculture.gov.au

Aseel DG, Rashad YM, Hammad SM (2019) Arbuscular mycorrhizal fungi trigger transcriptional expression of flavonoid and chlorogenic acid biosynthetic pathways genes in tomato against tomato mosaic virus. Sci Rep 9:9692

Bahrulolum H, Nooraei S, Javanshir N, Tarrahimofrad H, Mirbagheri VS, Easton AJ, Ahmadian G (2021) Green synthesis of metal nanoparticles using microorganisms and their application in the agrifood sector. J Nanobiotech 19:86

Barton J (2012) Predictability of pathogen host range in classical biological control of weeds: an update. BioControl 57:289–305

Bastías DA, Martínez-Ghersa MA, Newman JA, Card SD, Mace WJ, Gundel PE (2018) Jasmonic acid regulation of the anti-herbivory mechanism conferred by fungal endophytes in grasses. J Ecol 106:2365–2379

Bhattacharya J, Nitnavare R, Shankhapal A, Ghosh S (2022) Chapter 14 – Microbially synthesized nanoparticles: aspect in plant disease management. In: Kumar A, Aswani R (eds) Radhakrishnan EK. Academic, Biocontrol mechanisms of endophytic microorganisms, pp 303–325

Broberg M, Dubey M, Iqbal M, Gudmundssson M, Ihrmark K, Schroers HJ, Funck Jensen D, Brandström Durling M, Karlsson M (2021) Comparative genomics highlights the importance of drug efflux transporters during evolution of mycoparasitism in *Clonostachys* subgenus *Bionectria* (Fungi, Ascomycota, Hypocreales). Evol Appl 14:476–497

Card S, Johnson L, Teasdale S, Caradus J (2016) Deciphering endophyte behaviour: the link between endophyte biology and efficacious biological control agents. FEMS Microbiol Ecol 92:fiw114

Chadha N, Mishra M, Rajpal K, Bajaj R, Choudhary DK, Varma A (2015) An ecological role of fungal endophytes to ameliorate plants under biotic stress. Arch Microbiol 197:869–881

Collinge DB, Jensen DF, Rabiey M, Sarrocco S, Shaw MW, Shaw RH (2022) Biological control of plant diseases – what has been achieved and what is the direction? Plant Pathol 71:1024–1047

Cruz-Luna AR, Cruz-Martínez H, Vásquez-López A, Medina DI (2021) Metal nanoparticles as novel antifungal agents for sustainable agriculture: current advances and future directions. J Fungi 7:1033

Darshan K, Aggarwal R, Bashyal BM, Singh J, Shanmugam V, Gurjar MS, Solanke AU (2020) Transcriptome profiling provides insights into potential antagonistic mechanisms involved in *Chaetomium globosum* against *Bipolaris sorokiniana*. Front Microbiol 11:2971

Demissie ZA, Witte T, Robinson KA, Sproule A, Foote SJ, Johnston A, Harris LJ, Overy DP, Loewen MC (2020) Transcriptomic and exometabolomic profiling reveals antagonistic and defensive modes of *Clonostachys rosea* action against *Fusarium graminearum*. Mol Plant-Microbe Interact 33:842–858

Deshmukh SK, Verekar SA, Bhave SV (2015) Endophytic fungi: a reservoir of antibacterials. Front Microbiol 5:715

De Vries S, von Dahlen JK, Schnake A, Ginschel S, Schulz B, Rose LE (2018) Broad-spectrum inhibition of *Phytophthora infestans* by fungal endophytes. FEMS Microbiol Ecol 94:fiy037

De Silva NI, Brooks S, Lumyong S, Hyde KD (2019) Use of endophytes as biocontrol agents. Fungal Biol Rev 33:133–148

Djonovic S, Vargas AW, Kolomiets VM, Horndeski M, Wiest A, Kenerley CM (2007) A proteinaceous elicitor sm1 from the beneficial fungal *Trichoderma virens* is required for induced systemic resistance in maize. Plant Physiol 145:875–889

Droby S (2006) Biological control of postharvest diseases of fruits and vegetables: difficulties and challenges. Phytopathol Pol 39:105–117

Elijah A, Adebayo MA, Azeez MB, Alao AM, Oke DA (2021) Fungi as veritable tool in current advances in nanobiotechnology. Heliyon 7:e08480

Faust K (2019) Microbial consortium design benefits from metabolic modeling. Trends Biotechnol 37:123–125

Fraceto LF, Maruyama CR, Guilger M, Mishra S, Keswani C, Singh HB, de Lima R (2018) *Trichoderma harzianum*-based novel formulations: potential applications for management of next-gen agricultural challenges: applications of *Trichoderma harzianum*-based novel formulations. J Chem Technol Biotechnol 93:2056–2063

Gade A, Ingle A, Whiteley C, Rai M (2010) Mycogenic metal nanoparticles: progress and applications. Biotechnol Lett 32(5):593–600

Gardner DE (2006) Plant pathogens as biocontrol agents in native Hawaiian ecosystems. Am Phytopathol Soc 17:225–228

Ghorbanpour M, Omidvari M, Abbaszadeh-Dahaji P, Omidvar R, Kariman K (2018) Mechanisms underlying the protective effects of beneficial fungi against plant diseases. Biol Control 117:147–157

Ghosh S, Patil S, Ahire M, Kitture R, Kale S, Pardesi K, Cameotra SS, Bellare J, Dhavale DD, Jabgunde A, Chopade BA (2012) Synthesis of silver nanoparticles using *Dioscorea bulbifera* tuber extract and evaluation of its synergistic potential in combination with antimicrobial agents. Int J Nanomedicine 7:483–496

Guilger-Casagrande M, Lima RD (2019) Synthesis of silver nanoparticles mediated by fungi: a review. Front Bioeng Biotechnol 7:287

Guilger-Casagrande M, Germano-Costa T, Pasquoto-Stigliani T, Fraceto LF, de Lima R (2019) Biosynthesis of silver nanoparticles employing *Trichoderma harzianum* with enzymatic stimulation for the control of *Sclerotinia sclerotiorum*. Sci Rep 9:14351

Hanafy MH (2018) Myconanotechnology in veterinary sector: status quo and future perspectives. Int J Vet Sci Med 6(2):270–273

Hasan S, Wapshere AJ (1973) The biology of *Puccinia chondrillina*, a potential biological control agent of skeleton weed. Ann Appl Biol 74:325–332

Hennecke B, Arrowsmith L, Ten J (2021) Prioritising targets for biological control of weeds. Department of Agriculture, Fisheries and Forestry, Australia

Hilbig BE, Allen EB (2019) Fungal pathogens and arbuscular mycorrhizal fungi of abandoned agricultural fields: potential limits to restoration. Invasive Plant Sci Manag 12:186–193

Hou S, Zhang Y, Li M, Liu H, Wu F, Hu J, Lin X (2019) Concomitant biocontrol of pepper *Phytophthora* blight by soil indigenous arbuscular mycorrhizal fungi via upfront film-mulching with reductive fertilizer and tobacco waste. J Soils Sediments 20:452–460

Huang D, Ma M, Wang Q, Zhang M, Jing G, Li C, Ma F (2020) Arbuscular mycorrhizal fungi enhanced drought resistance in apple by regulating genes in the MAPK pathway. Plant Physiol Biochem 149:245–255

Inbakani SA, Siva R (2017) Biosynthesis of silver nanoparticles using edible mushrooms and its bactericidal activities. Res J Pharm Tech 10(2):467–472

Ireland KB, Hunter GC, Wood A, Delaisse C, Morin L (2019) Evaluation of the rust fungus *Puccinia rapipes* for biological control of *Lycium ferocissimum* (African boxthorn) in Australia: life cycle, taxonomy and pathogenicity. Fung Biol 123(11):811–823

Jaloot AS, Owaid MN, Naeem GA, Muslim RF (2020) Mycosynthesizing and characterizing silver nanoparticles from the mushroom *Inonotus hispidus* (Hymenochaetaceae), and their antibacterial and antifungal activities. Environ Nanotechnol Monit Manag 14:100313

Janisiewicz WJ, Korsten L (2002) Biological control of postharvest diseases of fruits. Annu Rev Phytopathol 40(1):411–441

Jensen DF, Karlsson M, Lindahl BD (2017) Fungal–fungal interactions: from natural ecosystems to managed plant production, with emphasis on biological control of plant diseases. In: Dighton J, White JF (eds) The fungal community – its organization and role in the ecosystem. CRC Press, Boca Raton, pp 549–562

Juntarawijit C, Juntarawijit Y (2018) Association between diabetes and pesticides: a case-control study among Thai farmers. Environ Health Prev Med 23:1–10

Keyser CA, Jensen B, Meyling NV (2016) Dual effects of *Metarhizium* spp. and *Clonostachys rosea* against an insect and a seed- borne pathogen in wheat. Pest Manag Sci 72:517–526

Khande P, Shahi SK (2018) Mycogenic nanoparticles and their bio-prospective applications: current status and future challenges. J Nanostruct Chem 8(4):369–391

Klaus A, Petrovic P, Vunduk J, Pavlovic V, Van Griensven LJLD (2020) The antimicrobial activities of silver nanoparticles synthesized from medicinal mushrooms. Int J Med Mushrooms 22(9):869–883

Köhl J, Kolnaar R, Ravensberg WJ (2019) Mode of action of microbial biological control agents against plant diseases: relevance beyond efficacy. Front Plant Sci 10:845

Konappa N, Udayashankar AC, Dhamodaran N, Krishnamurthy S, Jagannath S, Uzma F, Pradeep CK, De Britto S, Chowdappa S, Jogaiah S (2021) Ameliorated antibacterial and antioxidant properties by *Trichoderma harzianum* mediated green synthesis of silver nanoparticles. Biomol Ther 11:535

Lahlali R, Ezrari S, Radouane N, Kenfaoui J, Esmaeel Q, El Hams H, Belabess Z, Barka EA (2022) Biological control of plant pathogens: a global perspective. Microorganisms 10:596

Larran S, Simon MR, Moreno MV, Siurana MS, Perelló A (2016) Endophytes from wheat as biocontrol agents against tan spot disease. Biol Control 92:17–23

Li G, He D, Qian Y, Guan B, Gao S, Cui Y, Yokoyama K, Wang L (2012) Fungus-mediated green synthesis of silver nanoparticles using *Aspergillus terreus*. Int J Mol Sci 13:466–476

Li F, Guo Y, Christensen MJ, Gao P, Li Y, Duan T (2018) An arbuscular mycorrhizal fungus and *Epichloë festucae* var. *lolii* reduce *Bipolaris sorokiniana* disease incidence and improve perennial ryegrass growth. Mycorrhiza 28:159–169

Lin P, Zhang M, Wang M, Li Y, Liu J, Chen Y (2021) Inoculation with arbuscular mycorrhizal fungus modulates defense-related genes expression in banana seedlings susceptible to wilt disease. Plant Signal Behav 16:1884782

Liu K, Newman M, McInroy JA, Hu CH, Kloepper JW (2017) Selection and assessment of plant growth-promoting rhizobacteria for biological control of multiple plant diseases. Phytopathology 107:928–936

Liu K, McInroy JA, Hu CH, Kloepper JW (2018) Mixtures of plant-growth-promoting rhizobacteria enhance biological control of multiple plant diseases and plant-growth promotion in the presence of pathogens. Plant Dis 102:67–72

Lysøe E, Dees MW, Brurberg MB (2017) A three-way transcriptomic interaction study of a biocontrol agent (*Clonostachys rosea*), a fungal pathogen (*Helminthosporium solani*), and a potato host (*Solanum tuberosum*). Mol Plant-Microbe Interact 30:646–655

Maharjan S, Devkota A, Shrestha BB, Baniya CB, Rangaswamy M, Jha PK (2020) Prevalence of *Puccinia abrupta* var. *partheniicola* and its impact on *Parthenium hysterophorus* in Kathmandu Valley, Nepal. J Ecol Environ:44–25

Mansoor S, Zahoor I, Baba TR, Padder SA, Bhat ZA, Koul AM, Jiang L (2021) Fabrication of silver nanoparticles against fungal pathogens. Front Nanotechnol 3:679358

Massart S, Martinez-Medina M, Jijakli MH (2015a) Biological control in the microbiome era: challenges and opportunities. Biol Control 89:98–108

Massart S, Perazzolli M, Höfte M, Pertot I, Jijakli MH (2015b) Impact of the omic technologies for understanding the modes of action of biological control agents against plant pathogens. BioControl 60:725–746

McDougal R, Stewart A, Bradshaw R (2012) Transformation of *Cyclaneusma minus* with green fluorescent protein (GFP) to enable screening of fungi for biocontrol activity. Forests 3(1):83–94

Mhlongo MI, Piater LA, Madala NE, Labuschagne N, Dubery IA (2018) The chemistry of plant–microbe interactions in the rhizosphere and the potential for metabolomics to reveal signaling related to defense priming and induced systemic resistance. Front Plant Sci 9:112

Minchev Z, Kostenko O, Soler R, Pozo MJ (2021) Microbial consortia for effective biocontrol of root and foliar diseases in tomato. Front Plant Sci 12:2428

Mishra V, Ellouze W, Howard R (2018) Utility of arbuscular mycorrhizal fungi for improved production and disease mitigation in organic and hydroponic greenhouse crops. J Hortic 5:237

Mittal D, Kaur G, Ali S (2020) Nanoparticle-based sustainable agriculture and food science: recent advances and future outlook. Front Nanotechnol 2:5

Mitter B, Brader G, Pfaffenbichler N, Sessitsch A (2019) Next generation microbiome applications for crop production - limitations and the need of knowledge-based solutions. Curr Opin Microbiol 49:59–65

Mohanta YK, Nayak D, Biswas K, Singdevsachan SK, Abd Allah EF, Hashem A, Alqarawi AA, Yadav D, Mohanta TK (2018) Silver nanoparticles synthesized using wild mushroom show potential antimicrobial activities against food borne pathogens. Molecules 23(3):655

Mohanta Y, Singdevsachan S, Parida U, Panda S, Mohanta TK, Bae H (2016) Green synthesis and antimicrobial activity of silver nanoparticles using wild medicinal mushroom *Ganoderma applanatum* (Pers.) Pat. from the Similipal Biosphere Reserve, Odisha, India. IET Nanobiotechnol 10:184–189

Molnár Z, Bódai V, Szakacs G, Erdélyi B, Fogarassy Z, Sáfrán G (2018) Green synthesis of gold nanoparticles by thermophilic filamentous fungi. Sci Rep 8(1):1–12

Moradi F, Sedaghat S, Moradi O, Salmanabadi SA (2021) Review on green nano-biosynthesis of silver nanoparticles and their biological activities: with an emphasis on medicinal plants. Inorg Nano-Met Chem 51:133–142

Morin L, Evans KJ, Jourdan M, Gomez DR, Scott JK (2011) Use of a trap garden to find additional genetically distinct isolates of the rust fungus *Phragmidium violaceum* to enhance biological control of European blackberry in Australia. Eur J Plant Pathol 131:289–303

Morin L, Aveyard R, Lidbetter JR, Wilson PG (2012) Investigating the host-range of the rust fungus *Puccinia psidii* sensu lato across tribes of the family Myrtaceae present in Australia. PLoS One 7:e35434

Morley TB, Morin L (2008) Progress on boneseed (*Chrysanthemoides monilifera* subsp. *monilifera* (L.) Norlindh) biological control: the boneseed leaf bucklemite *Aceria* (Keifer) sp., the lacy-winged seed fly *Mesoclanis magnipalpis* Bezzi and the boneseed rust *Endophyllum osteospermi* (Doidge) A. R. Wood. Plant Prot Q 23:29–31

Nally MC, Pescea VM, Maturanoa YP, Muñoze CJ, Combinab M, Toroa ME (2012) Biocontrol of *Botrytis cinerea* in table grapes by non-pathogenic indigenous *Saccharomyces cerevisiae* yeasts isolated from viticultural environments in Argentina. Postharvest Biol Technol 64:40–48

Narayanan KB, Sakthivel N (2010) Biological synthesis of metal nanoparticles by microbes. Adv Colloid Interf Sci 156:1–13
Niu B, Wang W, Yuan Z, Sederoff RR, Sederoff H, Chiang VL, Borriss R (2020) Microbial interactions within multiple-strain biological control agents impact soil-borne plant disease. Front Microbiol 11:585404
Numata M, Hasegawa T, Fujisawa T, Sakurai K, Shinkai S (2004) β-1,3-glucan (Schizophyllan) can act as a one-dimensional host for creation of novel poly(aniline) nanofiber structures. Org Lett 6(24):4447–4450
O'Brien PA (2017) Biological control of plant diseases. Australas Plant Pathol 46(4):293–304
Ons L, Bylemans D, Thevissen K, Cammue BPA (2020) Combining biocontrol agents with chemical fungicides for integrated plant fungal disease control. Microorganisms 8(12):1930
Owaid MN (2019) Green synthesis of silver nanoparticles by *Pleurotus* (oyster mushroom) and their bioactivity: review. Environ Nanotechnol Monit Manag 12:100256
Owaid MN, Ibraheem IJ (2017) Mycosynthesis of nanoparticles using edible and medicinal mushrooms. Eur J Nanomed 9:5–23
Owaid MN, Naeem GA, Muslim RF, Oleiwi RS (2020) Synthesis, characterization and antitumor efficacy of silver nanoparticle from *Agaricus bisporus* pileus, Basidiomycota. Walailak J Sci Technol 17:75–87
Pal KK, McSpadden Gardener B (2006) Biological control of plant pathogens. Plant Health Instruct 2:1117–1142
Palmieri D, Vitullo D, De Curtis F, Lima G (2017) A microbial consortium in the rhizosphere as a new biocontrol approach against *fusarium* decline of chickpea. Plant Soil 412:425–439
Palmieri D, Ianiri G, Del Grosso C, Barone G, De Curtis F, Castoria R, Lima G (2022) Advances and perspectives in the use of biocontrol agents against fungal plant diseases. Horticulturae 8:577
Pandit MA, Kumar J, Gulati S, Bhandari N, Mehta P, Katyal R, Rawat CD, Mishra V, Kaur J (2022) Major biological control strategies for plant pathogens. Pathogens 11(2):273
Peng Y, Li SJ, Yan J, Tang Y, Cheng JP, Gao AJ, Yao X, Ruan JJ, Xu BL (2021) Research progress on phytopathogenic fungi and their role as biocontrol agents. Front Microbiol 12:670135
Pollard KM, Gange AC, Seier MK, Ellison CA (2022) A semi-natural evaluation of the potential of the rust fungus *Puccinia komarovii* var. *glanduliferae* as a biocontrol agent of *Impatiens glandulifera*. Biol Control 165:104786
Poveda J, Baptista P (2021) Filamentous fungi as biocontrol agents in olive (*Olea europaea* L.) diseases: mycorrhizal and endophytic fungi. Crop Prot 146:105672
Poveda J, Abril-Urias P, Escobar C (2020) Biological control of plant-parasitic nematodes by filamentous fungi inducers of resistance: *Trichoderma*, mycorrhizal and endophytic fungi. Front Microbiol 11:992
Poveda J, Roeschlin RA, Marano MR, Favaro MA (2021) Microorganisms as biocontrol agents against bacterial citrus diseases. Biol Control 158:104602
Pozo MJ, Jung SC, Martínez-Medina A, López-Ráez JA, Azcón-Aguilar C, Barea JM (2013) Root allies: arbuscular mycorrhizal fungi help plants to cope with biotic stresses. In: Aroca R (ed) Symbiotic endophytes. Springer, Cham, pp 289–307
Pozo MJ, Zabalgogeazcoa I, Vazquez de Aldana BR, Martinez-Medina A (2021) Untapping the potential of plant mycobiomes for applications in agriculture. Curr Opin Plant Biol 60:102034
Rabiey M, Hailey LE, Roy SR, Grenz K, Al-Zadjali MA, Barrett GA, Jackson RW (2019) Endophytes vs tree pathogens and pests: can they be used as biological control agents to improve tree health? Eur J Plant Pathol 155:711–729
Rai M, Bonde S, Golinska P, Trzcińska-Wencel J, Gade A, Abd-Elsalam K (2021) *Fusarium* as a novel fungus for the synthesis of nanoparticles: mechanism and applications. J Fungi 7(2):139
Ramírez-Valdespino CA, Orrantia-Borunda E (2021) *Trichoderma* and nanotechnology in sustainable agriculture: a review. Front Fungal Biol 2:764675
Raymaekers K, Ponet L, Holtappels D, Berckmans B, Cammue BPA (2020) Screening for novel biocontrol agents applicable in plant disease management—a review. Biol Control 144:104240

Salvadori MR, Ando RA, Oller Do Nascimento CA, Corrêa B (2014) Bioremediation from wastewater and extracellular synthesis of copper nanoparticles by the fungus *Trichoderma koningiopsis*. J Environ Sci Health 49(11):1286–1295

Sharma V, Salwan R, Sharma PN, Gulati A (2017) Integrated translatome and proteome: approach for accurate portraying of widespread multifunctional aspects of *Trichoderma*. Front Microbiol 8:1602

Shaw S, Le Cocq K, Paszkiewicz K, Moore K, Winsbury R, de Torres ZM, Studholme DJ, Salmon D, Thornton CR, Grant MR (2016) Transcriptional reprogramming underpins enhanced plant growth promotion by the biocontrol fungus *Trichoderma hamatum* GD12 during antagonistic interactions with *Sclerotinia sclerotiorum* in soil. Mol Plant Pathol 17:1425–1441

Silva ME, Uriostegui MA, Millán-Orozco J, Gives PM, Hernández EL, Braga FR (2017) Predatory activity of *Butlerius* nematodes and nematophagous fungi against *Haemonchus contortus* infective larvae. Rev Bras Parasitol Vet 26(1):92–95

Singh I, Giri B (2017) Arbuscular mycorrhiza mediated control of plant pathogens. In: Varma A, Prasad R, Tuteja N (eds) Mycorrhiza—nutrient uptake, biocontrol, ecorestoration. Springer, Cham, pp 131–160

Singh P, Kim YJ, Zhang D, Yang DC (2016) Biological synthesis of nanoparticles from plants and microorganisms. Trends Biotechnol 34:588–599

Singh V, Naveenkumar R, Muthukumar A (2019) Arbuscular mycorrhizal fungi and their effectiveness against soil borne diseases. In: Khan MR, Mukhopadhyay AN, Pandey RN, Thakur MP, Singh D (eds) Bio-intensive approaches: application and effectiveness in plant diseases management. Today & Tomorrow's Printers and Publishers, New Delhi, pp 183–199

Smith SE, Read DJ (2008) Mycorrhizal Symbiosis, 3rd edn. Academic, London

Sousa F, Ferreira D, Reis S, Costa P (2020) Current insights on antifungal therapy: novel nanotechnology approaches for drug delivery systems and new drugs from natural sources. Pharmaceuticals 13(9):248

Srivastava DA, Harris R, Breuer G, Levy M (2021) Secretion-based modes of action of biocontrol agents with a focus on *Pseudozyma aphidis*. Plan Theory 10:210

Stenberg JA, Sundh I, Becher PG, Björkman C, Dubey M, Egan PA, Friberg H, Gil JF, Jensen DF, Jonsson M, Karlsson M, Khalil S, Ninkovic V, Rehermann G, Vetukuri RR, Viketoft M (2021) When is it biological control? A framework of definitions, mechanisms, and classifications. J Pest Sc 94:665–676

Tanner RA, Pollard KM, Varia S, Evans HC, Ellison CA (2015) First release of a fungal classical biocontrol agent against an invasive alien weed in Europe: biology of the rust, *Puccinia komarovii* var. *glanduliferae*. Plant Pathol 64:1130–1139

Tariq M, Khan A, Asif M, Khan F, Ansari T, Shariq M, Siddiqui MA (2020) Biological control: a sustainable and practical approach for plant disease management. Acta Agric Scand, Section B Soil Plant Sci 70(6):507–524

Thakkar KN, Mhatre SS, Parikh RY (2010) Biological synthesis of metallic nanoparticles. Nanomedicine 6(2):257–262

Thambugala KM, Daranagama DA, Phillips AJL, Kannangara SD, Promputtha I (2020) Fungi vs. fungi in biocontrol: an overview of fungal antagonists applied against fungal plant pathogens. Front Cell Infect Microbiol 10:604923

Tomah AA, Alamer ISA, Li B, Zhang JZ (2020) Mycosynthesis of silver nanoparticles using screened *Trichoderma* isolates and their antifungal activity against *Sclerotinia sclerotiorum*. Nano 10:1955

Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK (2020) Plant–microbiome interactions: from community assembly to plant health. Nat Rev Microbiol 18:607–621

Vahabi K, Mansoori GA, Karimi S (2011) Biosynthesis of silver nanoparticles by fungus *Trichoderma reesei* (a route for large-scale production of AgNPs). Insciences J 1:65–79

Vahabi K, Reichelt M, Scholz SS, Furch AC, Matsuo M, Johnson JM, Sherameti I, Gershenzon J, Oelmüller R (2018) *Alternaria brassicae* induces systemic jasmonate responses in Arabidopsis which travel to neighboring plants via a Piriformospora indica hyphal network and activate abscisic acid responses. Front Plant Sci 9:626

Vargas-Inciarte L, Fuenmayor-Arrieta Y, LuzardoMéndez M, Costa-Jardin MD, Vera A, Carmona D, Homen-Pereira M, Costa-Jardin PD, San-Blas E (2019) Use of different *Trichoderma* species in cherry type tomatoes (*Solanum lycopersicum* L.) against *Fusarium oxysporum* wilt in tropical greenhouses. Agronomía Costarricense 43:85–100

Varma A, Choudhary DK (2019) Mycorrhizosphere and pedogenesis. Springer, Singapore

Vigneshwaran N, Ashtaputre NM, Varadarajan PV, Nachane RP, Paralikar KM, Balasubramanya RH (2007) Biological synthesis of silver nanoparticles using the fungus *Aspergillus flavus*. Materials Lett 61(6):1413–1418

Vigo C, Norman JR, Hooker JE (2000) Biocontrol of the pathogen *Phytophthora parasitica* by arbuscular mycorrhizal fungi is a consequence of effects on infection loci. Plant Pathol 49:509–514

Kannan V, Sureendar R (2009) Synergistic effect of beneficial rhizosphere microflora in biocontrol and plant growth promotion. J Basic Microbiol 49:158–164

Vinale F, Sivasithamparam K, Ghisalberti EL, Marra R, Woo SL, Lorito M (2008) *Trichoderma*–plant–pathogen interactions. Soil Biol Biochem 40:1–10

Vos C, Claerhout S, Mkandawire R, Panis B, De Waele D, Elsen A (2012) Arbuscular mycorrhizal fungi reduce root-knot nematode penetration through altered root exudation of their host. Plant Soil 354:335–345

Wang CX, Li XL, Song FQ, Wang GQ (2012) Effects of arbuscular mycorrhizal fungi on fusarium wilt and disease resistance-related enzyme activity in cucumber seedling root. Chin J Eco-Agric 20:53–57

Wang Q, Coleman JJ (2019) Progress and challenges: development and implementation of CRISPR/Cas9 technology in filamentous fungi. Comput Struct Biotechnol J 17:761–769

Weng W, Yan J, Zhou M, Yao X, Gao A, Ma C, Cheng J, Ruan J (2022) Roles of arbuscular mycorrhizal fungi as a biocontrol agent in the control of plant diseases. Microorganisms 10:1266

Win TT, Bo B, Malec P, Fu P (2021) The effect of a consortium of *Penicillium* sp. and *Bacillus* spp. in suppressing banana fungal diseases caused by *Fusarium* sp. and *Alternaria* sp. J Appl Microbiol 131:1890–1908

Youssef K, Hashim AF, Hussien A, Abd-Elsalam KA (2017) Fungi as ecosynthesizers for nanoparticles and their application in agriculture. Fungal nanotechnology Springer 116:55–75

Yandoc-Ables CB, Rosskopf EN, Charudattan R (2006) Plant pathogens at work: progress and possibilities for weed biocontrol. The American Phytopathological Society, Plant Pathology, Department, University of Florida, Gainesville

Zaki SA, Ouf SA, Albarakaty FM, Habeb MM, Aly AA, Abd-Elsalam KA (2021) *Trichoderma harzianum*-mediated ZnO nanoparticles: a green tool for controlling soil-borne pathogens in cotton. J Fungi 7:952

Zaki SA, Ouf SA Abd-Elsalam, K.A, Asran AA, Hassan MM, Kalia A, Albarakaty FM (2022) Trichogenic silver-based nanoparticles for suppression of fungi involved in damping-off of cotton seedlings. Microorganisms 10:344

Zhao H, Zhou T, Xie J, Cheng J, Chen T, Jiang D, Fu Y (2020) Mycoparasitism illuminated by genome and transcriptome sequencing of *Coniothyrium minitans*, an important biocontrol fungus of the plant pathogen *Sclerotinia sclerotiorum*. Microb Genom 6:e000345

New Perspectives on Fungal Siderophores

Tarek A. A. Moussa, Younes M. Rashad, and Zakaria A. M. Baka

1 Introduction

Fungi play a significant role in ecology and have a variety of effects on human life, both positively and negatively: they are key players in saprobic decomposition, significant plant symbionts (mycorrhiza), pathogens of plants and animals that affect human health as well as food production and preservation (decay, toxin production), serve as food or are used in the production of food (such as mushrooms, alcohol, bread, and mold cheese), and are crucial workhorses. Iron is a critical nutrient that affects all of these processes. Most fungal species handle iron using siderophores, which are ferric iron chelators unique to those particular fungi.

Iron is a transition metal, which has redox properties that enable it to exist in two oxidation states, ferrous (Fe^{2+}) and (Fe^{3+}) for the donation and acceptance of electrons, respectively (Haas et al. 2008; Blatzer et al. 2011; Johnson et al. 2012). Iron is the fourth most abundant metal on earth (Huber 2005; Gamit and Tank 2014), but its bioavailability is very low in an aerobic environment (in the presence of oxygen and at neutral pH) because iron is present as ferric hydroxides which is the major oxidized form found in aerobic environments (Oberegger et al. 2001; Johnson et al. 2012; Beckmann et al. 2013), it is insoluble and display a solubility below 10^{-9} M at neutral pH, which is not enough to conduct vital processes (Ratledge and Dover 2000).

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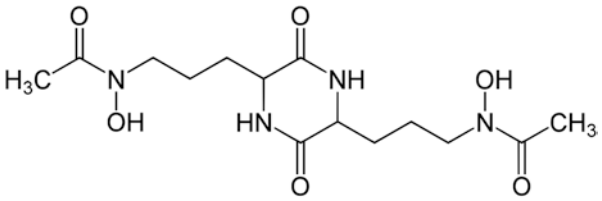
Siderophores (Greek for the iron carrier) are low molecular weight (500–1000 Daltons), organic, negatively charged molecules, high-affinity ferric iron-specific chelating compounds which are excreted by microorganisms to compete for iron with the host (Bruns et al. 2018). Siderophores' biosynthesis depends on iron availability, and their function is to supply iron to the cell. In the iron-limited environment, siderophores are excreted to mobilize extracellular iron while in an iron-supplemented environment, they are produced intracellularly for iron storage. In contrast to the reductive iron system uptake, siderophore is an essential determinant of the virulence of *A. fumigatus* and other pathogens (Leal et al. 2013).

According to the chemical nature of the moieties donating the oxygen ligands for Fe^{3+}, siderophores are classified into three main groups (Wencewicz et al. 2009): (i) aryl caps (catecholate and phenolates), (ii) carboxylates, and (iii) hydroxamates. Several bacteria produce mixed-type-siderophores that combine different Fe^{3+} ligands in one molecule but all fungi produce hydroxamate siderophores except certain zygomycetes which produce carboxylate siderophore rhizoferrin (Holinsworth and Martin 2009).

2 Structure and Biosynthesis of Siderophores

Hydroxamates siderophores can be grouped into four structural families according to non-proteinogenic amino acid ornithine and different acyl groups:

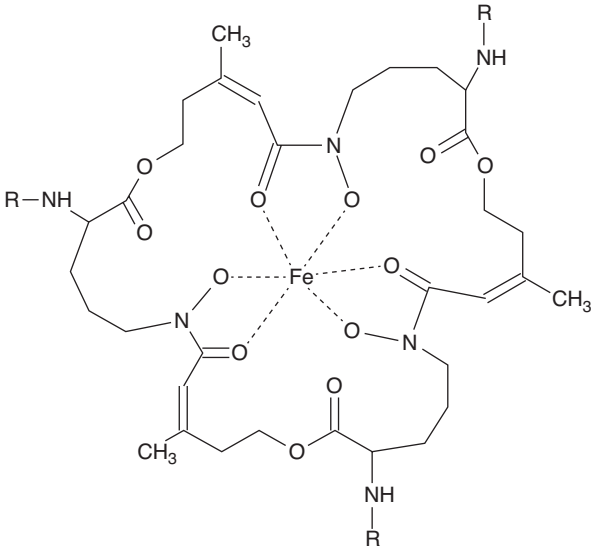
(i) **Rhodotorulic acid**, the N-acetyl-l-N-hydroxyornithine diketopiperazine. It has primarily been discovered in basidiomycetous yeasts (van der Helm and Winkelmann 1994, 2020). The iron-bearing ligand is created by combining 3 mol of dimerum acid (DA), a dihydroxamate derivative of rhodotorulic acid, with 2 mol of iron ($Fe_2(DA)_3$). Comparatively speaking to the other three-hydroxamate groups, the binding of iron is weaker. Some phytopathogenic fungi, such as *Stemphylium botryosum* and *Epicoccum purpurescens* (Frederick et al. 1981; Manulis et al. 1987), and some therapeutically significant fungi, such as *H. capsulatum* (Burt 1982) and *Blastomyces dermatitidis*, generate dimerum acid.



Rhodotorulic acid

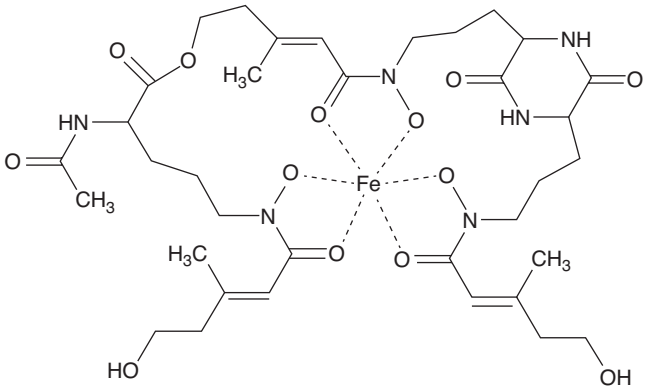
(ii) **Fusarinines**, also called fusigens, may be cyclic or linear hydroxamates. N-hydroxyornithine is N-acylated by anhydromevalonic acid to form fusarinine. The zoopathogens *Fusarium* spp., *Paecilomyces* spp., and *Aspergillus* spp. all

contain different fusarinines (van der Helm and Winkelmann 1994, 2020). *H. capsulatum* culture filtrates contained substances identified as trans-fusarinine and an unknown monohydroxamate, although they lacked biological activity (that is, they did not promote the growth of the fungus) (Burt 1982). Because it is generally known that *H. capsulatum* does not clone in its yeast cell phase of growth on most culture media in vitro, research on the siderophores of the fungus was started (Burt 1982). Burt employed culture filtrate-isolated hydroxamates to alleviate the growth restriction (Burt 1982). The same technique growth stimulation was employed in a *Paracoccidioides brasiliensis* study (Castaneda et al. 1988). *B. dermatitidis* siderophores coprogen B and DA were employed to increase *P. brasiliensis* plating efficiency (Castaneda et al. 1988).



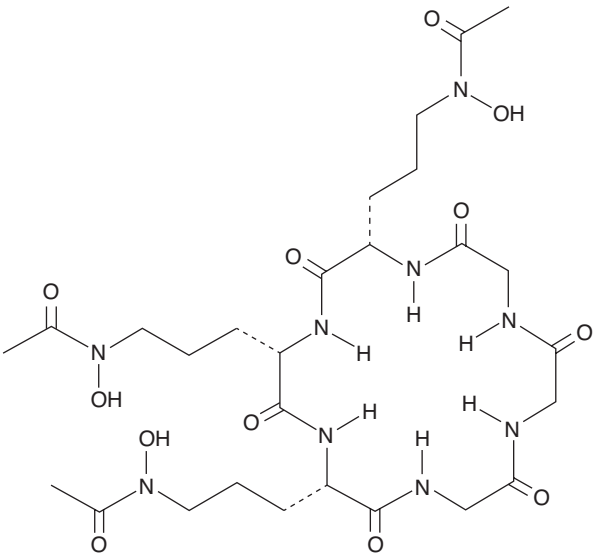
N,N ,N -triacetylfusarinine C (triacetylfusigen) (R = CO-CH_3) and fusarinine C (fusigen) (R = H)

(iii) **Coprogens**, include 1 mol of acetic acid, 3 mol of anhydromevalonic acid, and 3 mol of N-acyl-N-hydroxyl-l-ornithine. In the coprogen, ferrichrome, and fusarinine families, 1 mol of iron combines with one ligand, in contrast to the case with the rhodotorulic acid family (van der Helm and Winkelmann 1994, 2020). Numerous plant pathogens, including *H. capsulatum* (Burt 1982), *B. dermatitidis*, and occasionally human infections *Fusarium dimerum* and *Curvularia lunata*, create coprogens (Manulis et al. 1987; Höfte 1993; van der Helm and Winkelmann 1994, 2020). The number of hydroxamate families would be reduced to three if the coprogens were thought of as trihydroxamate derivatives of rhodotorulic acid with a linear structure. It is understood that 1 mol of dimerum acid and 1 mol of trans-fusarinine arise from the hydrolysis of the ester group of coprogen B (Winkelmann 1993).



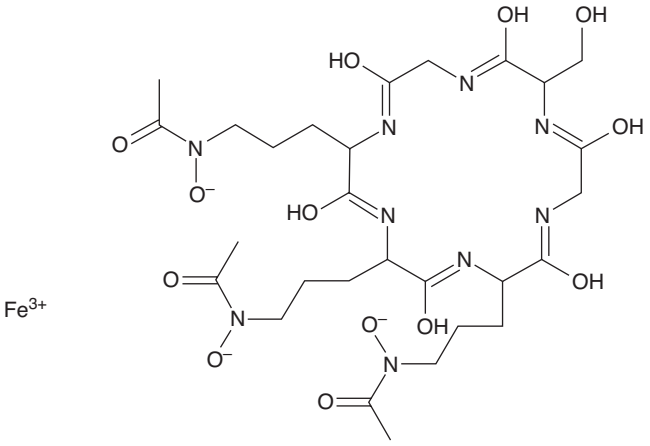
Coprogen

(iv) **ferrichrome**, cyclic peptides with combinations of glycine, serine, or alanine, as well as the tripeptide N-acyl-N-hydroxy ornithine (Haas et al. 2008). Some phytopathogenic fungi (Höfte 1993), *Microsporum* spp. (Bentley et al. 1986; Mor et al. 1992), *Trichophyton* spp. (Mor et al. 1992), and *Aspergillus* spp., including the significant pathogen *A. fumigatus*, are among the pathogenic fungi that make ferrichrome (van der Helm and Winkelmann 1994, 2020; Leong and Winkelmann 1998). Iron storage within cells is another use of ferrichrome.



Ferrichrome (iron-free)

Numerous hydroxamate siderophores, including ferricrocin, ferrichrome, ferrichrome C, and N,N,N-triacetylfusarinine C (TafC), are produced by *A. fumigatus* (Wallner et al. 2009). To maintain iron homeostasis, the four siderophores are secreted (Haas et al. 2008). TafC and ferricrocin are generated in the greatest amounts in iron-limited environments, particularly media-containing serum (Hissen et al. 2004). In addition to the two intracellular siderophores desferri-ferricrocin (DF-FC) and hydroxyferricrocin (HFC) for hyphal iron distribution and storage, fusarinine C (FsC) and desferri-triacetylfusarinine C (DF-TafC) are generated for the solubilization and uptake of iron (Haas et al. 2008; Wallner et al. 2009).



Ferricrocine

The main precursor of siderophores is the non-proteinogenic amino acid ornithine (Orn) which is produced in mitochondria from glutamate (Eisendle et al. 2003; Schrettl et al. 2004). The produced ornithine is either transported to the cytosol by *AmcA* (ortholog of *S. cerevisiae Arg11*) or converted into citrulline by the ornithine transcarbamoyl transferase (*ArgB*) in *A. fumigatus* (Jadoun et al. 2004). Production of ornithine involve six enzymes: acetylglutamate synthase, acetylglutamate kinase and acetylglutamyl phosphate- reductase that are encoded by *argEF* gene in *A. fumigatus* (ortholog of *Saccharomyces cerevisiae ARG5,6*), acetylornithine-aminotransferase, acetylornithine-deacetylase, and arginine biosynthesis bi-functional enzyme (Boonchird et al. 1991). The acetylglutamate kinase may be the rate-limiting step in arginine biosynthesis (Hilger et al. 1973).

The first shared step in the biosynthesis of all siderophores is the N5-hydroxylation of L-ornithine catalysed by the L-ornithine-N5-monooxygenase *SidA* (Eisendle et al. 2003; Hissen et al. 2004; Schrettl et al. 2004; Haas 2012, 2014). Then, the pathways for biosynthesis of extra- and intracellular siderophores to attach different acyl residues and formation of fusarinines and ferrichromes. For biosynthesis of fusarinine, the transacylase *SidF* transfers anhydromevalonyl (derived from mevalonate by CoA-ligation) to N5-hydroxy-L-ornithine and dehydration is stimulated

by the enzymes *SidI* and *SidH* (Schrettl et al. 2007; Yasmin et al. 2012). Non-ribosomal peptide synthetases (NRPSs) is an enzyme family that is best known from secondary metabolism and responsible for formation of both of fusarinines and ferrichromes. The NRPS SidD links three N5-cis-anhydromevalonyl-N5-hydroxy-L-ornithine residues by ester bonds and produce fusarinine C (FsC) and affinity for Fe(III) is increased (Eisendle et al. 2003; Schrettl et al. 2007). TAFC is derived by triple N2-acetylation of FsC catalysed by *SidG* (GNAT protein family) which its activity is important for biosynthesis of TAFC.

For biosynthesis of ferrichromes, two transacetylases are required for the N5-acetylation of N5-hydroxy-L-ornithine: the main enzyme *SidL* and an unidentified enzyme, which is upregulated by iron starvation (Blatzer et al. 2011). Both *SidF* and *SidL* belong to the GCN5-related N-acetyltransferases (GNAT). The NRPS *SidC* links three N5-acetyl-N5-hydroxy-L-ornithine, two L-glycine and one L-serine residue by peptide bonds and form the hexapeptide ferricrocin that improves the chemical stability. Hydroxy ferricrocin (HFC) is derived by single hydroxylation of ferricrocin (FC) stimulated by an unidentified gene product (Eisendle et al. 2003; Schrettl et al. 2007).

3 The Function of Siderophores

Fungal siderophores have main functions: (i) uptake of iron bound to organic molecules such as citrate or haem, (ii) the absorption of iron by membrane-bound uptake systems, (iii) the secretion of siderophores, which are considered as secondary metabolites that form soluble Fe^{3+} complexes; these complexes are then actively taken up via specific receptors, (iv) iron storage within mycelia and conidiospores (Boiteau et al. 2016). Additionally, Siderophores are responsible for their ability to access transferrin-bound iron and allow the growth of *A. fumigatus* in the presence of serum (Hissen et al. 2004; Tekaia and Latgé 2005). Also, the siderophore system is essential for the virulence of *A. fumigates,* particularly in pathogens that encode multiple siderophores (Bachman et al. 2012).

4 Mechanism of Siderophores-Mediated Iron Uptake

Chelation of iron, uptake of the siderophore-iron complex, and intracellular release of iron are the steps involved in siderophore-mediated iron uptake. The iron is then supplied to the microbe via high affinity siderophore uptake mechanisms (Table 1). The breakdown product and iron-free siderophore are expelled at the conclusion. Numerous fungi have the ability to retain internal iron linked to cellular siderophores that are not expelled. When the hard Lewis acid Fe (III) is strongly solved in

Table 1 Mechanisms of iron acquisition by pathogenic fungi

Mechanism	Examples	Reference
Reduction of ferric to ferrous iron	*Candida albicans*	Morrissey et al. (1996)
	Cryptococcus neoformans	Jacobson et al. (1998)
	Geotrichum candidum	Mor et al. (1988)
	Saccharomyces cerevisiae	Lesuisse and Labbe (1994)
Siderophore acquisition of ferric iron Hydroxamates (families)		
Rhodotorulic acid	*Epicoccum purpurescens*	Frederick et al. (1981)
	Histoplasma capsulatum	Burt (1982)
	Stemphilium botryosum	Manulis et al. (1987)
Coprogens	*Curvularia lunata*	van der Helm and Winkelmann (1994, 2020)
	Epicoccum purpurescens	Frederick et al. (1981)
	Fusarium dimerum	van der Helm and Winkelmann (1994, 2020)
	Histoplasma capsulatum	Burt (1982)
	Neurospora crassa	van der Helm and Winkelmann (1994, 2020)
	Stemphilium botryosum	Manulis et al. (1987)
Ferrichromes	*Aspergillus* spp.	Charlang et al. (1981)
	Epicoccum purpurescens	Frederick et al. (1981)
	Microsporum spp.	Bentley et al. (1986)
	Neurospora crassa	van der Helm and Winkelmann (1994, 2020)
	Trichophyton spp.	Mor et al. (1988)
	Ustilago maydis	Ardon et al. (1997, 1998)
Fusarinines	*Aspergillus* spp.	van der Helm and Winkelmann (1994, 2020)
	Epicoccum purpurescens	Frederick et al. (1981)
	Fusarium spp.	van der Helm and Winkelmann (1994, 2020)
	Histoplasma capsulatum	Burt (1982)
	Paecilomyces spp.	van der Helm and Winkelmann (1994, 2020)

(continued)

Table 1 (continued)

Mechanism	Examples	Reference
Unidentified in report referenced		
	Absidia corymbifera	Holzberg and Artis (1983)
	Candida albicans	Holzberg and Artis (1983) and Ismail et al. (1985)
	Madurella mycetomatis	Mezence and Boiron (1995)
	Pseudallescheria boydii	De Hoog et al. (1994)
	Rhizopus arrhizus	Holzberg and Artis (1983)
	Rhizopus oryzae	Holzberg and Artis (1983)
	Scedosporium prolificans	De Hoog et al. (1994)
	Sporothrix schenckii	Holzberg and Artis (1983)
Polycarboxylates (rhizoferrin)		
	Zygomycetes	van der Helm and Winkelmann (1994, 2020)
Phenolates-catecholates (chemical structures not identified)		
	Candida albicans	Ismail et al. (1985)
	Wood-rotting fungi	Fekete et al. (1983, 1989)
Miscellaneous iron resources Hemin		
	Candida albicans	Moors et al. (1992)
	Histoplasma capsulatum	Worsham and Goldman (1988)
β-Keto aldehydes (phytotoxins)		
	Stemphylium botryosum	Barash et al. (1982)
Acidification and mobilization		
	Neurospora crassa	Winkelmann (1979)
	Saccharomyces cerevisiae	Lesuisse and Labbe (1994)

Adapted from Howard (1999)

an aqueous solution, siderophores can form a stable octahedral $(Fe\ (H_2O)_6)^{3+}$ complex with ferric iron (Raymond and Dertz 2004). For instance, certain ferric siderophore transporters (which are members of the Siderophore-Iron-Transporter (SIT) family) supply Ferri-TafC (TafC+Fe) to cells (Haas et al. 2003; Raymond-Bouchard et al. 2012).

Iron is transported to the metabolic machinery (for iron transport) or to the intracellular siderophore FC (for iron storage) after chelation of iron and uptake, where TafC is hydrolyzed by the esterase EstB, where TafC degradation products (fusarinines) are excreted and the iron is stored as ferri-FC (FC + Fe) (Gsaller et al. 2012).

5 Role of Siderophores

5.1 Siderophore and Microbial Community

Accordingly, siderophores can speed up the dissolution of insoluble phases in minerals by forming a Fe(III)-siderophore complex at the surface of the mineral SS (Shirvani and Nourbakhsh 2010), which is subsequently transported into the soil solution and made available for microbial or plant absorption (Kalinowski et al. 2000; Kraemer 2004). Siderophores make iron more bioavailable to microorganisms, which led to a rise in the microbial population and a change in the microbial community of the soil (Sullivan et al. 2012).

5.2 Siderophores Promotes Plant Growth

Aspergillus niger, *Penicillium citrinum*, and *Trichoderma harzianum* siderophores lengthen the shoot and root of chickpeas (*Cicer arietinum*) (Yadav et al. 2011). Additionally, *Trichoderma asperellum*'s siderophore promotes cucumber growth by reducing salt stress (Qi and Zhao 2013). A type of symbiotic interaction known as ectomycorrhiza occurs when a fungal symbiont and a plant species' roots work together to give iron to the host roots of the plant (van Schöll et al. 2006). Phenolic exudates released from roots of transgenic plants encourage the growth of siderophore-producing microorganisms to enhance the solubility and uptake of iron by plants (Jin et al. 2010). In addition, plants produce phyto-siderophore to directly chelate iron (Masalha et al. 2000).

5.3 Siderophores and Fungal Virulence

Here, the function of siderophores in virulence is briefly discussed. The function of siderophores in controlling host immune responses is then further discussed. There has been substantial research on how siderophores affect pathogen virulence in both plants and animals (Haas et al. 2008; Cornelis and Dingemans 2013; Franza and Expert 2013). Data on siderophores and plant defense mechanisms are limited in comparison to the extensive amount of research on animal defense mechanisms. However, current discoveries raise a number of intriguing issues about the siderophore-related immune manipulation pathways in plants.

Competition for iron between the host and the microbe may occur during a fungal infection. Fungi have created specialized systems to absorb haems or glycoproteins involved in iron transport, such as transferrin and lactoferrin, in order to steal iron from the host. In addition, due to siderophores' high affinity for iron, they can directly fight for this element (Caza and Kronstad 2013).

Furthermore, multiple investigations show that siderophore synthesis by microbial pathogens is necessary for full pathogenicity in mammalian hosts. For instance, both intracellular and external siderophores contribute to the virulence of the extremely deadly fungus Aspergillus fumigatus. Mice exhibit decreased virulence and oxidative stress resistance when important siderophores-producing genes are deleted (Schrettl et al. 2007).

For full pathogenicity in their respective hosts, maize, rice, wheat, and *Arabidopsis thaliana*, siderophores are necessary in four ascomycete species, *Cochliobolus miyabeanus*, *C. heterostrophus*, *Fusarium graminearum*, and *Alternaria brassicicola* (Oide et al. 2006). It has been demonstrated that the hemibiotrophic fungus *Colletotrichum graminicola* must produce siderophores in order to be virulent in maize and resistant to oxidative stress (Albarouki et al. 2014). A siderophore-deficient mutant of the pathogenic fungus *A. alternata* on citrus exhibits reduced virulence (Chen et al. 2013).

5.4 Siderophores and Plant Immune Responses

Because plants are subjected to a variety of biotic stressors, they have evolved a number of defense mechanisms to fend off possible plant diseases. Plants are capable of detecting pathogen attacks and activating complex signaling networks, which results in induced defenses that bestow a more tolerant condition, in addition to pre-formed physical and chemical barriers. Phosphorylation events, reactive oxygen species (ROS) buildup, cell wall rigidification, callose deposition, defense hormone signaling, and expression of genes encoding pathogenesis-related (PR) proteins are examples of induced innate immune activities (Nürnberger et al. 2004). Plants have sentry systems made up of proteins that recognize elicitors originating by possible microbial diseases in order to activate these defenses.

The coprogen production of the hemibiotrophic fungus *C. graminicola* on maize initiates defense reactions in the rhizosphere. It's interesting to note that during the early biotrophic phase of invasion, the genes involved in coprogen production are suppressed, and during the necrotrophic phase, they are up-regulated (Albarouki et al. 2014). Thus, at the early stages of infection, the fungus closely regulates the production of siderophores, likely to get around the plant's defense mechanisms.

The plant immune responses induced by the siderophores in A. thaliana were extensively examined to better understand the molecular pathways involved in siderophore-mediated immunity in leaves. The experiments conclusively demonstrate that iron scavenging causes immune responses using a number of potent iron chelators, including fungal siderophores and an artificial molecule called ethylene diaminedi (o-hydroxyphenylacetic) acid (EDDHA), which is not a natural product but is typically used as a fertilizer for plants in its Fe-EDDHA form (Dellagi et al. 2009; Aznar et al. 2014). As a result, the application of ferri-siderophores to leaves does not trigger an immune response. These findings call into question how siderophores trigger immunity.

A microarray investigation on the physiological processes that the siderophores induce was spurred by the question of the mechanism of action (Aznar et al. 2014). The most significant mechanism that this highly specialized iron chelator was predicted to regulate was iron homeostasis, and immunology was just a small response. Surprisingly, the most significant physiological function that siderophores in leaves appeared to trigger was plant immunity. Heavy metal homeostasis is the main process that is active in roots. Clearly, siderophore treatment simulates biotic stress.

By demonstrating the buildup of ROS and the defense hormones SA and JA in treated leaves, this biotic-stress-like response was confirmed. It's intriguing because although SA and JA signaling are typically antagonistic, the increase of both hormones after siderophore treatment seems incongruous. Although the consequences of crosstalk between SA and JA can vary depending on the spatiotemporal distribution of each hormone, it can be a very complex process (Thaler et al. 2012). Intriguingly, siderophore therapy that activates the SA pathway causes the JA pathway to be suppressed in *Arabidopsis* (Dellagi et al. 2009).

Therefore, siderophores have a function as elicitors but they can also disrupt the hormonal balance of the plant. In Arabidopsis leaves, siderophore infiltration results in cell wall rigidification, which is reflected in the buildup of callose along the leaf vascular system. The most likely explanation is that siderophores rapidly alter the iron status in the vascular system, which results in the formation of ROS and the deposition of callose along the veins. It has been shown that siderophore treatment causes several genes that are known to be up-regulated during iron deficiency to become up-regulated (Aznar et al. 2014). For instance, after treating leaves with various siderophores, the gene for the main iron transporter, iron-regulated transporter 1 IRT1, is highly up-regulated (Dellagi et al. 2009; Aznar et al. 2014). The ferritin-coding gene is also up-regulated 24 hours after siderophore therapy, indicating iron inflow in the cell or oxidative stress, and is down-regulated shortly after siderophore treatment due to a primary "iron deficiency"-like event. Iron and zinc concentrations in treated plant roots have increased, which suggests that siderophores affect the number of heavy metals in the plant. It's interesting to note that metal concentrations don't alter in leaves. However, the distribution of iron at the cellular level shows that siderophores lead to iron depletion in plastids and buildup in cell walls. Consequently, siderophores cause significant alterations in the distribution of heavy metals in the plant (Aznar et al. 2014).

These observations show that iron or other metal distributions are perturbed during immune activation, which is supported by other experiments. Treatment with a siderophore does not result in the expression of immunological markers in iron-deficient plants (Dellagi et al. 2009). Additionally, siderophores fail to elicit the immunological responses seen in the WT in an irt1 mutant impacted by the absorption of many metals (Zn^{2+}, Mn^{2+}, Fe^{2+}), including iron (Aznar et al. 2014). Metals can efficiently aid in the formation of ROS, one of the several processes by which plants defend themselves against diseases (Fones and Preston 2013). Changes in the distribution or status of the metal can prompt ROS and immunity locally as a quick response, but they can also do so as a secondary, delayed response after the metal has been taken up from the rhizosphere or perhaps after mobilization from other

organs. Furthermore, the MYB72 gene may be a significant contributor to siderophore-triggered immunity through interfering with metal homeostasis. The iron deficiency in Arabidopsis necessitated the use of MYB72 and MYB10 (Palmer et al. 2013).

Alternately, siderophores may target the function of one or more proteins, similar to how pathogen effectors do, in which case metalloprotein modification may be involved. Immune responses will be triggered if this target protein is protected by a resistance-like protein, such as a member of the family of nucleotide-binding leucine-rich repeat (NB-LRR) proteins. In conclusion, since particular identification and the scavenging action are not mutually exclusive, siderophores may cause both to occur. Additionally, there can be variations in sensing mechanisms between various plant species. The iron scavenging effect, for example, does not appear to be involved in the process of coprogen defense activation in maize (Albarouki et al. 2014).

References

Albarouki E, Schafferer L, Ye F et al (2014) Biotrophy-specific downregulation of siderophore biosynthesis in Colletotrichum graminicola is required for modulation of immune responses of maize. Mol Microbiol 92:338–355. https://doi.org/10.1111/mmi.12561

Ardon O, Weizman H, Libman J et al (1997) Iron uptake in Ustilago maydis: studies with fluorescent ferrichrome analogues. Microbiology 143:3625–3631

Ardon O, Nudelman R, Caris C et al (1998) Iron uptake in Ustilago maydis: tracking the iron path. J Bacteriol 180:2021–2026

Aznar A, Chen NWG, Rigault M et al (2014) Scavenging iron: a novel mechanism of plant immunity activation by microbial siderophores. Plant Physiol 164:2167–2183. https://doi.org/10.1104/pp.113.233585

Bachman MA, Lenio S, Schmidt L et al (2012) Interaction of lipocalin 2, transferrin, and siderophores determines the replicative niche of Klebsiella pneumoniae during pneumonia. MBio 3:e00224–e00211

Barash I, Pupkin G, Netzer D, Kashman Y (1982) A novel enolic β-ketoaldehyde phytotoxin produced by Stemphylium botryosum f. sp. lycopersici: partial chemical and biological characterization. Plant Physiol 69:23–27

Beckmann N, Schafferer L, Schrettl M et al (2013) Characterization of the link between ornithine, arginine, polyamine and siderophore metabolism in Aspergillus fumigatus. PLoS One 8:e67426

Bentley MD, Anderegg RJ, Szansiszlo PJ, Davenport RF (1986) Isolation and identification of the principal siderophore of the dermatophyte Microsporum gypseum. Biochemistry 25:1455–1457

Blatzer M, Barker BM, Willger SD et al (2011) SREBP coordinates iron and ergosterol homeostasis to mediate triazole drug and hypoxia responses in the human fungal pathogen Aspergillus fumigatus. PLoS Genet 7:e1002374. https://doi.org/10.1371/journal.pgen.1002374

Boiteau RM, Mende DR, Hawco NJ et al (2016) Siderophore-based microbial adaptations to iron scarcity across the eastern Pacific Ocean. Proc Natl Acad Sci 113:14237–14242. https://doi.org/10.1073/pnas.1608594113

Boonchird C, Messenguy F, Dubois E (1991) Characterization of the yeast ARG5,6 gene: determination of the nucleotide sequence, analysis of the control region and of ARG5,6 transcript. Mol Gen Genet 226:154–166. https://doi.org/10.1007/BF00273599

Bruns H, Crüsemann M, Letzel A-C et al (2018) Function-related replacement of bacterial siderophore pathways. ISME J 12:320–329. https://doi.org/10.1038/ismej.2017.137
Burt WR (1982) Identification of coprogen B and its breakdown products from Histoplasma capsulatum. Infect Immun 35:990–996
Castaneda AR, Truster GA, Paul MH et al (1988) The early results of treatment of simple transposition in the current era. J Thorac Cardiovasc Surg 95:14–28
Caza M, Kronstad JW (2013) Shared and distinct mechanisms of iron acquisition by bacterial and fungal pathogens of humans. Front Cell Infect Microbiol 3:80. https://doi.org/10.3389/fcimb.2013.00080
Charlang G, Ng B, Horowitz NH, Horowitz RM (1981) Cellular and extracellular siderophores of Aspergillus nidulans and Penicillium chrysogenum. Mol Cell Biol 1:94–100. https://doi.org/10.1128/mcb.1.2.94-100.1981
Chen T-W, Wardill TJ, Sun Y et al (2013) Ultrasensitive fluorescent proteins for imaging neuronal activity. Nature 499:295–300. https://doi.org/10.1038/nature12354
Cornelis P, Dingemans J (2013) Pseudomonas aeruginosa adapts its iron uptake strategies in function of the type of infections. Front Cell Infect Microbiol 3:75. https://doi.org/10.3389/fcimb.2013.00075
De Hoog GS, Marvin-Sikkema FD, Lahpoor GA et al (1994) Ecology and physiology of the emerging opportunistic fungi Pseudallescheria boydii and Scedosporium prolificans: Ökologie und Physiologie der opportunistischen Pilze Pseudallescheria boydii und Scedosporium prolificans. Mycoses 37:71–78
Dellagi A, Segond D, Rigault M et al (2009) Microbial siderophores exert a subtle role in Arabidopsis during infection by manipulating the immune response and the iron status. Plant Physiol 150:1687–1696. https://doi.org/10.1104/pp.109.138636
Eisendle K, Lang A, Eibl B et al (2003) Phenotypic and functional deficiencies of leukaemic dendritic cells from patients with chronic myeloid leukaemia. Br J Haematol 120:63–73. https://doi.org/10.1046/j.1365-2141.2003.03979.x
Fekete FA, Spence JT, Emery T (1983) A rapid and sensitive paper electrophoresis assay for the detection of microbial siderophores elicited in solid-plating culture. Anal Biochem 131:516–519
Fekete FA, Chandhoke V, Jellison J (1989) Iron-binding compounds produced by wood-decaying basidiomycetes. Appl Environ Microbiol 55:2720–2722
Fones H, Preston GM (2013) The impact of transition metals on bacterial plant disease. FEMS Microbiol Rev 37:495–519. https://doi.org/10.1111/1574-6976.12004
Franza T, Expert D (2013) Role of iron homeostasis in the virulence of phytopathogenic bacteria: an "à la carte" menu. Mol Plant Pathol 14:429–438. https://doi.org/10.1111/mpp.12007
Frederick CB, Szaniszlo PJ, Vickrey PE et al (1981) Production and isolation of siderophores from the soil fungus Epicoccum purpurascens. Biochemistry 20:2432–2436
Gamit D, Tank SK (2014) Effect of siderophore producing microorganism on plant growth of Cajanus cajan (Pigeon pea). Int J Res Pure Appl Microbiol 4:20–27
Gsaller F, Eisendle M, Lechner BE et al (2012) The interplay between vacuolar and siderophore-mediated iron storage in Aspergillus fumigatus. Metallomics 4:1262–1270
Haas H (2012) Iron – a key nexus in the virulence of Aspergillus fumigatus. Front Microbiol 3:28. https://doi.org/10.3389/fmicb.2012.00028
Haas H (2014) Fungal siderophore metabolism with a focus on Aspergillus fumigatus. Nat Prod Rep 31:1266–1276
Haas H, Schoeser M, Lesuisse E et al (2003) Characterization of the Aspergillus nidulans transporters for the siderophores enterobactin and triacetylfusarinine C. Biochem J 371:505–513
Haas H, Eisendle M, Turgeon BG (2008) Siderophores in fungal physiology and virulence. Annu Rev Phytopathol 46:149–187
Hilger F, Culot M, Minet M et al (1973) Studies on the kinetics of the enzyme sequence mediating arginine synthesis in Saccharomyces cerevisiae. Microbiology 75:33–41
Hissen AHT, Chow JMT, Pinto LJ, Moore MM (2004) Survival of Aspergillus fumigatus in serum involves removal of iron from transferrin: the role of siderophores. Infect Immun 72:1402–1408

Höfte M (1993) Classes of microbial siderophores. Iron chelation plants soil Microorg, 3–26
Holinsworth B, Martin JD (2009) Siderophore production by marine-derived fungi. Biometals Int J Role Met Ions Biol Biochem Med 22:625–632. https://doi.org/10.1007/s10534-009-9239-y
Holzberg M, Artis WM (1983) Hydroxamate siderophore production by opportunistic and systemic fungal pathogens. Infect Immun 40:1134–1139
Howard DH (1999) Acquisition, transport, and storage of iron by pathogenic fungi. Clin Microbiol Rev 12:394–404. https://doi.org/10.1128/CMR.12.3.394
Huber DL (2005) Synthesis, properties, and applications of iron nanoparticles. Small 1:482–501. https://doi.org/10.1002/smll.200500006
Ismail A, Bedell GW, Lupan DM (1985) Siderophore production by the pathogenic yeast, Candida albicans. Biochem Biophys Res Commun 130:885–891
Jacobson ES, Goodner AP, Nyhus KJ (1998) Ferrous iron uptake in Cryptococcus neoformans. Infect Immun 66:4169–4175
Jadoun J, Shadkchan Y, Osherov N (2004) Disruption of the Aspergillus fumigatus argB gene using a novel in vitro transposon-based mutagenesis approach. Curr Genet 45:235–241. https://doi.org/10.1007/s00294-003-0480-6
Jin G, He G-W, Wang L-P, Zhang J (2010) Subgrid scale fluid velocity timescales seen by inertial particles in large-eddy simulation of particle-laden turbulence. Int J Multiph Flow 36:432–437
Johnson DB, Kanao T, Hedrich S (2012) Redox transformations of iron at extremely low pH: fundamental and applied aspects. Front Microbiol 3:96. https://doi.org/10.3389/fmicb.2012.00096
Kalinowski BE, Liermann LJ, Brantley SL et al (2000) X-ray photoelectron evidence for bacteria-enhanced dissolution of hornblende. Geochim Cosmochim Acta 64:1331–1343
Kraemer SM (2004) Iron oxide dissolution and solubility in the presence of siderophores. Aquat Sci 66:3–18
Leal SMJ, Roy S, Vareechon C et al (2013) Targeting iron acquisition blocks infection with the fungal pathogens Aspergillus fumigatus and Fusarium oxysporum. PLoS Pathog 9:e1003436. https://doi.org/10.1371/journal.ppat.1003436
Leong SA, Winkelmann G (1998) Molecular biology of iron transport in fungi. Met Ions Biol Syst 35:147–186
Lesuisse E, Labbe P (1994) Reductive iron assimilation in Saccharomyces cerevisiae. In: Winkelmann G, Winge DR (eds) Metal ions in fungi. Marcel Dekker, New York, pp 149–178
Manulis S, Kashman Y, Barash I (1987) Identification of siderophores and siderophore-mediated uptake of iron in Stemphylium botryosum. Phytochemistry 26:1317–1320
Masalha J, Kosegarten H, Elmaci Ö, Mengel K (2000) The central role of microbial activity for iron acquisition in maize and sunflower. Biol Fertil Soils 30:433–439
Mezence MIB, Boiron P (1995) Studies on siderophore production and effect of iron deprivation on the outer membrane proteins of Madurella mycetomatis. Curr Microbiol 31:220–223
Moors MA, Stull TL, Blank KJ et al (1992) A role for complement receptor-like molecules in iron acquisition by Candida albicans. J Exp Med 175:1643–1651
Mor H, Pasternak M, Barash I (1988) Uptake of iron by Geotrichum candidum, a non-siderophore producer. Biol Met 1:99–105
Mor H, Kashman Y, Winkelmann G, Barash I (1992) Characterization of siderophores produced by different species of the dermatophytic fungi Microsporum and Trichophyton. Biometals 5:213–216
Morrissey JA, Williams PH, Cashmore AM (1996) Candida albicans has a cell-associated ferric-reductase activity which is regulated in response to levels of iron and copper. Microbiology 142:485–492
Nürnberger T, Brunner F, Kemmerling B, Piater L (2004) Innate immunity in plants and animals: striking similarities and obvious differences. Immunol Rev 198:249–266. https://doi.org/10.1111/j.0105-2896.2004.0119.x
Oberegger H, Schoeser M, Zadra I et al (2001) SREA is involved in regulation of siderophore biosynthesis, utilization and uptake in Aspergillus nidulans. Mol Microbiol 41:1077–1089

Oide S, Moeder W, Krasnoff S et al (2006) NPS6, encoding a nonribosomal peptide synthetase involved in siderophore-mediated iron metabolism, is a conserved virulence determinant of plant pathogenic ascomycetes. Plant Cell 18:2836–2853

Palmer CM, Hindt MN, Schmidt H et al (2013) MYB10 and MYB72 are required for growth under iron-limiting conditions. PLoS Genet 9:e1003953

Qi W, Zhao L (2013) Study of the siderophore-producing Trichoderma asperellum Q1 on cucumber growth promotion under salt stress. J Basic Microbiol 53:355–364. https://doi.org/10.1002/jobm.201200031

Ratledge C, Dover LG (2000) Iron metabolism in pathogenic bacteria. Annu Rev Microbiol 54:881–941. https://doi.org/10.1146/annurev.micro.54.1.881

Raymond KN, Dertz EA (2004) Biochemical and physical properties of siderophores. In: Crosa JH, Mey AR, Payne SM (eds) Iron transport in bacteria

Raymond-Bouchard I, Carroll CS, Nesbitt JR et al (2012) Structural requirements for the activity of the MirB ferrisiderophore transporter of Aspergillus fumigatus. Eukaryot Cell 11:1333–1344

Schrettl M, Bignell E, Kragl C et al (2004) Siderophore biosynthesis but not reductive iron assimilation is essential for Aspergillus fumigatus virulence. J Exp Med 200:1213–1219. https://doi.org/10.1084/jem.20041242

Schrettl M, Bignell E, Kragl C et al (2007) Distinct roles for intra- and extracellular siderophores during Aspergillus fumigatus infection. PLoS Pathog 3:e128

Shirvani M, Nourbakhsh F (2010) Desferrioxamine-B adsorption to and iron dissolution from palygorskite and sepiolite. Appl Clay Sci 48:393–397. https://doi.org/10.1016/j.clay.2010.01.012

Sullivan TS, Ramkissoon S, Garrison VH, et al (2012) Siderophore production of African dust microorganisms over Trinidad and Tobago. Aerobiologia (Bologna) 28:391–401

Tekaia F, Latgé J-P (2005) Aspergillus fumigatus: saprophyte or pathogen? Curr Opin Microbiol 8:385–392. https://doi.org/10.1016/j.mib.2005.06.017

Thaler JS, Humphrey PT, Whiteman NK (2012) Evolution of jasmonate and salicylate signal crosstalk. Trends Plant Sci 17:260–270. https://doi.org/10.1016/j.tplants.2012.02.010

van der Helm D, Winkelmann G (1994) Hydroxamates and polycar-boxylates as iron transport agents (siderophores) in fungi. In: Metal in ions fungi. Marcel Dekker, New York, pp 39–98

van der Helm D, Winkelmann G (2020) Hydroxamates and polycarboxylates as iron transport agents (siderophores) in fungi. In: Metal ions in fungi. CRC Press, pp 39–98

van Schöll L, Smits MM, Hoffland E (2006) Ectomycorrhizal weathering of the soil minerals muscovite and hornblende. New Phytol 171:805–813. https://doi.org/10.1111/j.1469-8137.2006.01790.x

Wallner A, Blatzer M, Schrettl M et al (2009) Ferricrocin, a siderophore involved in intra-and transcellular iron distribution in Aspergillus fumigatus. Appl Environ Microbiol 75:4194–4196

Wencewicz TA, Möllmann U, Long TE, Miller MJ (2009) Syntheses and biological studies of the naturally occurring salmycin "Trojan Horse" antibiotics and synthetic desferridanoxamine-antibiotic conjugates. Biometals 22:633–648

Winkelmann G (1979) Surface iron polymers and hydroxy acids. A model of iron supply in sideramine-free fungi. Arch Microbiol 121:43–51

Winkelmann G (1993) Kinetics, energetics, and mechanisms of siderophore iron transport in fungi. In: Barton LL (ed) Iron chelation in plants and soil microorganisms. Academic, New York, pp 219–239

Worsham P, Goldman W (1988) Quantitative plating of Histoplasma capsulatum without addition of conditioned medium or siderophores. J Med Vet Mycol 26:137–143

Yadav J, Verma J, Tiwari K (2011) Plant growth promoting activities of fungi and their effect on chickpea plant growth. Asian J Biol Sci 4:291–299. https://doi.org/10.3923/ajbs.2011.291.299

Yasmin S, Alcazar-Fuoli L, Gründlinger M et al (2012) Mevalonate governs interdependency of ergosterol and siderophore biosyntheses in the fungal pathogen Aspergillus fumigatus. Proc Natl Acad Sci 109:E497–E504

Biogenic Synthesis of Nanoparticles Mediated by Fungi

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1 Introduction

One of the most exciting developments in technology that the twenty-first century has brought forth is nanotechnology. The Greek word "Nanos," which means "dwarf" or "very little," is the source of the prefix "nano".

One nanometer is equal to one billionth of a metre, which is an incredibly minute measurement unit. Nanotechnology is a multidisciplinary discipline that merges several areas of science and technology through the use of materials in nanoform. It is important to recognize that the fundamentals of quantum physics have played a role in the revolutionary character of nanotechnology. The capacity to observe, measure, manipulate, assemble, control, and manufacture materials at the nanoscale scale is what is meant by "nanotechnology". Nanotechnology is the implementation of the theory behind nanoscience. It focuses on the synthesis of materials at a size of 1–100 nm and has applications in agriculture, medicine, the pharmaceutical industry, the environmental area, and other disciplines (Lateef et al. 2021). A significant aspect of nanotechnology is the creation and modification of materials at the nuclear level to give them innovative features that may be used in a variety of ways. As a result, this would result in the production of cutting-edge materials that have exceptional characteristics. In recent years, nanotechnology and nanoscience research has seen explosive growth, giving the topic the nickname "tiny science".

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When it comes to technological developments, nanotechnology has been at the forefront of the discussion and has garnered an increasing amount of attention over recent years. Nanotechnology has not only piqued the interest of people of all ages and backgrounds all around the globe, but it has also caught the attention of the general public. Because of the topic's possible uses in technology, there has been a significant rise in interest in it over the last several years, and there has been a meteoric rise in commercial interest (Romig Jr et al. 2007). As a scientific and engineering discipline, nanotechnology is about the designing, synthesis, characterization, and application of materials and devices that have at least one dimension of their functional organization on the nanoscale scale. At the nanoscale, quantum physics governs rather than classical physics governs the behavior of materials. Nanoscaled materials have unique qualities that make them superior and more desirable than bulk materials, owing to their extraordinary attributes (Bhagyaraj and Oluwafemi 2018). Moving from a macro to a micro perspective eliminates the possibility of this impact occurring. Nevertheless, once the nanoscale size range is reached, it emerges as the dominating force. In addition, a variety of physical characteristics, such as mechanical, electrical, optical, and so on, alter when nano-scales are compared to macroscopic ones. A change in the mechanical, thermal, and catalytic characteristics of materials may also result from an increase in the surface area to volume ratio at the nanoscale (Purohit et al. 2012).

2 Nanoparticles

The term "nanoparticles (NPs)" refers to a broad category of materials that includes particulate compounds and must have at least one dimension that is less than 100 nanometers, which is much smaller than the bulk material. In the last 10 years, there has been an explosion of interest in the production of nanoscale materials, particularly metallic NPs, owing to the unique properties that these materials possess (Elmer and White 2018). Because NPs aren't simple molecules, they have three distinct layers as illustrated in Fig. 1, (a) the surface layer, which has the potential to be functionalized with a wide range of small molecules, metal ions, surfactants, and polymers. (b) The shell layer is composed of a substance that is completely unlike the core in terms of its chemical composition; and (c) The core, which is basically the centre piece of the NP and most often, refers to the NP itself (Shin et al. 2016).

The term "natural" may relate to either the shape of the materials or the aspect of the process. There are a variety of options, each of which requires more investigation to realize its full potential as a renewable resource for the natural production of NPs. Several types of yeast and bacteria that are not harmful provide useful possibilities for the production of a variety of nanoscale soluble particles. On the other hand, other plant products, such as herbs and debris from harvesting, might be fascinating alternatives. In a similar vein, grinding and homogenizing plant material may release a wealth of hitherto unexplored creative avenues and opportunities

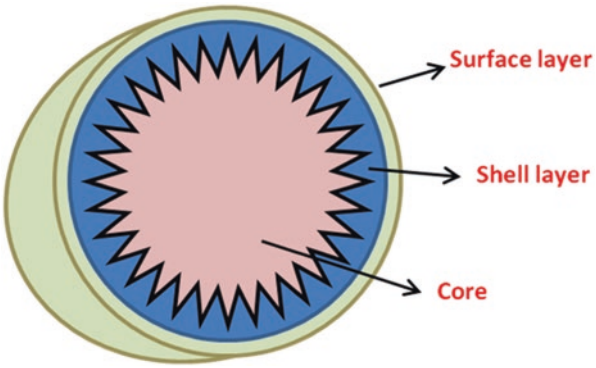

Fig. 1 Structure of nanoparticle (NP)

(Zhang et al. 2012; Liang et al. 2019). Bio-nanotechnology, together with phyto- or phyco-nanotechnology, is regarded as an exquisite twist in the realm of nanoscience. It gives a 'greener' aspect to the otherwise synthetic domain. As a component of bioremediation, the utilization of certain biogenic factories, the recovery of valuable materials from waste, and the efficient elimination of toxins are all now commonplace. Many applications in the natural and human sciences rely on NPs because of the large variety of activities in which they may be implemented, which is dependent on their size. It was the breakthrough in nanotechnology that signaled the beginning of a revolution in technology and a shift in the direction of human history (Nandini et al. 2017). Large quantities of bulk material were unable to compete with the widespread applications of nanoparticles because the latter owed their significance to the chemical, optical, mechanical, and magnetic properties that resulted from the increased surface area due to decreased particle size, while the former was devoid of this quality. Because of their one-of-a-kind characteristics and groundbreaking capabilities, NPs are increasingly being incorporated into everyday activities as well as the production of energy (Hasan 2015).

3 Biosynthesis of NPs

The production of non-hazardous and biodegradable nanoparticles may be accomplished using biosynthesis, which is an environmentally responsible and green approach. Instead of using conventional chemicals for bioreduction and capping, biosynthesis produces nanoparticles using bacteria, plant extracts, fungus, and other biological precursors and precursor compounds. Unique and improved characteristics of biosynthesized nanoparticles lead to their use in biological applications (Hasan 2015).

NPs are progressively being used in new products and devices having an excellent impact on completely different fields from sensoristics to biomedicine.

Microbial biosynthesis of nanoparticles is recently attracting interest as a brand new, exciting approach towards the development of 'greener' nanomanufacturing compared to classical chemical and physical approaches (Ribeiro et al. 2016). The most common microorganisms employed in nano-biosynthesis, mostly for medical applications, are bacteria and microalgae. Extracellular synthesis in yeasts and moulds is favourable for the potential re-use and for reducing the need for nanomaterial purification methods (Prasad et al. 2016).

The variation of microbiological systems needs a larger protocol standardization to get nanoparticles with increasingly uniform and reproducible chemical-physical characteristics (Hamida et al. 2021). In-depth knowledge of biosynthetic pathways and the potential benefits of genetic engineering are driving research into the development of ground-breaking microbial-based nano-synthesis for future scaling-up and potential economic exploitation of those promising nano-factories (Skeffington and Scheffel 2018).

The microbial nanoparticles synthesis has been extensively explored showing completely different advantages such as (i) synthesized nanoparticles have outlined chemical composition, size and morphology, (ii) biosynthesis is carried out under physicochemical conditions; (iii) simply handling and cultivating microbial cells and the possibility of cell culture scale-up; and (iv) Possibility of in vivo standardization of nanomaterial properties by genetic engineering methods or by adjusting critical cell culture operational starting parameters (Dragone et al. 2017).

It is crucial to understand the molecular biology and microbial genetics concepts behind the microbial nano-biosynthetic processes. Increased control over the chemical compositions, forms, and sizes of nanoparticles, for example, could result from the analysis of poorly understood biochemical mechanisms and the thorough identification of extracellular enzymes released by filamentous fungi (Al-Dhabi et al. 2018). The possibility of genetically engineering microorganisms to produce nanoparticles and calibrate their properties in vivo may be greatly increased by the availability of microorganism genome sequences (Voeikova et al. 2017).

The sequences of the genes involved in the synthesis of nanoparticles may be identified using biotechnological methods based on recombinant DNA technology, and their potential for heterologous expression (the controlled expression of the gene in a host organism) to increase the productivity of nanomaterials may also be explored (Husseiny et al. 2015).

3.1 Myconanotechnology

Through a variety of interrelated biomechanical and chemical mechanisms, fungi exhibit a variety of skills in influencing mineral formation, dissolution, and toxicity as well as metal speciation. The formation of nanoparticles, which can be in elemental, mineral, or compound form, is a result of several metal-mineral interactions. Since some mycogenic nanoparticles will act as nano-enzymes mimicking enzymes, such as peroxidase, organisms may profit from the development of such

nanomaterials by removing metal toxicity, being protected from environmental stress, and having better redox characteristics. As nanotechnology progresses, there is increased interest in using biological systems to produce nanomaterials, which could have positive economic effects and less negative environmental effects than traditional chemical synthesis. The formation of nanoparticles is a common result of many metal-mineral microbiological interactions, and fungi aren't an exception to the rule. The synthesis of CdS crystallites in yeasts is a prominent example of the latter, but the production may also be a direct or indirect result of metabolism and/or the reactivity of structural components (Rai et al. 2021).

Myconanotechnology is the production of nanoparticles by fungi and their subsequent usage, primarily in healthcare, environmental, and agricultural products. It looks into different ways to make metal nanoparticles, as well as process methods, environmental protection, and prospects (Rai et al. 2021). Soil mycobiota will influence metallic zinc mobilization from ZnO NPs in soils. Therefore, *Aspergillus niger*, a typical soil flora, was selected to assess microbial interactions with ZnO NPs. As expected, the *A. niger* strain had a major significant effect on the stability of particulate forms of ZnO due to the acidification of its environment. Developing effective synthesis and nanoparticle extraction methods may benefit from research on the actual production of nanoparticles as well as the effects of different factors on metal ion reduction. Mycogenic nanoparticles, risk evaluation, protection, and control will also be covered. Fungi can manufacture several extracellular enzymes that hydrolyze complex macromolecules and leave behind a hydrolysate (Castro-Longoria et al. 2017). The metabolic capacity of its use in bioprocesses has been a significant source of worry for the application of fungi. The diversity of fungi has resulted in significant consequences for the mycogenic synthesis of nanoparticles, a key component of myco-nanotechnology (Rai et al. 2011).

Myconanoparticles are widely employed as nematicides, to clean wastewater, preserve food, detect and regulate pathogenic organisms, and for a variety of alternative products. Numerous fungal species produce mycogenic nanoparticles, which could be employed in various agricultural applications to boost crop yield by promoting growth and preventing diseases (Hashem et al. 2021). Additionally, this can increase how hazardous chemical pesticides and herbicides are to plant environments. Human infectious disease-causing microorganisms have been effectively inhibited by fungal-mediated nanoparticles, especially when it comes to infections that are multi-resistant to conventional antibacterial treatments (Alghuthaymi et al. 2021).

In a very broad range of scientific fields, including medicine, pharmaceuticals, agriculture, and electronics, fungi-mediated nanoparticles are successfully applied. Because of this, several analyses concentrated on the application of mycogenic nanoparticles against plant diseases, post-harvest antibiotics, mycotoxin management, and plant pests, as well as specific animal pathogens. Additionally, fungus-based nanomaterials have great promise for improved diagnostics, biosensors, precision agriculture, and targeted smart delivery systems (Rai et al. 2021). The development of antifungal nanohybrid agents containing conjugates of organic or inorganic compounds, biological elements and biopolymers was researched to get

cheaper, additional dependable and effective products against most fungal infections of plants and animals (Kalia et al. 2020). Since myco-nanoparticles are still in their infancy, much research should be conducted in this field. Plants, animals, and humans will all substantially benefit, thus it is important to develop methods that are both affordable and environmentally benign (Jagtap et al. 2021).

Since most fungi are easily cultivated under controlled conditions and are well-known for the production of metabolites and enzymes linked to nanoparticles, we concentrate on fungi in this chapter. The production of nanoparticles can be a direct or indirect result of metabolism and/or the reactivity of structural elements, or it can be a part of a metal resistance mechanism. An example of the latter is the formation of CdS crystallites in some yeast, and the cell wall additionally offers abundant nucleation sites for their formation. Nanoparticles can be formed intracellularly or extracellularly (Jacob et al. 2016).

The mycogenic route for nanoparticles synthesis has been well recognized and chosen as better nano factories over bacteria and plants according to the following various reasons (Fig. 2):

(a) Exceptional protein secretor

Fungi produce large amounts of extracellular enzymes that catalyse the heavy metal ions and produce nanoparticles, and many may flourish within the presence of high metal concentrations due to various active and incidental mechanisms to combat metal toxicity due to which fungi can produce nanoparticles at a faster rate than chemical synthesis (Hashem et al. 2021).

(b) Easy culture

Fungi are easy to isolate and subculture as they have simple nutritional requirements. Serial dilutions, plating and hyphal extraction are the simple methods required to isolate fungi (Gade et al. 2010). A filamentous explorative mycelium

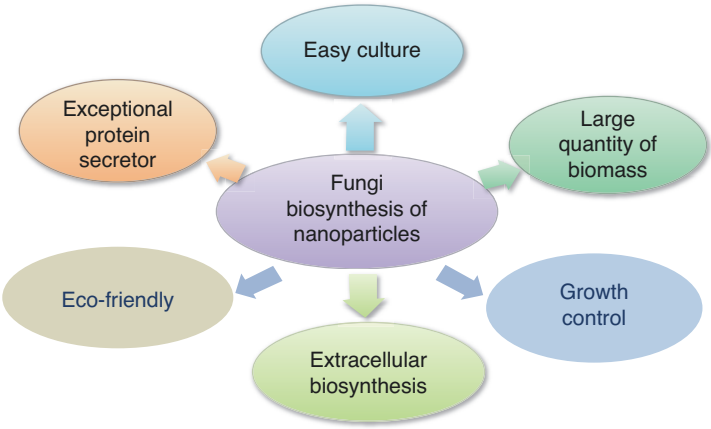

Fig. 2 Advantages of mycogenic synthesis of nanoparticles

made of fungal hyphae grows branches and fuses to have a high surface area to mass ratio and nutrient transfer capabilities. The hydrated mucilaginous sheath that frequently envelops hyphae serves as a matrix for geochemical reactions. Due to the numerous metal-binding functional groups inside the cell wall and accompanying extracellular polymeric substances (EPS) that serve as nucleation sites, the branching network offers an effective template for the creation of nanoparticles or nanominerals (Yu et al. 2020).

(c) Large quantity of biomass (Gade et al. 2010).
(d) Extracellular synthesis of nanoparticles

Fungi can produce nanoparticles extracellularly which is suitable for easier downstream processing and handling of biomass (Sahai 2010).

(e) Growth control

The enzymes secreted by fungi can be used to synthesize nanoparticles of defined size and shape. Fungi can sustain under high agitation and flow pressure as compared to other microorganisms and plants (Bhardwaj et al. 2020).

(f) Eco-friendly (Jagtap et al. 2021).

Several fungi species can be used to synthesize metal nanoparticles via extracellular and intracellular processes that are safe for the environment, clean, and non-toxic.

3.2 Strategies Used for the Fungal Biosynthesis of Nanoparticles

3.2.1 Top Down

This includes the formation of nano-size material from massive substrates. It involves cutting, etching, and grinding by mechanical, chemical or electrochemical methods (Fig. 2) depending upon the nature of basal matter. This may be due to lots of impurities and structural defects in synthesized nanoparticles by lithography (Behari 2010).

3.2.2 Bottom Up

It is mediated by the congregation of the substrate to atoms/molecules and assemblies into nanostructures like nanorods, nanotubes, nanowires or quantum dots. The key point in myco-synthesis of nanoparticles is the secretory enzymes having reducing power that is responsible for the reduction of metal compounds into a respective nanoparticle. The bottom-up approach for synthesis offers a diverse range of nanoparticles with more uniformity and fewer defects. The reason behind this is the

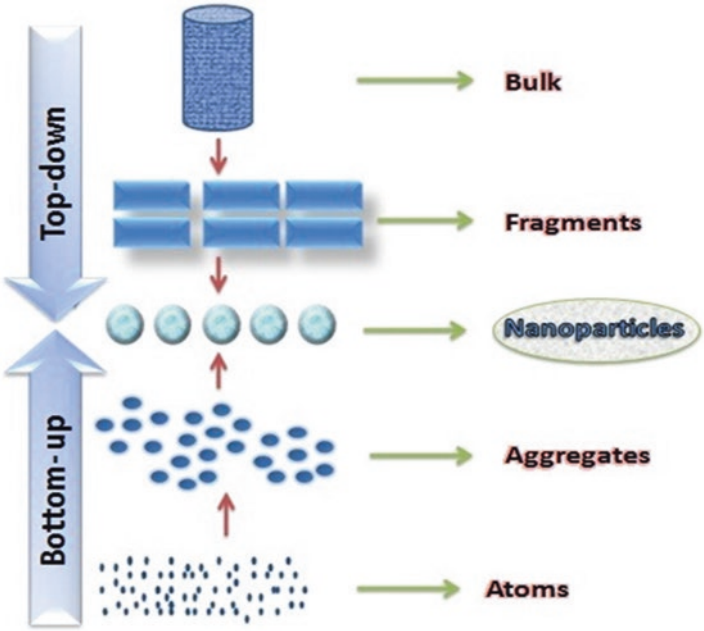

Fig. 3 Strategies of mycosynthesis of NPs

reduction of Gibbs free energy that results in the synthesis of nanoparticles which are close to thermodynamic equilibrium (Moghaddam 2010). Bottom-up approaches entail building structures through self- or positional assembly into crystals or tubes, followed by particle creation with nanoscale dimensions, which is the opposite of top-down approaches (Fig. 3).

Kashyap et al. (2013) reported the synthesis of nanoparticles by the use of fungi, which is a type of bottom-up strategy where most of the reaction is based on the reduction of the substrate, leading to the step-by-step formation of nanoparticles. There are several biotic and biotic factors which directly affect the myco-synthesis of nanoparticles such as temperature, pH, incubation conditions, time in the exposure of the substrate, the presence of a particular enzyme, metal species, biomass concentration of fungus and colloidal interaction conditions (Alghuthaymi et al. 2015).

3.3 Mechanism of Myco-synthesis of Nanoparticles

Fungi will manufacture nanoparticles as extracellularly or intracellularly, but the mechanism is not understood completely. Putative mechanisms during intracellular synthesis include heavy metal binding to the fungal cell wall by proteins or enzymes present on it via electrostatic interactions (Kashyap et al. 2013). Additionally, the

metal ions are reduced by enzymes present in the cell wall. This leads to the aggregation of metal ions and the formation of nanoparticles. Extracellular synthesis of nanoparticles has advantages because it doesn't require the lysis of fungal cells, a downstream process for the recovery and purification of nanoparticles. Whereas in the case of intracellular synthesis recovery and purification of nanoparticles from fungi biomass is a tedious task and thus analytical equipment and long processing techniques are needed (Zhang et al. 2011).

While some nanoparticles will operate as nanozymes, mediating redox processes and catalysis, altering iron speciation, and organic matter breakdown, and offering protection against reactive oxygen species, organisms may benefit from metal detoxification and protection from environmental stress. Nanozymes are inorganic nanoparticles made of metals and metal oxides that replicate the functions of enzymes in redox processes. Most of the catalytic reactions mediated by nanozymes involve oxidase (OXD), peroxidase (POD), catalase (CAT) and superoxide dismutase (SOD) activities (Yu et al. 2020). To prevent oxidative stress and preserve redox balance, the antioxidant enzyme eliminates extra reactive oxygen species (ROS), such as superoxide (O_2^-) and hydrogen peroxide (H_2O_2). What are the roles of biogenic nanomaterials in the co-evolution of the lithosphere and biosphere? is the question that is raised by the discovery that ferrihydrite nanoparticles produced by fungal transformation of hematite do indeed possess peroxidase activity, scavenge hydrogen peroxide for mitigation of cytotoxicity, and ensure the acquisition of essential iron. Moreover, several fungi are excellent candidates for metal immobilization, mineral dissolution and formation, and many can flourish in the presence of high metal concentrations due to various active and incidental mechanisms to combat metal toxicity (Chi et al. 2021).

3.4 Different Metallic Nanoparticles Are Produced During Myco-synthesis

Fungal nanotechnology examines a variety of metal nanoparticle syntheses, including processing methods, environmental preservation, and prospects. Certain nanomaterials, including *Trichoderma*, *mushrooms, Fusarium*, endophytic fungi, silver, gold, palladium, magnesium, zinc, copper, selenium, metal sulfides, cellulose, and titanium dioxide, as well as other important fungi (Prasad 2017). For example, *Rhizopus oryaze* metabolites were utilized as a biocatalyst for the green synthetization of magnesium oxide (MgO-NPs) nanoparticles (Hassan et al. 2021). Silver nanoparticle formation by *Trichoderma virens* also requires silver ion reduction by nitrate reductase (Devi et al. 2013). One of the most widespread genera of fungi, *Fusarium*, is crucial to the manufacturing of numerous nanoparticles and can be seen as a nanofactory. This issue discusses the production of silver nanoparticles (AgNPs) from Fusarium, also its mechanism and uses (Rai et al. 2021). Myco-fabrication can be described as the synthesis of various metal nanoparticles via fungal species (Table 1).

Table 1 Fungal biosynthesis of nanoparticles

Nanoparticles	Size (nm)	Shape	Species	Reference
Ag	–	Granular	*A. pullulans*, *D. hansenii*, *C. albicans*, *R. rubra*	Kierans et al. (1991)
	50–200	Spherical	*Phanerochaete chrysosporium*	Vigneshwaran et al. (2007)
	5–25	Monodispersed	*A. fumigatus*	Basavaraja et al. (2008)
	5–200	Pyramidal	*Cladosporium cladosporioides*	Balaji et al. (2009)
	8.92	–	*A. flavus*	Sanghi and Verma (2009)
	20	Spherical	*A. niger*	Gade et al. (2008)
	15	Spherical	*Volvariella volvacea*	Shaligram et al. (2009)
	16 ± 6	Spherical	*P. cyclopium*	Wanarska and Maliszewska (2019)
	20–60	Polydisperse spherical	*Alternaria alternata*	Bansal et al. (2005)
Au	20 ± 2.0	Spherical	*Rhizopus oryzae*	Das et al. (2012)
	43–63		*A. niger*	
	20		*A. niger*	
	8.7 ± 6		*A. niger*	
	6–37		*A. oryzae*	
	3.5 ± 3		*A. tamarii*	
	5		*F. oxysporum*	
	7.7 ± 4.3		*Penicillium ochro-chloron*	
	75	Heterogeneous	*Penicillium* sp.	
	15–20	Spherical	*S. cerevisiae*	Sen et al. (2011)
$BaTiO_3$	20–30	Spherical	*F. oxysporum*	Riddin et al. (2006)
$BiMnO_3$	50	Spherical	*Humicola* sp.	Mazumder et al. (2007)
$CdCO_3$	55–870	Granular	*Neurospora crassa*	Li et al. (2014)
CdTe	15–20	Spherical	*F. oxysporum*	Syed and Ahmad (2013)
CeO_2	5–20	Spherical	*A. niger*	Gopinath et al. (2015)
$CePO_4$	100–200, 500	Needles, spherical	*S. cerevisiae*	Jiang et al. (2010)
CO_3O_4	54.85	Spherical	*S. cerevisiae*	Li et al. (2018)

(continued)

Table 1 (continued)

Nanoparticles	Size (nm)	Shape	Species	Reference
$Cu_2CO_3(OH)_2$, $Cu_3(OH)_2(CO_3)_2$	10–20	Granular	*Neurospora crassa*	Li and Gadd (2017a)
Cu, CuO	5–20	Spherical	*Stereum hirsutum*	Cuevas et al. (2015)
CuS	10–40	Irregular	*F. oxysporum*	Schaffie and Hosseini (2014)
$CuAlO_2$	5	Spherical	*Humicola* sp.	Ahmad et al. (2007)
$FeCO_3$, Fe	~80	Granular	*Neurospora crassa*	Li et al. (2020)
Fe_3O_4	20–50	Quasi-spherical	*F. oxysporum*	Vainshtein et al. (2014)
Hydronium-jarosite	–	Spherical	*Purpureocillium lilacinum*	Oggerin et al. (2013)
$LaCO_3$	~80	Needles	*Neurospora crassa*	Li and Gadd (2017b)
$LiFePO_4$	–	Blocky	*S. cerevisiae*	Cao et al. (2018)
	–	Amorphous	*S. cerevisiae*	Zhang et al. (2013)
MgO	45.12–95.37	Heterogeneous	*Trichoderma viride*	Alrabadi et al. (2017)
$MnCO_3/Mn_2O_3$	20	Lamellar	*Neurospora crassa*	Li et al. (2016)
$NiCO_3$	60	Granular	*Neurospora crassa*	Li et al. (2019)
Ni oxide	1.25–3.8	Spherical	*Hypoxealixii*	Salvadori et al. (2015)
PbSe	20–160	Rods	*A. terreus*	Jacob et al. (2014)
Pt	10–100	Hexagonal, pentagonal, spherical, cuboid	*F. oxysporum*	Riddin et al. (2006)
Pd	10–20	Spherical	*S. cerevisiae*	Saitoh et al. (2020)
Se	70–90	Spherical	*Magnusiomyces ingens*	Lian et al. (2019)
Se, Te	48–78	Granular	*Aureobasidium pullulans*, *Mortierella humilis*, *Trichoderma harzianum*, *Phoma glomerata*	Liang et al. (2019)
$SmPO_4$	50–200	–	*S. cerevisiae*	Jiang et al. (2018)
$SrCO_3$	10–50	Needles	*Fusarium oxysporum*	Rautaray et al. (2004)
Te	20–465	Needles	*P. chrysosporium*	Espinosa-Ortiz et al. (2017)

(continued)

Table 1 (continued)

Nanoparticles	Size (nm)	Shape	Species	Reference
Ti/TiO_2	2–16	Spherical	*Trichoderma harzianum*	Jayaseelan et al. (2013)
TiO_2	6.7 ± 2.2	Spherical, oval	*S. cerevisiae*	Peiris et al. (2018)
	10	Oval	*S. cerevisiae*	He et al. (2011)
U(VI)	50–100	Needles	*Geotrichum* sp.	Zhao et al. (2016)
ZnO	–	Cuboid	*Pichia fermentans*	Chauhan et al. (2015)
ZnS	42	Spherical	*F. oxysporum*	Mirzadeh et al. (2013)
$Zn_3(PO_4)_2$	10–80 nm in width and 80–200 nm in length	Butterfly-like	*S. cerevisiae*	Yan et al. (2009)
ZrO_2	7–8	Spherical	*F. oxysporum*	Bansal et al. (2004)

3.4.1 Silver Nanoparticle Production (AgNP)

Min et al. (2009) reported that silver nanoparticles have a high fraction of surface atoms which shows a more antimicrobial effect compared to bulk silver. Synthesis of silver nanoparticles has been investigated utilizing several ubiquitous fungal species including *Trichoderma* (Vahabi et al. 2011), *Fusarium* (Durán et al. 2005), *Penicillium* (Hemath Naveen et al. 2010), and *Aspergillus* (Bhainsa and D'Sousa 2006). Extracellular synthesis has been demonstrated by *Trichoderma virde*, *Fusarium oxysporm*, *F. semitectum*, *F. solani*, *Aspergillus niger*, *A. flavus* (Jain et al. 2011), *Pleurotus ostreatus*, *Cladosporium cladosporioides* (Vahabi et al. 2011), *Penicillium brevicompactum*, *Epicoccum nigrum*, *Chrysosporium tropicum*, and *Phoma glomerata*, while intracellular synthesis was shown to occur in a *Verticillium* species, and in *Neurospora crassa* (Mukherjee et al. 2001).

Rathod and Ranganath (2011) have reported the extracellular synthesis of monodispersed AgNPs by *Rhizopus stolonifer* which is cost-effective as well as ecofriendly and characterized by UV-Vis, SEM, TEM, FTIR and AFM. Further, they have also extended their studies on determining the antibacterial activity against multidrug-resistant as *Pseudomonas aeruginosa*, *E. coli* and *S. aureus*. Jain et al. (2011) confirmed the presence of an extracellular protein of molecular weight 32 kDa during the synthesis of silver nanoparticles using cell filtrate of *A. flavus*.

Furthermore, Endophytic *Pestalotia* sp. isolated from leaves of *Syzgium cumini* has been used to produce spherical and polydispersed AgNP having an average size of 12.4 nm. They have reported this silver nanoparticle as a better antimicrobial agent by evaluating its antibacterial activity against *S. aureus* and *S. typhi*. Sanghi and Verma (2009) synthesized protein-capped AgNP using fungus proteins of *Coriolus versicolor*. The amino group of protein was found to be bound on AgNP

as determined by FTIR. The endophytic *Penicillium* sp. isolated from *Curcuma longa* leaves were found to be an excellent producer of silver nanoparticles as reported recently. Qian et al. (2013) synthesized AgNps from an endophytic fungi *Epicoccum nigrum* isolated from the cambium of *Phellodendron amurense*. The synthesized AgNP was found to be highly stable even at varied pH and temperature.

3.4.2 Gold Nanoparticle Production (AuNP)

Being more harmful to the fungus than silver, the synthesis of gold nanoparticles has been investigated utilizing *Fusarium* (Mukherjee et al. 2002), *Neurospora* (Castro-Longoria et al. 2011), *Verticillium*, *yeasts* (Chauhan et al. 2011) and *Aspergillus*. Extracellular gold nanoparticle synthesis was demonstrated by *Fusarium oxysporum*, *Aspergillus niger* and *Candida albican*. Intracellular gold nanoparticle synthesis has been detected by a *Verticillum* species (Gericke and Pinches 2006). Das et al. (2009) also reported that gold nanoparticles synthesized from *Rhizopus oryzae* have strong adsorption capacity. *Fusarium oxysporum*-mediated AuNP showed more aggregation and irregularity in shape and size (Anitha and Palanivelu 2011). Intracellular synthesis of AuNPs by using *Penicillium* sp. has been reported by Zhang et al. (2009). Variation in the temperature was found to control the size of biosynthesized gold nanoparticles.

Du et al. (2011) have reported that rapid extracellular synthesis of AuNP in cell filtrate and intracellular synthesis in fungal biomass by *Penicillium* sp. Shankar et al. (2003) synthesized AuNPs using endophytic fungi. *Colletotrichum* sp. isolated from leaves of *Pelargonium graveolus* as determined by TEM analysis. The *Sclerotium rolfsii*-mediated gold nanoparticles were found to be spherical and anisotropic which is of variable shapes such as triangle, hexagonal rod and decahedral in shape. The size shape and state of aggregation of the nanoparticle are determined by various factors including various concentrations of precursor salts, and different cellular fractions of culture. Deepa and Panda (2014) synthesized AuNPs from the culture filtrate of *F. oxysporum* and found diverse shapes and sizes of AuNPs in the presence of different cellular fractions. The specificity and sensitivity of the assay determine the pathogen detection in less time with more accuracy. Synthesis of AuNPs by edible mushroom *Pleurotus florida* has been documented. The synthesized AuNPs showed anticancer activity against cancer in vitro as human lung carcinoma, leukaemia, and human adenocarcinoma mammary gland (MDA-MB) (Bhat et al. 2013).

3.4.3 Miscellaneous Nanoparticle Production

Add to silver and gold, *F. oxysporum* has been used to synthesize zirconia, cadmium sulfide, titanium and cadmium selenide. The white-rot fungus *Phanerochaete chrysosporium* has incontestable that can synthesize elemental selenium nanoparticles

(Syed and Ahmad 2013). Cadmium sulfide nanoparticles have been synthesized by *Trametes versicolor*, *Schizosaccharomyces pombe* and *Candida glabrata*. Prasad and Jha (2010) reported the synthesis of CdS nanoparticles using *S. cerevisiae* as a rapid and low-cost green method.

In addition to the above, several other metallic nanoparticles were synthesized using fungi as the synthesis of nanosized magnetite by *Mucor javanicus* (Meng et al. 2014), Selenium nanoparticle by *A. alternate* (Sarkar et al. 2011), Silica nanoparticle by *F. oxysporum* (Bansal et al. 2006), Barium titanate nanoparticle by *F. oxysporum* (Bansal et al. 2006), Bi_2O_3 nanoparticle by *F. oxysporum* (Uddin et al. 2008) and Platinum nanoparticle by *F. oxysporum* (Govender et al. 2009). The biologically produced nanoparticles exhibit improved antibacterial activity against both Gram-positive and Gram-negative bacteria.

3.5 Potential Uses for Mycogenic Nanoparticles

Due to their distinctive characteristics, nanoparticles are utilised in everyday life. It has been discovered that nanoparticles are used in a variety of products. However, pharmacological and biological science is where nanoparticles are most useful (Golinska et al. 2014). The extensive use of NPs in numerous fields has recently raised awareness of fungus-mediated NP production. Also, Fungi are great choices among the different microorganisms utilized to produce nanoparticles for both internal and exogenous MtNPs which have good dispersion and stability properties (Bahrulolum et al. 2021).

The positive effects of nanotechnology are shown in various facets of agriculture. Currently, plant diseases are controlled through the myco-synthesis of nanomaterials in different structures (El-Batal et al. 2020). Myconanotechnology opened the door for the development of nano-devices and nano-structures, which have potential new applications in the agricultural fields (Raliya et al. 2015). Additionally, NPs produced by several fungal species are utilized to prevent plant pathogens from infecting plants and to protect them from pests and insects (Raliya et al. 2016). Fungi-produced nanoparticles play a significant role not only in inhibiting or killing harmful insects but also, in the decomposition of dangerous pesticides such as the silver nanoparticles formed from *Penicillium pinophilum* can degrade chlorpyrifos pesticide under different conditions. Both *Culex quinquefasciatus* and *Anopheles stephensi* larvae were shown to be vulnerable to gold nanoparticles and silver nanoparticles created by the entomogenous fungus *Chrysosporium tropicum* (Soni and Prakash 2012).

Researchers have previously focused on the antimicrobial examination of fungi-produced nanoparticles against microbes in the agricultural field (Sandhu et al. 2019). Fungal cells are a key component in the production of nanomaterials used to combat plant cell disease. Because of their high metal tolerance and capacity to accumulate metals, they are widely used in the production of NPs such as platinum, silver, iron, and gold, among others. It is reported that Ag-NPs formed by *Mucor*

hiemalis were potent against different pathogenic fungi (Aziz et al. 2016). According to Bansal et al. (2005), *F. oxysporum* is capable of myco-synthesizing silica NPs, which has significant in improving disease resistance in plant cells. CuO-NPs produced by *P. chrysogenum* were effective against many plant pathogenic fungi (El-Batal et al. 2020). The silver nanoparticles formed extracellularly by *Trichoderma longibrachiatum* significantly decreased the fungal growth of *Fusarium verticillioides*, *Fusarium moniliforme*, *Helminthosporium oryzae*, *Penicillium brevicompactum* and *Pyricularia grisea* (Elamawi et al. 2018). The plant pathogen *Fusarium solani*, isolated from wheat, was a good producer of AgNPs that have antifungal effects against different species of fungal pathogens that infect wheat, barley, and maize kernels (Vigneshwaran et al. 2007).

Environmental bioremediation is one of the most significant applications of nanoparticles. Nano-remediation employs active nanoparticles to stimulate and reduce pollution. Nanoparticles are now effective oxidizing agents for removing environmental pollutants and they have considerable permeability and reactivity to various organic contaminants (El-Sayed et al. 2020). Nanoparticles such as Au-NPs, ZnO-NPs, and Ag-NPs play a catalyst role in the dye-removal process by increasing the reaction rate while decreasing the time it takes to finish the degradation process (Rabeea et al. 2020). According to other studies, the biosynthesized Se-NPs and Au-NPs by the *Monascus purpureus* and *Cladosporium oxysporum* have proteins surface which enhances the adsorption of dyes (methylene blue and rhodamine B) as amino acids linked to rings of aromatic compounds creating hydrophobic areas that cause the interaction between nano-catalyst and dye molecules (El-Sayed et al. 2020). Many studies showed that the catalyst in the form of nano-silver has good effectiveness in eliminating pollutants, notably organic dyes, which results in an improved reaction rate and high efficiency. Also, the utilization of silver nano-catalysts leads to inhibition or decreasing the by-products generated during the production of propylene oxide, a common substance used for various industrial purposes. This highlights the industrial role that nano-metals play (Popli et al. 2018). In addition, silver nanoparticles created from fungi are employed in many environmental applications such as air decontamination, wastewater treatment and textile fabrics to minimize microbial infection (Durán et al. 2007; Zhang et al. 2014).

The advantages of NPs utilization in wastewater treatment are mostly through the adsorption of harmful substances including compounds, heavy metals, and other contaminants besides its antimicrobial metals and antioxidant characteristics (Gaur et al. 2014). Nowadays, this technique for wastewater treatment is capable of producing good-performance treated water containing fewer impurities, less toxic compounds and free from most heavy. Myconanotechnology has provided a new method for eliminating heavy metals like chromium, lead, and cadmium from wastewater using nanoparticles like iron oxide. This is ensured by the study of Mahanty et al. (2019) which recorded the removal of 90% of chromium content from water pollutants. Economically, myco-nanotechnology is regarded as a new approach to solving difficulties associated with wastewater treatment (Khandel and Shahi 2018).

Myconanotechnology is recently gaining attention in many industrial applications. In the field of the food industry, the applications of nanomaterials have proven their efficiency in food processing as its main focus is to reduce food spoilage. The nanoparticles are used in packaging food products taking into consideration food safety. Packaging materials containing AgNPs or ZnO-NPs were effective in preventing juices from spoilage without altering their characteristics although Ag-NPs have a higher antimicrobial activity on mould and yeast cells by comparing with ZnO-NPs. Ray et al. (2013) found that the addition of nano-gold to the packaging tissue gave it a new quality by raising its antimicrobial activity. A study on Se-NPs revealed that they can eliminate pollutants that lead to food spoiling and eradicate pathogens during the manufacturing process (Mosallam et al. 2018).

In the textile industry, one of the most significant industries, nano-metals were highly efficient in raising their quality by improving their antimicrobial activity and protection from harmful radiation. In this context, AgNPs have been successfully improved into textiles and wound dressings in eliminating microbial infections (Shaheen and Abd El Aty 2018). ZnO-NPs formed by *F. keratoplasticum*, *A. niger* and *A. terreus* enhanced the antibacterial efficiency of cotton fabrics against different bacterial strains and increased UV-blocking properties (Mohamed et al. 2019).

The appearance of new drug-resistant pathogens is a significant problem therefore, it was necessary to improve the characteristics of new drugs to increase their effectiveness against these organisms. The applications of NPs have several benefits in the medical field as disease diagnosis and treatment (Yousef et al. 2020). Numerous studies have shown that myco-synthesized Se-NPs, ZnO-NPs, Ag-NPs, Cu-NPs, and CuO-NPs have antibacterial properties against different pathogenic bacteria (Salem et al. 2021). Also, Mycosynthesized AgNPs have been reported as efficient antifungal agents against various pathogenic fungi such as *A. flavus*, *A. fumigatus*, *Candida parapsilosis*, *C. krusei*, *C. albicans*, *C. tropicalis*, *Sporothrix schenckii* and *F. solani* (Aziz et al. 2016; Parmar and Sharma 2020). This distinct antimicrobial effect of metal-NPs is attributed to its destructive effect on the microbial cell wall, degradation of cell components and/or oxidative damage of NPs (Qin et al. 2020). Different studies found a variation between Gram-negative bacteria than Gram-positive bacteria in response to metallic-NPs and this is attributed to the difference in their cell wall structure (Roy et al. 2019). Additionally, the disruption of membrane permeability due to electrostatic interaction between the NPs' positive charge and the negative charge of lipopolysaccharides in Gram-negative bacteria explained its higher sensitivity to NPs (Yun'an Qing et al. 2018). As the metallic-NPs enter a microbial cell, it binds with vital components like enzymes and nucleic acids, causing alteration of their normal structure (Qin et al. 2020).

Cancer diagnosis and therapy have drawn increased attention recently. Numerous nanomaterials have been studied to increase their effectiveness in treating cancer while minimizing side effects when compared to traditional medicines. The toxicity effects of mycogenic biosynthesized NPs are determined by Changes in survival, shape, and metabolic functions of the cells (Mohanta et al. 2018). Physico-chemical characteristics of NPs as nature, size, surface area and capping agents have an important role in their cytotoxicity impacts (Golinska et al. 2017; Mohamed et al.

2019). In recent years, to lessen the side effects of traditional anticancer medications and increase the performance of antitumor drug target therapies, a variety of NP-sized drug types have been studied in cancer therapy. The biosynthesized AgNPs from *Agaricus bisporus* and *Penicillium brevicompactum* showed an anticancer effect against the MCF-7 breast cancer cells (Majeed et al. 2016). Similar to this, gold nanoparticles made from *Chonemorpha fragrans* demonstrated efficacy against human breast and cervical cancer cell lines by induction of apoptosis in the cancer cell line (Clarance et al. 2020).

References

Ahmad A, Jagadale T, Dhas V, Khan S, Patil S, Pasricha R, Ravi V, Ogale S (2007) Fungus-based synthesis of chemically difficult-to-synthesize multifunctional nanoparticles of $CuAlO_2$. Adv Mater 19(20):3295–3299. https://doi.org/10.1002/adma.200602605

Al-Dhabi NA, Mohammed Ghilan AK, Arasu MV (2018) Characterization of silver nanomaterials derived from marine *Streptomyces* sp. al-dhabi-87 and its in vitro application against multidrug resistant and extended-spectrum beta-lactamase clinical pathogens. Nano 8(5):279. https://doi.org/10.3390/nano8050279

Alghuthaymi MA, Almoammar H, Rai M, Said-GalievE A-EKA (2015) Myconanoparticles: synthesis and their role in phytopathogens management. Biotechnol Biotechnol Equip 29(2):221–236. https://doi.org/10.1080/13102818.2015.1008194

Alghuthaymi MA, Kalia A, Bhardwaj K, Bhardwaj P, Abd-Elsalam KA, Valis M, Kuca K (2021) Nanohybrid antifungals for control of plant diseases: current status and future perspectives. J Fungi 7(1):48. https://doi.org/10.3390/jof7010048

Alrabadi NI, Thalij KM, Hussein EI, Al-Trad BM (2017) Antibacterial activity of ag and MgO nanoparticles synthesized by *Trichoderma viride*. J Appl Environ Biol Sci 7(8):94–101. https://doi.org/10.9734/bji/2017/29534

Anitha TS, Palanivelu P (2011) Synthesis and structural characterization of polydisperse silver and multishaped gold nanoparticles using *Fusarium oxysporum* MTCC 284. Digest J Nanomater Biostruct 6:1587–1595

Aziz N, Pandey R, Barman I, Prasad R (2016) Leveraging the attributes of *Mucor hiemalis*-derived silver nanoparticles for a synergistic broad-spectrum antimicrobial platform. Front Microbiol 7:1984. https://doi.org/10.3389/fmicb.2016.01984

Bahrulolum H, Nooraei S, Javanshir N, Tarrahimofrad H, Mirbagheri VS, Easton AJ, Ahmadian G (2021) Green synthesis of metal nanoparticles using microorganisms and their application in the agrifood sector. J Nanobiotechnol 19(1):1–26. https://doi.org/10.1186/s12951-021-00834-3

Balaji DS, Basavaraja S, Deshpande R, Mahesh DB, Prabhakar BK, Venkataraman A (2009) Extracellular biosynthesis of functionalized silver nanoparticles by strains of *Cladosporium cladosporioides* fungus. Colloids Surf B Biointerfaces 68(1):88–92. https://doi.org/10.1016/j.colsurfb.2008.09.022

Bansal V, Rautaray D, Ahmad A, Sastry M (2004) Biosynthesis of zirconia nanoparticles using the fungus *Fusarium oxysporum*. J Mater Chem 14(22):3303–3305. https://doi.org/10.1039/b407904c

Bansal V, Rautaray D, Bharde A, Ahire K, Sanyal A, Ahmad A, Sastry M (2005) Fungus-mediated biosynthesis of silica and titania particles. J Mater Chem 15(26):2583–2589. https://doi.org/10.1039/b503008k

Bansal V, Poddar P, Ahmad A, Sastry M (2006) Room-temperature biosynthesis of ferroelectric barium titanate nanoparticles. J Am Chem Soc 128(36):11958–11963

Basavaraja S, Balaji SD, Lagashetty A, Rajasab AH, Venkataraman A (2008) Extracellular biosynthesis of silver nanoparticles using the fungus *Fusarium semitectum*. Mater Res Bull 43(5):1164–1170. https://doi.org/10.1016/j.materresbull.2007.06.020

Behari J (2010) Principles of nanoscience: an overview. Indian J Exp Biol 48(10):1008–1019. https://doi.org/10.4103/0972-2327.31481

Bhagyaraj SM, Oluwafemi OS (2018) Nanotechnology: the science of the invisible. Elsevier, pp 1–18. https://doi.org/10.1016/b978-0-08-101975-7.00001-4

Bhainsa KC, D'souza SF (2006) Extracellular biosynthesis of silver nanoparticles using the fungus *Aspergillus fumigatus*. Colloids Surf B Biointerfaces 47(2):160–164

Bhardwaj K, Sharma A, Tejwan N, Bhardwaj S, Bhardwaj P, Nepovimova E et al (2020) *Pleurotus* macrofungi-assisted nanoparticle synthesis and its potential applications: a review. J Fungi 6(4):351. https://doi.org/10.3390/jof6040351

Bhat R, Sharanabasava VG, Deshpande R, Shetti U, Sanjeev G, Venkataraman A (2013) Photo-bio-synthesis of irregular shaped functionalized gold nanoparticles using edible mushroom *Pleurotus florida* and its anticancer evaluation. J Photochem Photobiol B Biol 125:63–69

Cao Y, Feng W, Su W (2018) Biosynthesis and characterization of LiFePO4/C composite using Baker's yeast. Int J Electrochem Sci 13:8022–8029. https://doi.org/10.20964/2018.08.61

Castro-Longoria E, Vilchis-Nestor AR, Avalos-Borja M (2011) Biosynthesis of silver, gold and bimetallic nanoparticles using the filamentous fungus *Neurospora crassa*. Colloids Surf B Biointerfaces 83(1):42–48

Castro-Longoria E, Garibo-Ruiz D, Martínez-Castro S (2017) Myconanotechnology to treat infectious diseases: a perspective. In: Fungal nanotechnology. Springer, Cham, pp 235–261

Chauhan A, Zubair S, Tufail S, Sherwani A, Sajid M, Raman S, Azam A, Owais M (2011) Fungus-mediated biological synthesis of gold nanoparticles: potential in detection of liver cancer. Int J Nanomedicine 6:2305–2319

Chauhan R, Reddy A, Abraham J (2015) Biosynthesis of silver and zinc oxide nanoparticles using *Pichia fermentans* JA2 and their antimicrobial property. Appl Nanosci 5(1):63–71. https://doi.org/10.1007/s13204-014-0292-7

Chi ZL, Zhao XY, Chen YL, Hao JL, Yu GH, Goodman BA, Gadd GM (2021) Intrinsic enzyme-like activity of magnetite particles is enhanced by cultivation with *Trichoderma guizhouense*. Environ Microbiol 23:893–907

Clarance P, Luvankar B, Sales J, Khusro A, Agastian P, Tack JC, Al Khulaifi MM, AL-Shwaiman HA, Elgorban AM, Syed A, Kim HJ (2020) Green synthesis and characterization of gold nanoparticles using endophytic fungi *Fusarium solani* and its in-vitro anticancer and biomedical applications. Saudi J Biol Sci 27(2):706–712. https://doi.org/10.1016/j.sjbs.2019.12.026

Cuevas R, Durán N, Diez MC, Tortella GR, Rubilar O (2015) Extracellular biosynthesis of copper and copper oxide nanoparticles by *Stereum hirsutum*, a native white-rot fungus from Chilean forests. J Nanomater 2015:1–7. https://doi.org/10.1155/2015/789089

Das SK, Das AR, Guha AK (2009) Gold nanoparticles: microbial synthesis and application in water hygiene management. Langmuir 25(14):8192–8199

Das SK, Dickinson C, Lafir F, Brougham DF, Marsili E (2012) Synthesis, characterization and catalytic activity of gold nanoparticles biosynthesized with *Rhizopus oryzae* protein extract. Green Chem 14(5):1322–1334. https://doi.org/10.1039/c2gc16676c

Deepa K, Panda T (2014) Synthesis of gold nanoparticles from different cellular fractions of *Fusarium oxysporum*. J Nanosci Nanotechnol 14(5):3455–3463

Devi TP, Kulanthaivel S, Kamil D, Borah JL, Prabhakaran N, Srinivasa N (2013) Biosynthesis of silver nanoparticles from *Trichoderma* species. Indian J Exp Biol 51(7):543–547

Dragone R, Grasso G, Muccini M, Toffanin S (2017) Portable bio/chemosensoristic devices: innovative systems for environmental health and food safety diagnostics. Front Public Health 5:80

Du L, Xian L, Feng JX (2011) Rapid extra−/intracellular biosynthesis of gold nanoparticles by the fungus *Penicillium* sp. J Nanopart Res 13(3):921–930

Durán N, Marcato PD, Alves OL, De Souza GI, Esposito E (2005) Mechanistic aspects of biosynthesis of silver nanoparticles by several *Fusarium oxysporum* strains. J Nanobiotechnol 3(1):1–7

Durán N, Marcato PD, De Souza GI, Alves OL, Esposito E (2007) Antibacterial effect of silver nanoparticles produced by fungal process on textile fabrics and their effluent treatment. J Biomed Nanotechnol 3(2):203–208

Elamawi RM, Al-Harbi RE, Hendi AA (2018) Biosynthesis and characterization of silver nanoparticles using *Trichoderma longibrachiatum* and their effect on phytopathogenic fungi. Egypt J Biol Pest Control 28(1):1–11. https://doi.org/10.1186/s41938-018-0028-1

El-Batal AI, El-Sayyad GS, Mosallam FM, Fathy RM (2020) *Penicillium chrysogenum*-mediated mycogenic synthesis of copper oxide nanoparticles using gamma rays for in vitro antimicrobial activity against some plant pathogens. J Clust Sci 31:79–90. https://doi.org/10.1007/s10876-019-01619-3

Elmer W, White JC (2018) The future of nanotechnology in plant pathology. Annu Rev Phytopathol 56:111–133. https://doi.org/10.1146/annurev-phyto-080417-050108

El-Sayed ESR, Abdelhakim HK, Ahmed AS (2020) Solid-state fermentation for enhanced production of selenium nanoparticles by gamma-irradiated *Monascus purpureus* and their biological evaluation and photocatalytic activities. Bioprocess Biosyst Eng 43(5):797–809

Espinosa-Ortiz EJ, Rene ER, Guyot F, van Hullebusch ED, Lens PN (2017) Biomineralization of tellurium and selenium-tellurium nanoparticles by the white-rot fungus *Phanerochaete chrysosporium*. Int Biodeterior Biodegrad 124:258–266. https://doi.org/10.1016/j.ibiod.2017.05.009

Gade AK, Bonde PP, Ingle AP, Marcato PD, Duran N, Rai MK (2008) Exploitation of *Aspergillus niger* for synthesis of silver nanoparticles. J Biobaased Mater Bioenergy 2(3):243–247. https://doi.org/10.1166/jbmb.2008.401

Gade A, Ingle A, Whiteley C, Rai M (2010) Mycogenic metal nanoparticles: progress and applications. Biotechnol Lett 32(5):593–600

Gaur N, Flora G, Yadav M, Tiwari A (2014) A review with recent advancements on bioremediation-based abolition of heavy metals. Environ Sci Process Impacts 16(2):180–193

Gericke M, Pinches A (2006) Biological synthesis of metal nanoparticles. Hydrometallurgy 83(1–4):132–140

Golinska P, Wypij M, Ingle AP, Gupta I, Dahm H, Rai M (2014) Biogenic synthesis of metal nanoparticles from actinomycetes: biomedical applications and cytotoxicity. Appl Microbiol Biotechnol 98(19):8083–8097

Golinska P, Rathod D, Wypij M, Gupta I, Składanowski M, Paralikar P, Dahm H, Rai M (2017) Mycoendophytes as efficient synthesizers of bionanoparticles: nanoantimicrobials, mechanism, and cytotoxicity. Crit Rev Biotechnol 37:765–778. https://doi.org/10.1080/07388551.2016.1235011

Gopinath K, Karthika V, Sundaravadivelan C, Gowri S, Arumugam A (2015) Mycogenesis of cerium oxide nanoparticles using *Aspergillus niger* culture filtrate and their applications for antibacterial and larvicidal activities. J Nano Chem 5(3):295–303. https://doi.org/10.1007/s40097-015-0161-2

Govender Y, Riddin T, Gericke M, Whiteley CG (2009) Bioreduction of platinum salts into nanoparticles: a mechanistic perspective. Biotechnol Lett 31(1):95–100

Hamida RS, Ali MA, Abdelmeguid NE, Al-Zaban MI, Baz L, Bin-Meferij MM (2021) Lichens – a potential source for nanoparticles fabrication: a review on nanoparticles biosynthesis and their prospective applications. J Fungi 7(4):291

Hasan S (2015) A review on nanoparticles: their synthesis and types. Res J Recent Sci 2277:2502

Hashem AH, Abdelaziz AM, Askar AA, Fouda HM, Khalil AM, Abd-Elsalam KA, Khaleil MM (2021) *Bacillus megaterium*-mediated synthesis of selenium nanoparticles and their antifungal activity against *Rhizoctonia solani* in Faba bean plants. J Fungi 7(3):195

Hassan SED, Fouda A, Saied E, Farag MM, Eid AM, Barghoth MG, Awad MA, Hamza MF, Awad MF (2021) *Rhizopus Oryzae*-mediated green synthesis of magnesium oxide nanoparticles

(MgO-NPs): a promising tool for antimicrobial, mosquitocidal action, and tanning effluent treatment. J Fungi 7(5):372. https://doi.org/10.3390/jof7050372

He W, Cui J, Yue Y, Zhang X, Xia X, Liu H, Lui S (2011) High-performance TiO2 from Baker's yeast. J Colloid Interface Sci 354(1):109–115. https://doi.org/10.1016/j.jcis.2010.10.035

Hemath Naveen KS, Kumar G, Karthik L, Bhaskara Rao KV (2010) Extracellular biosynthesis of silver nanoparticles using the filamentous fungus *Penicillium* sp. Arch Appl Sci Res 2(6):161–167

Husseiny SM, Salah TA, Anter HA (2015) Biosynthesis of size controlled silver nanoparticles by *Fusarium oxysporum*, their antibacterial and antitumor activities. Beni-Suef Univ J Basic Appl Sci 4(3):225–231

Jacob JM, Balakrishnan RM, Kumar UB (2014) Biosynthesis of lead selenide quantum rods in marine *Aspergillus terreus*. Mater Lett 124:279–281. https://doi.org/10.1016/j.matlet.2014.03.106

Jacob JM, Lens PN, Balakrishnan RM (2016) Microbial synthesis of chalcogenide semiconductor nanoparticles: a review. Microb Biotechnol 9:11–21

Jagtap P, Nath H, Kumari PB, Dave S, Mohanty P, Das J, Dave S (2021) Mycogenic fabrication of nanoparticles and their applications in modern agricultural practices & food industries. Fungi bio-prospects in sustainable agriculture. J Environ Nanotechnol:475–488

Jain N, Bhargava A, Majumdar S, Tarafdar JC, Panwar J (2011) Extracellular biosynthesis and characterization of silver nanoparticles using *Aspergillus flavus* NJP08: a mechanism perspective. Nanoscale 3(2):635–641

Jayaseelan C, Rahuman AA, Roopan SM, Kirthi AV, Venkatesan J, Kim SK, Iyappan M, Siva C (2013) Biological approach to synthesize TiO_2 nanoparticles using *Aeromonas hydrophila* and its antibacterial activity. Spectrochim Acta Mol BiomolSpectrosc 107:82–89. https://doi.org/10.1016/j.saa.2012.12.083

Jiang M, Ohnuki T, Kozai N, Tanaka K, Suzuki Y, Sakamoto F, Kamiishi E, Utsunomiya S (2010) Biological nano-mineralization of Ce phosphate by *Saccharomyces cerevisiae*. Chem Geol 277(1–2):61–69. https://doi.org/10.1016/j.chemgeo.2010.07.010

Jiang M, Ohnuki T, Utsunomiya S (2018) Biomineralization of middle rare earth element samarium in yeast and bacteria systems. Geomicrobiol J 35(5):375–384. https://doi.org/10.1080/01490451.2017.1377320

Kalia A, Abd-Elsalam KA, Kuca K (2020) Zinc-based nanomaterials for diagnosis and management of plant diseases: ecological safety and future prospects. J Fungi 6(4):222

Kashyap PL, Kumar S, Srivastava AK, Sharma AK (2013) Myconanotechnology in agriculture: a perspective. World J Microbiol Biotechnol 29(2):191–207

Khandel P, Shahi SK (2018) Mycogenic nanoparticles and their bio-prospective applications: current status and future challenges. J Nanostruct Chem 8:369–391. https://doi.org/10.1007/s40097-018-0285-2

Kierans M, Staines AM, Bennett H, Gadd GM (1991) Silver tolerance and accumulation in yeasts. Biol Met 4(2):100–106. https://doi.org/10.1007/bf01135386

Lateef A, Darwesh OM, Matter IA (2021) Microbial nanobiotechnology: the melting pot of microbiology, microbial technology and nanotechnology. In: Lateef A, Gueguim-Kana EB, Dasgupta N, Ranjan S (eds) Microbial nanobiotechnology. Materials horizons: from nature to nanomaterials. Springer, Singapore. https://doi.org/10.1007/978-981-33-4777-9_1

Li Q, Gadd GM (2017a) Biosynthesis of copper carbonate nanoparticles by ureolytic fungi. Appl Microbiol Biotechnol 101(19):7397–7407. https://doi.org/10.1007/s00253-017-8451-x

Li Q, Gadd GM (2017b) Fungal nanoscale metal carbonates and production of electrochemical materials. MicrobBiotechnol 10(5):1131–1136. https://doi.org/10.1111/1751-7915.12765

Li Q, Csetenyi L, Gadd GM (2014) Biomineralization of metal carbonates by *Neurospora crassa*. Environ Sci Technol 48(24):14409–14416. https://doi.org/10.1021/es5042546

Li Q, Liu D, Jia Z, Csetenyi L, Gadd GM (2016) Fungal biomineralization of manganese as a novel source of electrochemical materials. Curr Biol 26(7):950–955. https://doi.org/10.1016/j.cub.2016.01.068

Li G, Yu J, Jia J, Yang L, Zhao L, Zhou W, Liu H (2018) Cobalt–cobalt phosphide nanoparticles@ nitrogen-phosphorus doped carbon/graphene derived from cobalt ions adsorbed Saccharomycete yeasts as an efficient, stable, and large-current-density electrode for hydrogen evolution reactions. Adv Funct Mater 28(40):1801332. https://doi.org/10.1002/adfm.201801332

Li JF, Rupa EJ, Hurh J, Huo Y, Chen L, Han Y, Ahn JC, Park JK, Lee HA, Mathiyalagan R, Yang DC (2019) *Cordyceps militaris* fungus mediated zinc oxide nanoparticles for the photocatalytic degradation of methylene blue dye. Optik 183:691–697. https://doi.org/10.1016/j.ijleo.2019.02.081

Li Q, Liu D, Wang T, Chen C, Gadd GM (2020) Iron coral: novel fungal biomineralization of nanoscale zerovalent iron composites for treatment of chlorinated pollutants. Chem Eng J 402:126263. https://doi.org/10.1016/j.cej.2020.126263

Lian S, Diko CS, Yan Y, Li Z, Zhang H, Ma Q, Qu Y (2019) Characterization of biogenic selenium nanoparticles derived from cell-free extracts of a novel yeast *Magnusiomyces ingens*. 3 Biotech 9(6):1–8. https://doi.org/10.1007/s13205-019-1748-y

Liang X, Perez MAMJ, Nwoko KC, Egbers P, Feldmann J, Csetenyi L, Gadd GM (2019) Fungal formation of selenium and tellurium nanoparticles. Appl Microbiol Biotechnol 103(17):7241–7259. https://doi.org/10.1007/s00253-019-09995-6

Mahanty S, Bakshi M, Ghosh S, Gaine T, Chatterjee S, Bhattacharyya S, Das S, Das P, Chaudhuri P (2019) Mycosynthesis of iron oxide nanoparticles using manglicolous fungi isolated from Indian sundarbans and its application for the treatment of chromium containing solution: synthesis, adsorption isotherm, kinetics and thermodynamics study. Environ Nanotechnol Monit Manag 12:100276. https://doi.org/10.1016/j.enmm.2019.100276

Majeed S, Abdullah MSB, Nanda A, Ansari MT (2016) In vitro study of the antibacterial and anticancer activities of silver nanoparticles synthesized from *Penicillium brevicompactum* (MTCC-1999). J Taibah Univ Sci 10(4):614–620. https://doi.org/10.1016/j.jtusci.2016.02.010

Mazumder B, Uddin I, Khan S, Ravi V, Selvraj K, Poddar P, Ahmad A (2007) Bio-milling technique for the size reduction of chemically synthesized BiMnO3 nanoplates. J Mater Chem 17(37):3910–3914. https://doi.org/10.1039/b706154d

Meng X, Xu G, Zhou QL, Wu JP, Yang LR (2014) Highly efficient solvent-free synthesis of 1, 3-diacylglycerols by lipase immobilised on nano-sized magnetite particles. Food Chem 143:319–324

Min JS, Kim KS, Kim SW, Jung JH, Lamsal K, Kim SB, Jung M, Lee YS (2009) Effects of colloidal silver nanoparticles on sclerotium-forming phytopathogenic fungi. Plant Pathol J 25(4):376–380

Mirzadeh S, Darezereshki E, Bakhtiari F, Fazaelipoor MH, Hosseini MR (2013) Characterization of zinc sulfide (ZnS) nanoparticles biosynthesized by *Fusarium oxysporum*. Mater Sci Semicond Process 16(2):374–378. https://doi.org/10.1016/j.mssp.2012.09.008

Moghaddam K (2010) An introduction to microbial metal nanoparticle preparation method. J Young Investig 19(1)

Mohamed AA, Fouda A, Abdel-Rahman MA, Hassan SED, El-Gamal MS, Salem SS, Shaheen TI (2019) Fungal strain impacts the shape, bioactivity and multifunctional properties of green synthesized zinc oxide nanoparticles. Biocatal Agric Biotechnol 19:101103. https://doi.org/10.1016/j.bcab.2019.101103

Mohanta YK, Nayak D, Biswas K, Singdevsachan SK, Abd_Allah EF, Hashem A, Alqarawi AA, Yadav D, Mohanta TK (2018) Silver nanoparticles synthesized using wild mushroom show potential antimicrobial activities against food borne pathogens. Molecules 23:655. https://doi.org/10.3390/molecules23030655

Mosallam FM, El-Sayyad GS, Fathy RM, El-Batal AI (2018) Biomolecules-mediated synthesis of selenium nanoparticles using *Aspergillusoryzae* fermented Lupin extract and gamma radiation for hindering the growth of some multidrug-resistant bacteria and pathogenic fungi. Microb Pathog 122:108–116. https://doi.org/10.1016/j.micpath.2018.06.013

Mukherjee P, Ahmad A, Mandal D, Senapati S, Sainkar SR, Khan MI et al (2001) Fungus-mediated synthesis of silver nanoparticles and their immobilization in the mycelial matrix: a novel biological approach to nanoparticle synthesis. Nano Lett 1(10):515–519

Mukherjee P, Senapati S, Mandal D, Ahmad A, Khan MI, Kumar R, Sastry M (2002) Extracellular synthesis of gold nanoparticles by the fungus *Fusarium oxysporum*. Chem Bio Chem 3(5):461–463

Nandini B, Hariprasad P, Prakash HS, Shetty HS, Geetha N (2017) Trichogenic-selenium nanoparticles enhance disease suppressive ability of *Trichoderma* against downy mildew disease caused by *Sclerospora graminicola* in pearl millet. Sci Rep 7(1):1–1

Oggerin M, Tornos F, Rodríguez N, Del Moral C, Sánchez-Román M, Amils R (2013) Specific jarosite biomineralization by *Purpureocillium lilacinum*, an acidophilic fungi isolated from Río Tinto. Environ Microbiol 15(8):2228–2237. https://doi.org/10.1111/1462-2920.12094

Parmar S, Sharma VK (2020) Endophytic fungi mediated biofabrication of nanoparticles and their potential applications. In: Kumar A, Singh VK (eds) Microbial endophytes. Woodhead Publishing, pp 325–341. https://doi.org/10.1016/B978-0-12-818734-0.00013-9

Peiris MMK, Gunasekara TDCP, Jayaweera PM, Fernando SSN (2018) TiO_2 nanoparticles from Baker's yeast: a potent antimicrobial. J Microbiol Biotechnol 28:1664–1670. https://doi.org/10.4014/jmb.1807.07005

Popli D, Anil V, Subramanyam AB, Namratha MN, Ranjitha VR, Rao SN, Rai RV, Govindappa M (2018) Endophyte fungi, *Cladosporium* species-mediated synthesis of silver nanoparticles possessing in vitro antioxidant, anti-diabetic and anti-Alzheimer activity. Artif Cells Nanomed Biotechnol 46:676–683. https://doi.org/10.1080/21691401.2018.1434188

Prasad R (2017) Fungal nanotechnology: applications in agriculture, industry, and medicine. Springer

Prasad K, Jha AK (2010) Biosynthesis of CdS nanoparticles: an improved green and rapid procedure. J Colloid Interface Sci 342(1):68–72

Prasad R, Pandey R, Barman I (2016) Engineering tailored nanoparticles with microbes: quo vadis? Wiley Interdiscip Rev Nanomed Nanobiotechnol 8(2):316–330

Purohit K, Khitoliya P, Purohit R (2012) Recent advances in nanotechnology. Int J Sci Eng Res 3

Qian Y, Yu H, He D, Yang H, Wang W, Wan X, Wang L (2013) Biosynthesis of silver nanoparticles by the endophytic fungus *Epicoccum nigrum* and their activity against pathogenic fungi. Bioprocess Biosyst Eng 36(11):1613–1619

Qin W, Wang CY, Ma YX, Shen MJ, Li J, Jiao K, Tay FR, Niu LN (2020) Microbe-mediated extracellular and intracellular mineralization: environmental, industrial, and biotechnological applications. Adv Mater 32:1907833. https://doi.org/10.1002/adma.201907833

Rabeea MA, Owaid MN, Aziz AA, Jameel MS, Dheyab MA (2020) Mycosynthesis of gold nanoparticles using the extract of *Flammulina velutipes*, Physalacriaceae, and their efficacy for decolorization of methylene blue. J Environ Chem Eng 103841:103841. https://doi.org/10.1016/j.jece.2020.103841

Rai M, Gade A, Yadav A (2011) Biogenic nanoparticles: an introduction to what they are, how they are synthesized and their applications. In: Metal nanoparticles in microbiology. Springer, Berlin/Heidelberg, pp 1–14

Rai M, Bonde S, Golinska P, Trzcińska-Wencel J, Gade A, Abd-Elsalam KA, Shende S, Gaikwad S, Ingle AP (2021) *Fusarium* as a novel fungus for the synthesis of nanoparticles: mechanism and applications. J Fungi 7(2):139

Raliya R, Biswas P, Tarafdar J (2015) TiO_2 nanoparticle biosynthesis and its physiological effect on mung bean (*Vigna radiata* L.). Biotechnol Rep 5:22–26. https://doi.org/10.1016/j.btre.2014.10.009

Raliya R, Tarafdar JC, Biswas P (2016) Enhancing the mobilization of native phosphorus in the mung bean rhizosphere using ZnO nanoparticles synthesized by soil fungi. J Agric Food Chem 64:3111–3118. https://doi.org/10.1021/acs.jafc.5b05224

Rathod V, Ranganath E (2011) Synthesis of monodispersed silver nanoparticles by *Rhizopus stolonifer* and its antibacterial activity against MDR strains of *Pseudomonas aeruginosa* from burnt patients. Int J Environ Sci 1(7):1830–1840

Rautaray D, Sanyal A, Adyanthaya SD, Ahmad A, Sastry M (2004) Biological synthesis of strontium carbonate crystals using the fungus *fusarium oxysporum*. Langmuir 20(16):6827–6833. https://doi.org/10.1021/la049244d

Ray PC, Khan SA, Fan Z, Senapati D (2013) Gold nanotechnology for targeted detection and killing of multiple drug resistant bacteria from food samples. Advances in applied nanotechnology for agriculture. J Am Chem Soc:1–19. https://doi.org/10.1021/bk-2013-1143.ch001

Ribeiro BD, Coelho MA, de Castro AM (2016) Principles of green chemistry and white biotechnology. In: Coelho MAZ, Ribeiro BD (eds) White biotechnology for sustainable chemistry. The Royal Society of Chemistry, London, pp 1–8

Riddin TL, Gericke M, Whiteley CG (2006) Analysis of the inter-and extracellular formation of platinum nanoparticles by *Fusarium oxysporum* f. sp. *lycopersici* using response surface methodology. Nanotechnology 17(14):3482–3489. https://doi.org/10.1088/0957-4484/17/14/021

Romig AD Jr, Baker AB, Johannes J, Zipperian T, Eijkel K, Kirchhoff B, Mani HS, Rao CN, Walsh S (2007) An introduction to nanotechnology policy: opportunities and constraints for emerging and established economies. Technol Forecast Soc Change 74(9):1634–1642. https://doi.org/10.1016/j.techfore.2007.04.003

Roy A, Bulut O, Some S, Mandal AK, Yilmaz MD (2019) Green synthesis of silver nanoparticles: biomolecule-nanoparticle organizations targeting antimicrobial activity. RSC Adv 9:2673–2702. https://doi.org/10.1039/C8RA08982E

Sahai S (2010) Production of silver nanoparticles by a phytopathologic fungus *Bipolaris nodulosa* and its antimicrobial activity. Dig J Nanomater Biostruct 5:887–895

Saitoh N, Fujimori R, Yoshimura T, Tanaka H, Kondoh A, Nomura T, Konishi Y (2020) Microbial recovery of palladium by Baker's yeast through bioreductive deposition and biosorption. Hydrometallurgy 196:105413. https://doi.org/10.1016/j.hydromet.2020.105413

Salem SS, Fouda MMG, Fouda A, Awad MA, Al-Olayan EM, Allam AA, Shaheen TI (2021) Antibacterial, cytotoxicity and larvicidal activity of green synthesized selenium nanoparticles using *Penicillium corylophilum*. J Clust Sci 32(2):351–361. https://doi.org/10.1007/s10876-020-01794-8

Salvadori MR, Ando RA, Oller Nascimento CA, Correa B (2015) Extra and intracellular synthesis of nickel oxide nanoparticles mediated by dead fungal biomass. PLoS One 10(6):e0129799. https://doi.org/10.1371/journal.pone.0129799

Sandhu RS, Aharwal RP, Kumar S (2019) Green synthesis: a novel approach for nanoparticles synthesis. Int J Pharm Sci Res 10(8):3550

Sanghi R, Verma P (2009) Biomimetic synthesis and characterisation of protein capped silver nanoparticles. Bioresour Technol 100(1):501–504. https://doi.org/10.1016/j.biortech.2008.05.048

Sarkar J, Dey P, Saha S, Acharya K (2011) Mycosynthesis of selenium nanoparticles. Micro Nano Lett 6(8):599–602

Schaffie M, Hosseini MR (2014) Biological process for synthesis of semiconductor copper sulfide nanoparticle from mine wastewaters. J Environ Chem Eng 2(1):386–391. https://doi.org/10.1016/j.jece.2014.01.006

Sen K, Sinha P, Lahiri S (2011) Time dependent formation of gold nanoparticles in yeast cells: a comparative study. Biochem Eng J 55(1):1–6. https://doi.org/10.1016/j.bej.2011.02.014

Shaheen TI, Abd El Aty AA (2018) In-situ green myco-synthesis of silver nanoparticles onto cotton fabrics for broad spectrum antimicrobial activity. Int J Biol Macromol 118:2121–2130. https://doi.org/10.1016/j.ijbiomac.2018.07.062

Shaligram NS, Bule M, Bhambure R, Singhal RS, Singh SK, Szakacs G, Pandey A (2009) Biosynthesis of silver nanoparticles using aqueous extract from the compactin producing fungal strain. Process Biochem 44(8):939–943. https://doi.org/10.1016/j.procbio.2009.04.009

Shankar SS, Ahmad A, Pasricha R, Sastry M (2003) Bioreduction of chloroaurate ions by geranium leaves and its endophytic fungus yields gold nanoparticles of different shapes. J Mater Chem 13(7):1822–1826

Shin WK, Cho J, Kannan AG, Lee YS, Kim DW (2016) Cross-linked composite gel polymer electrolyte using mesoporous methacrylate-functionalized SiO2 nanoparticles for lithium-ion polymer batteries. Sci Rep 6(1):1

Skeffington AW, Scheffel A (2018) Exploiting algal mineralization for nanotechnology: bringing coccoliths to the fore. Curr Opin Biotechnol 49:57–63

Soni N, Prakash S (2012) Entomopathogenic fungus generated nanoparticles for enhancement of efficacy in *Culex quinquefasciatus* and *Anopheles stephensi*. Asian Pac J Trop Dis 2:S356–S361

Syed A, Ahmad A (2013) Extracellular biosynthesis of CdTe quantum dots by the fungus *Fusarium oxysporum* and their anti-bacterial activity. Spectrochim Acta Part A Mol BiomolSpectrosc 106:41–47

Uddin I, Adyanthaya S, Syed A, Selvaraj K, Ahmad A, Poddar P (2008) Structure and microbial synthesis of sub-10 nm Bi_2O_3 nanocrystals. J Nanosci Nanotechnol 8(8):3909–3913

Vahabi K, Mansoori GA, Karimi S (2011) Biosynthesis of silver nanoparticles by fungus *Trichoderma reesei* (a route for large-scale production of AgNPs). Insciences J 1:65–79. https://doi.org/10.5640/insc.010165

Vainshtein M, Belova N, Kulakovskaya T, Suzina N, Sorokin V (2014) Synthesis of magnetosensitive iron-containing nanoparticles by yeasts. J Ind Microbiol Biotechnol 41(4):657–663. https://doi.org/10.1007/s10295-014-1417-4

Vigneshwaran N, Ashtaputre NM, Varadarajan PV, Nachane RP, Paralikar KM, Balasubramanya RH (2007) Biological synthesis of silver nanoparticles using the fungus *Aspergillus flavus*. Mater Lett 61(6):1413–1418. https://doi.org/10.1016/j.matlet.2006.07.042

Voeikova TA, Zhuravliova OA, Bulushova NV, Veiko VP, Ismagulova TT, Lupanova TN, Shaitan KV, Debabov VG (2017) The "protein corona" of silver-sulfide nanoparticles obtained using gram-negative and-positive bacteria. Mol Genet Microbiol Virol 32(4):204–211

Wanarska E, Maliszewska I (2019) The possible mechanism of the formation of silver nanoparticles by *Penicillium cyclopium*. Bioorg Chem 93:102803. https://doi.org/10.1016/j.bioorg.2019.02.028

Yan S, He W, Sun C, Zhang X, Zhao H, Li Z, Zhou W, Tian X, Sun X, Han X (2009) The biomimetic synthesis of zinc phosphate nanoparticles. Dyes Pigments 80(2):254–258. https://doi.org/10.1016/j.dyepig.2008.06.010

Yousef S, Ibrahim NA, Farag SS, El-mehalawy A, Ismaiel A, Ahmed A (2020) Mycosynthesis of silver nanoparticles by the endophytic fungus *Alternaria tenuissima* AUMC 13621 and evaluation of their antimicrobial, antioxidant effect. Egypt J Microbiol 54:63–76. https://doi.org/10.21608/ejm.2019.13564.1101

Yu GH, Chi ZL, Kappler A, Sun FS, Liu CQ, Teng HH, Gadd GM (2020) Fungal nanophase particles catalyze iron transformation for oxidative stress removal and iron acquisition. Curr Biol 30(15):2943–2950

Yun'an Qing LC, Li R, Liu G, Zhang Y, Tang X, Wang J, Liu H, Qin Y (2018) Potential antibacterial mechanism of silver nanoparticles and the optimization of orthopedic implants by advanced modification technologies. Int J Nanomedicine 13:3311–3327. https://doi.org/10.2147/IJN.S165125

Zhang X, He X, Wang K, Wang Y, Li H, Tan W (2009) Biosynthesis of size-controlled gold nanoparticles using fungus, *Penicillium* sp. J Nanosci Nanotechnol 9(10):5738–5744

Zhang X, Yan S, Tyagi RD, Surampalli RY (2011) Synthesis of nanoparticles by microorganisms and their application in enhancing microbiological reaction rates. Chemosphere 82(4):489–494

Zhang L, Li D, Gao P (2012) Expulsion of selenium/protein nanoparticles through vesicle-like structures by *Saccharomyces cerevisiae* under microaerophilic environment. World J Microbiol Biotechnol 28(12):3381–3386

Zhang X, Zhang X, He W, Sun C, Ma J, Yuan J, Du X (2013) High-performance mesoporous LiFePO4 from Baker's yeast. Colloids Surf B: Biointerfaces 103:114–120. https://doi.org/10.1016/j.colsurfb.2012.10.002

Zhang M, Zhang K, De Gusseme B, Verstraete W, Field R (2014) The antibacterial and anti-biofouling performance of biogenic silver nanoparticles by *Lactobacillus fermentum*. Biofouling 30(3):347–357

Zhao C, Li X, Ding C, Liao J, Du L, Yang J, Yang Y, Zhang D, Tang J, Liu N, Sun Q (2016) Characterization of uranium bioaccumulation on a fungal isolate *Geotrichum* sp. dwc-1 as investigated by FTIR, TEM and XPS. J Radioanal Nucl Chem 310(1):165–175. https://doi.org/10.1007/s10967-016-4797-2

Plant Growth-Promoting Fungi for Growth Improvement and Resistance Induction

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1 Introduction

Plant diseases play a momentous role in destroying the productivity and quality of agricultural crops. These diseases are responsible for reducing the annual production of food in the world by 78% in fruit crops, 54% in vegetables, and 32% in cereals (Velásquez et al. 2018; Richard et al. 2022). The diseases caused by soil-borne pathogens are the most serious for the natural and production ecosystems, among them fungal plant pathogens that are the big group of plant disease agents and cause a voluminous reduction in the production of the five most crucial world crops, rice, wheat, corn, potatoes, and soybean with damage to as much as one-third of all crops annually according to the Food and Agriculture Organization of the United Nations (FAO) (Almeida et al. 2019; Manzar et al. 2022; Tyśkiewicz et al. 2022). In recent decades, synthetic pesticides are the main way for the control plant pathogens. However, the prolonged and excessive applications of these synthetic chemicals are associated with high levels of environmental pollution, toxicity, and carcinogenic properties in humans as well as the appearance of resistant strains from plant pathogens to pesticides (Rahman et al. 2018; Elsherbiny et al. 2019; Jacquet et al. 2022). Moreover, fertilizers have been used extensively worldwide for a long time, especially in developing countries. However, the outspread use of fertilizer leads to several adverse effects including soil degradation and yield losses which cause immense problems to soil sustainability and food security (Kohl et al. 2019; Chaudhary et al. 2022).

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Hence, plant growth-promoting fungi (PGPF) have received much attention to be used in both plant growth promotion and suppression of plant pathogens via induction of plant resistance for their distinctive properties and noteworthy applications (Busby et al. 2017; Francioli et al. 2021). PGPF are heterogeneous classes of non-pathogenic fungi associated with plants as non-symbiotic saprotrophic fungi, and non-obligate mutualism fungi with many different hosts (Murali et al. 2021; Mandal and Tiru 2022). PGPF can divide into endophytic fungi that live inside the root, seeds, stems, and leaves tissues or epiphytic fungi that live in the root and leaves surfaces or free-living fungi in the rhizosphere outside the root cells (Jahagirdar et al. 2019; Cantabella et al. 2022). PGPF include diverse taxonomic groups, a few the majority of these fungi primarily belong to the phylum Ascomycota like *Alternaria*, *Aspergillus*, *Botrytis*, *Chaetomium*, *Cladosporium*, *Colletotrichum*, *Penicillium*, *Trichoderma*, *Fusarium*, *Gliocladium*, *Phoma*, *Phomopsis*, and *Talaromyces*, and a few species belongs to Basidiomycota like *Rhodotorula*, and *Rhizoctonia*, and Zygomycota like *Mucor* and *Rhizopus* (Mishra et al. 2017; Hossain and Sultana 2020). Also, PGPF contains some sporeless fungi known as sterile black fungus (SBF), sterile dark fungus (SDF), and sterile red fungus (SRF) (Naseri and Younesi 2021).

The interaction between plants and PGPF leads to several positive tremendous effects on belowground and aboveground plant organs which support plant development and crop health (Abdel-Motaal et al. 2020; Ozimek and Hanaka 2021). PGPF promotes plant growth in various ways including increased yield, nitrogen fixation, enhanced photosynthesis, improve nutrient uptake, secretion of biomolecules like siderophores, phytohormone production like indole acetic acid (IAA), auxin, cytokinin, and gibberellin, antioxidative enzyme production, synthesize bioactive substances like volatile and non-volatile compounds, improve plant biochemical composition, and alleviation of heavy metal stress (Basavaraj et al. 2019; Ghosh and Panja 2021; Asghar and Kataoka 2022; Kumar et al. 2022). In addition, the application of PGPF as a biofertilizer, such in the forms of nitrogen fixer (N-fixer), potassium solubilizer (K-solubilizer), zinc solubilizer (Zn-solubilizer), phosphorus solubilizer (P-solubilizer), and sulfur oxidizer (S-oxidizer), is one of the best promising alternatives that cause considerable promotion in plant growth along with regaining fertility, organic form of nutrients, and sustainable biodiversity (Puga-Freitas and Blouin 2015; Nosheen et al. 2021; Bhatt et al. 2022).

Moreover, PGPF are able to adopt different strategies of eco-friendly disease management with a long-lasting induction of plant resistance by inducing systemic acquired resistance (SAR) and induced systemic resistance (ISR) in plants (Abdul Malik et al. 2020; Aboulila 2022). Plants have evolved different levels of active defense systems during the interaction between themselves and pathogens including pathogen-associated molecular patterns (PAMPs), which lead to the first type of induced defenses, known as pattern-triggered immunity (PTI), as well as effector-triggered immunity (ETI) (Cook et al. 2015; Berens et al. 2017; Zehra et al. 2021). PAMPs and ETI are described as elicitors that promote defense responses in plants and increase the production of new bioactive metabolites (Bigeard et al. 2015; Appu et al. 2021). These elicitors involve many different compounds inducing any type of

plant defense. PTI and ETI activate the induced resistance in plant tissues that are distal from the infection site, and this distinct form of pathogen-induced resistance is known as SAR (Cui et al. 2015; Yang et al. 2022). PGPF activates signaling pathways involving jasmonic acid (JA), and ethylene (ET), which trigger ISR throughout the plant as well as salicylic acid (SA) in SAR (Kushalappa et al. 2016; He et al. 2018). This chapter focuses on the properties of PGPF and their role in plant growth promotion and induction of resistance in plants as protective agents against plant pathogens along with a description of the potential mechanisms of PGPF activity.

2 Impact of PGPF on Plant Growth Promotion

PGPF possesses distinct beneficial properties for all plant species including improvement of seed germination rate, seedling growth, development and morphogenesis of plant roots, shoot growth, flowering, crop yield, phytohormone production, and photosynthetic efficiency (Priyadharsini and Muthukumar 2017; Bano et al. 2022). Most PGPF strains have the capacity to the production of siderophores, phytohormones (e.g., indole acetic acid, IAA, gibberellin, GA), volatile organic compounds (VOCs), solubilization of minerals (e.g., potassium, phosphorus, calcium, iron, copper), increases in nutrient uptake, and utilization of microbial enzymes (Burragoni and Jeon 2021; Hakim et al. 2021; Kour et al. 2021). PGPF impacts, directly and indirectly, the growth and productivity of plants. The direct way is by developing diverse mechanisms to mediate improvements in the plant growth, and productivity of crops, and the indirect way is by suppressing the plant pathogens (Breakfield et al. 2021; Zhang and White 2021). The PGPF promotes plant growth using one or more of these mechanisms (Malgioglio et al. 2022; Toppo et al. 2022). Table 1 recapitulates current studies showing that several strains of PGPF promote plant growth in many economic crops.

The inoculation of lettuce seeds by *Aspergillus niger* increased the plant diameter (6.9%), the number of leaves (8.1%), fresh weight (23.9%), and chlorophyll content (3.8%) as compared to the control groups. Also, the application of the conidial suspension of *A. niger* to the lettuce seedlings before transplanting produced similar results of all vegetative growth parameters using seed inoculation (Silva et al. 2022). The culture filtrates of *Chaetomium globosum* and *Minimedusa polyspora* displayed a direct plant growth-promoting effect through an increase of biomass, both in shoots and roots, number of leaves, and leaf area of chicory plants, *Cichorium intybus*. Based on ^{1}H-NMR spectra, the hydroalcoholic and chloroform extracts of chicory leaves and roots contain 49 molecules including amino acids, organic acids, sugars, organic compounds, fatty acids, secondary metabolites, and other compounds. The treatment with culture filtrates of both fungi stimulated the synthesis of 3-OH-butyrate by decreasing the synthesis of fatty acids and sterols as a mechanism balancing the NADPH/NADP^{+} ratio in *C. intybus* roots. The culture filtrate of *C. globosum* increased the phenylalanine and chicoric acid in the roots,

Table 1 Effect of PGPF on plant growth promotion

Crop	PGPF strain	Effect	References
Lettuce *Lactuca sativa*	*Aspergillus niger*	Seedling growth Shoot growth Plant growth	Silva et al. (2022)
Chicory *Cichorium intybus*	*Chaetomium globosum* *Minimedusa polyspora*	Root growth Shoot growth Bioactive compounds	Spinelli et al. (2022)
Cucumber *Cucumis sativus*	*Chaetomium globosum*	Seed germination and seedling growth Bioactive compounds Plant signaling pathways	Tian et al. (2022)
Apple *Malus hupehensis*	*Trichoderma asperellum*	Seedling growth Root growth Tree growth	Wang et al. (2022)
Potato *Solanum tuberosum*	*Paecilomyces variotii*	Root growth Shoot growth Crop yield Bioactive compounds	Cao et al. (2021)
Pakchoi *Brassica campestris*	*Trichoderma atroviride* *Trichoderma citrinoviride*	Seed germination and seedling growth Root growth Shoot growth	Chen et al. (2021)
Common bean *Phaseolus vulgaris*	*Aspergillus niger*	Root growth Shoot growth Bioactive compounds	Galeano et al. (2021)
Tobacco Tomato Kimchi cabbage Broccoli Bok choy Carrot	*Cladosporium halotolerans*	Volatile organic compounds (VOCs) Root growth Bioactive compounds Phytohormone production Plant signaling pathways	Jiang et al. (2021)
Tomato *Solanum lycopersicum*	*Botrytis cinerea*	Volatile organic compounds (VOCs) Root growth Shoot growth Plant signaling pathways	Kamaruzzaman et al. (2021)

(continued)

Table 1 (continued)

Crop	PGPF strain	Effect	References
Arabidopsis *Arabidopsis thaliana* Onion *Allium cepa*	*Aspergillus chiangmaiensis* *Aspergillus pseudopiperis* *Aspergillus pseudotubingensis*	Root growth Shoot growth Crop yield Bioactive compounds	Khuna et al. (2021)
Eggplant *Solanum melongena*	*Penicillium oxalicum* *Aspergillus brunneoviolaceus* *Aspergillus tubingensis*	Seedling growth Root growth Flowering Phytohormone production	Li et al. (2021)
Tobacco *Nicotiana tabacum*	*Byssochlamys spectabilis* *Chaetomium globosum* *Cephalotheca foveolate* *Penicillium melinii* *Alternaria tenuissima* *Nigrospora chinensis*	Seedling growth Root growth Shoot growth Phytohormone production Bioactive compounds	Tarroum et al. (2021)
Tomato *Solanum lycopersicum*	*Trichoderma afroharzianum*	Seed germination Root growth Shoot growth Bioactive compounds Plant signaling pathways	Zhao et al. (2021a)
Bean *Phaseolus vulgaris*	*Trichoderma harzianum*	Root growth Shoot growth Phytohormone production	Eslahi et al. (2020)
Chili pepper *Capsicum annuum*	*Alternaria solani*	Root growth Shoot growth Flowering	Mauricio-Castillo et al. (2020)
Tomato *Solanum lycopersicum* Pepper *Capsicum annuum*	*Paecilomyces variotii*	Seed germination Root growth Shoot growth Phytohormone production	Moreno-Gavíra et al. (2020)
Chilli *Capsicum annuum*	*Talaromyces* sp.	Seed germination and seedling vigor Shoot growth Bioactive compounds	Naziya et al. (2020)

(continued)

Table 1 (continued)

Crop	PGPF strain	Effect	References
Lettuce *Lactuca sativa*	*Trichoderma asperellum*	Volatile organic compounds (VOCs) Root growth Shoot growth Antifungal activity	Wonglom et al. (2020)
Tobacco *Nicotiana tabacum* Pepper *Capsicum annuum*	*Cladosporium sphaerospermum*	Root growth Shoot growth Flowering Crop yield	Li et al. (2019)

whereas the compound 4-OH-benzoate was increased by the treatment of *M. polyspora* culture filtrate (Spinelli et al. 2022).

On similar lines, the cucumber seeds inoculated with the fungus *Chaetomium globosum* ND35 had higher seed radicle length, fresh weight, and dry weight, and seedlings had higher plant height and root height length, shoot dry weight, and root dry weight after 15 days compared with non-inoculated groups. The differentially expressed genes (DEGs) caused by strain ND35 were mainly involved in phenylpropanoid biosynthesis, plant hormone signal transduction, plant-pathogen interaction, and photosynthesis through transcriptome analysis. The levels of reactive oxygen species (ROS), hydrogen peroxide (H_2O_2), indole-3-acetic acid (IAA), gibberellin (GA), zeatin (ZT), salicylic acid (SA), jasmonic acid (JA) and the activity of phenylalanine ammonia-lyase (PAL), 4-coumarate-CoA ligase (4CL), cinnamyl alcohol dehydrogenase (CAD), and peroxidase (POD) were higher in seedlings inoculated with *C. globosum* ND35 than those of non-inoculated groups according to Tian et al. (2022). The application of *Trichoderma asperellum* strain 6S-2 promoted the seedlings growth of *Malus hupehensis* Rehd and apple trees 2-year-old. The use of *T. asperellum* 6S-2 fertilizer increased the root dry and fresh weights of *M. hupehensis* Rehd seedlings as compared to the control group under greenhouse conditions and increased the number of branches and branch elongation of young apple trees under field conditions (Wang et al. 2022).

In a different study, Cao et al. (2021) used Zhinengcong (ZNC), an ethanol extract from the fungus *Paecilomyces variotii*, as a plant growth promotion and biocontrol tool in potato plants. The extract increased potato height, leaf area, stem diameter, root length, root weight, and yield as well as induced the production of reactive oxygen species (ROS), and the expression of indole acetic acid (IAA) related genes. The irrigation with ZNC significantly increased the output by 18.83% or more in 2 years of field trials with improvement in potato tubers quality including the content of vitamin C, protein, sugar, and starch. Likewise, ZNC significantly reduced the incidence and severity of late blight disease caused by the oomycete *Phytophthora infestans* in both greenhouse and field conditions. Also, Chen et al. (2021) used a mixture of two *Trichoderma* strains (*Trichoderma atroviride* LX-7 and *Trichoderma citrinoviride* HT-1) to promote the growth of pakchoi plants. Both

strains *T. atroviride* LX-7 and *T. citrinoviride* HT-1 showed the ability of siderophore and indole acetic acid (IAA) production and the strain LX-7 was efficient for potassium solubilization. The combination of LX-7 + HT-1 (1:1) gave the highest percentage of seed germination, germination energy, germination index, vitality index, growth of radicles and plumules, and fresh and dry weight of seedlings as well as the mixture of LX-7 + HT-1 (1:2) caused the highest biomass and quality of plants. Also, the two strains caused a strong increase in shoot length, root length, leaf length × width, and fresh, and dry weight of pakchoi plants in greenhouse experiments with an increase in the content of chlorophyll, vitamin C, soluble sugar, and soluble protein.

The fungal *Aspergillus niger* 9-P was isolated from forage grass and it was able to produce indole-3-acetic acid (IAA), siderophores, ammonia (NH3), hydrogen cyanide (HCN), 1-aminocyclopropane-1-carboxylic acid (ACC), and high phosphorus solubilizing activity with an increase in the activity of phosphatases, proteases, amylase, and pectinase. Moreover, isolate *A. niger* 9-P caused a strong increase in the growth parameters of common bean plants compared with the uninoculated plants (Galeano et al. 2021). In yet another example, the volatile organic compounds (VOCs) emitted by *Cladosporium halotolerans* NGPF1 enhanced the fresh weight of leaf and root, leaf number, root length, and chlorophyll content in broccoli, tobacco, tomato, bok choy, kimchi cabbage, and carrot in vitro conditions. Seven compounds were identified from NGPF1 grown in potato dextrose (PD) liquid medium using headspace solid-phase microextraction (HS-SPME) coupled with gas chromatography-mass spectrometry (GC-MS). The compounds 2-methyl-butanal and 3-methyl-butanal individually or in a mixture enhanced the plant growth and root system development (Jiang et al. 2021).

Similarly, the volatile organic compounds (VOCs) of the hypovirulent strain QT5-19 of *Botrytis cinerea* increased plant height, basal stem diameter, root number per plant, fresh weight per plant, and dry weight per plant of tomato seedlings after incubation at 20 °C for 16 days. The compounds, 2-butyl-1-octanol, 2-heptanal, 2-heptylfuran, and 1-octene-3-ol, as appearing in the VOC profile of QT5-19 promoted the plant growth parameters of tomato seedlings. The values of photosynthetic assimilation, stomatal conductance, transpiration, water use efficiency, and chlorophyll content increased in the tomato plants exposed to the VOCs of hypovirulent strain QT5-19 as compared with the control treatments (Kamaruzzaman et al. 2021). Seven new fungal strains namely *Aspergillus chiangmaiensis* (SDBR-CMUI4 and SDBRCMU15), *Aspergillus pseudopiperis* (SDBR-CMUI1 and SDBR-CMUI7), and *Aspergillus pseudotubingensis* (SDBR-CMUO2, SDBR-CMUO8, and SDBR-CMU20) were able to solubilize the insoluble mineral form of phosphorus, calcium, manganese, magnesium, iron, copper, zinc, cobalt, feldspar, and kaolin in the agar plate assay. All fungal strains significantly increased the leaf number, leaf length, dried biomass of shoot and root, chlorophyll content, and cellular inorganic phosphate content in both Arabidopsis and onion plants. Also, all strains improved the yield and quercetin content of the onion bulb (Khuna et al. 2021). Nevertheless, Li et al. (2021) isolated 162 fungal strains from different abandoned wastelands. Only four isolates, *Penicillium oxalicum* HZ06, *Aspergillus*

brunneoviolaceus HZ23, HZ10, and *Aspergillus tubingensis* HZ123, had the capacity to produce siderophore, and indole acetic acid (IAA) with the ability of phosphate-solubilizing. The inoculation of *P. oxalicum* HZ06 and *A. brunneoviolaceus* HZ23 and HZ10 caused an increase in the growth parameters of eggplant under greenhouse conditions including seedling fresh and dry weight, seedling length, root fresh and dry weight, root length, leaf size, and early flowering.

Tarroum et al. (2021) isolated *Byssochlamys spectabilis*, *Chaetomium globosum*, *Cephalotheca foveolata*, *Penicillium melinii*, *Alternaria tenuissima*, and *Nigrospora chinensis* from the rhizosphere of *Aeluropus littoralis*. All of the tested fungi promoted tobacco seedling growth in liquid Murashige and Skoog medium and significantly increased plant height, leaf area, dry weight, and total chlorophyll content compared with the control plants. The cell-free filtrates of all fungal strains in nutrients solution significantly increased shoot length, root length, shoot dry weight, root dry weight, leaf number, and leaf area of tobacco plants. The culture filtrate of *Trichoderma afroharzianum* TM2-4 promoted tomato seed germination, with hypocotyl length, radical length, and vigor index increased by 28.7, 19.4 and 62.1%, respectively by the production of bioactive substances. Also, *T. afroharzianum* significantly enhanced tomato plant growth including plant height, dry weight, number of leaves per plant, and root activity, through colonization in the rhizosphere and plant root system. A total of 984 differentially expressed genes in tomato roots inoculated with *T. afroharzianum* were identified by transcriptome analyses, which have a vital role in phytohormone homeostasis, antioxidant activity, and metabolic pathways including phenylpropanoid biosynthesis and glutathione metabolism (Zhao et al. 2021a).

Also, the strains of *Trichoderma harzianum* (T13, T15, and Tw) were able to produce indole acetic acid (IAA), and siderophore as well as high activity in solubilizing phosphorus and potassium in the soil. These strains also enhanced the expression of genes associated with plant growth promotion such as *chit42*, *Thpg1*, *qid74*, and *tex10*. *T. harzianum* significantly increased the growth parameters in bean plants in both the presence and absence of the pathogen *Rhizoctonia solani* including root fresh weight, root dry weight, shoot height, stem diameter, shoot fresh weight, and shoot dry weight with enhanced expression of the growth-related genes (NAC1, EXP1, DGL1) according to Eslahi et al. (2020). In the same way, Mauricio-Castillo et al. (2020) isolated the fungus *Alternaria solani* IA300 from mature seeds of *Phaseolus vulgaris*. This isolate IA300 showed the ability to promote the growth in chili plants *Capsicum annuum*, including root length, aerial part length, root fresh weight, aerial fresh weight, root dry weight, aerial dry weight, number of leaves, flowers, and buttons after 15, 30, 45, and 60 days of inoculation. *Paecilomyces variotii* showed a high ability to produce siderophores and indole-3-acetic acid (IAA), but a low ability to solubilize phosphorus. The inoculation of tomato and pepper seeds by spores of *P. variotii* increased the seed germination, root and shoot length, and seed vigor index as well as the growth parameters of tomato and pepper seedlings including stem length, stem diameter, leaf number, leaf area, root dry weight, aerial dry weight as compared with the experimental control (Moreno-Gavíra et al. 2020).

The isolate of *Talaromyces* sp. significantly enhanced seed germination and seedling vigor with promoted growth parameters in chilli plants e.g., plant height, shoot fresh and dry weight, shoot dry weight, and total chlorophyll. Furthermore, *Talaromyces* sp. can solubilize phosphate and produce cellulase, chitinase, siderophore, indoleacetic acid, and hydrogen cyanide (Naziya et al. 2020). In a different study, the volatile organic compounds (VOCs) emitted by *Trichoderma asperellum* T1 enhanced the defense-related enzymes in lettuce plants, β-1,3-glucanase, and chitinase, as the cell-wall degrading enzymes after 2 weeks of exposure. The fresh and dry weight of shoots and roots, the number of leaves, plant biomass, and total chlorophyll content were increased in lettuce plants after 14 days of exposure to the VOCs of *T. asperellum* T1. 22 compounds were identified as acids, alcohols, aldehydes, alkanes, pyran, and fatty acid groups as VOCs of *T. asperellum* T1, and the compound, 6-pentyl-2H-pyran-2-one (6-PP), was the major one by 14.2% using GC-MS analysis. In addition, these VOCs inhibited the fungal growth of *Corynespora cassiicola* and *Curvularia aeria* as the two important leaf spot fungal pathogens in lettuce (Wonglom et al. 2020). The fungus *Cladosporium sphaerospermum* TC09 increased stem length, shoot biomass, root biomass, leaf biomass, and length of the leaf of tobacco seedlings under *in vitro* conditions after 20 days exposed to TC09 cultures. The expression of the genes associated with phytohormone homeostasis, photosynthesis, and defense responses increased in the tobacco seedlings after 10 days using comparative transcriptome analyses. Also, the pepper seedlings treated with *C. sphaerospermum* TC09 for 20 days in the greenhouse conditions flowered 20 days earlier and yielded 213% more than the control plants (Li et al. 2019).

3 Impact of PGPF on Plant Resistance Induction

Several members of PGPF have been found to be potential inducers of systemic resistance such as *Trichoderma*, *Aspergillus*, *Mucor*, *Penicillium*, *Talaromyces*, *Chaetomium*, and *Phoma* against plant pathogens (Hossain et al. 2017; Verma et al. 2022). The PGPF employs multifarious mechanisms in controlling plant diseases including direct antagonism like parasitism, hyperparasitism, and commensalism, and indirect antagonism such as systemic acquired resistance (SAR) and induced systemic resistance (ISR) (Fig. 1) (Walters et al. 2013; Fontana et al. 2021).

SAR is induced in plants as a response to the primary infection by a virulent pathogen which causes a hypersensitive reaction (HR) or local necrotic lesions on the host plant to arrest the pathogen growth (Durrant and Dong 2004; Salman et al. 2022). These lesions are characterized by different types of pathogenesis-related (PR) proteins such as hydrolase [β-1,3-glucanase] (PR-2) and chitinase (PR-3), which inhibit the growth of phytopathogens as well as by the increased expression of the pathogenesis-related genes (PR genes) (Gao et al. 2015; Eccleston et al. 2022). SAR is typically triggered by activation of a pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI), and effector-triggered immunity (ETI)

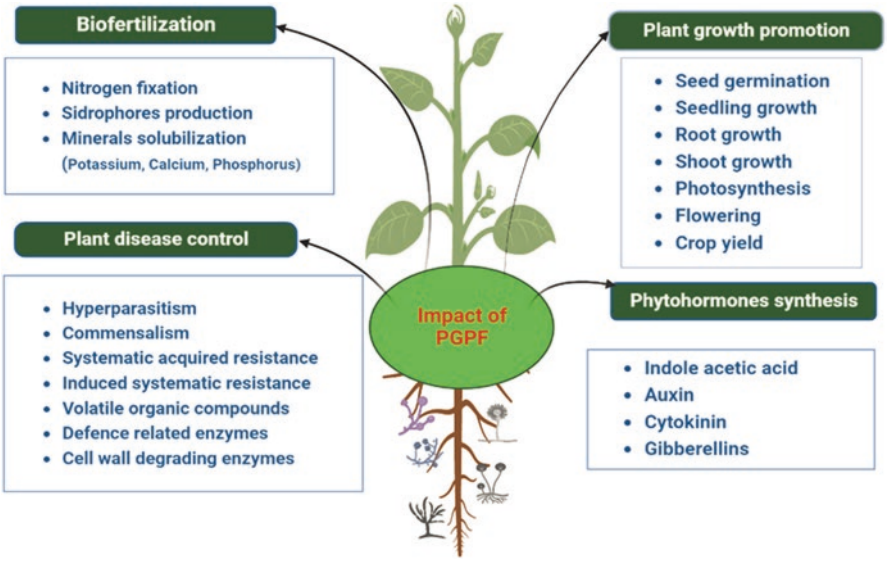

Fig. 1 Impact of PGPF on plant growth promotion and plant diseases suppression

response (Meena et al. 2022). The high level of endogenous salicylic acid (SA) in systemic tissues is one of the hallmarks of SAR (Klessig et al. 2018).

ISR is triggered upon colonization of plants by biological agents like plant growth-promoting rhizobacteria (PGPR) and plant growth-promoting fungi (PGPF) or chemical inducers (Pieterse et al. 2014; Olowe et al. 2020). ISR leads to resistance priming in root parts and aerial parts of plants (Romera et al. 2019). Therefore, ISR is known to reduce the incidence and severity of various plant diseases (Walters et al. 2013; Thankappan et al. 2022). Unlike SAR, ISR does not include the accumulation of pathogenesis-related proteins or salicylic acid (SA), but jasmonic acid (JA) and ethylene (ET)-mediated pathways are responsible for the ISR as well as the production of defense-related enzymes and defense chemicals diseases (Vlot et al. 2021). Table 2 summarizes findings related to the effect of some PGPF as biological inducers on the induction of plant resistance.

For instance, the ethyl acetate extracts of *Aspergillus flavus*, *A. niger*, *Mucor circinelloides*, and *Penicillium oxalicum* significantly inhibited *Fusarium oxysporum* f. sp. *lycopersici* using the agar well diffusion method and reduced wilt disease severity in tomato plants by 16.6, 20.83, 37.5, and 45.83%, respectively. The PGPF enhanced the total soluble proteins and carbohydrates, total phenol, and total proline in treated plants compared to control plants as well as the activity of oxidative enzymes including peroxidase (POD), and polyphenoloxidase (PPO) (Attia et al. 2022). In the same way, *Aspergillus terreus* ANU-301 inhibited the growth of *Fusarium oxysporum* f. sp. *lycopersici* by 58.5% in the dual culture assay, while culture filtrate of the fungus caused only 20.2% inhibition of the pathogen growth. Also, the isolate ANU-301 significantly reduced the wilt disease symptoms in

Table 2 Effect of PGPF on plant resistance induction

Crop	Pathogen (disease)	PGPF strain	Mechanism	References
Tomato	*Fusarium oxysporum* f. sp. *lycopersici* (Fusarium wilt)	*Aspergillus flavus* *Aspergillus niger* *Mucor circinelloides* *Penicillium oxalicum*	Antifungal activity Significantly reduced disease severity	Attia et al. (2022)
Tomato	*Fusarium oxysporum* f. sp. *lycopersici* (Fusarium wilt)	*Aspergillus terreus*	Antifungal activity Reduce disease severity Bioactive compounds	Choi and Ahsan (2022)
Maize	*Cephalosporium maydis* (Late wilt)	*Chaetomium globosum*	Antifungal activity Reduce incidence and severity of disease Enzymes activity	Elshahawy and Khattab (2022)
Ginseng	*Alternaria panax* *Botrytis cinerea* *Cylindrocarpon destructans* *Fusarium oxysporum* *Sclerotinia nivalis* *Sclerotinia sclerotiorum* (Root rot)	*Trichoderma Pleuroticola* *Trichoderma atroviride*	Antifungal activity Volatile organic compounds (VOCs)	Joo and Hussein (2022)
Tobacco Cotton	*Verticillium dahliae* (Verticillium wilt)	*Trichoderma koningiopsis*	Antifungal activity Volatile organic compounds (VOCs) Reduce disease severity	Kong et al. (2022)
Macadamia	*Lasiodiplodia theobromae* (kernel rot)	*Trichoderma hamatum*	Antifungal activity Volatile and non-volatile metabolites Reduce the disease severity	Li et al. (2022)
Rice	*Rhizoctonia solani* (Sheath blight)	*Talaromyces* spp.	Reduce disease index Plant signaling pathways Plant growth promotion	Abbas et al. (2021)

(continued)

Table 2 (continued)

Crop	Pathogen (disease)	PGPF strain	Mechanism	References
Tomato	*Rhizoctonia solani* (Crown rot)	*Acrophialophora jodhpurensis*	Antifungal activity Volatile and non-volatile metabolites Decrease the disease index Enzymes activity	Daroodi et al. (2021)
Peanut	*Fusarium solani* (Brown root rot)	*Trichoderma harzianum*	Antifungal activity Bioactive compounds Reduce incidence and severity of disease	Erazo et al. (2021)
Tomato	*Alternaria alternata* (Early blight)	*Trichoderma viride* *Chaetomium globosum*	Antifungal activity Reduce incidence and severity of disease Enzymes activity	Khalil et al. (2021)
Muskmelon	*Stagonosporopsis cucurbitacearum* (Gummy stem blight)	*Trichoderma asperelloides*	Antifungal activity Reduce disease severity index (DSI) Enzymes activity	Ruangwong et al. (2021)
Tomato	*Botrytis cinerea* (Gray mold)	*Trichoderma asperellum*	Antifungal activity Reduce incidence and severity of disease Plant growth promotion	Wang et al. (2021)
Chilli	*Colletotrichum truncatum* (Anthracnose)	*Trichoderma harzianum* *Trichoderma asperellum*	Antifungal activity Induced systemic resistance (ISR) Reduce disease severity Enzymes activity	Yadav et al. (2021)
Cotton	*Verticillium dahlia* (Verticillium wilt)	*Chaetomium globosum*	Antifungal activity Reduce disease incidence Bioactive compounds	Zhang et al. (2021)

(continued)

Table 2 (continued)

Crop	Pathogen (disease)	PGPF strain	Mechanism	References
Tomato	*Botrytis cinerea* (Grey mould)	*Trichoderma afroharzianum*	Antifungal activity Reduce incidence and severity of disease Enzymes activity Plant signaling pathways	Zhao et al. (2021b)
Wheat	*Rhizoctonia solani* (Wilt disease)	*Aspergillus flavus* *Aspergillus niger* *Penicillium citrinum* *Penicillium chrysogenum* *Trichoderma koningiopsis*	Reduce disease severity Induced systemic resistance (ISR)	El-Maraghy et al. (2020)
Chilli	*Colletotrichum capsici* (Anthracnose)	*Talaromyces* sp.	Antifungal activity Reduce incidence and severity of disease Lignin and callose deposition Enzymes activity	Naziya et al. (2020)
Cucumber	*Rhizoctonia solani*	*Trichoderma brevicrassum*	Antifungal activity Reduce incidence and severity of disease Plant growth promotion	Zhang and Zhuang (2020)
Onion	*Sclerotium cepivorum* (White rot)	*Phoma* sp. *Trichoderma asperellum* *Fusarium equiseti* *Penicillium simplicissmum*	Antifungal activity Reduce incidence and severity of disease Enzymes activity	Elsharkawy and El-Khateeb (2019)

tomato plants inoculated with *F. oxysporum* f. sp. *lycopersici,* and *A. terreus*. Twenty compounds were identified in the culture filtrate of *A. terreus* by GC-MS/MS analysis, and 2,4-bis(1-methyl-1-phenylethyl)-phenol and 2,3,4,5-tetraphenyl-1H-pyrrole were the major components in the filtrate (Choi and Ahsan 2022). The fungus *Chaetomium globosum* Chg-1 caused a voluminous inhibition on the growth of *Cephalosporium maydis* by 91% in the dual culture test. Hexane, ethyl acetate, and methanol extracts of *C. globosum* Chg-1 were highly effective in the reduction of the mycelial growth and conidial germination of *C. maydis* at different concentrations. In greenhouse trials, the treatments of *C. globosum* Chg-1 significantly reduced late wilt disease incidence and severity in two maize cultivars by inducing

resistance mechanisms in maize plants via the induction of antioxidant enzymes (Elshahawy and Khattab 2022).

In yet another example, Joo and Hussein (2022) isolated different strains of *Trichoderma* from the rhizosphere of Korean ginseng and pine soils (*T. harzianum* KNU1, *T. reesei* KNU4, *T. harzianum* KNU10, *T. harzianum* H22, *T. atroviride* 24, *T. koningii* 27, *T. virens* 19, *T. longibrachiatum* 28, *T. Pleuroticola* P22, and *T. asperellum* 18). The fungus *T. Pleuroticola* P22 showed high antifungal activity against *Alternaria panax*, *Botrytis cinerea*, *Cylindrocarpon destructans*, *Fusarium oxysporum*, *Sclerotinia nivalis,* and *S. sclerotiorum*. Moreover, volatile organic compounds (VOCs) produced by *T. atroviride* showed a decisive inhibition of *A. panax*, *B. cinerea*, *C. destructans*, and *S. nivalis*. The volatile organic compounds (VOCs) produced by *Trichoderma koningiopsis* T2 significantly inhibited the growth of *Verticillium dahliae*. *Trichoderma* VOCs reduced the severity of Verticillium wilt by preventing the colonization of *V. dahliae* on tobacco and cotton. Six volatile compounds were identified by GC-MS analysis, and the major compounds were 3-octanone, 3-methyl-1-butanol, butanoic acid ethyl ester, and 2-hexyl-furan. The VOCs of *T. koningiopsis* T2 significantly inhibited the microsclerotia formation of *V. dahliae* and decreased the activity of cell wall-degrading enzymes of the pathogen (Kong et al. 2022). On similar lines, *Trichoderma hamatum* C9 inhibited the growth of *Lasiodiplodia theobromae* by 56.3% in the dual confrontation assay. The cell-free culture filtrate of *T. hamatum* markedly inhibited the mycelial growth of *L. theobromae* at a concentration ranging from 0.5% to 10% and the volatile organic compounds (VOCs) of the strain C9 caused 32.4% inhibition on the pathogen growth. The lesion area caused by *L. theobromae* on macadamia leaves was reduced after spraying the leaves with a conidial suspension of *T. hamatum* as well as the disease severity index (DSI) according to Li et al. (2022).

Talaromyces spp. were isolated from the paddy soil and caused more protection from the damage by rice sheath blight caused by *Rhizoctonia solani* compared with the control plants under greenhouse conditions. The defense-related genes were highly expressed in the plants treated with isolates of *Talaromyces* such as OsPR1a (General defense), OsEIN2 (Ethylene signaling), OsJAMYB (Jasmonic acid biosynthesis), and OsAOS2 (Jasmonic acid response). Concurrently, these isolates caused an increase in the total plant height, fresh and dry biomass, the number of tillers and productive tillers, panicle length, and grain yield (Abbas et al. 2021). The strain *Acrophialophora jodhpurensis* inhibited the growth of *Rhizoctonia solani* AG4-HG II in the dual culture test on PDA. Both volatile and non-volatile metabolites of *A. jodhpurensis* inhibited *R. solani* growth especially non-volatile metabolites at the concentration of 15%. The isolate of *A. jodhpurensis* decreased the disease index of crown rot in tomato seedlings by more than 40% compared to the control groups. Also, *A. jodhpurensis* induced the activity of antioxidant enzymes including catalase (CAT), ascorbate peroxidase (APX), peroxidase (GPX), and superoxide dismutase (SOD) as well as phenolic content, lignin accumulation, relative water content, cell membrane stability, hydrogen peroxide (H_2O_2), superoxide (O_2) and iron ions (Daroodi et al. 2021).

Trichoderma harzianum ITEM 3636 inhibited the growth of *Fusarium solani* RC 386 in the dual culture experiment by 48.4, and 30% when used the media of peanut root extract agar (PREA), and malt extract agar (MEA), respectively, and 78.2% inhibition with the used filtered liquid cultures of *T. harzianum*. Also, *T. harzianum* ITEM 3636 was able to synthesize a high level of some enzymes including protease (prb1), N-acetyl-β-D-glucosaminidase or NAGase (exc1 and exc2), β-1,3-glucanase (b13glu), and chitinases (chit33, chit42) as a mechanism of antagonistic activity against *F. solani* RC386. The genes, *prb1*, *chit33*, and *bgn13.1*, were detected with the interaction between *T. harzianum* and *F. solani* mycelia as biocontrol-associated genes. The application of *T. harzianum* ITEM 3636 on peanut plants in the greenhouse assays reduced both the incidence and the severity of peanut brown root rot by 3.8 and 63.98% respectively (Erazo et al. 2021). In this context, *Trichoderma viride* and *Chaetomium globosum* showed antagonistic activities against *Alternaria alternata* with inhibition zones reaching 1.6 and 1.4 cm, respectively. The foliar application on tomato plants by *T. viride* and *C. globosum* either alone or in combination reduced the incidence of early blight disease by 73.3, 37.6, and 59.1%, respectively and the disease severity was 18.7, 46.4, and 37.6%, respectively, compared with the control groups. Also, these treatments enhanced the antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT) with an increase in chlorophyll content and a decrease in hydrogen peroxide (H_2O_2), membrane ion leakage, and Malondialdehyde (MDA) levels in the treated plants (Khalil et al. 2021). Similarly, *Trichoderma asperelloides* PSU-P1 caused a tremendous inhibition of the growth of *Stagonosporopsis cucurbitacearum* by 96.08% in the dual culture assay. The seedlings of muskmelon treated with *T. asperelloides* showed a disease severity index (DSI) of gummy stem blight by 10% as compared to the control by 75% DSI. Also, the activity of defense-related enzymes, peroxidase (POD) and polyphenol oxidase (PPO), and cell wall degrading enzymes, chitinase, and β-1,3-glucanase, in muskmelon seedlings treated with *T. asperelloides* PSU-P1 were higher than in the control groups (Ruangwong et al. 2021).

Wang et al. (2021) tested 23 *Trichoderma* strains isolated from tomato rhizosphere soil against *Botrytis cinerea* in the dual culture assay. Among them, *Trichoderma asperellum* strain DQ-1 caused a strong inhibition of the pathogen growth by 88.41%. The disease incidence and severity of gray mold were reduced by 38 and 64% in tomato plants inoculated with *T. asperellum* DQ-1 and then with *B. cinerea* as compared with the control groups. The isolate *T. asperellum* DQ-1 caused an increase in the expression levels of disease resistance-related genes PR2 and TPX, ethylene pathway-related genes ETR1 and CTR1, and jasmonic acid pathway-related genes LOX1 and PAL with triggered the systemic acquired resistance (SAR) and induced systemic resistance (ISR) pathway. Also, the strain DQ-1 increased tomato seeds germination rate and root length by 5.55 and 37.86%, respectively. In another study, *Trichoderma harzianum* and *T. asperellum* showed a strong radial growth inhibition against *Colletotrichum truncatum* by 75.46, and 73.09%, respectively in the dual culture plates. The seeds of chilli treated with *T. asperellum*, *T. harzianum*, and *T. asperellum* + *T. harzianum* inflicted an induced systemic resistance (ISR) against a *C. truncatum* under greenhouse conditions with

a considerable reduction in the anthracnose disease index percentage in chilli plants. Additionally, increasing the relative chlorophyll content in plants and accumulating phenolic compounds as well as enhanced the activity of defense-related enzymes including superoxide dismutase (SOD), peroxidase (POX), polyphenol oxidase (PPO), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX) and phenylalanine ammonia-lyase (PAL) (Yadav et al. 2021). The fungus *Chaetomium globosum* CEF-082 inhibited the colony expansion of the pathogen *Verticillium dahliae* in the dual-culture antagonism bioassay. Also, *C. globosum* CEF-082 and its metabolic filtrate reduced the incidence of cotton Verticillium wilt and increased the cotton plant height. The compound chaetoviridin A was identified from the metabolic crude extract of *C. globosum* CEF-082 through HPLC and NMR analysis and caused strong inhibition of the growth and microsclerotia germination of *V. dahliae*. This compound caused cell necrosis and mycelial deformation of *V. dahliae* with an increase in the production of reactive oxygen species and nitrous oxide (Zhang et al. 2021).

Trichoderma afroharzianum TM24 inhibited the growth of *Botrytis cinerea* by 74.2% with continuous overgrowth on the mycelia of the pathogen. Also, after 5 days of incubation, isolate TM24 exhibited the highest activities of chitinase and β-1,3-glucanase. The isolate TM24 displayed a significantly reduced in both disease incidence and disease severity on tomato leaves and the biocontrol efficiency was 56.7% against grey mould in greenhouse experiments with an increase in the activity of defense-related enzymes including polyphenol oxidase, phenylalanine ammonia-lyase, superoxide dismutase, and peroxidase. A total of 1941 differentially expressed genes (DEGs) were obtained in tomato leaves treated with *T. afroharzianum* and then inoculated with *B. cinerea* by transcriptome analysis. These genes were related to defense-related pathways, like flavonoid, phenylpropanoid, jasmonic acid, and ethylene metabolisms as well as the MAPK signaling pathway and plant hormones signal transduction pathway (Zhao et al. 2021b). Furthermore, the rhizosphere fungi *Aspergillus flavus*, *A. niger*, *Penicillium citrinum*, *P. chrysogenum*, and *Trichoderma koningiopsis* significantly decreased the disease severity (lesions size) in wheat plants via stimulated induced systemic resistance (ISR) against wilt disease caused by *Rhizoctonia solani* R43. Also, all fungi showed a high capability to produce siderophores and solubilize tri-calcium phosphate (El-Maraghy et al. 2020). Also, the fungus *Talaromyces* sp. record the maximum inhibition against *Colletotrichum capsici*, the causal agent of chilli anthracnose disease, by 88.64% during the antagonism test with root colonization ability in the plants. Also, *Talaromyces* sp. caused great protection in chilli plants against anthracnose by 78.75% under greenhouse conditions. The PGPF fungus directly activated lignin and callose deposition in chilli seedlings as well as the enzymes of phenylalanine ammonia-lyase (PAL), peroxidase (POX), β-1,3-glucanase, and chitinase (Naziya et al. 2020).

Among 278 *Trichoderma* strains belonging to 139 species, *Trichoderma brevicrassum* TC967 caused the highest inhibition on the growth of *Rhizoctonia solani* by 72.14% in the dual culture experiment. The disease index was only 37.5% in the cucumber seedlings treated with *T. brevicrassum* TC967. Also, this strain

significantly reduced disease symptoms in cucumber plants under greenhouse conditions. The strain TC967 induced the expression of systemic acquired resistance (SAR) genes such as PR1 (encoding pathogenesis-related protein), PR5 (encoding thaumatinlike protein), and PR4 (encoding chitinase for induced systemic resistance, ISR) in cucumber plants treated with TC967 and the pathogen as compared with the control. At the same time, the shoot length and dry weight of cucumber seedlings were increased after treatment with the strain TC967 than those of the control (Zhang and Zhuang 2020). The PGPF isolates, *Phoma* sp. GS8-1, *Phoma* sp. GS8-3, *Trichoderma asperellum* SKT-1, *Fusarium equiseti* GF18-3, and *Penicillium simplicissmum* GP17-2, strongly inhibited the growth and germination of the sclerotia of *Sclerotium cepivorum* and the four culture filtrate of PGPF isolates significantly decreased the germination of sclerotia. The treatments with PGPF isolates significantly reduced both disease incidence and severity in onion plants in greenhouse and field trials with an increase in the levels of peroxidase (POX) and polyphenol oxidase (PPO) enzymes (Elsharkawy and El-Khateeb 2019).

4 Conclusions

Plant growth-promoting fungi (PGPF) are promising agents for sustainable agriculture. The use of PGPF proves to be an outstanding alternative to chemical fertilizers and synthetic pesticides in the long term with numerous potentials in biofertilization, biocontrol, and biostimulation. PGPF are a powerful tool for scientific research and agricultural companies to develop viable strategies in crop productivity and plant disease management with maintaining the agroecosystems, biodiversity, and soil health. The application of PGPF improves plant growth and yield, directly suppresses plant pathogens, and indirectly enhances induced resistance in plants including SAR and ISR in an eco-friendly, non-toxic, and cost-effective manner. Understanding the underlying mechanisms of PGPF activity will be useful and highly vital for developing new tools to boost crop productivity, plant disease control, and involvement in a sustainable ecosystem.

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References

Abbas A, Fu Y, Qu Z, Zhao H, Sun Y, Lin Y, Xie J, Cheng J, Jiang D (2021) Isolation and evaluation of the biocontrol potential of *Talaromyces* spp. against rice sheath blight guided by soil microbiome. Environ Microbiol 23:5946–5961. https://doi.org/10.1111/1462-2920.15596

Abdel-Motaal F, Kamel N, El-Zayat S, Abou-Ellail M (2020) Early blight suppression and plant growth promotion potential of the endophyte *Aspergillus flavus* in tomato plant. Ann Agric Sci 65:117–123. https://doi.org/10.1016/j.aoas.2020.07.001

Abdul Malik NA, Kumar IS, Nadarajah K (2020) Elicitor and receptor molecules: orchestrators of plant defense and immunity. Int J Mol Sci 21:963. https://doi.org/10.3390/ijms21030963

Aboulila AA (2022) Efficiency of plant growth regulators as inducers for improve systemic acquired resistance against stripe rust disease caused by *Puccinia striiformis* f. sp. *tritici* in wheat through up-regulation of PR-1 and PR-4 genes expression. Physiol Mol Plant Pathol 121:101882. https://doi.org/10.1016/j.pmpp.2022.101882

Almeida FB, Rodrigues LM, Coelho C (2019) The still underestimated problem of fungal diseases worldwide. Front Microbiol 10:214. https://doi.org/10.3389/fmicb.2019.00214

Appu M, Ramalingam P, Sathiyanarayanan A, Huang J (2021) An overview of plant defense-related enzymes responses to biotic stresses. Plant Gene 27:100302. https://doi.org/10.1016/j.plgene.2021.100302

Asghar W, Kataoka R (2022) Different green manures (*Vicia villosa* and *Brassica juncea*) construct different fungal structures, including plant-growth-promoting effects, after incorporation into the soil. Agronomy 12:323. https://doi.org/10.3390/agronomy12020323

Attia MS, Abdelaziz AM, Al-Askar AA, Arishi AA, Abdelhakim AM, Hashem AH (2022) Plant growth-promoting fungi as biocontrol tool against Fusarium wilt disease of tomato plant. J Fungi 8:775. https://doi.org/10.3390/jof8080775

Bano A, Waqar A, Khan A, Tariq H (2022) Phytostimulants in sustainable agriculture. Front Sustain Food Syst 6:801788. https://doi.org/10.3389/fsufs.2022.801788

Basavaraj GL, Murali M, Lavanya SN, Amruthesh KN (2019) Seed priming with biotic agents invokes defense response and enhances plant growth in pearl millet upon infection with *Magnaporthe grisea*. Biocatal Agric Biotechnol 21:101279. https://doi.org/10.1016/j.bcab.2019.101279

Berens ML, Berry HM, Mine A, Argueso CT, Tsuda K (2017) Evolution of hormone signaling networks in plant defense. Annu Rev Phytopathol 55:401–425. https://doi.org/10.1146/annurev-phyto-080516-035544

Bhatt K, Suyal DC, Kumar S, Singh K, Goswami P (2022) New insights into engineered plant-microbe interactions for pesticide removal. Chemosphere 309:136635. https://doi.org/10.1016/j.chemosphere.2022.136635

Bigeard J, Colcombet J, Hirt H (2015) Signaling mechanisms in pattern-triggered immunity (PTI). Mol Plant 8:521–539. https://doi.org/10.1016/j.molp.2014.12.022

Breakfield N, Collett DP, Frodyma M (2021) Plant growth-promoting microbes-An industry view. Emerg Top Life Sci 5:317–324. https://doi.org/10.1042/ETLS20200313

Burragoni SG, Jeon J (2021) Applications of endophytic microbes in agriculture, biotechnology, medicine, and beyond. Microbiol Res 245:126691. https://doi.org/10.1016/j.micres.2020.126691

Busby PE, Soman C, Wagner MR, Friesen ML, Kremer J, Bennett A, Morsy M, Eisen JA, Leach JE, Dangl JL (2017) Research priorities for harnessing plant microbiomes in sustainable agriculture. PLoS Biol 15:e2001793. https://doi.org/10.1371/journal.pbio.2001793

Cantabella D, Dolcet-Sanjuan R, Teixidó N (2022) Using plant growth-promoting microorganisms (PGPMs) to improve plant development under in vitro culture conditions. Planta 255:117. https://doi.org/10.1007/s00425-022-03897-0

Cao J, Liu B, Xu X, Zhang X, Zhu C, Li Y, Ding X (2021) Plant endophytic fungus extract ZNC improved potato immunity, yield, and quality. Front Plant Sci 12:707256. https://doi.org/10.3389/fpls.2021.707256

Chaudhary P, Singh S, Chaudhary A, Sharma A, Kumar G (2022) Overview of biofertilizers in crop production and stress management for sustainable agriculture. Front Plant Sci 13:930340. https://doi.org/10.3389/fpls.2022.930340

Chen D, Hou Q, Jia L, Sun K (2021) Combined use of two *Trichoderma* strains to promote growth of pakchoi (*Brassica chinensis* L.). Agronomy 11:726. https://doi.org/10.3390/agronomy11040726

Choi HW, Ahsan SM (2022) Biocontrol activity of *Aspergillus terreus* ANU-301 against two distinct plant diseases, tomato Fusarium wilt and potato soft rot. Plant Pathol J 38:33–45. https://doi.org/10.5423/PPJ.OA.12.2021.0187

Cook DE, Mesarich CH, Thomma BP (2015) Understanding plant immunity as a surveillance system to detect invasion. Ann Rev Phytopathol 53:541–563. https://doi.org/10.1146/annurev-phyto-080614-120114

Cui H, Tsuda K, Parker JE (2015) Effector-triggered immunity: from pathogen perception to robust defense. Annu Rev Plant Biol 66:487–511. https://doi.org/10.1146/annurev-arplant-050213-040012

Daroodi Z, Taheri P, Tarighi S (2021) Direct antagonistic activity and tomato resistance induction of the endophytic fungus *Acrophialophora jodhpurensis* against *Rhizoctonia solani*. Biol Control 160:104696. https://doi.org/10.1016/j.biocontrol.2021.104696

Durrant WE, Dong X (2004) Systemic acquired resistance. Annu Rev Phytopathol 42:185–209. https://doi.org/10.1146/annurev.phyto.42.040803.140421

Eccleston L, Brambilla A, Vlot AC (2022) New molecules in plant defence against pathogens. Essays Biochem 66:683–693. https://doi.org/10.1042/EBC20210076

El-Maraghy SS, Tohamy TA, Hussein KA (2020) Role of plant-growth promoting fungi (PGPF) in defensive genes expression of *Triticum aestivum* against wilt disease. Rhizosphere 15:100223. https://doi.org/10.1016/j.rhisph.2020.100223

Elshahawy IE, Khattab AEA (2022) Endophyte *Chaetomium globosum* improves the growth of maize plants and induces their resistance to late wilt disease. J Plant Dis Protect 129:1125–1144. https://doi.org/10.1007/s41348-022-00626-3

Elsharkawy MM, El-Khateeb NMM (2019) Antifungal activity and resistance induction against *Sclerotium cepivorum* by plant growth-promoting fungi in onion plants. Egypt J Biol Pest Control 29:68. https://doi.org/10.1186/s41938-019-0178-9

Elsherbiny EA, Taher MA, Elsebai MF (2019) Activity of *Purpureocillium lilacinum* filtrates on biochemical characteristics of *Sclerotinia sclerotiorum* and induction of defense responses in common bean. Eur J Plant Pathol 155:39–52. https://doi.org/10.1007/s10658-019-01748-5

Erazo JG, Palacios SA, Pastor N, Giordano FD, Rovera M, Reynoso MM, Venisse JS, Torres AM (2021) Biocontrol mechanisms of *Trichoderma harzianum* ITEM 3636 against peanut brown root rot caused by *Fusarium solani* RC 386. Biol Control 164:104774. https://doi.org/10.1016/j.biocontrol.2021.104774

Eslahi N, Kowsari M, Moghaddam A, Zamani M (2020) Influence of recombinant *Trichoderma* strains on growth of bean (*Phaseolus vulgaris* L.) by increased root colonization and induction of root growth related genes. Sci Hortic 261:108932. https://doi.org/10.1016/j.scienta.2019.108932

Fontana DC, de Paula S, Torres AG, de Souza VHM, Pascholati SF, Schmidt D, Dourado Neto D (2021) Endophytic fungi: biological control and induced resistance to phytopathogens and abiotic stresses. Pathogens 10:570. https://doi.org/10.3390/pathogens10050570

Francioli D, van Rijssel SQ, van Ruijven J, Termorshuizen AJ, Cotton TE, Dumbrell AJ, Raaijmakers JM, Wei-gelt A, Mommer L (2021) Plant functional group drives the community structure of saprophytic fungi in a grassland biodiversity experiment. Plant Soil 461:91–105. https://doi.org/10.1007/s11104-020-04454-y

Galeano RMS, Franco DG, Chaves PO, Giannesi GC, Masui DC, Ruller R, Corrêa BO, Brasil MDS, Zanoelo FF (2021) Plant growth promoting potential of endophytic *Aspergillus niger* 9-p isolated from native forage grass in Pantanal of Nhecolândia region, Brazil. Rhizosphere 18:100332. https://doi.org/10.1016/j.rhisph.2021.100332

Gao Q-M, Zhu S, Kachroo P, Kachroo A (2015) Signal regulators of systemic acquired resistance. Front Plant Sci 6:228. https://doi.org/10.3389/fpls.2015.00228

Ghosh SK, Panja A (2021) Signatures of signaling pathways underlying plant-growth promotion by fungi. In: Jogaiah S (ed) Biocontrol agents and secondary metabolites. Elsevier Inc. https://doi.org/10.1016/B978-0-12-822919-4.00013-2

Hakim S, Naqqash T, Nawaz MS, Laraib I, Siddique MJ, Zia R, Mirza MS, Imran A (2021) Rhizosphere engineering with plant growth-promoting microorganisms for agriculture and ecological sustainability. Front Sustain Food Syst 5:617157. https://doi.org/10.3389/fsufs.2021.617157

He M, He C-Q, Ding N-Z (2018) Abiotic stresses: general defenses of land plants and chances for engineering multistress tolerance. Front Plant Sci 9:1771. https://doi.org/10.3389/fpls.2018.01771

Hossain MM, Sultana F (2020) Application and mechanisms of plant growth promoting fungi (PGPF) for Phytostimulation. In: Das SK (ed) Organic agriculture. IntechOpen, London. https://doi.org/10.5772/intechopen.92338

Hossain MM, Sultana F, Islam S (2017) Plant growth-promoting fungi (PGPF): phytostimulation and induced systemic resistance. In: Singh D, Singh H, Prabha R (eds) Plant-microbe interactions in agro-ecological perspectives. Springer, Singapore, pp 135–191. https://doi.org/10.1007/978-981-10-6593-4_6

Jacquet F, Jeuffroy M-H, Jouan J, Le Cadre E, Litrico I, Malausa T, Reboud X, Huyghe C (2022) Pesticide-free agriculture as a new paradigm for research. Agron Sustain Dev 42:8. https://doi.org/10.1007/s13593-021-00742-8

Jahagirdar S, Kambrekar DN, Navi SS, Kunta M (2019) Plant growth-promoting fungi: diversity and classification. In: Jogaiah S, Abdelrahman M (eds) Bioactive molecules in plant defense. Springer, Cham. https://doi.org/10.1007/978-3-030-27165-7_2

Jiang L, Lee MH, Kim CY, Kim SW, Kim PI, Min SR, Lee J (2021) Plant growth promotion by two volatile organic compounds emitted from the fungus *Cladosporium halotolerans* NGPF1. Front Plant Sci 12:794349. https://doi.org/10.3389/fpls.2021.794349

Joo JH, Hussein KA (2022) Biological control and plant growth promotion properties of volatile organic compound-producing antagonistic *Trichoderma* spp. Front Plant Sci 13:897668. https://doi.org/10.3389/fpls.2022.897668

Kamaruzzaman M, Wang Z, Wu M, Yang L, Han Y, Li G, Zhang J (2021) Promotion of tomato growth by the volatiles produced by the hypovirulent strain QT5-19 of the plant gray mold fungus *Botrytis cinerea*. Microbiol Res 247:126731. https://doi.org/10.1016/j.micres.2021.126731

Khalil MI, Youssef SA, Tartoura KA, Eldesoky AA (2021) Comparative evaluation of physiological and biochemical alteration in tomato plants infected by *Alternaria alternata* in response to *Trichoderma viride* and *Chaetomium globosum* application. Physiol Mol Plant Pathol 115:101671. https://doi.org/10.1016/j.pmpp.2021.101671

Khuna S, Suwannarach N, Kumla J, Frisvad JC, Matsui K, Nuangmek W, Lumyong S (2021) Growth enhancement of Arabidopsis (*Arabidopsis thaliana*) and onion (*Allium cepa*) with inoculation of three newly identified mineral-solubilizing fungi in the genus *Aspergillus* section *Nigri*. Front Microbiol 12:705896. https://doi.org/10.3389/fmicb.2021.705896

Klessig DF, Choi HW, Dempsey DA (2018) Systemic acquired resistance and salicylic acid: past, present, and future. Mol Plant-Microbe Interact 31:871–888. https://doi.org/10.1094/MPMI-03-18-0067-CR

Kohl J, Kolnaar R, Ravensberg WJ (2019) Mode of action of microbial biological control agents against plant diseases: relevance beyond efficacy. Front Plant Sci 10:845. https://doi.org/10.3389/fpls.2019.00845

Kong W-L, Ni H, Wang W-Y, Wu X-Q (2022) Antifungal effects of volatile organic compounds produced by *Trichoderma koningiopsis* T2 against *Verticillium dahliae*. Front Microbiol 13:1013468. https://doi.org/10.3389/fmicb.2022.1013468

Kour D, Rana KL, Kaur L, Yadav N, Yadav AN, Kumar M, Kumar V, Dhaliwal HS, Saxena AK (2021) Biodiversity, current developments and potential biotechnological applications of phosphorus-solubilizing and -mobilizing microbes: a review. Pedosphere 31:43–75. https://doi.org/10.1016/S1002-0160(20)60057-1

Kumar M, Poonam AS, Singh RP (2022) Plant growth promoting microbes: diverse roles for sustainable and ecofriendly agriculture. Energy Nexus 7:100133. https://doi.org/10.1016/j.nexus.2022.100133

Kushalappa AC, Yogendra KN, Karre S (2016) Plant innate immune response: qualitative and quantitative resistance. Crit Rev Plant Sci 35:38–55. https://doi.org/10.1080/07352689.2016.1148980

Li ZT, Janisiewicz WJ, Liu Z, Callahan AM, Evans BE, Jurick WM II, Dardick C (2019) Exposure *in vitro* to an environmentally isolated strain TC09 of *Cladosporium sphaerospermum* triggers plant growth promotion, early flowering, and fruit yield increase. Front Plant Sci 9:1959. https://doi.org/10.3389/fpls.2018.01959

Li X, Li D, Yan J, Zhang Y, Wang H, Zhang J, Ahmed T, Li B (2021) Effect of plant-growth-promoting fungi on eggplant (*Solanum melongena* L.) in new reclamation land. Agriculture 11:1036. https://doi.org/10.3390/agriculture11111036

Li X, Leng J, Yu L, Bai H, Li X, Wisniewski M, Liu J, Sui Y (2022) Efficacy of the biocontrol agent *Trichoderma hamatum* against *Lasiodiplodia theobromae* on macadamia. Front Microbiol 13:994422. https://doi.org/10.3389/fmicb.2022.994422

Malgioglio G, Rizzo GF, Nigro S, Lefebvre du Prey V, Herforth-Rahmé J, Catara V, Branca F (2022) Plant-microbe interaction in sustainable agriculture: the factors that may influence the efficacy of PGPM application. Sustainability 14:2253. https://doi.org/10.3390/su14042253

Mandal P, Tiru Z (2022) Soil application of plant growth promoting fungi for sustainable agriculture in the new decade. In: Roy S, Mathur P, Chakraborty AP, Saha SP (eds) Plant stress: challenges and Management in the new decade. Advances in science, technology & innovation. Springer, Cham. https://doi.org/10.1007/978-3-030-95365-2_20

Manzar N, Kashyap AS, Goutam RS, Rajawat MVS, Sharma PK, Sharma SK, Singh HV (2022) *Trichoderma*: advent of versatile biocontrol agent, its secrets and insights into mechanism of biocontrol potential. Sustainability 14:12786. https://doi.org/10.3390/su141912786

Mauricio-Castillo JA, Salas-Muñoz S, Reveles-Torres LR, Salas-Luevano MA, Salazar-Badillo FB (2020) Could *Alternaria solani* IA300 be a plant growth-promoting fungus? Eur J Plant Pathol 157:413–419. https://doi.org/10.1007/s10658-020-01984-0

Meena M, Yadav G, Sonigra P, Nagda A, Mehta T, Swapnil P, Marwal A (2022) Role of elicitors to initiate the induction of systemic resistance in plants to biotic stress. Plant Stress 5:100103. https://doi.org/10.1016/j.stress.2022.100103

Mishra J, Singh R, Arora NK (2017) Plant growth-promoting microbes: diverse roles in agriculture and environmental sustainability. In: Kumar V, Kumar M, Sharma S, Prasad R (eds) Probiotics and plant health. Springer, Singapore. https://doi.org/10.1007/978-981-10-3473-2_4

Moreno-Gavíra A, Diánez F, Sánchez-Montesinos B, Santos M (2020) *Paecilomyces variotii* as a plant-growth promoter in horticulture. Agronomy 10:597. https://doi.org/10.3390/agronomy10040597

Murali M, Naziya B, Ansari MA, Alomary MN, AlYahya S, Almatroudi A, Thriveni MC, Gowtham HG, Singh SB, Aiyaz M, Kalegowda N, Lakshmidevi N, Amruthesh KN (2021) Bioprospecting of rhizosphere-resident fungi: their role and importance in sustainable agriculture. J Fungi 7:314. https://doi.org/10.3390/jof7040314

Naseri B, Younesi H (2021) Beneficial microbes in biocontrol of root rots in bean crops: a meta-analysis (1990–2020). Physiol Mol Plant Pathol 116:101712. https://doi.org/10.1016/j.pmpp.2021.101712

Naziya B, Murali M, Amruthesh KN (2020) Plant growth-promoting fungi (PGPF) instigate plant growth and induce disease resistance in *Capsicum annuum* L. upon infection with *Colletotrichum capsici* (Syd.) Butler & Bisby. Biomol Ther 10:41. https://doi.org/10.3390/biom10010041

Nosheen S, Ajmal I, Song Y (2021) Microbes as biofertilizers, a potential approach for sustainable crop production. Sustainability 13:1868. https://doi.org/10.3390/su13041868

Olowe OM, Akanmu AO, Asemoloye MD (2020) Exploration of microbial stimulants for induction of systemic resistance in plant disease management. Ann Appl Biol 117:282–293. https://doi.org/10.1111/aab.12631

Ozimek E, Hanaka A (2021) Mortierella species as the plant growth-promoting fungi present in agricultural soils. Agriculture 11:7. https://doi.org/10.3390/agriculture11010007

Pieterse CM, Zamioudis C, Berendsen RL, Weller DM, Van Wees SCM, Bakker PA (2014) Induced systemic resistance by beneficial microbes. Annu Rev Phytopathol 52:347–375. https://doi.org/10.1146/annurev-phyto-082712-102340

Priyadharsini P, Muthukumar T (2017) The root endophytic fungus *Curvularia geniculata* from *Parthenium hysterophorus* roots improves plant growth through phosphate solubilization and phytohormone production. Fungal Ecol 27:69–77. https://doi.org/10.1016/j.funeco.2017.02.007

Puga-Freitas R, Blouin M (2015) A review of the effects of soil organisms on plant hormone signalling pathways. Environ Exp Bot 114:104–116. https://doi.org/10.1016/j.envexpbot.2014.07.006

Rahman SF, Singh E, Pieterse CMJ, Schenk PM (2018) Emerging microbial biocontrol strategies for plant pathogens. Plant Sci 267:102–111. https://doi.org/10.1016/j.plantsci.2017.11.012

Richard B, Qi A, Fitt BDL (2022) Control of crop diseases through integrated crop management to deliver climate-smart farming systems for low-and high-input crop production. Plant Pathol 71:187–206. https://doi.org/10.1111/ppa.13493

Romera FJ, García MJ, Lucena C, Martínez-Medina A, Aparicio MA, Ramos J, Alcántara E, Angulo M, Pérez-Vicente R (2019) Induced systemic resistance (ISR) and Fe deficiency responses in dicot plants. Front Plant Sci 10:287. https://doi.org/10.3389/fpls.2019.00287

Ruangwong O-U, Wonglom P, Phoka N, Suwannarach N, Lumyong S, Ito S-I, Sunpapao A (2021) Biological control activity of *Trichoderma asperelloides* PSU-P1 against gummy stem blight in muskmelon (*Cucumis melo*). Physiol Mol Plant Pathol 115:101663. https://doi.org/10.1016/j.pmpp.2021.101663

Salman EK, Ghoniem KE, Badr ES, Aboulila AA, Emeran AA (2022) Identification of chlorpromazine hydrochloride role as a new systemic acquired resistance inducer against *Magnaporthe oryzae* in rice. Physiol Mol Plant Pathol 117:101770. https://doi.org/10.1016/j.pmpp.2021.101770

Silva PV, Pereira LM, Mundim GSM, Maciel GM, de Arau'jo Gallis RB, de Mendes GO (2022) Field evaluation of the effect of *Aspergillus niger* on lettuce growth using conventional measurements and a high-throughput phenotyping method based on aerial images. PLoS One 17:e0274731. https://doi.org/10.1371/journal.pone.0274731

Spinelli V, Brasili E, Sciubba F, Ceci A, Giampaoli O, Miccheli A, Pasqua G, Persiani AM (2022) Biostimulant effects of *Chaetomium globosum* and *Minimedusa polyspora* culture filtrates on *Cichorium intybus* plant: growth performance and metabolomic traits. Front Plant Sci 13:879076. https://doi.org/10.3389/fpls.2022.879076

Tarroum M, Ben Romdhane W, Ali AAM, Al-Qurainy F, Al-Doss A, Fki L, Hassairi A (2021) Harnessing the rhizosphere of the halophyte grass *Aeluropus littoralis* for halophilic plant-growth-promoting fungi and evaluation of their biostimulant activities. Plan Theory 10:784. https://doi.org/10.3390/plants10040784

Thankappan S, Narayanasamy S, Sridharan AP, Binodh AK, Kumari AN, Parasuraman P, Uthandi S (2022) Rhizospheric volatilome in modulating induced systemic resistance against biotic stress: a new paradigm for future food security. Physiol Mol Plant Pathol 120:101852. https://doi.org/10.1016/j.pmpp.2022.101852

Tian Y, Fu X, Zhang G, Zhang R, Kang Z, Gao K, Mendgen K (2022) Mechanisms in growth-promoting of cucumber by the endophytic fungus *Chaetomium globosum* strain ND35. J Fungi 8:180. https://doi.org/10.3390/jof8020180

Toppo P, Subba R, Roy K, Mathur P (2022) Elucidating the strategies for isolation of endophytic fungi and their functional attributes for the regulation of plant growth and resilience to stress. J Plant Growth Regul. https://doi.org/10.1007/s00344-022-10638-w

Tyśkiewicz R, Nowak A, Ozimek E, Jaroszuk-Ściseł J (2022) *Trichoderma*: the current status of its application in agriculture for the biocontrol of fungal phytopathogens and stimulation of plant growth. Int J Mol Sci 23:2329. https://doi.org/10.3390/ijms23042329

Velásquez AC, Castroverde CDM, He SY (2018) Plant-pathogen warfare under changing climate conditions. Curr Biol 28:R619–R634. https://doi.org/10.1016/j.cub.2018.03.054

Verma A, Shameem N, Jatav HS, Sathyanarayana E, Parray JA, Poczai P, Sayyed RZ (2022) Fungal endophytes to combat biotic and abiotic stresses for climate-smart and sustainable agriculture. Front Plant Sci 13:953836. https://doi.org/10.3389/fpls.2022.953836

Vlot AC, Sales JH, Lenk M, Bauer K, Brambilla A, Sommer A, Chen Y, Wenig M, Nayem S (2021) Systemic propagation of immunity in plants. New Phytol 229:1234–1250. https://doi.org/10.1111/nph.16953

Walters DR, Ratsep J, Havis ND (2013) Controlling crop diseases using induced resistance: challenges for the future. J Exp Bot 64:1263–1280. https://doi.org/10.1093/jxb/ert026

Wang R, Chen D, Khan RAA, Cui J, Hou J, Liu T (2021) A novel *Trichoderma asperellum* strain DQ-1 promotes tomato growth and induces resistance to gray mold caused by *Botrytis cinerea*. FEMS Microbiol Lett 368:fnab140. https://doi.org/10.1093/femsle/fnab140

Wang H, Zhang R, Mao Y, Jiang W, Chen X, Shen X, Yin C, Mao Z (2022) Effects of *Trichoderma asperellum* 6S-2 on apple tree growth and replanted soil microbial environment. J Fungi 8:63. https://doi.org/10.3390/jof8010063

Wonglom P, Ito S, Sunpapao A (2020) Volatile organic compounds emitted from endophytic fungus *Trichoderma asperellum* T1 mediate antifungal activity, defense response and promote plant growth in lettuce (*Lactuca sativa*). Fungal Ecol 43:100867. https://doi.org/10.1016/j.funeco.2019.100867

Yadav M, Dubey MK, Upadhyay RS (2021) Systemic resistance in chilli pepper against anthracnose (caused by *Colletotrichum truncatum*) induced by *Trichoderma harzianum*, *Trichoderma asperellum* and *Paenibacillus dendritiformis*. J Fungi 7:307. https://doi.org/10.3390/jof7040307

Yang B, Yang S, Zheng W, Wang Y (2022) Plant immunity inducers: from discovery to agricultural application. Stress Biol 2:5. https://doi.org/10.1007/s44154-021-00028-9

Zehra A, Raytekar NA, Meena M, Swapnil P (2021) Efficiency of microbial bio-agents as elicitors in plant defense mechanism under biotic stress: a review. Curr Res Microb Sci 2:100054. https://doi.org/10.1016/j.crmicr.2021.100054

Zhang Q, White JF (2021) Bioprospecting desert plants for endophytic and biostimulant microbes: a strategy for enhancing agricultural production in a hotter, drier future. Biology 10:961. https://doi.org/10.3390/biology10100961

Zhang Y, Zhuang W-Y (2020) *Trichoderma brevicrassum* strain TC967 with capacities of diminishing cucumber disease caused by *Rhizoctonia solani* and promoting plant growth. Biol Control 142:104151. https://doi.org/10.1016/j.biocontrol.2019.104151

Zhang Y, Zhu H, Ye Y, Tang C (2021) Antifungal activity of chaetoviridin A from *Chaetomium globosum* CEF-082 metabolites against *Verticillium dahliae* in cotton. Mol Plant-Microbe Interact 34:758–769. https://doi.org/10.1094/MPMI-02-21-0032-R

Zhao J, Liu T, Liu WC, Zhang DP, Dong D, Wu HL, Zhang TT, Liu DW (2021a) Transcriptomic insights into growth promotion effect of *Trichoderma afroharzianum* TM2-4 microbial agent on tomato plants. J Integr Agric 20:1266–1276. https://doi.org/10.1016/S2095-3119(20)63415-3

Zhao J, Liu T, Zhang D, Wu H, Zhang T, Dong D (2021b) Biocontrol potential of *Trichoderma afroharzianum* TM24 against grey mould on tomato plants. Curr Microbiol 78:4115–4126. https://doi.org/10.1007/s00284-021-02671-x

An Insight into Fungi in Forest Ecosystems

Meenambiga Setti Sudharsan, Kalyanaraman Rajagopal, and Narasimhan Banu

1 Introduction

In nature, any organism does not exist in isolation. All living organisms in an ecosystem interact with each other for their survival. The Physico-chemical environment makes up the habitat for each organism for example if the plant is the organism, it grows in two environments: the aerial environment (shoot system) for light, temperature, precipitation, wind, etc., and the soil (edaphic factor) environment (root system) for inorganic nutrients and water. The microorganisms depend on living as well as dead organic matter from plants and animals for food, and shelter and release minerals bound to the organic matter for plant reuse. A forest ecosystem is a highly organized system the predominant elements are plants, particularly trees, which form a canopy cover and serve as habitats for the microorganisms particularly bacteria, fungi, insects, and animals. In a forest ecosystem both living as well as dead wood serves as the substrate for the fungi, lichens, small plants, etc. Fungi establish different associations with forest plants such as mycorrhizal, epiphytic, endophytic, saprophytic, and parasitic. In a forest, ecosystem fungi play a vital role in mineral recycling, decomposing dead organic matter, absorption of minerals from the soil, acting as biocontrol agents, etc.

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2 Mycorrhizal Fungi

Intimate connections between plant roots and rhizosphere microorganisms are represented by mycorrhizas, a symbiotic link between fungi and plant roots (Giovannini et al. 2020). In the carbon sequestration within forest soil, mycorrhizal fungi are crucial. Mycorrhizae, which act as a carbon sink, are crucial for distributing carbon and have an impact on the ecosystem's nutrient cycling. Through a mutualistic interaction, mycorrhizal association enhances plant development and existence in the ecosystem (Juan-Ovejero et al. 2020). The principal energy source for mycorrhizal fungi is simple sugars, which are transported to the roots of plants as photosynthates. The plant *Sequoiadendron giganteum* produces a type of mycorrhizae known as vesicular-arbuscular mycorrhizae; seedlings inoculated with these fungi in nurseries can be two to three times larger than non-inoculated manageable seedlings. Mycorrhizal fungi have a role in the cycling of nutrients in the soil. As well as their reproductive organs (spores, mushrooms, and Truffles) are essential parts of the intricate woodland food chain. Management techniques that safeguard the soil's biological composition will safeguard the overall well-being and functionality of the forest ecosystem (Molina 1994). Some of the common mycorrhizal fungi are listed in (Table 1).

2.1 Ectomycorrhizal Fungi (EMF)

In symbioses with over 60 percent of the trees, these types of fungi constitute an essential part of the forest soil microbiome (Bueno et al. 2017; Steidinger et al. 2019). The absence of data on the population of ectomycorrhizal fungi and the growth rate of trees has made it difficult to study the data on other in situ variations in the environment. This paved the way for ectomycorrhizal fungi to study the growth rate by taking into account the climatic effects, nitrogen deposition, and other tree morphological characteristics. We were also able to explicitly correlate

Table 1 Common Mycorrhizal fungi and their host plant

Host	Family	Mycorrhiza
Clusia multiflora	Clusiaceae	*Acaulospora scrobiculata, Glomus* sp., *Gigaspora* sp., *Racocetra fulgida*
Ipomoea batatas	Convolvulaceae	*Gigaspora margarita*
Liriodendron tulipifera	Magnoliaceae	*Acaulospora morrowiae, Claroideoglomus claroideum, Rhizoglomus clarum, Paraglomaus brasilianum*
Andropogon virginicus	Poaceae	*Fuscutata heterogama*
Panicum virgatum L.	Poaceae	*Glomus diaphanum, Claroideoglomus etunicatum, Gigaspora albida*
Malus prunifolia	Rosaceae	*Cetraspora pellusida, Acaulospora scrobiculata*

the composition of the EMF community & genomic functional potentials with forest tree growth. The ability to statistically account for well-known determinants of tree development makes it particularly crucial to include these environmental factors in our mode everywhere this work was done in the forest network, particularly age and stand density, nitrogen deposition, and climate (Etzold et al. 2020).

2.2 Endomycorrhizal Fungi (EF)

The majority of vegetative crops such as grasses, fruit trees, and vegetables constitute endomycorrhizal fungi that penetrate the cortical cells. In other words, endomycorrhiza has an exchange system inside the root, & the fungi's hyphae extend outside the root. Compared to ectomycorrhiza, this connection is more intrusive. Spores, fragments of colonized roots, & vegetative hyphae are the three main inoculum sources that endomycorrhizal fungus uses to colonize plants. Propagules, the conventional unit of measurement indicated on the majority of commercially available mycorrhizal products, refer to these inoculants collectively (Sutela et al. 2020; Coque et al. 2020).

2.3 Arbuscular Mycorrhizal Fungi (AMF)

The development of arbuscles inside the roots is the characteristic feature of Endomycorrhizal filamentous fungi. AMF includes hundreds of species from the phyla of Glomeromycota which have the potential to colonize around 80% of terrestrial plants (Lee 2019). Arbuscular mycorrhizal fungi are helpful soil microorganisms that form mutualistic symbioses with the roots of the most significant food crops and are essential to maintaining the long-term fertility and health of the soil. By choosing AMF inoculum based on their colonization capacity and effectiveness, which are influenced by fungal and plant genotypes and a variety of environmental factors, the enormous inter and intra-specific AMF diversity can be fully used. The several functions of AMF, which include nitrogen fixation, phosphorus solubilization, and the generation of phytohormones, siderophores, and antibiotics, are the consequence of the cooperative efforts of the bacterial populations that inhabit the mycorrhizosphere. Host plants, mycorrhizal symbionts, and related microorganisms exhibit advantageous newly emerging traits that could be effectively utilized in sustainable agriculture (Giovannini et al. 2020).

2.4 Ericoid Mycorrhizal Fungi (ERM)

The first Leotiomycetes species isolated from ERM roots was *Rhizoscyphus ericae*. It was formerly assigned to the genus *Pezizella* but was then transferred to *Hymenoscyphus* and finally to *Rhizoscyphus***.** Ericaceae plants are essential as they store 20% of the total carbon storage of the planet. These infertile soils have a high concentration of resistant polyphenolic chemicals and acidic conditions, which cause the organic matter in the soil to decompose very slowly. Ericaceous plants' endomycorrhizal relationships with fungi, which help them extract nutrients from the soil by breaking down a variety of intricate and resistant organic substrates, are essential to their survival in these habitats. Ericaceous plants also make up the understory in forest ecosystems. In colder temperate and altitudinal forests, the ERM fungal biomass may help to store a significant amount of soil organic matter. Because of their role in decomposition and the possibility that their fungal biomass itself is rich in refractory carbon compounds. Four widespread species of Leotiomycetes have recently had the genetic machinery underlying their exceptional saprotrophic powers revealed. These ERM fungi are less like other mycorrhizal fungi and more like saprotrophs and pathogens due to their enzyme machinery (Perotto et al. 2018).

2.5 Orchid Mycorrhizal Fungi (OMF)

Some orchid species lack the ability to synthesize chlorophyll, while others only do so once they have developed past the seedling stage. Every time, at least a portion of the plant's life is dependent on sugars produced by a fungus partner. Although the tiny orchid seeds can germinate aseptically when given the "fungal sugar" trehalose, they will not grow unless a fungus infects them since they have very little nutritional reserves. Because the plant in essence parasitizes the fungus that invades it, these mycorrhizas are uncommon. *Rhizoctonia solani*, a common plant pathogen, is similar to the fungus in these partnerships, although current taxonomic investigations have placed them in multiple related genera. They are mostly saprotrophic, meaning that they develop by breaking down organic matter in the soil, although they may also obtain trace minerals or other nutrients., Although they are mostly saprotrophic, which means they grow by consuming soil organic matter, they may also get trace elements or other nutrients from plants. *Armillaria* species indirectly parasite non-photosynthetic plants such as *Monotropa* species even though they are termed as mycorrhizal fungi (Alghamdi 2019).

3 Role of Mycorrhizal Fungi

Plants can take up more phosphorus and trace elements with the help of mycorrhizas. They achieve this by increasing the amount of soil the plant explores. Extremely thin hyphae, measuring between 1 and 10 thousandths of a millimeter in width, are a distinctive feature of mycorrhizal fungus. These hyphae search the soil for nutrients, carry them back to the host plant, and aid in aggregating soil particles. This property of mycorrhizal fungus is particularly crucial for plant uptake of phosphorous, which does not travel as easily in the soil solution as nitrogen. When phosphorus is low in the soil, plants with mycorrhizas on their root systems have better access to and absorb more phosphorus than other plants. Plant roots must scour the soil for trace elements like phosphorus, copper, and zinc, which act similarly in soil. The aggregate of soil can also be increased by mycorrhizal fungus. The hyphae create networks between adjacent soil particles, roots and soil particles, roots of the same plant, and roots of various plants. Inside the roots they colonize, they also create networks. There is also some evidence to suggest that the fungi may aid in plant adaptation to drought (Alghamdi 2019).

More nutrients and water are absorbed by plants from the soil as a result of mycorrhizae. Additionally, they improve plants' resistance to numerous harmful environmental stressors. Additionally, mycorrhizae play a significant part in the process of soil structure and promote advantageous microbial activity, increase the capacity of the soil to hold water and nutrients for the soil, boost the permeability and porosity of the soil, create a favorable habitat for increased microbial activity, and nutrient cycling in the soil. Root survival is increased and established when seeds are sown or plants are transplanted which enhances the plant's capacity to absorb minerals and gain access to other nutrition sources shared by colonized plants. They increase the ability of plants to resist soil diseases, viruses, drought, salt stress, and pests, among other things, and lead to the healthy growth of the plant's root system (Sutela et al. 2020). The mycorrhizal connection is crucial to the health of the forest ecosystem. Changes in CO_2 content may have a significant impact on roots and mycorrhizal fungi. Despite the fact that they serve as a substantial carbon sink; Hence, detailed analysis is required to predict their function. Using mycorrhizas behave in a variety of ways to high CO_2 that could change soil-plant interactions, nutrient uptake, and plant growth patterns of carbon allocation. The data indicate that increased CO_2 could be affecting forests through modified C inputs from plant systems. Future carbon sequestration should be evaluated. The interactions between the improved carbon inputs restrictions enhanced mycorrhizal activity and functions with increased capacity for resource acquisition. One of the more common types of forest creatures, forest fungi are essential to the productivity of ecosystems by aiding in soil fertility, nitrogen cycle, and nutrient uptake. They serve as pillars in the intricate woodland food web. Forest plants and symbiotic root fungus have co-evolved in mutualistic partnerships such that both parties' life and fitness depend on the other. We must safeguard the invisible and underappreciated

below-ground ecology, just as woods make enormous financial investments in the form of photosynthates to support beneficial soil species.

4 Phyllosphere Epiphytic and Endophytic Fungi

Plant-microbe interactions are essential in plant diversity, population or community stability, and in turn, ecosystem dynamics (Wardle et al. 2004). Epiphytic fungi serve as an important component of the forest microbial population that survives on the leaf surface. Those fungi living inside the host are termed endophytes which do not cause any symptoms or injury to the host. Endophytic fungi are highly diverse & play several important roles in forest ecosystems (Arnold et al. 2003; Guerreiro et al. 2018) These fungi play a crucial role in carbon & nitrogen recycling in forest ecosystems (Sun et al. 2011). Microenvironments with which they reside vary for epiphytes and endophytes. The former rest on the external environment whereas the latter depends on nutrients from host tissues. So, the host plants therefore apparently have more control over the endophytic fungi than epiphytic fungi (Inácio et al. 2002; Clay and Schardl 2002; Santamaria and Bayman 2005).

Phylloplane, which denotes the surface of the leaf is an important niche for the survival and growth of a diversity of microorganisms. Knowing the diversity of epiphytes & their role in the ecosystem dynamics has gained attention worldwide. Epiphytes have frequently been viewed as commensals, pathogens, & parasites. Some mycologists have described epiphyllous as epifoliar fungi or nutrition guilds & epifoliar fungi are functionally commensal (Whipps et al. 2008; Anthony et al. 2002; Li et al. 2016; Gilbert and Strong 2007). Fungal spores are present on the surface of the leaf depending on the moisture conditions for their germination. Conversely, some spores are washed away without deposition (Jones 1994; Braun and Howard 1994). During germination of fungal spores on the surface of the leaf, rapid changes can take place in temperature, fluctuation in humidity & nutrients are also in short supply apart from this competition among epiphytes for space. Epiphytic fungi which are exposed to radiations and high-intensity light are susceptible to failure in spore germination (Shepherd and Wagner 2012). Pigment melanin which provides spores and hyphae dark color protects fungal hyphae from ultraviolet damage (Whipps et al. 2008).

Dechnik-Vázquez et al. (2016); Terborgh and Peres (2017), and Mežaka et al. (2020) reported that the distribution of epiphyllous fungi on the leaf surface is determined by both environments and leaf chemistry. The distribution of epiphyllous fungi also differs between closed forest sites and ground-rooted plants. The diversity of epiphyllous communities in the forests does not follow similar patterns instead shows species vary depending on the leaf age. However, an intense study is required for interactions between early colonizers of epiphyllous fungi and later colonizers. Phylloplane fungi like *Vizella* Sacc obtain protection by growing below or inside leaf cuticles (Gadgil 2005). Phylloplane fungi grow on the surface with minimum or low nutrient conditions but the saprotrophic fungi obtain nutrients by

breaking down dead hyphae and other leaf exudates (Cooke and Rayner 1984). Some epiphyllous fungi are parasitic, they enter the host by developing haustoria that break the epidermal layer and gain entry into and absorbs the food.

5 Fungal Endophytes

Anton De Bary coined the term endophyte describing it as fungi or bacteria living in plants without showing any disease symptoms (Wilson 1995). Endophytes differ from other organisms such as epiphytes and mycorrhiza in which the latter resides in the external (Saikkonen et al. 1998). Fungal endophytes survive inside the healthy plant tissues as dormant structures and form symbiotic relations with the host plants. Most mycologists agreed on the fact that the presence of fungal endophytes is ubiquitous. Yet they may not be exposed to the varying external environment as the epiphytic (phylloplane) fungi are, they come across the defense reactions of the host. So, their life strategies are likely to be different from those of other fungi (Rajagopal 1999). Nearly 400,000 types of plants that exist on earth are associated with one or more fungal endophytes. The diversity and distribution of fungal endophytes were found to be diverse in each host plant it is attributed to plant health, leaf age, climate, canopy cover, etc. Litter and fungal endophyte, microfungi are found to occur in almost every plant on earth and have been reported from all plants studied to date. Bills and Polishook (1994) have reported that tropical plants harbor various fungi in abundance than temperate plants. Fungal endophytes are a collection of endosymbionts with distinct biological niches and have high range of diversity that hosts seeds, leaves, roots, and stems (Tiwari et al. 2010). Like mycorrhizal fungi, fungal endophytes form symbiotic plant-fungi associations. But, unlike mycorrhiza fungi which colonize plant roots & grow into the rhizosphere, fungal endophytes infect above-ground parts and reside completely within plant tissues (Caroll 1988). Fungal endophytes comprise various groups of species that vary in symbiotic and ecological functions. Rodriguez et al. (2009) grouped endophytes into four functional classes based on host range, colonization, tissue specificity, transmission patterns, and fitness benefits conferred to hosts. Class I Class of endophyte belongs to clavicipitaceous fungi infecting grasses whereas classes II, III, and IV are nonclavicipitaceous fungal endophytes, present in asymptomatic plant tissues of nonvascular plants, ferns, gymnosperms, and angiosperms (Tables 2 and 3).

6 Role of Endophytic Fungi

Fungal endophytes prevent pathogenic microorganisms by infecting host plants and they are capable of producing an array of biologically active compounds which are essential for host endophyte relationships (Strobel and Daisy 2003). Several endophytic fungi synthesize antimicrobial compounds active against pathogens infecting

Table 2 Fungal endophytes from forest trees (angiosperms)

Host	Family	Fungal endophyte
Avicennia marina	Acanthaceae	*Pseudocercospora* sp. *Capnodiales* sp. *Basidiomycota* sp. *Sporidiobolales* sp
Carpinus caroliniana	Betulaceae	*Pestalotiopsis guepinii Trichoderma harzianum*
Alnus rubra	Betulaceae	*Gnomonia setacea,* *Gnomoniella tubiformis*
Betula pubescens	Betulaceae	*Venturia ditricha* *Phomopsis* sp. *Ophiovalsa betulae Trimmatostroma betulinum*
Alnus glutinosa	Betulaceae	*Ophiovalsa suffusa* *Pezicula cinnamomea Pleurophomopsis lignicola*
Alnus rubra	Betulaceae	*Phomopsis* sp. *Ophiovalsa suffuse*
Betula pendula	Betulaceae	*Ophiovalsa betulae* *Pseudovalsa lanciformis*
Carpinus betulus	Betulaceae	*Pezicula carpinea* *Diaporthe carpini*
Excoecaria agallocha	Euphorbiaceae	*Phyllosticta* sp. *Botryosphaeriaceae* sp. *Pseudocercospora* sp. *Erythrobasidium* sp. *Dothideomycetes* sp. *Jaminaea* sp. *Uwebraunia* sp. *Mycosphaerellaceae* sp. *Zasmidium*sp *Pleosporales* sp. *Mycosphaerellaceae* sp. *Erythrobasidiales* sp. *Symmetrospora* sp
Rhododendron arboretum	Ericaceae	*Alternaria alternata* *Chaetomium indium* *Cochliobolus lunatas* *Fusarium* sp. *Humicola* sp. *Sporormiella* sp. *Aspergillus niger* *Chaetomiun indicum* *Cladosporium* sp. *Emericella nidulans* *Phoma* sp. *Trichoderma* sp
Acacia melanoxylon	Fabaceae	*Penicillium* sp. *Botrytis* sp. *Chaetomium globosum* *C. incomptum* *Cladosporium* sp. *Fusarium* sp. *Sporormiella* sp

(continued)

Table 2 (continued)

Host	Family	Fungal endophyte
Acacia decurrens	Fabaceae	*Aspergillus flavus* *Aspergillus niger* *Drechslera* sp.
Dalbergia latifolia	Fabaceae	*Pestalotiopsis* sp. *Curvularia* sp. *Curvularia lunata*
Pterocarpus marsupium	Fabaceae	*Nigrospora oryzae*
Acacia dealbata	Fabaceae	*Drechslera* sp. *Fusarium* sp
Quercus robur	Fagaceae	*Dicarpella dryina* *Apiognomonia quercina Ulocladium* sp. *Trichoderma viride* *Amphiporthe leiphaemia* *Phomopsis quercina* *Colpoma quercinum Nodulisporium* sp. *Eutypella* sp
Quercus petraea	Fagaceae	*Apiognomonia quercina, Aureobasidium apocryptum,* *Colpoma quercinum, Apiognomonia errabunda*
Quercus cerris	Fagaceae	*Cladosporium cladosporioides Phomopsis quercina* *Diplodia mutila* *Dicarpella dryina, Dendrodochium* sp
Fagus sylvatica	Fagaceae	*Apiognomonia errabunda Dicarpella dryina* *Pezicula livida* *Botryosphaeria quercuum Diaporthe eres* *Asterosporium asterospermum Neohendersonia kickxii*
Quercus alba	Fagaceae	*Dicarpella dryina* *Dicarpella subglobosa*
Fagus crenata	Fagaceae	*Apiognomonia* sp. *Geniculosporium* sp. *Ascochyta* sp. *Tritirachium* sp. *Periconiella* sp. *Phomopsis* sp.
Quercus emoryi	Fagaceae	*Asteromella* sp.
Quercus pubescens	Fagaceae	*Cladosporium cladosporioides Ulocladium* sp. *Phomopsis quercina, Apiognomonia quercina*
Quercus ilex	Fagaceae	*Phyllosticta ilicina* *Phomopsis glandicola Acremonium strictum* *Biscogniauxia* sp. *Nodulisporium* sp. *Phoma* sp.
Quercus garryana	Fagaceae	*Apiognomonia quercina*
Castanea sativa	Fagaceae	*Cryptodiaporthe castanea, Pezicula cinnamomea*
Acer pseudoplatanus	Malvaceae	*Petrakia irregularis* *Phomopsis* sp. *Phialocephala dimorphospora*

(continued)

Table 2 (continued)

Host	Family	Fungal endophyte
Tilia cordata	Malvaceae	*Apiognomonia tiliae Mycosphaerella punctiformis*
Grewia tiliifolia	Malvaceae	*Nigrospora oryzae*
M. nilagirica	Magnoliaceae	*Phyllosticta* sp. *Chaetomium globosum* *Fusarium* sp.
Michelia champaca	Magnoliaceae	*Curvularia* sp. *Drechslera* sp. *Penicillium* sp
Eucalyptus globulus	Myrtaceae	*Cladosporium* sp. *Scopulariopsis* sp. *Trichoderma* sp. *C. indicum*
Fraxinus excelsior	Oleaceae	*Phomopsis* sp.
Aegiceras corniculatum	Primulaceae	*Neodevriesia* sp. *Cladosporium* sp. *Pestalotiopsis* sp. *Capnodiales* sp. *Agaricostilbales* sp. *Dothideomycetes* sp. *Davidiellaceae* sp
Rhizophora stylosa	Rhizophoraceae	*Phaeoramularia* *Zymoseptoria* sp. *Toxicocladosporium* sp. *Dothideomycetes* sp. *Meira* sp
Acer macrophyllum	Sapindaceae	*Phomopsis* sp. *Diaporthe eres* *Cryptodiaporthe hystrix* *Pezicula livida*
Acer pseudoplatanus	Sapindaceae	*Phloeospora aceris Cryptodiaporthe hystrix*
Populus tremula	Salicaceae	*Penicillium* sp. *Cladosporium maculicola*
Salix fragilis	Salicaceae	*Cryptodiaporthe salicella* *Daldinia* sp. *Microsphaeropsis* sp.
Populus tremula	Salicaceae	*Valsa sordida* *Trichoderma viride*

plants (Rajagopal 1999). Fisher et al. (1984a) reported that several fungal endophytes that they tested possess antibacterial and antifungal compounds. Fisher et al. (1984b) have isolated a broad-spectrum antibiotic from fungal endophyte isolated from *Vaccinium* sp. Fungal endophytes have the capacity to tolerate or metabolize phenolics and other defense chemicals of the host plants (Carroll and Petrini 1983). Endophytes serve as biocontrol agents in many countries against fungal pathogens for plant crops (Petrini 1991). Fungal endophytes represent natural genomes bestowed with beneficial attributes that could be identified and introduced into other plants for required characteristics. Then again, fungal endophytes could be used as

Table 3 Fungal endophytes from forest trees (gymnosperms)

Host	Family	Fungal endophyte
Juniperus communis	Cupressaceae	*Kabatia juniper* *Anthostomella formosa Pezicula cinnamomea*
Sequoia sempervirens	Cupressaceae	*Chloroscypha chloromela Cryptocline* sp. *Pezicula livida*
Calocedrus decurrens	Cupressaceae	*Linodochium* sp. *Geniculosporium* sp.
Thuja plicata	Cupressaceae	*Chloroscypha seaveri Geniculosporium* sp.
Chamaecyparis lawsoniana	Cupressaceae	*Scolecosporiella* sp. *Nodulisporium* sp.
Juniperus occidentalis	Cupressaceae	*Sarea difformis*
Larix sibirica	Pinaceae	*Monilinia laxa*
Abies magnifica	Pinaceae	*Phyllosticta* sp. *Cryptocline abietina*
Picea abies	Pinaceae	*Lophodermium piceae, Tiarosporella parca*
Abies lasiocarpa	Pinaceae	*Cryptocline* sp.
Picea glauca	Pinaceae	*Lophodermium piceae Mycosphaerella* sp.
Abies balsamea	Pinaceae	*Phyllosticta* sp. *Lophodermium* sp.
Picea mariana	Pinaceae	*Cryptocline abietina*
Abies procera	Pinaceae	*Phyllosticta* sp. *Lophodermium* sp.
Abies concolor, Abies grandis	Pinaceae	*Phyllosticta* sp. *Cryptocline* sp.
Abies amabilis	Pinaceae	*Phyllosticta* sp. *Lophodermium* sp.
Taxus brevifolia	Taxaceae	*Phyllosticta* sp.
Pinus thunbergii x densiflora	Pinaceae	*Lophodermium pinastri Phialocephala* sp.
Tsuga heterophylla	Pinaceae	*Cryptocline* sp
Pseudotsuga menziesii	Pinaceae	*Rhabdocline parkeri Phyllosticta abietis*
Tsuga mertensiana	Pinaceae	*Lophodermium* sp. *Phyllosticta* sp.
Pinus contorta	Pinaceae	*Lophodermium* sp.
Pinus lambertiana	Pinaceae	*Lophodermium* sp. *Cyclaneusma minus*
Pinus nigra	Pinaceae	*Cyclaneusma niveum Cenangium ferruginosum*
Pinus resinosa	Pinaceae	*Lophodermium* sp. *Pragmopycnis* sp
Pinus sylvestris	Pinaceae	*Anthostomella Formosa Lophodermium seditiosum* *Cyclaneusma minus Cenangium ferruginosum* *Lophodermium pinastri*
Picea sitchensis	Pinaceae	*Lophodermium piceae* *Rhizosphaera kalkhoffii Phomopsis* sp.

(continued)

Table 3 (continued)

Host	Family	Fungal endophyte
Pinus banksiana	Pinaceae	*Coccomyces* sp. *Phomopsis* sp
Pinus mugo	Pinaceae	*Cenangium ferruginosum* *Cyclaneusma minus Lophodermium pinastri*
Pinus ponderosa	Pinaceae	*Lophodermium* sp. *Sydowia polyspora*
Pinus strobus	Pinaceae	*Lophodermium nitens Hormonema* sp
Pinus monticola	Pinaceae	*Lophodermium* sp. *Hormonema* sp.
Pinus attenuata	Pinaceae	*Cyclaneusma* sp. *Lophodermium* sp
Pinus densiflora	Pinaceae	*Lophodermium pinastri Phialocephala* sp.
Larix decidua	Pinaceae	*Tympanis* sp. *Phialocephala dimorphospora*
Pinus tabulaeformis	Pinaceae	*Rhodotorula pinicola*
Picea abies	Pinaceae	*Tryblidiopsis pinastri* *Mollisia cinera* *Pezicula livida* *Tympanis* sp. *Pocillopycnis umensis*
Pinus sylvestris	Pinaceae	*Pezicula livida* *Tympanis* sp.
Abies alba	Pinaceae	*Diaporthe eres* *Grovesiella abieticola* *Pezicula* sp. *Cryptocline abietina,* *Gloeosporidiella* sp.

vectors of genes to be delivered artificially into other hosts (Petrini et al. 1992). Fungal endophytes provide the greatest potential for biocontrol because these fungi are integrated into the host system. Dewan and Sivasithamparam (1989) stated that "Take all" diseases caused by fungus in wheat are protected by fungal endophytes. The fungal endophyte also confers protection against insects and pests for example the needles of Douglas fir harbor a fungal endophyte *Rhabdocline parkeri* this fungal endophyte controls the gall midge caused by *Contarina* sp. (Carroll and Carroll 1978).

Pugh (1972) demonstrated the synthesis of the growth-promoting substances IAA from the fungal endophytes *Aureobasidium pullulans* and *Epicoccum purpurascens*. Fungal endophytes isolated from Neem leaves are known to produce bioactive compounds that interfere with plant cell division (Suryanarayanan and Rajagopal 1998). The fungal endophytes such as *Aureobasidium pullulans* & *Epicoccum purpurascens* produce phytohormones that fasten seed germination in plants. Fungal endophytes are being investigated in commercial sectors such as medical, pharmaceutical, & agricultural industries (Monaghan et al. 1995) because

most of the fungal endophytic fungi are an unexploited pool of secondary metabolites. Hence, the presence of fungal endophytes is an advantage to plants.

Fungal endophytes are symbionts that survive inside the aerial part of the plants. They may augment host resistance to grazing herbivores by synthesizing various alkaloids Endophyte infection also increase nutrient uptake and play a key role in increasing host tolerance to various stress conditions such as heat, salinity, etc. and affect evolution and plant biodiversity (Clay and Shardl 2002; Redman et al. 2002; Brundrett 2006). Fungal endophyte provides disease resistance to host plants and increases the productivity of host plants in resisting abiotic stresses (Lewis 2004; Newsham et al. 1998; Hesse et al. 2003 Fungal endophyte increases host biomass by enhancing photosynthetic efficiency. Under stress conditions, enhancement of tillering ability plays a major role Enhanced tillering ability is advantageous for both host expansion & fungal endophyte transmission, particularly under stress conditions. This improvement in host plant growth might be attributed to the enhanced production of indole acetic acid (De Battista et al. 1990). Fungal endophytes are recognized as dormant saprobes or latent pathogens and are involved in important functions such as deterrent to pest and herbivory, release growth-promoting stimuli, and increasing competitive ability in the host. They are known to synthesize metabolites useful in the biocontrol of plant pests and pharmaceuticals (Bacon et al. 1986; Bills 1996; Wagner and Lewis 2000).

Recently, it was found that fungal endophyte and bacterial infections in plants were found to enhance tolerance to aluminum in tall fescue and tolerance to zinc in perennial ryegrass. Fungal endophytes protect plants from heavy metal exposure and thus difference in the growth rate of fungal endophyte-free and infected plants showed remarkable differences (Ren et al. 2006). During Cd stress, fungal endophyte infection augmented Cd uptake more than EF hosts, and therefore phytoextraction efficiency of tall fescue increased due to fungal endophyte infection. Tumau et al. (1996) predicted that possible mechanisms of Cd uptake by fungal endophytes gather Cd in mycelia and store it in *Pinus sylvestris*, Cd is retained by ectomycorrhizal fungi in the fungal mantle. Fungi might use another mechanism by secreting metal-chelating compounds like phenolic or organic acid molecules into the rhizosphere. More exudate production by endophyte infection has been reported in tall fescue and in regress. Hence, exudates might be accountable for the increased Cd transport to the shoot region in EI tall fescue. Besides, heavy metal mobilization would occur by the production of siderophores in endophyte bacteria (Abou-shanab et al. 2003). reported that metal ions were incorporated in the glucan-chitin complex of *Acremonium pinkertoniae* by forming bonds with nitrogen & oxygen atoms of the fungal cell wall polysaccharides. This mechanism of binding is similar to that in the tall fescue infected with EI. Due to human interference and natural activities, heavy metal contamination drastically increases in the ecosystem. Currently, physical or chemical, or phytoremediation is employed. But, in phytoremediation the plant species are used even though they are called hyperaccumulators of metal ions, unfortunately, most of the plant species are very slow growing so it has restricted the use of this method in phytoremediation metal contaminated soils. However, metal ion uptake by plants can be influenced by microorganisms that are closely

associated with the host plants. The use of such indigenous organisms as endobacteria and fungal endophytes including mycorrhizal are effective in heavy metal sequestration (Wieshammer et al. 2007). Several studies indicated that endophyte infection could considerably increase plant biomass and heavy metal uptake of the host plants. Endophyte infection significantly protects the host plant from abiotic stresses such as drought and mineral scarcity which occur in heavy metal polluted sites. Host-specific endophyte-plant symbionts can be used in phytoremediation, or tolerant endophyte species can be horizontally transferred into other plants, increasing their phytoremediation competence (Wang et al. 2004). The root fungal endophytes can enhance and improve the ecological adaptations of plants living in extreme environments. The fungal endophytes in roots can improve the stress tolerance of the host plants to abiotic and biotic stress. Some of the major stress factors include heat, salt, drought, herbivores, and pathogens (Weiss 2011, 2016; Nguyen et al. 2016; Rodriguez et al. 2008; Arnold et al. 2003). Fungal endophytes present in roots are dark-septate endophytes (DSE) which provide tolerance of plants to heavy metal stress through antioxidative mechanisms by altering heavy-metal distribution in plant cells, and detoxification of heavy metals (Nisa et al. 2015).

7 Pathogenic Fungi

Forest plants are essential for sustainable wildlife habitat and have a greater contribution to the industry for their harvesting value. Fungal pathogens affect healthy natural forest ecosystems, although they are beneficial in eliminating unfit flora from the forest ecosystem (Hyde et al. 2019; Castello et al. 1995). Plant diversity in the forest ecosystem is maintained by soil-borne pathogens and also has detrimental effects during the distribution of seedlings. A difference in the juvenile population is caused when the host-specific pathogens kill the plants present close to them (Packer and Clay 2000). Fungi possess a parasitic and pathogenic relationship with the host which varies depending on favorable and unfavorable conditions (Rai and Agarkar 2016). Pathogenic fungi prevail as necrotrophs in the form of latent pathogens where they get triggered by physiological changes of the host and re-establishes their growth (Brown 1998; Slippers and Wingfield 2007). Hemibiotrophs transform into necrotrophs by initially occurring as biotrophs (De Silva et al. 2017). A natural ecosystem is greatly affected as pathogenic fungi pose a serious threat causing a reduction of its viability and vitality. (Fisher et al. 2020). The emergence of new pathogens leads to the generation of dangerous strains which negatively impact plant health and biodiversity conservation (Avila-Quezada et al. 2018). A high virulence rate is observed in emerging pathogens and they also arise from new taxa on native hosts. Depletion of keynote species causes a modification in the basic nature of the forest ecosystem. Non-indigenous fungal species effectively remove many different types of foundation species which helps in stabilizing water levels and many other ecological processes. Deletion of such species from the ecosystem leads to serious impacts on food webs, nutrient fluxes, and biodiversity (Ellison et al.

2005). Some major factors such as abiotic stresses, change in climatic conditions, and migration of pathogens contribute to the devastating effects of fungal diseases on forest trees (La Porta et al. 2008).

8 Emerging Forest Pathogenic Fungi

Emerging fungal pathogens are diverse which attributes to many factors with climatic changes as the predominant factor. *Phytophthora cinnamomi*, a soil-borne oomycete is a unique example of a fungal pathogen related to climatic changes (Brasier and Kirk 2001). The *P. cinnamomi*, a native of Southeast Asia, is now prevalent in most parts of temperate and tropical areas. The major symptoms of the disease are necroses involving root, collar, and stem leading to major diseases such as stem cankers and declines (Hardham and Blackman 2018). *P. cinnamomi* move to warmer regions as they are sensitive to host and infect plant species present in warmer areas (Bergot et al. 2004). The *P. cinnamomi* not only infects plants within South Asia and infects plant trees worldwide, particularly in South-west Australia.

Common symptoms related to fungal diseases range from spots, wilts, blights, rots, cankers, and damping-off (Jayawardena et al. 2019). Fungus-like pathogens and fungi threaten biodiversity with regard to their gene expression levels and biogeography (Scott et al. 2019). Globally, newly emerging pathogens are the primary cause of disease for plant pathogens (Rafiqi et al. 2018). Climatic changes are ranked as the top contributing drivers for emerging fungal pathogens in addition to natural calamities such as floods, hurricanes, and storms. (Nnadi and Carter 2021). Worldwide migration of pathogens is due to the migration of living plants across international borders and those pathogens have severe ecological consequences. Native pathogens have a less deleterious effect on host plants and these pathogens when migrating to new places show alarming damages to the endemic plants with lesser resistance. Previously unaffected hosts are affected by *P. cinnamaomi* which expands its geographic range. Latent pathogens are the major source of emerging pathogens causing virulence and they are cryptically associated with plants. They lead to unanticipated diseases and are similar to known species with little variations in some traits (Stergiopoulos and Gordon 2014). The pathogen shows symptoms of diseases if the host is immunocompromised or nutritional conditions get altered. (Photita et al. 2004).

9 Major Plant Diseases

Pathogenic fungi contribute to plant diseases through various invasion mechanisms. They have diverse dispersal mechanisms, reproduction patterns, growth, and parasitism (Porras-Alfaro and Bayman 2011). Spore dispersal can occur through pollen dispersal or independent of the host such as water, insect vector, or wind (Doehlemann

et al. 2017). Spores secrete an extracellular matrix for attaching to the host surface and penetrate through phloem or through wounds. Some fungi penetrate the hosts using cell wall degrading enzymes or using appressoria (Dean et al. 2012). A high turgor pressure causes the fungus to penetrate through the cuticle to enter the hosts and obtain nutrients as necrotrophs. Forest pathogenic fungi affect the forest ecosystem by causing canker, dieback, gall, leaf spot, rust, butt rot, chestnut blight, Dutch elm disease, honey fungus, oak decline, *Gremmeniella abietina*, Red and brown band needle blight of pines, Citrus and black spot, Beech bark disease, red needle cast disease, Leaf rust disease, leaf spot diseases, powdery mildew etc. (La Porta et al. 2008).

9.1 Dutch Elm Disease

Dutch elm disease causing vascular wilt predominantly affects *Ulmus* sp. in the Northern hemisphere. *Scolytid* bark beetles are the vectors infecting healthy bark beetles leading to tree death. (Webber 2000). *Ophiostoma ulmi* was identified as the causative fungi during the first pandemic which affected Europe and North America. In 1940, the pandemic reduced causing the death of most of the trees, and around the 1950s, the disease reappeared in Western Asia, Northern America, and Europe with a new name as *Ophiostoma novo-ulmi*. The first Dutch elm disease caused by *Ophiostoma ulmi* was not as severe as the first pandemic due to the viral infection of the fungi. (Mitchell and Brasier 1994).

9.2 Canker

Fusarium circinatum results in canker disease of *Pinus radiata* and is found to be one of the most important phytopathogens affecting a group of crops and trees. This pathogen affects pine trees globally. It was reported in California initially in 1986 and later was found to infect Europe (Correll et al. 1991). *Fusarium* sp. Is highly prevalent in tropical regions when compared to temperate regions and its dispersion depends mainly on climatic conditions. They do not prefer cooler temperatures and are less prevalent in northern latitudes in spite of the presence of susceptible hosts (Drenkhan et al. 2020). The plantation trees in the United States and Southern Europe were killed by the pathogenic fungus *Ceratocystis platani* and also affected plantations in Italy in 1972. In Europe, genetic variations have been introduced in the fungus which is transmitted through wounds or pruning. The fungus damages the cambium and bark and causes ink disease which causes death in 3–6 years. The spread of fungal infection could be prevented by destroying diseased trees but the eradication of fungus in stumps remains a challenge (Maire and Vigouroux 2004)

9.3 Ash Dieback

Hymenoscyphus fraxineus, an invasive discomycte infects *Fraxinus excelsior* causing dieback which is prevalent in both tropical and temperate regions of Asia, Europe, Central America, and North America. The origin of *Hymenoscyphus fraxineus* is in Eastern Asia and is misidentified as *Lambertella albida* which is less virulent than *H. fraxineus* (Gross et al. 2014). *H. fraxineus* produces dieback symptoms in ash trees which were detected in Poland and subsequently had an impact on many European countries (Mckinney et al. 2014). *H. fraxineus*, an aggressive pathogen infects ash trees through ascospores dispersed by wind and present on the leaf petioles. This leads to symptoms of crown dieback, premature leaf fall, leaf necrosis and finally leading to mortality of the tree. This also induces necrosis of bark lesions and seedlings are exposed to an increased death rate whereas aged trees develop long-term infection (Gross et al. 2014).

9.4 Red Needle Cast Disease

Phytophthora pluvialis, which causes red needle cast disease in *Pinus radiata* was found in New Zealand. *P. pluvialis*, an aerial homothallic fungus produces oogonia with caducous sporangia which produce zoospores and these zoospores move to the needle surfaces of the *Pinus* plant. Subsequently, zoospores move to intercellular spaces. Again, a new cycle is started when they develop sporangia from the stomata (Gómez-Gallego et al. 2019)

9.5 Foliar Rust Disease

Melamspora species infect trees worldwide causing foliar rust disease which leads to reduced photosynthetic activity, reduced biomass, and early leaf drop by *M. medusae, M. occidentalis, M. allii-populina* and *M. laricis-populina* are some common species of *Melamspora* (Newcombe et al. 2000). The trees mostly affected by *Melamspora* are *Populus* species native to Northern America. Natural hybridization between *M. medusae* and *M. occidentalis* results in a new hybrid that has a greater impact in the USA. Thus, novel virulent traits in *Populus* sp. are a result of such hybridization.

9.6 Oak Decline

Throughout Europe, a reduction in oak forests has been associated with climatic changes, and the fungal pathogen *Phytophthora cinnamomi* results in root rot disease at higher temperatures. *P. cinnamomi*, resistant to osmotic stresses and the strong influence of climate and pathogen interaction causes a drastic reduction in mature oaks. Also, endophytic fungi play a significant role in oak decline. Mediterranean *Quercus* sp. are predominantly affected by four endophytic fungi among the 27 endophytic fungi reported (Ragazzi et al. 2003). The colonization frequency of such endophytes is higher in diseased plants than in healthy plants. *Discula quecina*, an endophyte of Turkish oak exhibits an unstable equilibrium between mutualism and pathogenesis. Climatic factors play a major role in the endophytic nature of *Discula quecina*.

9.7 Cypress Canker

Cypress canker is caused by the imperfect fungus *Seiridium cardinale* in recent decades. *Seridium cardinale* is the most pathogenic species among other species of *Seiridium*. The colonies of *S. cardinale* can grow up to 35 °C with 25 °C being optimal. The landscape and amenity values of the plants are largely affected.

9.8 Shoot Blight

Sphaeropsis sapinea causes shoot blight in Pines which is an opportunistic pathogen and causes the death of trees in a few years. It was identified in Italy in 1900 and during water stress, it was found to damage different parts of the plant causing blue necrosis, crown dieback, and death of cones. The colonization frequency of the fungus *Sphaeropsis sapinea* was drastically reduced during drought in Europe with some species commonly found in pine plantations (Paoletti et al. 2001). Cones are damaged by the fungus in drought-reduced areas where the trees show browning of needles. *Sphaeropsis sapinea* has been found as an invasive species in Estonia in 2008. Fungal pathogens *Dothistroma pini* and *Dothistroma septosporum* causes red and brown band needle blight of pines and distinguishing both the species was found to be difficult and could be overcome by the molecular level of identification.

10 Mushrooms and Wood Decay Fungi

Mushroom is one of the organisms that have a wide diversity after insects. Fungi estimates at about 1.5 million across the globe, but only 70,000 species have been identified. Mushrooms inhabit different locations but most of them reside in association with forest trees. Mushrooms live as saprophytes & serve as an agent of wood decay. Basidiomycota and Ascomycota constitute the majority of the wood-decaying fungi (Arnstadt et al. 2016; Swift 1982). They are very much important as decomposers since they have cellulose and other plant polymer degrading abilities. Generally, they serve as nature's trash burner and replenisher of soil and thus help in the rejuvenation of the forest ecosystem.

A number of species of wild & medicinal mushrooms occur in all biologically diverse regions during the rainy season. They are found on the wood of living or dead trees, on leaf litter, & in soil (Arora 2008; Karwa and Rai 2010). Tropical rainforests are well known for a variety of organisms based on biogeographical regions. Although tropical habitats occupy only 25.7% of Earth's land, they are the house of most of the world's species (Deshmukh 1986). The availability of the mushroom in nature highly depends on many environmental conditions which include, soil moisture, air humidity, pH, temperature, light intensity, and substrate. The spread & growth of an organism in the world is also influenced by environmental factors. Depending on the enzymes they have, mushrooms grow in different habitats. The fruit body production of mushrooms is not well understood to date as many factors interact with mushroom growth in nature. Nearly 5000 macromycetes have been documented in Switzerland. Among them reported, 30% are mycorrhizal, and the remaining occur in forests. Worldwide, there are about 92 medicinal fungi have been grown (Boa 2004) but none belong to mycorrhizal species.

Mycorrhizal fungi depend on host trees for extending fixing carbon to extend their mycelium in the soil. Mycorrhizal colonization & fruit body production are affected by the interruption of carbon flow from the host to the roots. Tree girdling, shading & herbivores decrease mycorrhizal colonies and their community (Hogberg et al. 2001; Hacskaylo 1965; Gehring and Whitham 2002). Mycorrhizal fungi are host specific and the host tree plays a stronger role in community building than climatic changes (Rineau et al. 2010). Fungal communities and its population is strongly affected during forest succession (Hintikka 1988).

A geographic Information System (GIS) was used to study the area of Grevena, a city in Greece. Grevena has enriched fungal diversity and the mushrooms present in that area were studied extensively. Molasse, ophiolites, & flysch are the dominant geological formations found in the forest of Grevena. Mushrooms found in the Grevena forest ecosystem could be classified into four major categories based on GIS. Mushrooms are found in more than one forest (Table 3) habitat found in molasse, ophiolite, and flysch. Based on the data obtained by GIS, mushrooms found in the forest ecosystem of Grevena can be classified into four major categories (Table 4).

Table 4 Different mushroom groups in forest ecosystem

Oak Forest	Beech forest	Coniferous forest	Mixed forest
Amanita caesarea	*Amanita muscaria*	*Agaricus silvaticus*	*Macrolepiota procera*
Amanita phalloides	*Boletus edulis*	*Agaricus silvicola*	*Boletus reticulates*
Amanita pantherina	*Boletus regius*	*Gyromitra esculenta*	*Cantharellus cibarius*
Amanita verna	*Coprinus silvaticus*	*Gyromitra gigas*	*Gyromitra infula*
Amanita rubescens	*Ramaria aurea*	*Morchella deliciosa*	*Inocybe geophylla*
Amanita vaginata	*Ramaria sanguinea*	*Morchella elata*	*Hydnum rufescens*
Boletus satanas	*Russula mariae*	*Galerina marginata*	*Suillellus luridus*
Boletus aereus	*Plallus impudicus*	*Lactarius deliciosus*	*Boletus rhodopurpurus*
Boleus lupinus	*Laccaria amethyslina*	*Russula sanguinaria*	*Mycena rosea*
Boletus subtomentosus	*Hygrophoropsis aurantiaca*	*Suillus collinitus*	*Russula cyanoxantha*
Boletus queletii	*Lycoperdon echinatum*	*Suillus luteus*	*Stropharia aeruginosa*
Craterellus cornucopioides	*Cortinarius cinnabarinus*	*Suillus variegates*	*Lyiphyllus decastes*
Lactarius piperatus	*Cortinarius elegantissimus*	*Suillus bovinus*	*Lycoperdon perlatus*
Ramaria formosa	*Cortinarius*	*Hygrocybe coccinea*	*Hydnum repandus*
Russula maculata	*Elegantissimu*	*Coronaria*	*Laccaria laccata*
Entoloma sinuatum	*Pluteus cervinus*	*Caloscypha fulgens*	*Plleurotus ostreatus*
Lactarius volemus	*Albatrellus cristatus Mycena renati Pholiota suarrosa*	*Tricholoma aurdrtium*	*Pleurotus ostreatus*

Currently, soil microbiologists and ecologists are engaged in understanding the biological interactions below the soils of the forest floor of different forest ecosystems. The interaction among microbes, plants, and animals greatly influences the dynamics of forest ecosystems (Copely 2000). Rossman and others (1998) reported that among the various groups of soil biota fungi, which are more diverse play a major role in the forest ecosystem. Considering the various functions of fungi in forest ecosystems their activity determines the succession and stability of other biological entities' establishment like trees. Hence, soil fungi multiplication and their diversity can offer insight into sustaining fungi as valuable resources. Fungi are able to survive in different habitats because they degrade complex food materials into simpler food extracellularly, the degraded food materials are absorbed across the cell membrane and fungi are capable to inhibit the activity of compounds that reduce the fungal growth in soil. The diversity of fungi is enormous in any forest ecosystem as they use different organic and inorganic substrates for their survival. It is difficult to assess the exact number and diversity in a forest ecosystem. Different

groups of fungi isolated from forest woods belong to different classes like Ascomycetes, Basidiomycetes, and Deuteromycetes (imperfect fungi-asexual fungi) however fungi associated with woody tree roots were poorly studied.

The process of wood decay is linked to the ecological functions of fungi. Many fungi isolated from forest woods include various groups such as ascomycetes, basidiomycetes, Deuteromycetes, and zygomycetes. In the forest, the function of wood decay fungi is to recycle carbon and nitrogen and convert wastes into humus. They are important for the recycling of wood components particularly carbon in biogeochemical cycles. The forest wood mainly consists of lignocellulose. Lignocellulose is a recalcitrant material that contains cellulose, hemicellulose, & lignin, along with proteins, pectin, fatty acids, & other compounds. The ratio of lignocellulosic materials varies between Angiosperms & Gymnosperms, species to species, and varies in different parts of the plant (Cote 1968; Sjostrom 1993). More amount of cellulose and less lignin is present in angiosperms than in Gymnosperm trees. Wood decaying fungi are classified based on the degradation of cell wall components such as cellulose, hemicellulose, & lignin, they are (i) Brown rot fungi (ii) Soft rot fungi, and (iii) White rot fungi.

Brown rot fungi actively degrade cellulose and hemicelluloses the lignin was degraded only partially by brown rot fungi by the process of dealkylation and demethoxylation deposits wood residues (Floudas et al. 2012). Floudas et al. (2012) described that white rot could be the ancestors of brown rot fungi**.** Riley et al. (2014) proposed that the changeover from white rot to brown rot would have happens in two steps. (i) By losing some of the genes encoding degrading enzymes peroxidases essential for white rot decay mechanisms or (ii) The lignocellulosic complex was rapidly degraded by the wood decay brown rot by redox reactions and thus, the brown rot fungi utilize carbohydrate polymers of the wood and leave lignin as a brown residue. eg. *Gloeophyllum trabeum*. Soft rot fungi perform incomplete degradation of cellulose, and hemicellulose which results in cavities with a soft appearance cell wall. Most of the soft rot fungi primarily belong to ascomycetes, from different groups e.g., *Aspergillus, Phialocephala dimorphospora, Trichoderma,* and *Xylaria*. The white rot fungi destroy all three cell wall components of wood and make the wood consistency white and soft. The white rot is mainly caused by agaricomycetes a subphylum of basidiomycetes *Fomes* sp., *Heterobasidion* sp., *Phanerochaete chrysoporium*, *Trametes*, and *Trichaptum*. Some ascomycetous fungi like *Coccomyces* sp. and *Xylaria* sp., are also capable of causing white rot fungi (Makela et al. 2015). The descendants of wood decay fungi are from white rot fungi, which would have evolved into brown rot fungi by loss of ligninolytic enzyme genes such as manganese & lignin peroxidases. Based on substrate utilization the white rot fungi are classified into (i) Necrotrophs- killing all living cells for ensuing saprotrophic colonization, (ii) Saprotrophs that survive on either living or dead organic matter, and (iii) Biotrophs they grow on living wood cells without killing them. The saprobic wood decay fungi mainly belong to basidiomycetes, while saprobic fungi decomposing plant litter belong to both ascomycetes and basidiomycetes. Generally, the white rot, brown rot, and wood rot fungi are gilled pleurotoid, polypore, or corticoid agaricomycetes species belonging to class basidiomycetes which includes

grassland and forest soil-inhabiting and litter decomposing mushrooms. The wood degrading fungi secrete both enzymes or nonenzymatic mechanisms to destroy wood and at the same time resist wood defense chemicals (Deroy et al. 2015). The fungi overcome host defense by different modes like secreting secretome, proteins by fungal hyphae, degrading or modifying toxic substances, and producing detoxifying enzymes belonging to Cytochrome p450 monooxygenase (cytP450) and Glutathione transferase (GST) families (Alfaro et al. 2014; Morel et al. 2018). The ligninolytic fungi vary in their infection mode some of them have a narrow host range and others have a wide host range. Generally, brown rot fungi prefer gymnosperms as a host to attack over angiosperms, whereas white rot fungi prefer angiosperms to gymnosperms (Hibbett and Donnghue 2001). Some of the Pinus species not infected by the *Heterobasidion abietinum*, *H.occidantale*, and *H. Parviporum*, whereas the *Hannosum* sp. and *H.irregulare* could infect *Pinus* (Bruns et al. 1998; Johannesson and Stenlid 2003; Dalman et al. 2010; Garbelotto and Gonthier 2013). Hess et al. (2017) reported that the brown rot decay fungi *Serpula lacrymans* is suggested to be adapted to a habitat with large substrates in its natural habitat. The capability of this species to decay wood in a swift has been reported (Jennings 1991). The brown rot decays certain substrates more quickly than its close sister species *S. himantioides* (Skrede et al. 2011; Balasundaram et al. 2018). Therefore, it appears that S. Lacrymans is adapted to a very narrower habitat than its more prevalent species, *S. himantioides*. Hence, it appears that *Serpula* genus genomes carry more genes for CAZymes than other brown rots. Hess et al. (2017) reported that the brown rot decay fungi *Serpula lacrymans* is suggested to be adapted to a habitat with large substrates in its natural habitat. The capability of this species to decay wood in a swift has been reported (Jennings 1991). The brown rot decays certain substrates more quickly than its close sister species *S. himantioides* (Skrede et al. 2011; Balasundaram et al. 2018). Hence, it appears that Serpula genus genomes carry more genes for CAZymes than other brown rots. Hess et al. (2017) stated that *S. lacrymans* number of CAZymes is fewer than in *S.himantioides*, indicating that *S. Lacrymans* causes brown rot decay which is characterized by a non-enzymatic energy efficient decay system. Generally, fungi can secure their substrate in different methods like altering the pH, oozing oxidative enzymes, or emitting volatiles. The primary colonizers were established initially & must adapt to the substrate rapidly using an efficient defense mechanism. Usually, the primary colonizers are overcome by secondary colonizers by the latter producing metabolites that sustain them. Nowadays biocontrol agents were used by forest industries to overcome forest pathogens. For example, the wood decay species *Phlebiopsis gigantea* stops diseases caused by *H.annosum*, as the latter cannot outcompete *P. gigantea* (Garbelotto and Gonthier 2013). The *P.gigantea* is incapable of killing alive tress as *H. annosum* does, hence, *P.gigantea* is a preferred fungal species as a biocontrol agent by the forest owners.

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References

Abou-Shanab RA, Angle JS, Delorme TA et al (2003) Rhizobacterial effects on nickel extraction from soil and uptake by *Alyssum murale*. New Phytol 158(1):219–224

Alfaro M, Oguiza JA, Ramírez L, Pisabarro AG (2014) Comparative analysis of secretomes in basidiomycete fungi. J Proteome 102:28–43

Alghamdi SA (2019) Influence of mycorrhizal fungi on seed germination and growth in terrestrial and epiphytic orchids. Saudi J Biol Sci 26(3):495–502

Anthony PA, Holtum JA, Jackes BR (2002) Shade acclimation of rainforest leaves to colonization by lichens. Funct Ecol 16(6):808–816

Arnold AE, Mejía LC, Kyllo D et al (2003) Fungal endophytes limit pathogen damage in a tropical tree. Proc Natl Acad Sci 100(26):15649–15654

Arnstadt T, Hoppe B, Kahl T et al (2016) Dynamics of fungal community composition, decomposition and resulting deadwood properties in logs of *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*. For Ecol Manag 382:129–142

Avila-Quezada GD, Esquivel JF, Silva-Rojas HV et al (2018) Emerging plant diseases under a changing climate scenario: threats to our global food supply. Emir J Food Agric 30(6):443–450

Bacon CW, Lyons PC, Porter JK, Robbins JD (1986) Ergot toxicity from endophyte-infected grasses: a review 1. J Agron 78(1):106–116

Balasundaram SV, Hess J, Durling MB et al (2018) The fungus that came in from the cold: dry rot's pre-adapted ability to invade buildings. ISME J 12(3):791–801

Bergot M, Cloppet E, Pérarnaud V et al (2004) Simulation of potential range expansion of oak disease caused by *Phytophthora cinnamomi* under climate change. Glob Chang Biol 10(9):1539–1552

Bills GF (1996) Endophytic fungi in grasses and woody plants: isolation and analysis of endophytic fungal communities from woody plants. In: Redlin SC, Carris LM (eds) Systematics, ecology and evolution. APS Press, The American Phytopathological Society, St. Paul, pp 31–65

Bills GF, Polishook JD (1994) Abundance and diversity of microfungi in leaf litter of a lowland rain forest in Costa Rica. J Mycol 86(2):187–198

Boa E (2004) Wild edible fungi. In: A global overview of their use and importance to people. Non-wood forest products. FAO, Rome

Brasier CM, Kirk SA (2001) Comparative aggressiveness of standard and variant hybrid *alder phytophthoras, Phytophthora cambivora* and other Phytophthora species on bark of *Alnus, Quercus* and other woody hosts. Plant Pathol 50(2):218–229

Braun EJ, Howard RJ (1994) Adhesion of fungal spores and germlings to host plant surfaces. Protoplasma 181(1):202–212

Brown KB (1998) Preliminary studies on endophytic fungal communities of *Musa acuminata* species complex in Hong Kong and Australia. Fung Divers 1:27–51

Brundrett MC (2006) Understanding the roles of multifunctional mycorrhizal and endophytic fungi. In: Schulz BJE, Boyle CJC, Sieber TN (eds) Microbial root endophytes Berlin. Springer, Germany, pp 281–293

Bruns TD, Szaro TM, Gardes M (1998) A sequence database for the identification of ectomycorrhizal basidiomycetes by phylogenetic analysis. Mol Ecol 7(3):257–272

Bueno CG, Moora M, Gerz M et al (2017) Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. Glob Ecol Biogeogr 26(6):690–699

Carroll G (1988) Fungal endophytes in stems and leaves: from latent pathogen to mutualistic symbiont. Ecology 69(1):2–9

Carroll GC, Carroll FE (1978) Studies on the incidence of coniferous needle endophytes in the Pacific northwest. Canadian J Bot 56(24):3034–3043

Carroll G, Petrini O (1983) Patterns of substrate utilization by some fungal endophytes from coniferous foliage. Mycologia 75(1):53–63

Castello JD, Leopold DJ, Smallidge PJ (1995) Pathogens, patterns, and processes in forest ecosystems. Bioscience 45(1):16–24

Clay K, Schardl C (2002) Evolutionary origins and ecological consequences of endophyte symbiosis with grasses. Am Nat 160(S4):S99–S127
Cooke RC, Rayner AD (1984) Ecology of saprotrophic fungi. Longman Publishing Group, London
Copley J (2000) Ecology goes underground. Nature 406(6795):452–455
Coque JJ, Álvarez-Pérez JM, Cobos R et al (2020) Advances in the control of phytopathogenic fungi that infect crops through their root system. Adv Appl Microbiol 111:123–170
Correll JC, Gordon TR, McCain AH et al (1991) Pitch canker disease in California: pathogenicity, distribution, and canker development on Monterey pine (*Pinus radiata*). Plant Dis 75(7):676–682
Côté WA (1968) Biological deterioration of wood. In: Principles of wood science and technology. Springer, Berlin, pp 97–135
Dalman K, Olson Å, Stenlid J (2010) Evolutionary history of the conifer root rot fungus *Heterobasidion annosum* sensu lato. Mol Ecol 19(22):4979–4993
De Battista JP, Bacon CW, Severson R et al (1990) Indole acetic acid production by the fungal endophyte of tall fescue. J Agron 82(5):878–880
De Silva DD, Crous PW, Ades PK et al (2017) Life styles of *Colletotrichum* species and implications for plant biosecurity. Fungal Biol Rev 31(3):155–168
Dean R, Van Kan JA, Pretorius ZA (2012) The top 10 fungal pathogens in molecular plant pathology. Mol Plant Pathol 13(4):414–430
Dechnik-Vázquez YA, Meave JA, Pérez-García EA et al (2016) The effect of treefall gaps on the understorey structure and composition of the tropical dry forest of Nizanda, Oaxaca, Mexico: implications for forest regeneration. J Trop Ecol 32(2):89–106
Deroy A, Saiag F, Kebbi-Benkeder Z et al (2015) The GSTome reflects the chemical environment of white-rot fungi. PLoS One 10(10):e0137083
Deshmukh I (1986) Ecology and tropical biology. Blackwell scientific publications
Dewan MM, Sivasithamparam K (1989) Growth promotion of rotation crop species by a sterile fungus from wheat and effect of soil temperature and water potential on its suppression of take-all. Mycol Res 93(2):156–160
Doehlemann G, Ökmen B, Zhu W, Sharon A (2017) Plant pathogenic fungi. Microbiol Spectr 5(1):5–1
Drenkhan R, Ganley B, Martín-García J et al (2020) Global geographic distribution and host range of *Fusarium circinatum*, the causal agent of pine pitch canker. Forests 11(7):724
Ellison AM, Bank MS, Clinton BD et al (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ 3(9):479–486
Etzold S, Ferretti M, Reinds GJ et al (2020) Nitrogen deposition is the most important environmental driver of growth of pure, even-aged and managed European forests. For Ecol Manag 458:117762
Fisher PJ, Anson AE, Petrini O (1984a) Antibiotic activity of some endophytic fungi from ericaceous plants. Bot Helv 94(2):249–253
Fisher PJ, Anson AE, Petrini O (1984b) Novel antibiotic activity of an endophytic *Cryptosporiopsis* sp. isolated from *Vaccinium myrtillus*. Trans Br Mycol Soc 83(1):145–148
Fisher MC, Gurr SJ, Cuomo CA (2020) Threats posed by the fungal kingdom to humans, wildlife, and agriculture. M Biol 11(3):e00449–e00420
Floudas D, Binder M, Riley R (2012) The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. Science 336(6089):1715–1719
Gadgil M (2005) Ecological journeys. Permanent Black, New Delhi.
Garbelotto M, Gonthier P (2013) Biology, epidemiology, and control of Heterobasidion species worldwide. Annu Rev Phytopathol 51(1):39–59
Gehring CA, Whitham TG (2002) Mycorrhizae-herbivore interactions: population and community consequences. In: van der Heijden MGA, Sanders I (eds) Mycorrhizal ecology. Springer, Berlin, pp 295–320
Gilbert GS, Strong DR (2007) Fungal symbionts of tropical trees. Ecology 88:539–540

Giovannini L, Palla M, Agnolucci M et al (2020) Arbuscular mycorrhizal fungi and associated microbiota as plant biostimulants: research strategies for the selection of the best performing inocula. Agronomy 10(1):106

Gómez-Gallego M, LeBoldus JM, Bader MK et al (2019) Contrasting the pathogen loads in co-existing populations of *Phytophthora pluvialis* and *Nothophaeocryptopus gaeumannii* in Douglas fir plantations in New Zealand and the Pacific Northwest United States. Phytopathology 109(11):1908–1921

Gross A, Holdenrieder O, Pautasso M et al (2014) *Hymenoscyphus fraxinus*, the causal agent of European ash dieback. Mol Plant Pathol 15(1):5–21

Guerreiro MA, Brachmann A, Begerow D, Peršoh D (2018) Transient leaf endophytes are the most active fungi in 1-year-old beech leaf litter. Fungal Divers 89(1):237–251

Hacskaylo E (1965) *Thelephora terrestris* and mycorrhizae of Virginia pine. For Sci 11(4):401–404

Hardham AR, Blackman LM (2018) Phytophthora cinnamomi. Mol Plant Pathol 19(2):260–285

Hess JM, Wang Q, Kraft C, Slavin JL (2017) Impact of *Agaricus bisporus* mushroom consumption on satiety and food intake. Appetite 117:179–185

Hesse U, Schöberlein W, Wittenmayer L et al (2003) Effects of *Neotyphodium* endophytes on growth, reproduction and drought-stress tolerance of three *Lolium perenne* L. genotypes. Grass Forage Sci 58(4):407–415

Hibbett DS, Donoghue MJ (2001) Analysis of character correlations among wood decay mechanisms, mating systems, and substrate ranges in homobasidiomycetes. Syst Biol 50(2):215–242

Hintikka V (1988) On the macromycete flora in oligotrophic pine forests of different ages in South Finland. Acta Bot Fenn 136:89–94

HoÈgberg P, Nordgren A, Buchmann N et al (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411(6839):789–792

Hyde KD, Xu J, Rapior S (2019) The amazing potential of fungi: 50 ways we can exploit fungi industrially. Fungal Divers 97(1):1–36

Inácio J, Pereira P, Carvalho DM (2002) Estimation and diversity of phylloplane mycobiota on selected plants in a mediterranean–type ecosystem in Portugal. Microb Ecol 44(4):344–353

Jayawardena RS, Hyde KD, McKenzie EH et al (2019) One stop shop III: taxonomic update with molecular phylogeny for important phytopathogenic genera: 51–75. Fungal Divers 98(1):77–160

Jennings DH (1991) The spatial aspects of fungal growth. Sci Prog:141–156

Johannesson H, Stenlid J (2003) Molecular markers reveal genetic isolation and phylogeography of the S and F intersterility groups of the wood-decay fungus *Heterobasidion annosum*. Mol Phylogenet Evol 29(1):94–101

Jones EG (1994) Fungal adhesion. Mycol Res 98(9):961–981

Juan-Ovejero R, Briones MJ, Öpik M (2020) Fungal diversity in peatlands and its contribution to carbon cycling. Appl Soil Ecol 146:103393

Karwa AL, RAI MK (2010) Tapping into the edible fungi biodiversity of Central India. Biodiversitas J Biol Divers 11(2)

La Porta N, Capretti P, Thomsen IM et al (2008) Forest pathogens with higher damage potential due to climate change in Europe. Can J Plant Pathol 30(2):177–195

Lee SJ (2019) The evolution of RNA interference system, blue light sensing mechanism and circadian clock in *Rhizophagus irregularis* give insight on Arbuscular mycorrhizal symbiosis, Dissertation, University of Montreal, Canada

Lewis GC (2004) Effects of biotic and abiotic stress on the growth of three genotypes of *Lolium perenne* with and without infection by the fungal endophyte *Neotyphodium lolii*. Ann App Biol 144(1):53–63

Li X, Zhai X, Shu Z et al (2016) *Phoma glomerata* D14: an endophytic fungus from *salvia miltiorrhiza* that produces salvianolic acid C. Curr Microbiol 73(1):31–37

Maire F, Vigouroux A (2004) Plane tree canker stain: a study of the persistence of the causal parasite in stumps of cutdown trees. Phytoma 572:29–23

Mäkelä MR, Marinović M, Nousiainen P et al (2015) Aromatic metabolism of filamentous fungi in relation to the presence of aromatic compounds in plant biomass. Adv Appl Microbiol 91:63–137
McKinney LV, Nielsen LR, Collinge DB et al (2014) The ash dieback crisis: genetic variation in resistance can prove a long-term solution. Plant Pathol 63(3):485–499
Mežaka A, Bader MY, Salazar Allen N, Mendieta-Leiva G (2020) Epiphyll specialization for leaf and forest successional stages in a tropical lowland rainforest. J Veg Sci 31(1):118–128
Mitchell AG, Brasier CM (1994) Contrasting structure of European and north American populations of *Ophiostoma ulmi*. Mycol Res 98(5):576–582
Molina R (1994) The role of mycorrhizal symbioses in the health of giant redwoods and other forest ecosystems. USDA Forest Service Gen Tech Rep PSW 151:78–81
Monaghan RC, Polishook JD, Pecore VJ (1995) Discovery of novel secondary metabolites from fungi-is it really a random walk through a random forest? Can J Bot 73:925–931
Morel S, Arnould S, Vitou M et al (2018) Antiproliferative and antioxidant activities of wild Boletales mushrooms from France. Int J Med Mushrooms 20(1):13–29
Newcombe G, Stirling B, McDonald S, Bradshaw HD (2000) *Melampsora*× *Columbiana*, a natural hybrid of *M. medusae* and *M. occidentalis*. Mycol Res 4(3):261–274
Newsham KK, Lewis GC, Greenslade PD, McLeod AR (1998) *Neotyphodium lolii*, a fungal leaf endophyte, reduces fertility of *Lolium perenne* exposed to elevated UV-B radiation. Ann Bot 81(3):397–403
Nguyen NH, Song Z, Bates ST et al (2016) FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecol 20:241–248
Nisa H, Kamili AN, Nawchoo IA et al (2015) Fungal endophytes as prolific source of phytochemicals and other bioactive natural products: a review. Microb Pathog 82:50–59
Nnadi NE, Carter DA (2021) Climate change and the emergence of fungal pathogens. PLoS Pathog 17(4):e1009503
Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404:278–281
Paoletti E, Danti R, Strati S (2001) Pre-and post-inoculation water stress affects *Sphaeropsis sapinea* canker length in *Pinus halepensis* seedlings. Forest Pathol 31(4):209–218
Perotto S, Daghino S, Martino E (2018) Ericoid mycorrhizal fungi and their genomes: another side to the mycorrhizal symbiosis? New Phytol 220(4):1141–1147
Petrini O (1991) Fungal endophytes of tree leaves. In: Andrew JH, Hirano SS (eds) Microbial ecology of leaves. Springer, New York, pp 179–197
Petrini O, Sieber TN, Toti L, Viret O (1992) Ecology, metabolite production, and substrate utilization in endophytic fungi. Nat Toxins 1(3):185–196
Photita W, Lumyong S, Lumyong P et al (2004) Are some endophytes of Musa acuminata latent pathogens? Fungal Divers 16:131–140
Porras-Alfaro A, Bayman P (2011) Hidden fungi, emergent properties: endophytes and microbiomes. Ann Rev Phytopathol 49(1):291–315
Pugh GJF (1972) Saprophytic fungi and seeds. In: Heydecker W (ed) Seed ecology. Butterworth, London, pp 337–345
Rafiqi M, Saunders D, McMullan M et al (2018) Plant-killers: fungal threats to ecosystems. In: Willis KJ (ed) State of the world's fungi repot. Royal Botanic Gardens, Kew, p 56
Ragazzi A, Moricca S, Capretti P et al (2003) Differences in composition of endophytic mycobiota in twigs and leaves of healthy and declining *Quercus* species in Italy. For Pathol 33(1):31–38
Rai M, Agarkar G (2016) Plant–fungal interactions: what triggers the fungi to switch among lifestyles? Crit Rev Microbiol 42(3):428–438
Rajagopal K (1999) Biology and ecology of fungal endophytes of forest trees with special reference to neem (*Azadirachta indica A. Juss*), Doctoral dissertation, University of Madras
Redman RS, Sheehan KB, Stout RG et al (2002) Thermotolerance generated by plant/fungal symbiosis. Science 298(5598):1581

Ren A, Gao Y, Zhang L, Xie F (2006) Effects of cadmium on growth parameters of endophyte-infected endophyte-free ryegrass. J Plant Nutr Soil Sci 169(6):857–860
Riley R, Salamov AA, Brown DW et al (2014) Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. Proc Natl Acad Sci USA 111(27):9923–9928
Rineau F, Maurice JP, Nys C et al (2010) Forest liming durably impact the communities of ecto-mycorrhizas and fungal epigeous fruiting bodies. Ann For Sci 67(1):110
Rodriguez RJ, Henson J, Van Volkenburgh E et al (2008) Stress tolerance in plants via habitat-adapted symbiosis. ISME J 2(4):404–416
Rodriguez RJ, White JF Jr, Arnold AE et al (2009) Fungal endophytes: diversity and functional roles. New Phytol 182(2):314–330
Rossman AY (1998) Protocols for an all-taxa biodiversity inventory of fungi in a Costa Rican conservation area. Parkway Publishers, Inc.
Saikkonen K, Faeth SH, Helander M et al (1998) Fungal endophytes: a continuum of interactions with host plants. Annu Rev Ecol Evol S 29:319–343
Santamaría J, Bayman P (2005) Fungal epiphytes and endophytes of coffee leaves (Coffea arabica). Microb Ecol 50(1):1–8
Scott P, Bader MK, Burgess T et al (2019) Global biogeography and invasion risk of the plant pathogen genus *Phytophthora*. Environ Sci Policy 101:175–182
Shepherd RW, Wagner GJ (2012) Fungi and leaf surfaces. In: Southworth D (ed) Biocomplexity of plant-fungal interactions. Wiley, Ames, p 131
Sjostrom E (1993) Wood chemistry – fundamentals and applications. Gulf Professional Publishing, Academic Press, San Diego
Skrede I, Engh IB, Binder M et al (2011) Evolutionary history of Serpulaceae (Basidiomycota): molecular phylogeny, historical biogeography and evidence for a single transition of nutritional mode. BMC Evol 11(1):1–3
Slippers B, Wingfield MJ (2007) Botryosphaeriaceae as endophytes and latent pathogens of woody plants: diversity, ecology and impact. Fungal Biol Rev 21(2–3):90–106
Steidinger BS, Crowther TW, Liang J et al (2019) Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. Nature 569(7756):404–408
Stergiopoulos I, Gordon TR (2014) Cryptic fungal infections: the hidden agenda of plant pathogens. Front Plant Sci 5:506
Strobel G, Daisy B (2003) Bioprospecting for microbial endophytes and their natural products. Microbiol Mol Bio Rev 67(4):491–502
Sun X, Guo LD, Hyde KD (2011) Community composition of endophytic fungi in Acer truncatum and their role in decomposition. Fungal Divers 47(1):85–95
Suryanarayanan TS, Rajagopal K (1998) Fungal endophytes in leaves of some south Indian tree species. In: Proceedings of the Asia–Pacific mycological conference on biodiversity and biotechnology. Hua-Hin, Thailand, pp 252–256
Sutela S, Forgia M, Vainio EJ et al (2020) The virome from a collection of endomycorrhizal fungi reveals new viral taxa with unprecedented genome organization. Virus Evol 6(2):veaa076
Swift MJ (1982) Basidiomycetes as components of forest ecosystems. In: Frankl JC, Hedger JN (eds) Decomposer basidiomvcetes: their biologv and ecology. Cambridge University Press, Cambridge, pp 203–256
Terborgh J, Peres CA (2017) Do community-managed forests work? A biodiversity perspective. Land 6(2):22
Tiwari A, Mahajan CS, Mishra DK et al (2010) Comparative in vitro antioxidant activity of *Pongamia pinnata* Linn. Leaves extracts and isolated compound. Inter J Pharm Biol Arch 1:69–75
Turnau K, Kottke I, Dexheimer J (1996) Toxic element filtering *in Rhizopogon roseolus/Pinus sylvestris* mycorrhizas collected from calamine dumps. Mycol Res 100(1):16–22
Wagner BL, Lewis LC (2000) Colonization of corn, Zea mays, by the entomopathogenic fungus *Beauveria bassiana*. Appl Environ Microbiol 66(8):3468–3473

Wang J, Machado C, Panaccione DG et al (2004) The determinant step in ergot alkaloid biosynthesis by an endophyte of perennial ryegrass. Fungal Genet Biol 41(2):189–198
Wardle DA, Bardgett RD, Klironomos JN et al (2004) Ecological linkages between aboveground and belowground biota. Science 304(5677):1629–1633
Webber JF (2000) Insect vector behavior and the evolution of Dutch elm disease. In: Dunn CP (ed) The elms. Springer, Boston, MA, pp 47–60
Weiss M, Sýkorová Z, Garnica S et al (2011) Sebacinales everywhere: previously overlooked ubiquitous fungal endophytes. PLoS One 6(2):e16793
Weiß M, Waller F, Zuccaro A et al (2016) Sebacinales–one thousand and one interactions with land plants. New Phytol 211(1):20–40
Whipps JM, Hand P, Pink D et al (2008) Phyllosphere microbiology with special reference to diversity and plant genotype. J Appl Microbiol 105(6):1744–1755
Wieshammer G, Unterbrunner R, García TB et al (2007) Phytoextraction of Cd and Zn from agricultural soils by Salix ssp. and intercropping of Salix caprea and Arabidopsis halleri. Plant Soil 298(1):255–264
Wilson D (1995) Endophyte: the evolution of a term, and clarification of its use and definition. Oikos 73:274–276
Xiao AD (2008) Ren ren: the “little people” of Yunnan. Econ Bot 62(3):540–544

Recent Progress on Fungal Enzymes

Neveen M. Khalil

1 Introduction

In light of the many developments that are taking place around us, we cannot but always search for what is new to keep pace with this tremendous development of the era. Meanwhile, it is clear that enzymes play a pivotal role in many applications that keep pace with such enormous progress. There is always a rising demand for enzymes production to satisfy the need for them.

In general, enzymes are proteins in nature. All living organisms produce them to catalyze specific reactions. Enzymes are manipulated in fields of industry, medicine and environment. Enzymatic processes are more advantageous when compared with the conventional chemical ones. This appears in the gentler reaction conditions and the more advanced specificity which led to higher production of desired products and less production of byproducts (de Souza et al. 2020), moreover more efficient and cleaner processes thus contributing to the sustainable growth concept (Dhevagi et al. 2021).

While all living organisms are capable of producing enzymes, it is noticed that animals and plants cannot satisfy the industrial demands. This drew the attentions towards microbial enzymes (Guerrand 2018). Microbial enzymes can be produced at much higher rates. They are also cost-effective, scalable and more genetically compliant (Singh et al. 2019). Regarding fungal enzymes, they are more stable and more retaining of their activity (Verma et al. 2020). Fungal enzymes show higher production potency, easier purification steps, especially in case of filamentous fungi. Furthermore, since ancient times, fungi have been utilized for different purposes such as baking and brewing. From this perspective, fungi can be considered safe and thus justifying the continuity of their recent use in more than half of commercial enzymes. For all of the previous fungal enzymes are of more significance in various

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application fields (Kango et al. 2019). Some species belonging to genera of *Aspergillus*, *Penicillium*, *Rhizopus* and *Trichoderma*, and recently mushroom are fulfilling the enzyme market requirements. The rapid growth of this market led to continuous attempts to find novel enzymes producers satisfying the industrial characteristics (Kumla et al. 2020).

According to their mode of nutrition, fungi are considered chemo-organo-heterotrophs getting their nutrients via the breakdown of extracellular organic matter. They could be parasites if the source of organic matter used is from a living host or they could be saprophytes if the source is dead organic matter. (Devi et al. 2020; Suman et al. 2015). In either way, fungi produce an array of hydrolytic (glycolytic, proteolytic and lipolytic) and oxidative enzymes to breakdown the complex organic matters forming simple ones (Kour et al. 2019). Fungal enzymes are mainly produced during the log phase of growth. Extracellular enzymes are secreted to the outside of the cell for digestion of complex nutrients prior to being absorbed within the cells, then endocellular enzymes (found inside the cells) further assimilate the absorbed nutrients (Dhevagi et al. 2021). Extracellular enzymes could also participate in protection of fungi against the naturally existing hazardous materials or those resulting from substrates hydrolysis (Verma et al. 2020). Enzymes are classified where an enzyme could belong to a hydrolase, lyase, oxidoreductase, translocase, transferase, ligase or an isomerase group (Jeske et al. 2019). Hydrolases and oxidoreductases are the most commercially valuable fungal enzymes (Berbee et al. 2017).

There is a variety of enzymes secreted by fungi namely amylases, xylanases, cellulases, lipases, proteases, peroxidases, catalases and laccases (Marco et al. 2013). It is always desirable to use enzymes instead of corrosive chemicals to perform specific functions at the ambient temperatures. Fungal enzymes when purified, their application could be expensive due to the number of phases in the purification process. Nevertheless, their employment could be cost-effective if recyclable biocatalysts are utilized (Godfrey and Reichelt 1996; Gianfreda and Rao 2004).

This chapter discusses the production and purification of fungal enzymes with emphasis on their recent biotechnological applications. Such applications will be outlined in the industrial, biomedical and environmental fields.

2 Production of Fungal Enzymes

Large-scale production of enzymes was developed through the numerous researches conducted in the recent period using specific strains. Studies are concerned with developing fermentation processes, recombinant DNA cloning and enzymes engineering, introducing them to many application fields (Gurung et al. 2013).

2.1 Optimization of Medium

Economically important compounds with applications in various fields are produced by fermentation technology (Dubey et al. 2008). Studies for medium optimization are performed to enhance production of the desired yield. Many investigations were concerned with the microbial nutritional requirements for enhancing metabolites (e.g. enzymes) production (Shih et al. 2002; Singh et al. 2012). It must be taken into consideration that medium optimization should fulfil minimal microbial growth to obtain maximum production of the desired metabolite. This is to have maximum efficiency and minimum cost and wastes thus competing the traditional methods (Singh et al. 2017).

Various strategies are proposed for designing and optimizing the medium for highest efficiency for production. In the classical experimental technique for fermentation medium optimization, the one-factor-at-a-time (OFAT), one factor is changed at each experiment while the other factors are kept constant. Then the concentrations of each selected medium component is varied over a tested range. The OFAT is easy and convenient. Hence, many researchers prefer it (Gonzalez et al. 1995) and they still follow this method (Singh et al. 2017). On the other hand, using the statistical design of experiments (DOE) technique for optimizing the fermentation medium can overcome some of the limitations of the OFAT technique. In 1992, Fisher proposed the theory of experimental design. This theory describes that varying more than one of the medium factors at a time is more efficient than varying only one factor at a time (Fisher 1992).

Optimization of fermentation medium reached new dimensions with the advancements in the statistical methodology. There were improvements in the process efficiency, reduction in experimental time and cost, consequently contributing in the process economics. The microbial process is biological in nature containing relatively many natural variables. Microbial reactions are associated together in a complex network, where several factors influencing different parts in this network. Applying the rational experimental design statistically evaluating the results, leads to increasing the reliability of the obtained experimental data. Furthermore, using the experimental design reduces the number of experiments needed for obtaining reliable data (Elibol 2004).

The experimental design is considered a study plan for achieving certain objectives. Experiments have to be well-planned and the sample size should be enough for obtaining sufficient data so as to answer the objectives of the study. In the full factorial design, all factors, e.g. strain, medium constituents, temperature, pH etc. are studied. Meanwhile, in the partial factorial one, a few number of factors are chosen to be tested, which is usually done if the full factorial design cannot be applied due to little availability of knowledge about all the interactions of medium constituents (Singh et al. 2017).

Since not all medium constituents contribute in the production of the desired product, then the unimportant factors should be removed from the study. R.L. Plackett and J.P. Burman issued their study in 1946 about designing optimal factorial

experiments to precisely set and select the major effects in any process. This is the Placket-Burman Design (PBD), which is a two-level design. It is economically useful in finding the main effectors when assuming that other interacting effects are negligible, to compare the important ones. In other words, the effect of a factor will be superior or will be underestimated if there are no interactions (Vaidya et al. 2003).

2.2 Genetic Approaches

Genetic engineering (transcriptomics, proteomics and designing recombinant strains) is used in analyzing and improving enzymes production with least alterations in strains genome (Meyer et al. 2010; Liu et al. 2013). For instance, in *Saccharomyces cerevisiae*, overexpression of several transcription factors (TFs) resulted in enhancing TF target genes expression, whether under inducing or non-inducing effects (Chua et al. 2006). While in *Neurospora crassa*, inducer-independent cellulases production was accomplished by the constitutive overexpression of *clr-2* via the *ccg-1* promoter (Coradetti et al. 2013). *Aspergillus tamarii* was subjected to Illumina RNA-seq transcriptome profiling to identify genes responsible for encoding proteins managing plant biomass degradation. There were 209 CAZyme (carbohydrate-active enzyme) genes identified. Another five genes belonging to AA9 (GH61) family and related to LPMO (lytic polysaccharide monooxygenase) were identified. It was noticed that there was up-regulation of transcription factor gene XlnR, responsible for hemicellulases induction, and ClrA gene, involved in regulating cellulases, as well as more than 150 transporter genes (Midorikawa et al. 2018). In *Aspergillus niger*, it was found that overexpression of *gaaR* via *A. nidulans* promotor, *gpdA*, lead to the constitutive expression of genes responsible for encoding pectinases (Alazi et al. 2018). Another study revealed that in order to achieve stable and safe cellulase gene (*sestc*) expression, clustered regularly interspaced short palindromic repeats-Cas9 (CRISPR-Cas9) approach was applied to integrate the *sestc* expression cassette, which contains *Agaricus biporus* gpd (glyceraldehyde-3-phosphate-dehydrogenase) gene promoter, in the chromosome of *Saccharomyces cerevisiae*. Ethanol production showed 37.7-fold increase in the engineered *S. cerevisiae* strain compared with the wild type (Yang et al. 2018).

Properties of fungal enzymes can be improved through protein engineering (Ribeiro and Ribeiro 2013). Work began in the field of protein engineering in the eighties of the last century. Protein engineering is concerned with constructing proteins that are modified via site directed mutagenesis. Researches extended to study the catalytic mechanisms of enzymes and the relationship between their structure and function (Brannigan and Wilkinson 2002). By conducting advanced gene manipulation techniques, the proteins macromolecular structure can be changed to allow the manipulation of the enzymes target functions (Fan et al. 2009).

Site directed mutagenesis is a traditional technique of rational enzyme designing. It is used for evaluating the impact of a certain amino acid or more on the characteristics of the studied enzyme. The thermostable endoglucanase of *Humicola*

grisea Cel12A showed three uncommon free cysteines. These were Cys175, Cys206 and Cys216. They were used to construct mutants by site directed mutagenesis. The study demonstrated that these cysteines have a role in enzyme stability (Sandgren et al. 2005).

Another type of rational approaches is creation of multifunctional, chimera, enzymes. Such strategy aids in reducing costs when enzymes are economically used. When enzymes are engineered to have multi-domains along a single polypeptide chain, this would simplify production and purification processes. A natural linker was used to fuse a domain having laccase activity and obtained from *Pycnoporus cinnabarinus* with an *Aspergillus niger* CBM1 domain (Ravalason et al. 2009). The CBM1 domain is responsible for connection to molecules of cellulose, while the laccase domain manages lignin degradation around cellulose with good end results when applied in pulp and paper industries (Ibarra et al. 2006).

In the directed evolution approach, protein engineering employs the natural selection basis for the creation of novel characteristics of proteins and RNAs. Molecular diversity is generated here by random mutations using selective pressure. Survivors to these pressures are selected (Otten and Quax 2005). An example of the random mutagenesis methods is the error occurring in a PCR (polymerase chain reaction), where there is a controllable mis-incorporation of bases during amplification of genes (Cadwell and Joyce 1994). Another method for random mutagenesis is EP-RCA that employs rolling circle amplification (RCA) (Fujii et al. 2004). EP-RCA was used in the small DNA which encodes glucoamylase signal peptide in a recombinant *Saccharomyces cerevisiae*. This DNA was circularized and then it served as an EP-RCA template (Luhe et al. 2010). The technique of DNA shuffling was developed for random recombination mimicking natural evolution (Stemmer 1994a, b). An example for DNA shuffling technique is the staggered extension process (StEP). For instance, GOase (galactose oxidase) was obtained from *Fusarium* and then it was evolved by StEP and expressed in functional form inside *E. coli*. The evolved enzymes showed same substrate specificity and activity but showed more thermostbility and higher expression levels compared with native fungal oxidase (Sun et al. 2001).

In the semi-rational design, semi-rational mutagenesis can be considered a combination of directed and random mutagenesis. Here, hot spots can be defined by the structural or the functional information, which are then randomized for all the amino acids. This is to enhance the enzyme activity or change substrate specificity or the enantioselectivity mutations found close to the active site which are more important than those found on the enzyme surface (Bornscheuer and Pohl 2001). In this relation, an up-shift took place in the optimum pH of *Trichoderma reesei* endoglucanase II variants which occurred when a library was constructed by strand overlap extension (SOE) saturation mutagenesis technique (Qin et al. 2008). Another strategy with less number of cloning steps than SOE is *in vivo* overlap extension (IVOE) which was explored in ascomycetes and basidiomycetes (Mate et al. 2011). The *Pycnoporus cinnabarinus* laccase activity was 8000-fold increased using the error-prone PCR technique together with the *in vivo* shuffling and also the IVOE site directed mutation and recombination (Camarero et al. 2012).

3 Purification of Fungal Enzymes

It has become pivotal that researchers should try to find new methods replacing the traditional ones for fungal enzymes recovery and purification (Polizeli et al. 1991). We also cannot ignore that it is necessary to investigate the biochemical characteristics and the correlation between the structure and function of the purified enzyme (Gupta et al. 2003). Furthermore, its purity as well as its molecular weight are usually examined by SDS-PAGE (Patil and Chaudhari 2010).

Various procedures are employed for fungal enzymes purification. The purification process usually starts with precipitating proteins found in crude enzyme extract to concentrate them. In this step, ammonium sulfate or an organic solvent such as ethanol or acetone can be used. Next steps include dialysis and chromatographic techniques such as ion exchange or gel filtration (Kiiskinen et al. 2004). If the organic solvent step is only applied, where it is tested in different percentages to separate different protein types, the obtained precipitated protein in this case is only partially purified (Kumarevel et al. 2005; Yadav et al. 2019).

The liquid-liquid extraction technique surpasses the traditional ones in that several early stages can be cut short. This technique is based on the fact that when immiscible liquids are brought together, molecules transfer from phase to another. For instance, the ATPS (acqeuous two-phase system) technique avoids organic solvents use, but molecules are separated between two phases whether it is salt/salt or polymer/salt or polymer/polymer immiscible aqueous phases (Albertsson 1958). The ATPS method is preferred in extracting enzymes since high amounts of water are present (Freire et al. 2012), lower cost than when utilizing chromatography, more environmentally friendly and can be scaled up to reach higher purification folds (Naganagouda and Mulimani 2008; Schwienheer et al. 2015). In this relation, *Penicillium candidum* protease was purified using a system of PEG and sodium citrate and it was amended with sodium chloride to enrich the salt phase thus increasing the purification level (Alhelli et al. 2016).

On the other hand, the emerging TPP (three-phase partitioning) technique is developed for proteins, especially enzymes, extraction. It is characterized by high potential for concentrating proteins from multi-component crude broths and exhibiting higher purification levels compared with conventional methods of protein concentration (Gagaoua and Hafid 2016). The basis of this rising tool is combining the crude protein extract with a solid salt, ammonium sulfate, and organic solvent (e.g. butanol) for obtaining three phases (Ketnawa et al. 2017). The major drawback here is using an organic solvent, which limits the large-scale utilization of this technique (Alvarez-Guerra et al. 2014) since enzymes activity is reduced in presence of organic solvents (Ketnawa et al. 2017). However, butanol delivered a 7.2-fold of purity and a 184-recovery percentage for a laccase obtained from *Pleurotus ostreatus* (Kumar et al. 2011).

4 Recent Applications of Fungal Enzymes

In this section, different fungal enzymes will be reviewed while elucidating their progress in industrial, biomedical and environmental fields (Fig. 1).

4.1 Industrial Applications

Fungal enzymes are widely used in various industrial applications (Table 1). In the biofuel field, Rice straw was used for the production of cellulase-hemicellulase consortium by *Aspergillus niger* P-19. This enzyme preparation caused saccharification (70 g/L reducing sugars) of rice straw pretreated with 0.25 N NaOH. Fermentation of reducing C6 sugars yielded 15.6 g/L ethanol, with possibility of increasing the yield by targeting C5 sugars (Kaur et al. 2020). On the other hand, the enzymes hydrolysate (lignin peroxidase, manganese peroxidase, cellulase, xylanase) obtained from *Pycnoporus sanguineus* MCA 16 achieved saccharification of sugarcane bagasse. This hydrolysate was utilized for the production of ethanol by *Saccharomyces cerevisiae* CAT-1 (Scarpa et al. 2019).

As for microbial fuel cells (MFCs), their performance is influenced by microbial growth and metabolism. Fungi are eukaryotic microorganisms characterized by complex cell organization. In fungi, electron transfer occurs in two pathways. While oxidation of the substrate glucose by glycolysis produces two molecules of NADH for each glucose molecule, we find that interaction of mediators as methylene blue with a constituent of the electron transport chain (ETC) results in continuous functioning of the ETC and generation of electrons from Krebs cycle. These two pathways are therefore crucial for the simultaneous electrons providing and waste removal from substrate. Basically, there are two designs for constructing MFCs;

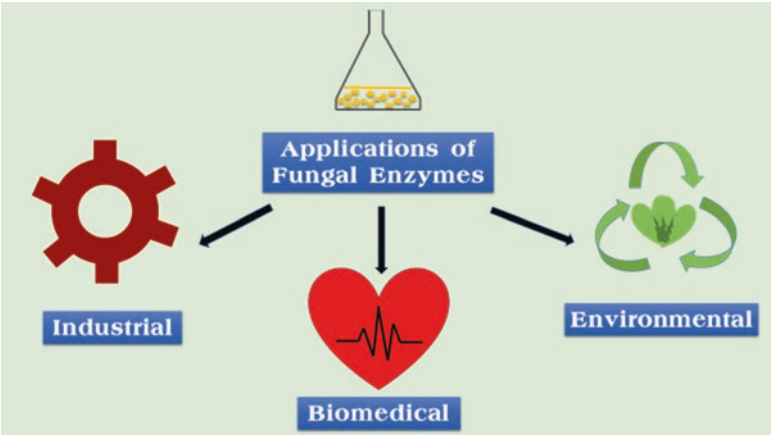

Fig. 1 Applications of fungal enzymes in different fields

Table 1 Some recent industrial applications of fungal enzymes

Enzyme	Fungal source	Industrial aspect	References
Cellulases and hemicellulases	*Aspergillus Niger*	Ethanol production	Kaur et al. (2020)
Lignin peroxidase manganese peroxidase, cellulase, xylanase	*Pycnoporus sanguineus*	Ethanol production	Scarpa et al. (2019)
Oxidoreductases	*Aspergillus sydowii*	Single-chamber microbial fuel cell embedded in interior design elements	Abdallah et al. (2019)
Oxidoreductases	*Trichoderma harzianum*	Dual-chamber microbial fuel cell	Shabani et al. (2021)
Xylanase	*Sclerotium rolfsii*	Paper and pulp, and fuel industries	Moussa et al. (2014)
Ligninolytic enzyme cocktails	*Aspergillus* sp., *Trichoderma* sp. and *Trametes versicolor*	Food additive	Margetic et al. (2021)
L-asparaginase	*Penicillium crustosum*	Acrylamide reduction in coffee	Khalil et al. (2021)
Polygalacturonases	*Talaromyces Leycettanus*	Clarification of grape juice	Li et al. (2017)
α-Amylase	*Geomyces Pannorum*	Bread making	He et al. (2017)
β-Glucosidase	*Meyerozyma guilliermondii*	Wine making	da Silva et al. (2019)
Lipase	*Thermomyces lanuginosus*	Fats interesterification, green apple flavoring	Shekarchizadeh and Kadivar (2012), Sadighi et al. (2017)
Protease	*Aspergillus oryzae*	Cheese making	Kumura et al. (2017)
Protease	*Pleurotus albidus*	Milk clotting	Abdel-Rahman et al. (2018)
Protease	*Aspergillus terreus*	Detergent and leather industries	Abu-Tahon et al. (2020)

single and dual chambers MFCs (Sarma et al. 2021). An example of the single-chambered fungal MFC is the one constructed by Abdallah et al. (2019). In their work, *Aspergillus sydowii* NYKA 510 was utilized as a cathodic biocatalyst in an MFC, where its oxidoreductases were responsible for performance of the MFC at 2000 Ω, which achieved 160 mWm^{-2}, 0.4 W, 0.76 V as well as 380 mAm^{-2}. A project was designed for a lighting unit that was implemented by using a system of two sets of four MFCs each, and connected in series, to generate electricity. The scanning electron microscope image of the utilized *A. sydowii* NYKA 510 was used in algorithmic form generation equations to design the lighting unit. On the other hand, Shabani et al. (2021) constructed a dual-chambered fungal MFC with the pure culture of *Trichoderma harzianum*. Another MFC was constructed with a mixed

culture of *Trichoderma harzianum* and *Pseudomonas fluorescens*, which were used as bioanodes as sources of oxidoreductases. The MFC recorded a 1.7 mW m^{-2} power density for the MFC system working with mixed biofilm, while that of the pure fungal biofilm achieved 0.13 mW m^{-2}.

Beside the ability of xylanases to improve the overall utilization of lignocellulosic matters in generation of biofuels and chemicals, they have also attracted much attention in the paper and pulp technological industries. Fungi are broadly used as producers of xylanases more than bacteria. A xylanase was purified from *Sclerotium rolfsii* with high thermal and pH stabilities making it a good candidate for such industrial applications (Moussa et al. 2014).

Acrylamide has been encountered in some foods that are subjected to heat treatments, e.g. French fries, bread and coffee beans. One of its formation mechanisms is the Maillard reaction, where at highly elevated temperatures the amino group in the amino acid L-asparagine reacts with the carbonyl group in another compound (e.g. reducing sugar). L-asparaginase can be used to hydrolyze L-asparagine to L-aspartic acid and ammonia, thus contributing in decreasing acrylamide generation (Xu et al. 2016). A heterodimer L-asparaginase was purified from *Penicillium crustosum* NMKA 511 that was highly specific towards L-asparagine. The enzyme reduced the acrylamide levels up to 80.7% and 75.8% for light-roasted coffee beans and dark-roasted ones, respectively (Khalil et al. 2021).

Increasing the daily supply of dietary fibers is of great priority while searching for novel sources and production technologies. Lignocellulosic materials hydrolysis by enzyme cocktails from *Aspergillus* and *Trichoderma* could be efficiently improved after *Trametes versicolor* laccase action. The procured soluble dietary fibers exhibited a 20-fold increase in the antioxidant activity when compared with the untreated (Margetic et al. 2021). The endo- and exopolygalacturonases synergistic action ensures effective pectic substances hydrolysis. Exo-TePG28a and endo-TePG28b polygalacuronases from *Talaromyces leycettanus* JCM12802 were overexpressed in the yeast *Pichia pastoris* and it was then characterized. Both enzymes showed high pH (2–7) and thermal (70 °C) stabilities. They caused a 140% pectin degrading efficiency making them worthy to be applied in the juice industry (Li et al. 2017).

In starch industrial applications, such as bread making, α-amylase could be of great value. The α-amylase (AmyA1) gene from the fungus *Geomyces pannorum* was cloned and expressed in *Aspergillus oryzae*. The enzyme could increase bread cohesiveness and decrease gumminess. Furthermore, the immobilized AmyA1 enzyme displayed thermal and pH stabilities and reusability (He et al. 2017). On the other hand, in the winemaking industry, β-glucosidase breaks down the glycoside-terpene complexes releasing the terpene groups, which promote wine flavor and quality. The β-glucosidase obtained from *Meyerozyma guilliermondii* revealed ethanol-glucose tolerance which is important to be applied in final saccharification during winemaking (da Silva et al. 2019).

The lipase from *Thermomyces lanuginosus* was immobilized. It was then used in the interesterification process of fats procured from camel hump. This is to be a potential analogue of cocoa butter manufacture (Shekarchizadeh and Kadivar 2012).

Another immobilized lipase, with high catalytic activity, from *Thermomyces lanuginosus* was exploited for the synthesis of ethyl valerate which is responsible for the green apple flavoring (Sadighi et al. 2017).

Owing to their high stable activity at acidic pHs and flavor enhancing property, it is becoming popular nowadays to use milk-clotting proteases as substitutes for calf rennin in cheese manufacture (Mamo et al. 2020). The protease secreted by *Aspergillus oryzae* is considered safe; accordingly, it can be applied as a milk-clotting agent in dairy industries (Kumura et al. 2017). In addition, *Pleurotus albidus*, the edible mushroom, was utilized as safe and efficient producer of milk-clotting enzyme (Abdel-Rahman et al. 2018).

Other applications of proteases are recognized for the alkaline protease produced by *Aspergillus terreus*. The purified protease was highly stable at wide temperature and alkaline pH ranges. It was also compatible with surfactants and detergents and exhibited good washing performance. Moreover, it showed a dehairing ability for animal hides without added chemicals thus it could be exploited in the leather industry (Abu-Tahon et al. 2020).

4.2 Biomedical Applications

Different biomedical activities are explored for fungal enzymes that vary between antimicrobial, antitumor, antioxidant, as well as therapeutic (Table 2). Fungal enzymes can cause cell membrane rupturing which results in losing cytoplasmic constituents. Moreover, they can inhibit synthesis of DNA, essential enzymes, or electron transport chain, in addition to blocking receptors of bacteria. This accounts for their antimicrobial activity (Fuglsang et al. 1995).

Table 2 Some recent biomedical applications of fungal enzymes

Enzyme	Fungal source	Biomedical aspect	References
Chitinase	*Trichoderma harzianum*	Antifungal activity	Deng et al. (2019)
Collagenase	*Penicillium aurantiogriseum*	Antibacterial and antioxidant activities	Lima et al. (2015)
Tyrosinase	*Saccharomyces cerevisiae*	Antioxidant, protective effect of normal cells.	Abdel-Rahman et al. (2019)
L-phenylalanine ammonia lyase	*Rhodosporidium toruloides*	Anticancer activity against breast cancer MCF7 and prostate cancer DU145 cells	Babich et al. (2013)
Ribonuclease	*Hohenbuehelia serotina*	Antiproliferative activity towards leukemia, lymphoma cells and HIV-1 reverse transcriptase	Zhang et al. (2014)
Asparaginase	*Lasiodiplodia theobromae*	Antileukemia	Moubasher et al. (2022)
β-Glucosidase	*Aspergillus* sp.	Neurological disorders treatment	Oh et al. (2018)

Chitinases acquired from fungi have potent antifungal activity, which enables their use in biocontrol applications (Le and Yang 2018). In this relation, the chitinase obtained from *Trichoderma harzianum* caused efficient retardation in growth of the phytopathogenic fungus *Botrytis cinerea* (Deng et al. 2019). The collagenase from *Penicillium aurantiogriseum* URM 4622 caused hydrolysis of collagen resulting in formation of peptides having molecular weights less than two kDa. These peptides showed antibacterial activities against *Bacillus subtilis*, *Escherichia coli* and *Staphylococcus aureus*, in addition to an antioxidant activity (Lima et al., 2015). Antioxidant compounds are of great importance since they augment in avoiding oxidative stresses generated by the harmful reactive oxygen species (ROSs). ROSs can cause cell damage by modifying structures of compounds like lipids, proteins and nucleic acids (Aklakur 2016). Fungal enzyme antioxidants can protect against severe actions of ROSs by transforming them into water and molecular oxygen (Rafi et al. 2016). Tyrosinase is a copper-containing monooxygenase, which is involved in the formation of the melanin pigment. The purified tyrosinase obtained from *Saccharomyces cerevisiae* showed an antioxidant activity. It also caused an increase in the viable count of MFB-4 cell line (normal skin melanocytes) before and after exposure to UV-irradiation indicating the protective and healing actions against UV (Abdel-Rahman et al. 2019).

The enzyme L-phenylalanine ammonia lyase (PAL) was purified from *Rhodosporidium toruloides*. The enzyme showed remarkable *in vitro* and *in vivo* antitumor activities against the cell lines MCF7 (breast cancer) and DU145 (prostate cancer), suggesting their potential application in cancer treatment (Babich et al. 2013). Meanwhile, the ribonuclease (RNase) purified from the fruiting bodies of the mushroom *Hohenbuehelia serotina* caused inhibition of reverse transcriptase of HIV-1 (human immunodeficiency virus type 1), in addition to decreasing the uptake of [^{3}H-methyl]-thymidine by the leukemia cells L1210 and the lymphoma cells MBL2 (Zhang et al. 2014).

It is noted that normal as well as leukemia cells require asparagine amino acid for their proliferation. However, only normal cells are capable of synthesizing asparagine using asparagine synthetase, while leukemia cells lack this enzyme. Asparaginase administration to ALL (acute lymphoblastic leukemia) patients causes hydrolysis of serum asparagine, consequently, proliferation of leukemic cells will be prohibited (El-Naggar et al. 2014). The endophytic fungus *Lasiodiplodia theobromae* was used as a source of asparaginase which exhibited a potential to be utilized as a reliable anticancer agent against leukemic cell line M-NFS-60 (Moubasher et al. 2022).

On the other hand, extracellular β-glucosidases, BGL1 and BGL2, were isolated from *Aspergillus* sp. YDJ216. They presented a potential to be applied in pharmaceutical industries. The flavone glycosides hydrolysis showed an inhibitory action on monoamine oxidase. This suggests their possible application in treating neurological disorders (Oh et al. 2018).

It is worthy to point out that, lectins, non-immunogenic proteins, do not have the catalytic activity of enzymes. However, they can bind without catalysis to certain carbohydrates (Lam and Ng 2011). Fungi are important producers of lectins, where

mushrooms constitute for 82% of fungal lectins (Diaz et al. 2011; Varrot et al. 2013). They have various applications regarding their antiproliferative, immune stimulating, antioxidant, antimicrobial and therapeutic potentials. In this regard, a lectin purified from *Pleurotus ostreatus* SS89 was stable over wide temperature and pH ranges. It showed significant antiproliferative activities towards the colorectal cancer cells HCT and the hepatic cancer cells HepG2. It also exhibited antibacterial activities towards *Escherichia Coli, Bacillus subtilis*, *Pseudomonas aeruginosa*, *Staphylococcus aureus* and *Streptococcus faecalis* (Kamel et al. 2021).

4.3 Environmental Applications

The continuous growth of the world population along with employing environmental resources is offset by an increase in pollution levels of waste materials as well as xenobiotics in the environment, which could be hazardous (Moussa and Khalil 2022). Table 3 depicts some fungal enzymes exploited in the environmental field. In this regard, the alkaline keratinase of *Scopulariopsis brevicaulis*, obtained from Egyptian black sand, showed hydrolyzing activities towards different keratinaceous waste materials (human hair, human nails, chicken feathers). The highest degrading ability was achieved against chicken feathers (Sharaf and Khalil 2011). Marchut-Mikolajczyk et al. (2015) found that the immobilized enzymes, lipases, laccases and peroxidases of *Mucor circinelloides* enhanced the biodegradation efficiency of diesel oil hydrocarbons by 20–30%.

Table 3 Some recent environmental applications of fungal enzymes

Enzyme	Fungal source	Environmental aspect	References
Keratinase	*Scopulariopsis brevicaulis*	Keratinaceous wastes degradation	Sharaf and Khalil (2011)
Lipases, laccases and peroxidases	*Mucor circinelloides*	Diesel oil hydrocarbons degradation	Marchut-Mikolajczyk et al. (2015)
Ligninolytic enzymes	*Aspergillus terreus*	Naphthalene and anthracene degradation	Ali et al. (2012)
Laccase	*Aspergillus flavus*	Dye decolorization	Khalil et al. (2016)
Cellulase laccase	*Aspergillus oryzae Ganoderma lucidum*	Detoxification of ink	Saini et al. (2020)
Laccase	*Trametes versicolor*	Tetracycline removal	Wen et al. (2019)
Manganese peroxidase	*Anthracophyllum discolor*	Removal of dyes	Siddeeg et al. (2020)
Lignin peroxidase	*Pichia methanolica*	Degradation of organic pollutants	Guo et al. (2019)
CYP450	*Trametes versicolor*	Removal of the herbicide diuron and the insecticides acetamiprid and imidacloprid	Hu et al. (2022)

The pollutants polycyclic aromatic hydrocarbons (PAHs) are, due to their hydrophobicity, quite resistant to biodegradation (Antizar-Ladislao et al. 2006). They can be chemically, physically or biologically remediated (Wu et al., 2010). Fungal ligninolytic enzymes can degrade PAHs. A potent *Aspergillus terreus* isolate producing lignin peroxidase and manganese peroxidase, degraded efficiently naphthalene (98.5%) and anthracene (91%) in tested soil models (Ali et al. 2012).

Synthetic dyes are found in the effluents of textile, cosmetics, paper and leather industries (Rezaei et al. 2015). Laccases can decolorize these dyes. For instance, a laccase purified from *Aspergillus flavus* NG85, a Saint Catherine Protectorate isolate, showed remarkable decolorization efficiencies against different dyes especially malachite green. Moreover, laccase decolorized a real textile effluent (Khalil et al. 2016).

Sustainable energy is meeting today's demands without jeopardizing the consumption of environmental resources for the future generations. In this context, wastes such as paper wastes can be used for production of bioethanol. However, this approach is obstructed due to presence of ink. A study was conducted where a cellulase from *Aspergillus oryzae* MDU-4 along with the laccase isozymes of *Ganoderma lucidum* MDU-7 showed significant effects in the toxic ink degradation. The CAZymes enzymatic consortium from *Trichoderma citrinoviride* MDU-1 caused solubilization of carbohydrate in the deinked papers. This was followed by fermentation of hexose sugars, which are free from the toxic ink to form bioethanol using *Saccharomyces cerevisiae* NCIM-3640 (Saini et al. 2020).

BDMMs (bentonite-derived mesoporous materials) were used to immobilize a laccase from *Trametes versicolor* to develop BDMMs-*Lac*. This was used for TC (tetracycline) removal. It showed 60% efficiency in TC removal (Wen et al. 2019).

Manganese peroxidase (MnP) has drawn the attention to be used in wastewater treatment. MnP was obtained from the fungus *Anthracophyllum discolor* and then immobilized on the nanocomposite Fe_3O_4/chitosan. It caused 96% ± 2% and 98% ± 2% removal of the dyes methylene blue and reactive orange 16, respectively, showing its potential in bioremediation of wastewater (Siddeeg et al. 2020).

Lignin peroxidase was procured from *Pichia methanolica* by heterologous expression. The enzyme was purified and immobilized on the nanoparticles Fe_3O_4@SiO_2@polydopamine. The immobilized enzyme caused remarkable dissipation of the organic pollutants phenol, 5-chlorophenol, dibutyl phthalate, tetracycline, phenanthrene and fluoranthene. The dissipation that occurred was due to degradation, primarily, and adsorption (Guo et al. 2019).

An investigation was performed to study the importance of the cytochrome P450 (CYP450) system of *Trametes versicolor* in removing the herbicide diuron, the insecticides acetamiprid (ACE) and imidacloprid (IMI). Presence of 1-ABT, CYP450 inhibitor, in the culture retarded the degradation of diuron. In addition, the half-life of ACE and IMI markedly increased when 1-ABT was present. Accordingly, the authors concluded that the system of CYP450 takes part in the degradation of the tested pollutants (Hu et al. 2022).

5 Conclusion

The global industrial demands for enzymes increases daily. Animal and plant enzymes cannot fulfil these demands; hence, the attention is drawn to microbial enzymes due to their feasible production in high quantities and more stability. Among microbial enzymes, enzymes derived from fungi are produced at larger scales and are more easily purified. They are inevitable in the industrial, biomedical and environmental sectors, as they can perform many tasks with high efficiency in production of foods and beverages, generation of biofuels, manufacture of detergents, leather, paper, textile and pharmaceuticals, and management of wastes. More research should be focused on exploring novel fungal sources for production of enzymes with desired features.

References

Abdallah YK, Estevez AT, Tantawy DEDM et al (2019) Employing laccase-producing *Aspergillus sydowii* NYKA 510 as a cathodic biocatalyst in self-sufficient lighting microbial fuel cell. J Microbiol Biotechnol 29(12):1861–1872. https://doi.org/10.4014/jmb.1907.07031

Abdel-Rahman TM, Khalil NM, Abdel-Ghany MN et al (2018) Purification and characterization of milk-clotting enzyme from the edible mushroom *Pleurotus albidus*. Res J Pharm Biol Chem Sci 9:49–63

Abdel-Rahman TM, Khalil NM, Abdel-Ghany MN et al (2019) Purification, characterization and medicinal application of tyrosinase extracted from *Saccharomyces cerevisiae*. J Inn Pharm Biol Sci 6(1):1–11

Abu-Tahon MA, Arafat HH, Isaac GS (2020) Laundry detergent compatibility and dehairing efficiency of alkaline thermostable protease produced from *Aspergillus terreus* under solid-state fermentation. J Oleo Sci 69(3):241–254. https://doi.org/10.5650/jos.ess19315

Aklakur M (2016) Natural antioxidants from sea: a potential industrial perspective in aquafeed formulation. Rev Aquac 10:385–399. https://doi.org/10.1111/raq.12167

Alazi E, Knetsch T, Di Falco MD et al (2018) Inducer-independent production of pectinases in *Aspergillus Niger* by overexpression of the D-galacturonic acid responsive transcription factor gaaR. Appl Microbiol Biotechnol 102:2723–2736. https://doi.org/10.1007/s00253-018-8753-7

Albertsson PA (1958) Partition of proteins in liquid polymer-polymer two-phase systems. Nature 182:709–711. https://doi.org/10.1038/182709a0

Alhelli AM, Abdul Manap MY, Mohammed AS et al (2016) Response surface methodology modelling of an aqueous two-phase system for purification of protease from *Penicillium candidum* (PCA 1/TT031) under solid state fermentation and its biochemical characterization. Int J Mol Sci 17(11):1872. https://doi.org/10.3390/ijms17111872

Ali MIA, Khalil NM, Abd El-Ghany MN (2012) Biodegradation of some polycyclic aromatic hydrocarbons by *Aspergillus terreus*. Afr J Microbiol Res 6:3783–3790. https://doi.org/10.5897/AJMR12.411

Alvarez-Guerra E, Ventura SPM, Coutinho JA et al (2014) Ionic liquid-based three phase partitioning (ILTPP) systems: ionic liquid recovery and recycling. Fluid Phase Equilib 371:67–74. https://doi.org/10.1016/j.fluid.2014.03.009

Antizar-Ladislao B, Lopez-Real J, Beck A (2006) Bioremediation of polycyclic aromatic hydrocarbons (PAH) in an aged coal–tar-contaminated soil using different in-vessel composting approaches. J Hazard Mater 137:1583–1588. https://doi.org/10.1016/j.jhazmat.2006.04.056

Babich OO, Pokrovsky VS, Anisimova NY et al (2013) Recombinant l-phenylalanine ammonia lyase from *Rhodosporidium toruloides* as a potential anticancer agent. Biotechnol Appl Biochem 60(3):316–322. https://doi.org/10.1002/bab.1089

Berbee ML, James TY, Strullu-Derrien C (2017) Early diverging fungi: diversity and impact at the dawn of terrestrial life. Annu Rev Microbiol 71:41–60. https://doi.org/10.1146/annurev-micro-030117-020324

Bornscheuer UT, Pohl M (2001) Improved biocatalysts by directed evolution and rational protein design. Curr Opin Chem Biol 5(2):137–143. https://doi.org/10.1016/S1367-5931(00)00182-4

Brannigan JA, Wilkinson AJ (2002) Protein engineering 20 years on. Nature Rev Mol Cell Biol 3(12):964–970. https://doi.org/10.1038/nrm975

Cadwell RC, Joyce GF (1994) Mutagenic PCR. PCR Methods Appl 3(6):S136–S140. https://doi.org/10.1101/gr.3.6.s136

Camarero SI, Pardo AI, Canas P et al (2012) Engineering platforms for directed evolution of laccase from *Pycnoporus cinnabarinus*. Appl Env Microbiol 78(5):1370–1384. https://doi.org/10.1128/AEM.07530-11

Chua G, Morris QD, Sopko R et al (2006) Identifying transcription factor functions and targets by phenotypic activation. Proc Natl Acad Sci U S A 103:12045–12050. https://doi.org/10.1073/pnas.0605140103

Coradetti ST, Xiong Y, Glass NL (2013) Analysis of a conserved cellulase transcriptional regulator reveals inducer-independent production of cellulolytic enzymes in *Neurospora crassa*. Microbiol Open 2:595–609. https://doi.org/10.1002/mbo3.94

da Silva RR, da Conceicao PJP, de Menezes CLA et al (2019) Biochemical characteristics and potential application of a novel ethanol and glucose-tolerant β-glucosidase secreted by *Pichia guilliermondii* G1.2. J Biotechnol 294:73–80. https://doi.org/10.1016/j.jbiotec.2019.02.001

de Souza JB, Michelin M, Amancio FL et al (2020) Sunflower stalk as a carbon source inductive for fungal xylanase production. Ind Crop Prod 153:112368. https://doi.org/10.1016/j.indcrop.2020.112368

Deng JJ, Shi D, Mao HH et al (2019) Heterologous expression and characterization of an antifungal chitinase (Chit46) from *Trichoderma harzianum* GIM 3.442 and its application in colloidal chitin conversion. Int J Biol Macromol 134:113–121. https://doi.org/10.1016/j.ijbiomac.2019.04.177

Devi R, Kaur T, Kour D et al (2020) Beneficial fungal communities from different habitats and their roles in plant growth promotion and soil health. Microb Biosyst 5:21–47. https://doi.org/10.21608/MB.2020.32802.1016

Dhevagi P, Ramya A, Priyatharshini S et al (2021) Industrially important fungal enzymes: productions and applications. In: Yadav AN (ed) Recent trends in mycological research. Fungal biology. Springer, Cham. https://doi.org/10.1007/978-3-030-68260-6_11

Diaz EM, Vicente-Manzanares M, Sacristan M et al (2011) Fungal lectin of *Peltigera canina* induces chemotropism of compatible *Nostoc* cells by constriction-relaxation pulses of cyanobiont cytoskeleton. Plant Signal Behav 6(10):1525–1536. https://doi.org/10.4161/psb.6.10.16687

Dubey KK, Ray A, Behera B (2008) Production of demethylated colchicine through microbial transformation and scale-up process development. Process Biochem 43:251–257. https://doi.org/10.1016/j.procbio.2007.12.002

Elibol M (2004) Optimization of medium composition for actinorhodin production by *Streptomyces coelicolor* A3 (2) with response surface methodology. Process Biochem 39:1057–1062. https://doi.org/10.1016/S0032-9592(03)00232-2

El-Naggar NEA, El-Ewasy SM, El-Shweihy NM (2014) Microbial l-asparaginase as a potential therapeutic agent for the treatment of acute lymphoblastic leukemia: the pros and cons. Int J Pharmacol 10(4):182–199. https://doi.org/10.3923/ijp.2014.182.199

Fan ZM, Werkman JR, Yuan L (2009) Engineering of a multifunctional hemicellulase. Biotechnol Lett 31(5):751–757. https://doi.org/10.1007/s10529-009-9926-3

Fisher RA (1992) The arrangement of field experiments. In: Kotz S, Johnson NL (eds) Breakthroughs in statistics. Springer-Verlag Inc, New York, NY, pp 82–91. https://doi.org/10.1007/978-1-4612-4380-9_8

Freire MG, Cláudio AFM, Araújo JMM et al (2012) Aqueous biphasic systems: a boost brought about by using ionic liquids. Chem Soc Rev 41:4966–4995. https://doi.org/10.1039/C2CS35151J

Fuglsang CC, Johansen C, Christgau S et al (1995) Antimicrobial enzymes: applications and future potential in the food industry. Trends Food Sci Technol 6:390–396. https://doi.org/10.1016/S0924-2244(00)89217-1

Fujii R, Kitaoka M, Hayashi K (2004) One-step random mutagenesis by error-prone rolling circle amplification. Nucleic Acids Res 32(19):e145. https://doi.org/10.1093/nar/gnh147

Gagaoua M, Hafid K (2016) Three phase partitioning system, an emerging non-chromatographic tool for proteolytic enzymes recovery and purification. Biosensors J, OMICS 5(1):100134

Gianfreda L, Rao MA (2004) Potential of extra-cellular enzymes in remediation of polluted soils: a review. Enzym Microb Technol 35:339–354. https://doi.org/10.1016/j.enzmictec.2004.05.006340L

Godfrey T, Reichelt J (1996) Industrial enzymology. The application of enzymes in industry, 2nd edn. Macmillan New York Nature Press. https://onlinelibrary.wiley.com/doi/abs/10.1002/star.19840360111

Gonzalez R, Islas L, Obregon AM et al (1995) Gentamicin formation in *Micromonospora purpurea*: stimulatory effect of ammonium. J Antibiot 48:479–483. https://doi.org/10.7164/antibiotics.48.479

Guerrand D (2018) Economics of food and feed enzymes: status and prospectives. In: Nunes CS, Kumar V (eds) Enzymes in human and animal nutrition: principles and perspectives. Academic Press, London, pp 487–514. https://doi.org/10.1016/B978-0-12-805419-2.00026-5

Guo J, Liu X, Zhang X et al (2019) Immobilized lignin peroxidase on Fe3O4@SiO2@polydopamine nanoparticles for degradation of organic pollutants. Int J Biol Macromol 138:433–440. https://doi.org/10.1016/j.ijbiomac.2019.07.105

Gupta R, Gigras P, Mohapatra H et al (2003) Microbial α-amylases: a biotechnological perspective. Process Biochem 38(11):1599–1616. https://doi.org/10.1016/S0032-9592(03)00053-0

Gurung N, Ray S, Bose S et al (2013) A broader view: microbial enzymes and their relevance in industries, medicine, and beyond. Biomed Res Int 2013:1–18. https://doi.org/10.1155/2013/329121

He L, Mao Y, Zhang L et al (2017) Functional expression of a novel α-amylase from Antarctic psychrotolerant fungus for baking industry and its magnetic immobilization. BMC Biotechnol 17(1):22. https://doi.org/10.1186/s12896-017-0343-8

Hu K, Barbieri MV, Lopez-Garcia E et al (2022) Fungal degradation of selected medium to highly polar pesticides by *Trametes versicolor*: kinetics, biodegradation pathways, and ecotoxicity of treated waters. Anal Bioanal Chem 414(1):439–449. https://doi.org/10.1007/s00216-021-03267-x

Ibarra DJ, Romero MJ, Martinez AT et al (2006) Exploring the enzymatic parameters for optimal delignification of eucalypt pulp by laccase-mediator. Enzym Microb Technol 39(6):1319–1327. https://doi.org/10.1016/j.enzmictec.2006.03.019

Jeske L, Placzek S, Schomburg I et al (2019) BRENDA in 2019: a European ELIXIR core data resource. Nucleic Acids Res 47:D542–D549. https://doi.org/10.1093/nar/gky1048

Kamel IS, Khalil NM, Atalla SMM et al (2021) Purification, molecular and biochemical characterization and biological applications of hemagglutinating lectin with anticancer activities from *Pleurotus ostreatus*. Plant Arch 21(S1):416–431. https://doi.org/10.51470/PLANTARCHIVES.2021.v21.S1.065

Kango N, Jana UK, Choukade R (2019) Fungal enzymes: sources and biotechnological applications. In: Satyanarayana T, Deshmukh SK, Deshpande MV (eds) Advancing frontiers in mycology & mycotechnology: basic and applied aspects of fungi. Springer, Singapore, pp 515–538. https://doi.org/10.1007/978-981-13-9349-5_21

Kaur J, Chugh P, Soni R et al (2020) A low-cost approach for the generation of enhanced sugars and ethanol from rice straw using in-house produced cellulase-hemicellulase consortium from *A. Niger* P-19. Bioresour Technol Rep 11:100469. https://doi.org/10.1016/j.biteb.2020.100469

Ketnawa S, Rungraeng N, Rawdkuen S (2017) Phase partitioning for enzyme separation: an overview and recent applications. Int Food Res J 24(1):1–24

Khalil NM, Ali MIA, Ouf SA et al (2016) Characterization of *aspergillus flavus* NG 85 laccase and its dye decolorization efficiency. Res J Pharm Biol Chem Sci 7:818–829

Khalil NM, Rodríguez-Couto S, El-Ghany MNA (2021) Characterization of *Penicillium crustosum* l-asparaginase and its acrylamide alleviation efficiency in roasted coffee beans at non-cytotoxic levels. Arch Microbiol 203(5):2625–2637. https://doi.org/10.1007/s00203-021-02198-6

Kiiskinen LL, Kruus K, Bailey M et al (2004) Expression of *Melanocarpus Albomyces* laccase in *Trichoderma reesei* and characterization of the purified enzyme. Microbiol 150:3065–3074. https://doi.org/10.1099/mic.0.27147-0

Kour D, Rana KL, Kaur T et al (2019) Extremophiles for hydrolytic enzymes productions: biodiversity and potential biotechnological applications. In: Molina G, Gupta VK, Singh B et al (eds) Bioprocessing for biomolecules production. Wiley, pp 321–372. https://doi.org/10.1002/9781119434436.ch16

Kumar VV, Sathyaselvabala V, Kirupha SD et al (2011) Application of response surface methodology to optimize three phase partitioning for purification of laccase from *Pleurotus ostreatus*. Separation Sci Technol 46:1922–1930. https://doi.org/10.1080/01496395.2011.583306

Kumarevel TS, Gopinath SCB, Hilda A et al (2005) Purification of lipase from *Cunninghamella verticillata* by stepwise precipitation and optimized conditions for crystallization. World J Microbiol Biotechnol 21:23–26. https://doi.org/10.1007/s11274-004-1005-2

Kumla J, Suwannarach N, Sujarit K et al (2020) Cultivation of mushrooms and their lignocellulolytic enzyme production through the utilization of agro-industrial waste. Molecules 25:2811. https://doi.org/10.3390/molecules25122811

Kumura H, Saito C, Taniguchi Y (2017) Adjunctive application of solid-state culture products from *Aspergillus oryzae* for semi-hard cheese. Adv Dairy Res 5(3):1–7. https://doi.org/10.4172/2329-888X.1000188

Lam SK, Ng TB (2011) Lectins: production and practical applications. Appl Microbiol Biotechnol 89(1):45–55. https://doi.org/10.1007/s00253-010-2892-9

Le B, Yang SH (2018) Characterization of a chitinase from *Salinivibrio* sp. BAO-1801 as an antifungal activity and a biocatalyst for producing chitobiose. J Basic Microbiol 58:848–856. https://doi.org/10.1002/jobm.201800256

Li Y, Wang Y, Tu T et al (2017) Two acidic, thermophilic GH28 polygalacturonases from *Talaromyces leycettanus* JCM 12802 with application potentials for grape juice clarification. Food Chem 237:997–1003. https://doi.org/10.1016/j.foodchem.2017.06.037

Lima CA, Campos JF, Filho JL et al (2015) Antimicrobial and radical scavenging properties of bovine collagen hydrolysates produced by *Penicillium aurantiogriseum* URM 4622 collagenase. J Food Sci Technol 52(7):4459–4466. https://doi.org/10.1007/s13197-014-1463-y

Liu G, Zhang L, Qin Y et al (2013) Long-term strain improvements accumulate mutations in regulatory elements responsible for hyper-production of cellulolytic enzymes. Sci Rep 3:1–7. https://doi.org/10.1038/srep01569

Luhe AL, Ting ENY, Tan L et al (2010) Engineering of small sized DNAs by error-prone multiply-primed rolling circle amplification for introduction of random point mutations. J Mol Catal B Enzym 67(1–2):92–97. https://doi.org/10.1016/j.molcatb.2010.07.011

Mamo J, Getachew P, Kuria MS et al (2020) Application of milk-clotting protease from *Aspergillus oryzae* DRDFS13 MN726447 and *Bacillus subtilis* SMDFS 2B MN715837 for Danbo cheese production. J Food Qual 1:1–12. https://doi.org/10.1155/2020/8869010

Marchut-Mikolajczyk O, Kwapisz E, Wieczorek D et al (2015) Biodegradation of diesel oil hydrocarbons enhanced with *Mucor circinelloides* enzyme preparation. Int Biodeterior Biodegrad 104:142–148. https://doi.org/10.1016/j.ibiod.2015.05.008

Marco E, Font X, Sanchez A et al (2013) Co-composting as a management strategy to reuse the white–rot fungus *Trametes versicolor* after its use in a biotechnological process. Int J Environ Waste Manag 11:100–108. https://doi.org/10.1504/IJEWM.2013.050637

Margetic A, Stojanovic S, Ristovic M et al (2021) Fungal oxidative and hydrolyzing enzymes as designers in the biological production of dietary fibers from triticale. LWT-Food Science and Technology 145:111291. https://doi.org/10.1016/j.lwt.2021.111291

Mate D, Garcia-Ruiz E, Camarero S et al (2011) Directed evolution of fungal laccases. Curr Genomics 12(2):113–122. https://doi.org/10.2174/138920211795564322

Meyer V, Ram AFJ, Punt PJ (2010) Genetics, genetic manipulation, and approaches to strain improvement of filamentous fungi. In: Baltz R, Demain A, Davies J et al (eds) Manual of industrial microbiology and biotechnology. ASM Press, Washington, DC, pp 318–329. https://doi.org/10.1128/9781555816827.ch22

Midorikawa GEO, Correa CL, Noronha EF et al (2018) Analysis of the transcriptome in *aspergillus tamarii* during enzymatic degradation of sugarcane bagasse. Front Bioeng Biotechnol 6:123. https://doi.org/10.3389/fbioe.2018.00123

Moubasher HA, Balbool BA, Helmy YA et al (2022) Insights into asparaginase from endophytic fungus *Lasiodiplodia theobromae*: purification, characterization and antileukemic activity. Int J Environ Res Public Health 19(2):680. https://doi.org/10.3390/ijerph19020680

Moussa TAA, Khalil NM (2022) Extremozymes from extremophilic microorganisms as sources of bioremediation. In: Kuddus M (ed) Microbial extremozymes. Academic Press, pp 135–146. https://doi.org/10.1016/B978-0-12-822945-3.00005-1

Moussa TAA, Khalil NM, Ali DMI, Mostafa FA (2014) Purification and biochemical characterization of xylanase from *Sclerotium rolfsii*. J Pure Appl Microbiol 8(6):4727–4733

Naganagouda K, Mulimani VH (2008) Aqueous two-phase extraction (ATPE): an attractive and economically viable technology for downstream processing of A*spergillus oryzae* α-galactosidase. Process Biochem 43:1293–1299. https://doi.org/10.1016/j.procbio.2008.07.016

Oh JM, Lee JP, Baek SC et al (2018) Characterization of two extracellular β-glucosidases produced from the cellulolytic fungus *aspergillus* sp. YDJ216 and their potential applications for the hydrolysis of flavone glycosides. Int J Biol Macromol 111:595–603. https://doi.org/10.1016/j.ijbiomac.2018.01.020

Otten LG, Quax WJ (2005) Directed evolution: selecting today's biocatalysts. Biomol Eng 22(1–3):1–9. https://doi.org/10.1016/j.bioeng.2005.02.002

Patil NP, Chaudhari BL (2010) Production and purification of pectinase by soil isolate *Penicillium* sp. and search for better agro-residue for its SSF. Rec Res Sci Technol 2:36–42

Polizeli MDLTM, Jorge JA, Terenzi HF (1991) Pectinase production by *Neurospora crassa*: purification and biochemical characterization of extracellular polygalacturonase activity. J Gen Microbiol 137:1815–1823. https://doi.org/10.1099/00221287-137-8-1815

Qin YQ, Wei XM, Song X et al (2008) The role of the site 342 in catalytic efficiency and pH optima of endoglucanase II from *Trichoderma reesei* as probed by saturation mutagenesis. Biocatal Biotransformation 26(5):378–382. https://doi.org/10.1080/10242420802249299

Rafi S, Shoaib A, Awan ZA et al (2016) Chromium tolerance, oxidative stress response, morphological characteristics, and FTIR studies of phytopathogenic fungus *Sclerotium rolfsii*. Folia Microbiol 62:207–219. https://doi.org/10.1007/s12223-016-0489-0

Ravalason H, Herpoel-Gimbert I, Record E et al (2009) Fusion of a family 1 carbohydrate binding module of *Aspergillus Niger* to the *Pycnoporus cinnabarinus* laccase for efficient softwood Kraft pulp biobleaching. J Biotechnol 142(3–4):220–226. https://doi.org/10.1016/j.jbiotec.2009.04.013

Rezaei S, Tahmasbi H, Mogharabia M et al (2015) Efficient decolorization and detoxification of reactive orange 7 using laccase isolated from *Paraconiothyrium variabile*, kinetics and energetics. J Taiwan Inst Chem Eng 56:113–121. https://doi.org/10.1016/j.jtice.2015.04.008

Ribeiro LF, Ribeiro LFC (2013) Improving fungal enzyme properties through protein engineering. In: Polizeli MDLTM, Rai M (eds) Fungal enzymes, 1st edn. CRC Press, pp 341–366. https://doi.org/10.1201/b15247

Sadighi A, Motevalizadeh SF, Hosseini M et al (2017) Metal-chelate immobilization of lipase onto polyethylenimine coated MCM-41 for apple flavor synthesis. Appl Biochem Biotechnol 182:1371–1389. https://doi.org/10.1007/s12010-017-2404-9

Saini S, Chutani P, Kumar P et al (2020) Development of an eco-friendly deinking process for the production of bioethanol using diverse hazardous paper wastes. Renew Energy 146:2362–2373. https://doi.org/10.1016/j.renene.2019.08.087

Sandgren M, Stahlberg J, Mitchinson C (2005) Structural and biochemical studies of GH family 12 cellulases: improved thermal stability, and ligand complexes. Prog Biophys Mol Biol 89(3):246–291. https://doi.org/10.1016/j.pbiomolbio.2004.11.002

Sarma H, Bhattacharyya PN, Jadhav DA et al (2021) Fungal-mediated electrochemical system: prospects, applications and challenges. Curr Res Microb Sci 2:100041. https://doi.org/10.1016/j.crmicr.2021.100041

Scarpa JDCP, Marques NP, Monteiro DA et al (2019) Saccharification of pretreated sugarcane bagasse using enzymes solution from *Pycnoporus sanguineus* MCA 16 and cellulosic ethanol production. Ind Crop Prod 141:111795. https://doi.org/10.1016/j.indcrop.2019.111795

Schwienheer C, Prinz A, Zeiner T et al (2015) Separation of active laccases from *Pleurotus sapidus* culture supernatant using aqueous two-phase systems in centrifugal partition chromatography. J Chromatogr B Analyt Technol Biomed Life Sci 1002:1–7. https://doi.org/10.1016/j.jchromb.2015.07.050

Shabani M, Pontié M, Younesi H et al (2021) Biodegradation of acetaminophen and its main by-product 4-aminophenol by *Trichoderma harzianum* versus mixed biofilm of *Trichoderma harzianum*/*Pseudomonas fluorescens* in a fungal microbial fuel cell. J Appl Electrochem 51:581–596. https://doi.org/10.1007/s10800-020-01518-w

Sharaf EF, Khalil NM (2011) Keratinolytic activity of purified alkaline keratinase produced by *Scopulariopsis brevicaulis* (Sacc.) and its amino acids profile. Saudi. J Biol Sci 18(2):117–121. https://doi.org/10.1016/j.sjbs.2010.12.011

Shekarchizadeh H, Kadivar M (2012) A study on parameters of potential cocoa butter analogue synthesis from camel hump by lipase-catalysed interesterification in supercritical CO_2 using response surface methodology. Food Chem 135(1):155–160. https://doi.org/10.1016/j.foodchem.2012.04.033

Shih I, Van Y, Chang Y (2002) Application of statistical experimental methods to optimize production of poly (**γ**-glutamicacid) by *Bacillus licheniformis* CCRC12826. Enzym Microb Technol 31:213–220. https://doi.org/10.1016/S0141-0229(02)00103-5

Siddeeg SM, Tahoon MA, Mnif W et al (2020) Iron oxide/chitosan magnetic nanocomposite immobilized manganese peroxidase for decolorization of textile wastewater. PRO 8:5. https://doi.org/10.3390/pr8010005

Singh N, Rai V, Tripathi C (2012) Production and optimization of oxytetracycline by a new isolate *Streptomyces rimosus* using response surface methodology. Med Chem Res 21:3140–3145. https://doi.org/10.1007/s00044-011-9845-4

Singh V, Haque S, Niwas R et al (2017) Strategies for fermentation medium optimization: an in-depth review. Front Microbiol 7:2087. https://doi.org/10.3389/fmicb.2016.02087

Singh R, Singh T, Pandey A (2019) Microbial enzymes—an overview. In: Singh RS, Singhania RR, Pandey A et al (eds) Advances in enzyme technology. Elsevier, Amsterdam, pp 1–40. https://doi.org/10.1016/B978-0-444-64114-4.00001-7

Stemmer WPC (1994a) DNA shuffling by random fragmentation and reassembly *in vitro* recombination for molecular evolution. Proc Natl Acad Sci U S A 91(22):10747–10751. https://doi.org/10.1073/pnas.91.22.10747

Stemmer WPC (1994b) Rapid evolution of a protein *in vitro* by DNA shuffling. Nature 370(6488):389–391. https://doi.org/10.1038/370389a0

Suman A, Verma P, Yadav AN et al (2015) Bioprospecting for extracellular hydrolytic enzymes from culturable thermotolerant bacteria isolated from Manikaran thermal springs. Res J Biotechnol 10:33–42

Sun LH, Petrounia IP, Yagasaki M et al (2001) Expression and stabilization of galactose oxidase in *Escherichia coli* by directed evolution. Protein Eng 14(9):699–704. https://doi.org/10.1093/protein/14.9.699

Vaidya R, Vyas P, Chhatpar H (2003) Statistical optimization of medium components for the production of chitinase by *Alcaligenes xylosoxydans*. Enzym Microb Technol 33:92–96. https://doi.org/10.1016/S0141-0229(03)00100-5

Varrot A, Basheer SM, Imberty A (2013) Fungal lectins: structure, function and potential applications. Curr Opin Struct Biol 5:678–685. https://doi.org/10.1016/j.sbi.2013.07.007

Verma ML, Thakur M, Randhawa JS et al (2020) Biotechnological applications of fungal enzymes with special reference to bioremediation. In: Gothandam K, Ranjan S, Dasgupta N et al (eds) Environmental biotechnology Vol 2. Environmental chemistry for a sustainable world, vol 45. Springer, Cham. https://doi.org/10.1007/978-3-030-38196-7_10

Wen X, Zeng Z, Du C et al (2019) Immobilized laccase on bentonite-derived mesoporous materials for removal of tetracycline. Chemosphere 222:865–871. https://doi.org/10.1016/j.chemosphere.2019.02.020

Wu ML, Nie MQ, Wang XC et al (2010) Analysis of phenanthrene biodegradation by using FTIR, UV and GC-MS. Spectrochim Acta A Mol Biomol Spectrosc 75(3):1047–1050. https://doi.org/10.1016/j.saa.2009.12.051

Xu F, Oruna-Concha M, Elmore J (2016) The use of asparaginase to reduce acrylamide levels in cooked food. Food Chem 210:163–171. https://doi.org/10.1016/j.foodchem.2016.04.105

Yadav M, Bista G, Maharjan R et al (2019) Secretory laccase from *Pestalotiopsis* species CDBT-F-G1 fungal strain isolated from high altitude: optimization of its production and characterization. Appl Sci 9:340. https://doi.org/10.3390/app9020340

Yang P, Wu Y, Zheng Z et al (2018) CRISPR-Cas9 approach constructing cellulase *sestc*-engineered *Saccharomyces cerevisiae* for the production of orange peel ethanol. Front Microbiol 9:2436. https://doi.org/10.3389/fmicb.2018.02436

Zhang R, Zhao L, Wang H et al (2014) A novel ribonuclease with antiproliferative activity toward leukemia and lymphoma cells and HIV-1 reverse transcriptase inhibitory activity from the mushroom, *Hohenbuehelia serotina*. Int J Mol Med 33:209–214. https://doi.org/10.3892/ijmm.2013.1553

Endophytic Fungi as Sources of Novel Natural Compounds

Adel Kamel Madbouly

1 Introduction

Currently, the scientists are searching for natural bioactive metabolites, which are useful in application for treatment of the various diseases; especially those diseases caused by the drug resistant microorganisms. This is in addition to their use in the sector of agriculture for the development of natural pesticides, which are less toxic and more efficient than the currently used chemical pesticides (de Carvalhoa et al. 2021). These natural products have been recently applied in agriculture as herbicides, fungicides, and insecticides, and have caused significant increase in the crop yield and quality, including the avermectin, spinosyn, and phosphinothricin (Yan et al. 2018).

There is a continuous search for microorganisms that are considered as vast reservoirs of bioactive secondary metabolites, including the endophytes. The increasing demands for secondary metabolites in the international markets imposed severe threats on many plant species. However, in recent years; the plant endophytes have emerged as promising alternative sources for the plant secondary metabolites (Gupta et al. 2020). These endophytes live symbiotically inside the plant tissues, and represent reservoirs of the novel bioactive compounds, which have widespread applications as promising agents for the development of novel agricultural and biomedical products (Petrini 1991 and Paramanantham et al. 2019).

The endophytes can release the same and\or similar secondary metabolites as their host plants (Strobel 2003; Puri et al. 2005). The produced bioactive metabolites have been recorded to possess several pharmacological potentials, including anti-microbial (Xing et al. 2011; Uche-Okereafor et al. 2019), immune-modulatory (Puri et al. 2007), anti-malarial (Baba et al. 2015), anti-cancer (Jia et al. 2014;

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Jinfeng et al. 2017), anti-inflammatory (Pretsch et al. 2014), and anti-oxidant (Singh et al. 2016). Moreover, several novel drug molecules have been recovered from the endophytic fungi, such as vinblastine (Guo et al. 1998), paclitaxel (Strobel et al. 1997), quercetin as an anti-inflammatory agent (Qiu et al. 2010), podophyllotoxin as an antitumor agent (Kour et al. 2008), borneol as an anti-oxidant (Chen et al. 2011), and berberine as an antibiotic (Duan et al. 2009).

Furthermore, the endophytes have several beneficial impacts on the development of large number of crop plants, including tomato; when grown under greenhouse (Anupama et al. 2014) and\or under field conditions (Babu et al. 2015). These beneficial endophytes involve the plant-growth-promoting fungi (PGPF), which promote the plant growth through several modes of action, including plant protection against the different pathogen infections (Jogaiah et al. 2018). Moreover, they support the crop plants to get the available nutrients in the soil, and stimulate the plant growth as well (Murali et al. 2012). The plant growth-promoting endophytes (PGPE) enhance the enzyme activity (Hassan 2017), promote hormones production in the plant tissue (Lin and Xu 2013), and facilitate the nutrients exchange. In addition, these endophytes have the ability to provide nitrogen to their host plants, and mobilize the insoluble phosphates (Matsuoka et al. 2013), thus they play an important role in providing the soil phosphorus as a low-cost input to their host plants.

The endophytes can bio-transform the plant-derived bioactive metabolites to their respective more effective derivatives, leading thus to functional and structural diversification (Tian et al. 2014; Ebada et al. 2016). Furthermore, several endophytes have the ability to up-regulate synthesis of the host bioactive compounds, and cause expression of the related genes in their host plants. Accordingly, biosynthesis of the plant-derived natural bioactive compounds by the fungal endophytes represents a promising technique for the specific and efficient production of the valuable bioactive compounds; using the endophytes as efficient “bio-laboratories” (Singh et al. 2021). The promising fungal endophytes can be modified to be more beneficial to the humankind; through manipulation of the modern biotechnologies, including genetic engineering, microbial fermentation, and recombinant DNA technology (Mahmud et al. 2020).

The objectives of the current study were to give a comprehensive insight on the efficacy of endofungi as potent producers of the novel natural bioactive compounds, define several types of these compounds, and recording their beneficial roles in the various medical and agricultural disciplines.

2 What Are Endophytes?

Endophytes are defined as endo-symbiotic groups of microorganisms, including bacteria and\or fungi that colonise the inter-and\or intracellular sites of the host plants (Pimentel et al. 2011; Singh and Dubey 2015). A previous study of Petrini (1991) defined endophytes as any microorganism that colonises the internal tissues of the host plant at some part of its life cycle; without causing any sort of

harm to this host. Recently, Mishra et al. (2021) added that endophytes are a group of plant-associated microorganisms, such as bacteria and fungi that inhabit the internal plant tissues. According to Jain et al. (2020) and Phurailatpam and Mishra (2020), these endophytes do not cause any disease symptoms to their hosts; however, they provide a merit to their hosts under the various biotic\ and abiotic stresses. Usually the most frequently detected endophytes in the tissues of their host plants are the fungi, although larger numbers of bacteria are often isolated. A previous study conducted by Brader et al. (2017) revealed that many endophytes might be either beneficial or pathogenic. Although the majority of these endophytes do not cause harmful effects on certain host plant species; however, they may be pathogenic when inhabiting the other plants. The endofungi alter the levels of gene expression, mitigate the stress conditions in the host plants, and modulate the biosynthetic pathways; accordingly, they play significant roles in establishing the plant's defence against the various pathogens (Deshmukh et al. 2020).

In general, the endophytes colonise the root; stem, leaf segments, petiole, fruit, seed, and buds, in addition to the dead and hollow cells of the host plants (Specian et al. 2012; Stepniewska and Kuzniar 2013). Meanwhile, Rosenblueth and Martínez-Romero (2006) previously reported that the endophytes have been divided into various subgroups, including the obligate or facultative endophytes that inhabit all types of the plants. Almost all endophytes that are recorded in the vascular plants employ a plant-fungal interaction, which is symbiotic, as most of the endophytes absorb nutrients from their host plants; however, they provide valuable benefits to these plants. These endophytes live within the tissues of their hosts harmlessly, thus provide an indirect defence against the various herbivores, as revealed by Bamisile et al. (2018).

The endophytes obtain nutrients and protection from their hosts; however, they encourage the uptake of nutrients by their host plants and protect them against the various abiotic and biotic stresses. Hardoim et al. (2015) reported that existence of the endophytes have several impacts on the plant health; growth, developments, the different types of the plant communities, population dynamic, and on the ecosystem functioning.

According to Wani et al. (2015), the endophytes have been divided into systemic and non-systemic or transient endophytes. The systemic endophytes are the same phylogenetically, as they colonise their host plants under the various environmental conditions. Conversely, the non-systemic endophytes are not phylogenetically the same, and they vary in their diversities and abundances with the variation in the environmental conditions (Higgins et al. 2014). On microbial infection, both of the host plants and the endophytes express mutual association, which allows them to develop molecular mechanisms and different strategies for their collaborated adaptation (Christensen et al. 2002). Depending on several factors, the interaction between the plant and an endophyte varies from commensalism to symbiosis and\or to parasitism (Eaton et al. 2011; Nair and Padmavathy 2014).

The pathogenicity traits of the endophytes are based on several biotic interactions and environmental factors. The fluorescent Pseudomonads are beneficial to most of the plants; however under certain conditions they may be pathogenic to the

leather leaf plants (Kloepper et al. 2013). The beneficial endophytes produce several compounds that enhance the host plants growth and sustainability, and protect the plants from the various environmental conditions; while being conveniently living inside these host plants. The populations of the endophytes are mainly controlled by the climatic conditions and the locations where their host plants naturally grow.

Several studies conducted by Franken (2012) and Chetia et al. (2019) reported that endophytes improve the growth and development of their host plants via providing several advantages that range from mutual survival in the harsh habitats to tolerance to the various abiotic and\ or biotic stresses.

According to Chutulo and Chalannavar (2018), the endophytes have proven to aid in the evolution and adaptation of the host plants to their environment. They are either partially or completely responsible for metabolite synthesis in their hosts, to help the plants in surviving in the harsh environment. *In vitro* and *in vivo* studies conducted by Li et al. (2019) confirmed that removal of the endophytes from the host plants has led to the loss of their resistance and adaptative properties toward the unfavorable environments; where the hosts live friendly with their endophytes. Gouda et al. (2016) pointed out that variations exist within populations of the endophytes that live within their host plants depending on several factors, including the host species; the developmental stage of the host, and the prevailing environmental conditions.

The previous study of Hardoim et al. (2008) reported that obligate endophytes depend on the metabolism of their host plants for survival, and they spread among their hosts through vertical transmission and through activities of the different types of vectors. On the other hand, the facultative endophytes live outside the bodies of their hosts during a certain stage of their life cycle, and they are mostly associated with plants from their atmosphere and from the neighboring soil environments (Abreu-Tarazi et al. 2010).

As a result of this long-term evolutionary association between the endophytes and their host plants, the native microbial endophytes have evolved to produce a wide range of metabolites. Sometimes these metabolites are synthesized via similar biochemical pathways; however, they can also be made by different pathways that exist in the plant or in the endophyte (Gupta et al. 2020). About 10% of the fungal endophytes recovered from *Taxus baccata* plant have the ability to produce taxanes (Caruso et al. 2000), which is a class of diterpenes usually isolated from the different *Taxus* spp. These compounds are known for their anti-mitotic potentials, due to stabilization of the microtubules (Crown and O'Leary 2000). Moreover, >73 genera of the endofungi isolated from plants have been reported to produce taxol that is originally isolated from *T. brevifolia*. Taxol expresses cytotoxic efficacy, and is thus used to treat several types of tumours (Gupta et al. 2020). This widespread production of taxol by the endofungi that belong to different taxonomic groups protects their niches inside the host plant tissues through inhibiting the invading fungi (Kusari et al. 2014). Furthermore, the bioactive compounds derived from the endophytes are used as a part of the plant chemical defences against the invading microbial pathogens and insects (Sahu et al. 2019, 2020).

The study of metabolites production by the endophytic fungi and their hosts using *in vitro* and *in silico* analyses may help in the prediction of new bioactive compounds, and their manipulation in human benefits (Nischitha and Shivanna 2022).

3 Isolation of the Fungal Endophytes

For effective selection of the promising plants as sources of fungal endophytes; 4 points should be considered, including: (i) Plants should be from a distinctive ecological niche, survival strategies, and unique biology, (ii) Plants must be of medical and ethnobotanical importance, (iii) Plants should be endemic to specific areas, and (iv) Plants should be from biodiversity attraction areas (Strobel and Daisy 2003).

4 Benefits of the Plant's Endofungi

Endophytes develop certain specific mechanisms to penetrate and then reside inside the tissues of their hosts. They possess the necessary exo-enzymes to grow well and then colonise the apoplastic fluid of their hosts (Chandra 2012). The association of endophytes with their hosts may become mutualistic when they colonise the roots, which will allow better growth of the host, and provide the endophyte with the adequate nutrients required to colonise their host's roots. Schulz et al. (2002) revealed that the concentrations of several plant defence metabolites are lower in the control host plant when becomes infected with a pathogen, compared to their concentrations in the presence of an endophyte. In general, there is an equilibrium between the fungal pathogenesis and the plant defence.

However, a disease develops, when this balance is disturbed by either an increase in fungal virulence or a decrease in the plant defence. Endophytes synthesize their various metabolites in order to compete with the pathogens on colonising the host and compete with the epiphytes, in addition to regulating the host metabolism, which are in a balanced association.

Moreover, endophytes have a significant tolerance toward the different host's metabolites. A previous study of Wang and Dai (2011) highlighted that endophytes' detoxification or transformation ability of these plant's defense bioactive compounds is an important characteristic, which will determine the range of colonization of the endophyte's hosts. Saunders and Kohn (2009) previously reported that the biotransformation ability of the endophytes will help in detoxification of the host's toxic metabolites, in addition to the production of novel bioactive secondary metabolites.

The fungal endophytes colonise their host tissues, and then help in producing the plant bioactive compounds and hormones, in addition to promoting the accumulation of their hosts secondary metabolites (Shwab and Keller 2008 and Waqas et al. 2012). Later, Schouten (2019) added that as a symbiotic relationship, the plants

assist their fungal endophytes through providing adequate nourishment and shelter, and cause seed dissemination, while the fungal endophytes transform the host's bioactive compounds into multifunctional products. Furthermore, several studies conducted by Khan et al. (2016) and Satheesan and Sabu (2020) highlighted that the fungal endophytes influence the biosynthesis of the host's phytohormones, enzymes, and their bioactive compounds.

A previous work conducted by Subbulakshmi et al. (2012) proved that microorganisms associated with their host plants rather than the plants themselves provide products with significant therapeutic potentialities. The plant endophytes produce phytohormones and bioactive compounds of high biotechnological interests, including the pharmaceutical drugs and the enzymes (Joseph and Priya 2011 and Parthasarathi et al. 2012).

According to several recent studies conducted by Ze-Hong et al. (2018), Salendra et al. (2018), Mondal (2019) and Wang et al. (2020), large numbers of endophytic fungi have attracted the attention due to the production of structurally complex secondary metabolites, which have various biological potentials.

The endophytes act as major resources of structurally unique natural bioactive metabolites, including benzoquinones; alkaloids, flavonoids, benzopyranones, steroids, phenols, terpenoids, xanthones, and tetralones, which deserve exploration in the novel therapy (Tan and Zou 2001). Furthermore, the endophytes are potent producers of antibacterial; antifungal, antiviral, immunosuppressive, and cytotoxic bioactive metabolites.

Siderophores are another group of biologically active compounds produced by the endophytes, which aid the microorganisms in chelating the F^{+3} ions to improve the plant growth (Fadiji and Babalola 2020). Moreover, the siderophores represent also important components of the microorganisms that express a virulence trait, thus affecting the people, animals, and plants. Several studies have been conducted on 5 different strains of an endophytic fungus named *Phialocephala fortinii*, which produces 3 types of siderophores; namely, ferrichrome C, ferrirubin, and ferricrocin. The secretion of these siderophores depends mainly on the F^{+3} ion concentration and on the pH of the growth medium (Nair and Padmavathy 2014). Accordingly, *P. fortinii* showed a promise for its use in the manufacture of siderophores on the industrial scale.

Currently, the endophytic resources are improved to provide us with several benefits, including the discovery of novel and effective metabolic compounds that may not be easily synthesized via the chemical routes. Another endophytic fungus identified as *Hypoxylon* sp. that is recorded as a resident in the *Persea indica* plant tissues produces several volatile organic compounds (VOCs), including 1,8–1-met hyl-1,4-cyclohexadiene and cineole, which are temporarily reported as alpha-m ethylene-alpha-fenchocamphorone. In addition, this endophyte produces a strong antimicrobial VOC, which is effective in inhibiting the growth of *Sclerotinia sclerotiorum*, *Phytophthora cinnamomi*, *Cercospora beticola,* and *Botrytis cinerea* (Fadiji and Babalola 2020). Furthermore, *Hypoxylon* sp. produces 1, 8-cineole (a monoterpene) that is a novel octane derivative, which can be used as a fuel additive. Fadiji

and Babalola (2020) study added that the search for more fungi that can produce VOCs will increase their use in the production of energy to improve the agricultural sectors, in addition to their utilization in medicine and in several other industries.

Singh et al. (2011) recorded a fungal endophyte termed *Phomopsis* sp. that has been isolated from *Odontoglossum* sp., which secretes a number of VOCs, such as ethanol, benzene, and 2-propanone, in addition to a monoterpene called sabinene that has a peppery odor. Moreover, the gases produced by *Phomopsis* sp. have antifungal traits, where as the mixtures of these VOCs have antibiotic activities against several phytopathogenic fungi.

5 Bioactive Metabolites Produced by the Endophytic Fungi

In addition to plants, microorganisms represent leading sources of natural compounds with desirable bioactive activities, where more than 20,000 bioactive metabolites have been recorded by the end of 2002 (Bérdy 2005). Fungi are one of the most important eukaryotic microorganisms, which are explored for using their metabolites in several clinical applications. Nowadays, the prevailing drugs of fungal origin include griseofulvin; β-lactam antibiotics, cyclosporine A, lovastatin, Taxol, and the ergot alkaloids.

A previous study by De Souza et al. (2011) reported that endophytes are the main producers of chemical compounds inside their host plants. Many of these endophytes are able to synthesize bioactive compounds, which can be used as growing sources of pharmaceutical drugs. Several endophytic fungi have been reported as sources of novel antifungal; antibacterial, antiviral, anti-tumour, and anti-inflammatory metabolites, in addition to other substances that belong to the steroids; alkaloids, flavonoids, and terpenoid extracts.

A previous study on the biosynthetic pathways that has been conducted by Jennewein et al. (2001) revealed that both the plants and the endophytic fungi have similar but distinct pathways for synthesis of the secondary metabolites. However, few studies reported that endophytes associated with the non taxol producing plants produce taxol. An endophytic taxol-producing fungus named *Colletotrichum gloeosporioides*, which is isolated from the leaves of *Justicia gendarussa* plant, produces about 163.4 µg\l of taxol (Gangadevi and Muthumary 2008).

A research study conducted by Ancheeva et al. (2019) proposed that the endophytic fungi represent growing sources of important metabolites, which may be beneficial such as antibiotics (i.e. penicillin), or detrimental such as mycotoxins (i.e. aflatoxins); with wide range of biological efficacies. The non-virulent nature of most of the fungal endophytes makes most of their secondary metabolites (SMs) more suitable for the human usage, as these metabolites are nontoxic to the mammalian cells.

5.1 Indole Alkaloids

Although several metabolites have been recovered from the fungal endophytes; however, prenylated indole alkaloids have attracted the attention of the biologists and the chemists due to their significant bioactivities and flexible frameworks. Several types of bioactive prenylated indole alkaloids such as fumitremorgins; versicolamides, α-cyclopiazonic acid, and paraherquamides (Cui et al. 2016), in addition to the ergot alkaloids (Ansari and Häubl 2016); have been recovered and identified from the genera of *Penicillium*, *Claviceps,* and *Aspergillus*. During the recent study conducted by Wang et al. (2021) several prenylated indole alkaloids have been isolated and identified (Fig. 1), including 2 new prenylated indole alkaloids named asperlenines A-B (1–2) and a new indole alkaloid termed asperlenine C (4) together with 12 known compounds, including asperorydine F (3) (Song 2012); butyrolactone I (5) (Dewi et al. 2015), auranthine (6) (Liu 2018), pyripyropene A (7) (Liang 2014) ardeemins (8) and (9) (Khalil 2014), paecilin B (10) (Mapook 2020), and five heterodimeric tetrahydroxanthone derivatives asperlentions D-H (11–15) (Li et al. 2016).

Results of evaluating the anticancer potentials of all these compounds against several tumor cell lines, such as H460, A549, and BT549, revealed that compounds 2, 4, 5, 13, and 15 have expressed moderate anti-cancer efficacy against A549 cell line with IC_{50} value of 18.74 to 45.76 μM. Moreover, all these prenylated indole

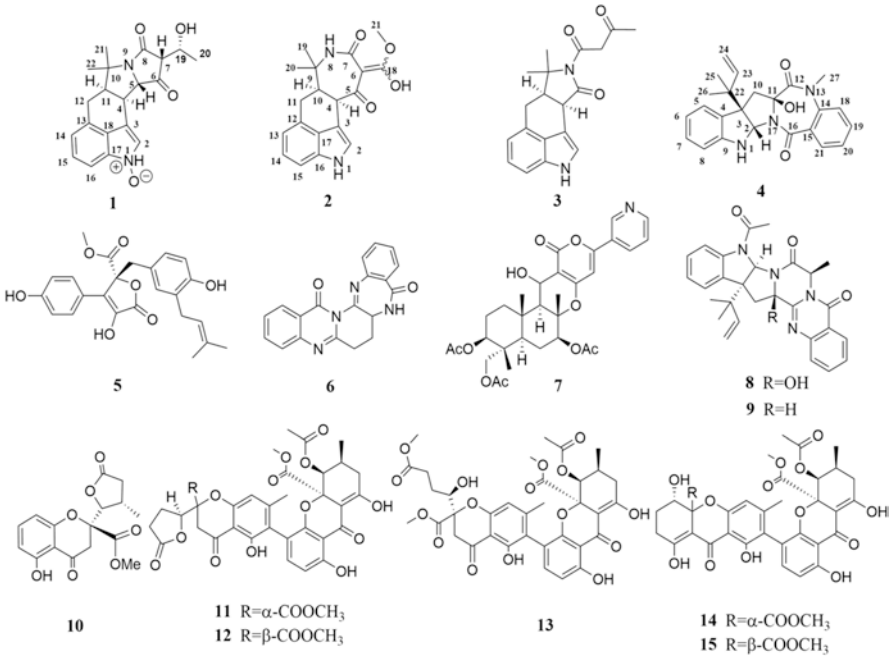


Fig. 1 The chemical structure of 1–15 compounds. (Wang et al. 2021)

alkaloids have also been screened for their anti-microbial potencies against 3 phytopathogeic fungi; namely *Fusarium oxysporum*, *Rhizoctonia solani,* and *Colletotrichum gloeosporioides* penz, and against 2 phytopathogenic bacteria, including *Xanthomonas oryzae* pv. *oryzicola* and *Xanthomonas oryzae* pv. *oryzae*. Compounds 13 and 15 have demonstrated significant anti-bacterial potential against *X. oryzae* pv. *oryzicola* recording MIC value of 25 µg/ ml.

Aconitine is a diterpenoid alkaloid observed in *Aconitum* spp., which is a voltage-gated sodium channel activator that opens the Na^+ channels effectively, thus causing prolonged presynaptic depolarization of the neurons and muscles. This alkaloid is also synthesized by *Cladosporium cladosporioides*; an endophytic fungus that inhabits *Aconitum leucostomum* (Yang et al. 2013). In the Chinese folk medicine, aconitine is used to relief the pain caused by the intercostal neuralgia, trigeminal, migraine, and rheumatism, in addition to the general debilitation (Singh et al. 2021).

Piperine is an anti-inflammatory and anticancer alkaloid that has been recorded in the fruits of *Piper nigrum* and *Piper longum*, and is responsible for their pungent taste. Piperine has also been extracted from cultures of several endophytic fungi; mainly *Mycosphaerella* sp., *C. gloeosporioides,* and *Periconia* sp. that have been originally isolated from *Piper* spp. (Chithra et al. 2014). This alkaloid decreases the renal glutathione concentration and renal glutathione reductase activity, and enhances the hepatic-oxidized glutathione, thus demonstrating an anti-diabetic efficacy.

5.2 Polyketides

Using a culture of *Alternaria* sp. that is an endophytic fungus, about 6 new polyketides have been isolated, including alternaritins A-D [(±)-1–4] and isoxanalteric acid I (8), in addition to 25 known toxins of *Alternaria* (Tian et al. 2021). The bioactivities of all these polyketides compounds have been evaluated. The 2 new compounds; 2 and 3, have displayed moderate inhibitory activity against COX-2 cell line, while the pair of isomers; 8 and 9 have demonstrated medium potential against COX-2 and against the uropathogenic bacterium *Escherichia coli* (Tian et al. 2021).

Cladosporitides A–C (Fig. 2) are 3 new polyketides, which are isolated from *Cladosporium tenuissimum*; an endophytic fungus obtained from the *Berberis*

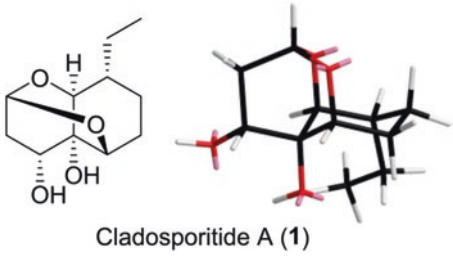


Fig. 2 Chemical structure of Cladosporitide A. (Feng et al. 2021)

heteropoda stem (Fig. 2). Using an anti-inflammatory assay, the compounds 1–3 manifested moderate inhibitory efficacies against LPS-induced NO production in RAW 264.7 cells; recording IC_{50} that ranged from 22.32–33.97 lM (Feng et al. 2021).

5.3 Alkaloids

According to the previous study conducted by Wang et al. (2011), alkaloids are defined as a class of nitrogenous organic compounds biosynthesized from amino acids. Moreover, they are well defined for their various biological activities, including antiviral, antifungal, and anticancer efficacies, in addition to being important sources of drugs. Barros and Rodrigues-Filho (2005) reported the production of spiroquinazoline alkaloids, such as alantrypinene, alanditrypinone, alantryleunone, and alantryphenone, by the endophytic fungus termed *Eupenicillium* sp., which has been isolated from *Murraya paniculata* leaves (Fig. 3).

5.4 Phenolic Compounds

The phenolic compounds represent the largest group of fungal secondary metabolites. Most of the plant phenolics are products of the shikimic acid pathway produced through the phenylpropanoid metabolism. The class of phenolics comprises important subclasses including the flavonoids and lignans. Meanwhile, the flavonoids include several subclasses, including tannins, isoflavonoids, anthocyanin

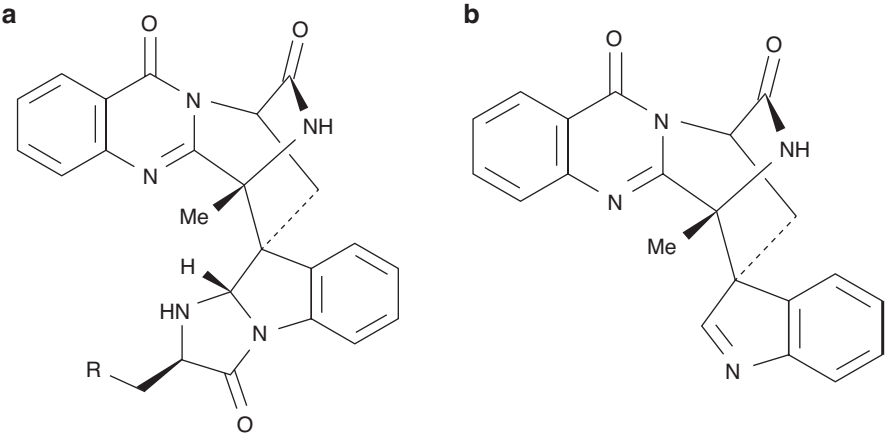
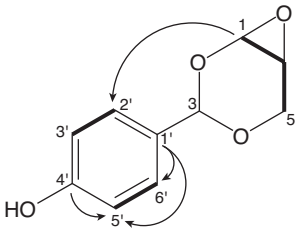
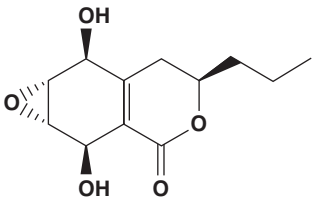


Fig. 3 Structures of some spiroquinazoline alkaloids recovered from *Eupenicillium* sp.; an endophytic fungus that has been isolated from the leaves of *Murraya paniculate*. (**a**) Alanditrypinone (R = 3-indolyl); Alantryphenone (R = Ph); Alantryleunone (R = CHMe2), and (**b**) Alantrypinene. (Mathur et al. 2021)

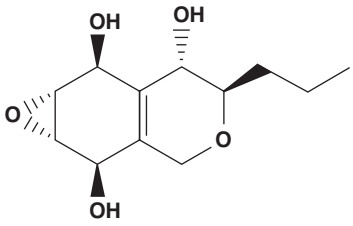
pigments, flavones, flavanones, catechins, leucoanthocyanidins, aurones, and chalcones. The tannins act as wood protectants and feeding deterrents. However, the isoflavonoids act as signaling molecules, in addition to being used by the plants as a defense mechanism (Croteau et al. 2000) (Fig. 4).



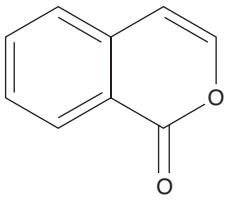
4-(2,4,7-trioxa-bicyclo[4.1.0]heptan-3-yl) phenol



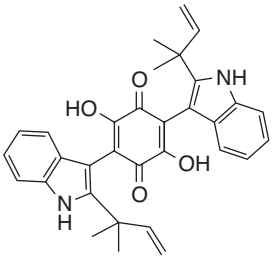
Cycloepoxylactone



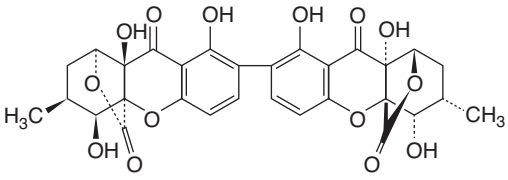
Cycloepoxytriol B



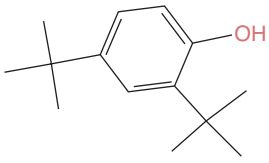
Isocoumarin



Hinnuliquinone



Ergoflavin



Phenol,2,4-bis (1,1-dimethylethyl)

Fig. 4 Chemical structures of some phenolic compounds recovered from the leaf endophytes. (Mathur et al. 2021)

The previous study conducted by Subban et al. (2013) reported that *Pestalotiopsis mangiferae;* an endophytic fungus that inhabits the leaves of *Mangifera indica,* synthesizes a phenolic compound termed 4-(2,4,7-trioxa-bicyclo [4.1.0] heptan-3-yl) phenol, which has displayed significant antifungal and antibacterial efficacies against *C. albicans*; *E. coli*, *P. aeruginosa*, *K. pneumoniae*, *B. subtilis,* and *Micrococcus luteus*. This phenolic compound forms pores in the bacterial cell wall leading to its destruction. Furthermore, *Phomopsis* sp. recovered from the leaves of *Laurus azorica* produces cycloepoxytriol B and cycloepoxylactone, which have demonstrated significant inhibitory activities against *Chlorella fusca*, *Bacillus megaterium,* and *Microbotryum violaceum*.

5.5 Lipids

Lipids are composed of several natural compounds such as essential oils; waxes, fixed oils, phospholipids, fat-soluble vitamins (i.e. vitamins A, D, E and K) and sterols (Hussein and El-Anssary 2018). The essential oils are defined as low molecular weight volatile compounds, including menthol; linalool, camphor, and menthone, which have analgesic; sedative, anesthetic, antiseptic, and spasmolytic activities. Manganyi et al. (2019) revealed that linoleic acid (A) and cyclodecasiloxane (B) produced by the endophytic fungus *Alternaria* sp. that is recovered from *Pelargonium sidoides* plant; expressed antibacterial potency against *Bacillus cereus*, *Enterococcus gallinarum,* and *Enterococcus faecium* (Fig. 5).

Meanwhile, the previous study conducted by Santos et al. (2015) reported that the leaves of *Indigofera suffruticosa* are colonised by about 65 fungal endophytes, where *Pestalotiopsis maculans* and *Nigrospora sphaerica* exhibited antibacterial efficacy against *Staphylococcus aureus*. Moreover, the endophytic bacterial strain of EML-CAP3 that is recovered from *Capsicum annuum* produced lipophilic

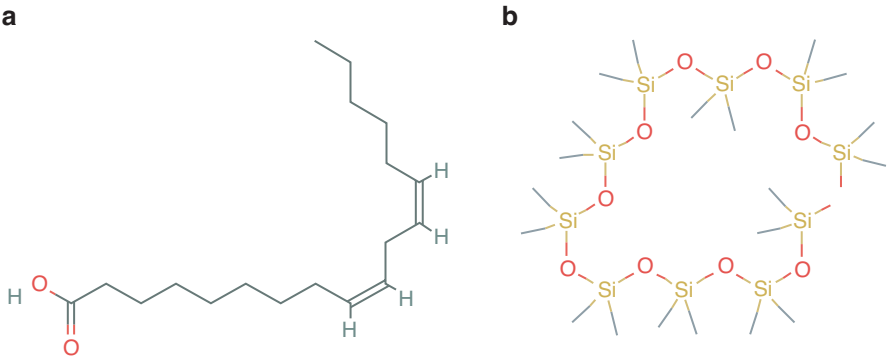


Fig. 5 Chemical structures of (**a**) Linoleic acid and (**b**) Cyclodecasiloxane recovered from *Pelargonium sidoides* leaf endophytes. (Mathur et al. 2021)

antimicrobial peptides, which are reported to exhibit anti-angiogenic potential (Jung et al. 2015).

5.6 *Terpenoids and Steroids*

Recently, Mathur et al. (2021) defined the terpenoids and steroids as the major classes of metabolites derived from isopentenyl diphosphate, which are biosynthesized through the glyceraldehyde 3-phosphate\pyruvate pathway and\or the acetate\mevalonate pathway. The diterpenes commonly include the gibberellin hormones, resins, and phytol. The triterpenoids include the toxins and phytoalexins, while the sesquiterpenes majorly comprise the essential oils (Croteau et al. 2000). The endophytic fungi produce sesquiterpenes, diterpenoids, and triterpenoids, which are mainly responsible for their antimicrobial potentials (Geetanjali 2017). The endophytic fungus *Alternaria alternata* recovered from the leaves of *Azadirachta indica* synthesizes more than 10 varieties of terpenes, which have shown antibacterial potency against *Listeria monocytogenes*, *B. subtilis*, *Staphylococcus aureus*, *E. coli,* and *Salmonella typhimurium*. Furthermore, these compounds demonstrated strong antioxidant efficacies (Chatterjee et al. 2019) (Fig. 6).

The Pestalotiopens A compound (Fig. 7) produced by endophytic fungus *Pestalotiopsis* sp. that is recovered from the leaves of *Rhizophora mucronate* has displayed antibacterial potential against *E. faecalis*, as revealed by Deshmukh et al. (2015).

Woodrow et al. (2005) reported that a sesquiterpene lactone with endoperoxide trioxane moiety called Artemisinin has been recovered from the *Artemisia annua*

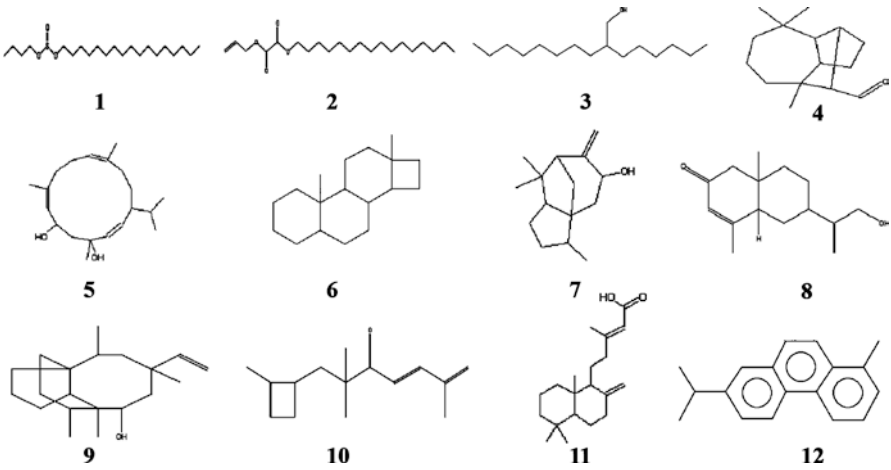


Fig. 6 Chemical structures of terpenes obtained from *Azadirachta indica* leaf endophytes (Chatterjee et al. 2019)

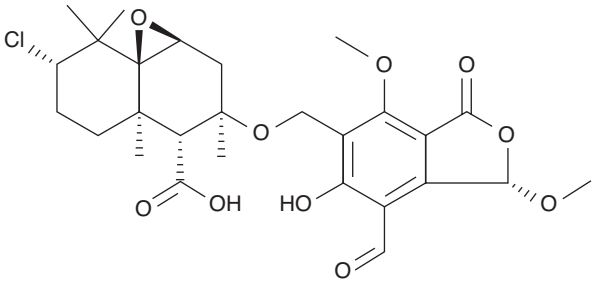


Fig. 7 Chemical structure of Pestalotiopens A. (Mathur et al. 2021)

plant; as its active antimalarial component. This terpene and its derivatives have several biological potentials, such as anti-inflammatory, anticancer, and immune-regulatory; without any risk of drug-resistance development (Das 2015). Recently, Bridgford et al. (2018) added that Artemisinin antimalarial potency operates through ROS generation, causing compromisation of the parasite proteasome function in addition to protein damage, thus inducing the stress response of the endoplasmic reticulum (ER).

5.7 Vinblastine

The terpenoid indole alkaloid derivatives such as vincristine and vinblastine are anti-cancerous agents, which are obtained by the combination of catharanthine and vindoline monomers (Selvakumar and Panneerselvam 2018). Vincristine interferes with the mitotic spindle dynamics and microtubule formation; decreases the tumor blood flow probably as a result of anti-angiogenesis, and causes disruption of the intracellular transport.

On the other hand, an early study conducted by Barnett et al. (1978) documented that vinblastine and vincristine are two natural alkaloids recovered from *Catharanthus roseus* or *Vinca rosea*, which are the major drugs used in treatment of lymphoma and leukemia, respectively. The importance of *Catharanthus roseus* plant is attributed to the presence of vinblastine and vincristine as 2 bisindole anti-tumor alkaloids. In addition, both of these alkaloids can lower the number of leukocytes. As anti-cancerous drugs, vinblastine and vincristine bind to the tubulin and prevent mitosis in the metaphase, thus preventing the cells from making the spindles that are needed for their division. Later, Creasey (1979) added that to mediate their cytotoxic action, vinblastine and vincristine bind intracellularly to the tubulin, thus causing subsequent dissolution of the microtubules and arrest of the cells during the mitosis phase.

5.8 Paclitaxel

A highly functionalized diterpenoid named Paclitaxel (Taxol) exists in yew (*Taxus*) species; however, it is mainly isolated from *Taxus brevifolia* plant. Taxol compound is the world's first expensive anticancer drug used for the treatment of breast and ovarian cancers, in addition to being currently used for the treatment of other human tissue-proliferating diseases. Furthermore, in South Carolina, several *Pestalotiopsis microspora* isolates have been recovered from the bald cypress and also produce Taxol. Many other endophytic fungi produce Taxol including *Periconia* sp. and *Pestalotiopsis guepini* (Strobel et al. 1997). Taxol has proven to exhibit an efficient action against several types of cancers, including ovarian; prostate, lung, and breast cancers. It acts through stabilizing the microtubules and then disrupts their dynamic equilibrium (Wang et al. 1999).

During the study reported by Zhao et al. (2010), about 19 genera of endophytic fungi, such as *Aspergillus*; *Alternaria*, *Botryodiplodia*, *Cladosporium*, *Botrytis*, *Ectostroma*, *Metarhizium*, *Fusarium*, *Monochaeti*a, Ozonium, *Mucor*, *Papulaspora*, *Pestalotia*, *Periconia*, *Pestalotiopsis*, *Pithomyces*, *Taxomyces*, *Phyllosticta,* and *Tubercularia*, have been screened for their capacity to produce Taxol and its analogues (i.e. baccatin III, 10-deacetylbaccatin III).

The hosts of paclitaxel-producing fungi include several *Taxus* spp.; mainly *T. cuspidate*, *T. baccata*, *T. yunnanensis,* and *T. media,* in addition to non-*Taxus* spp.; such as *Citrus medica*; *Cardiospermum helicacabum*, *Ginkgo biloba*, *Cupressus* sp., *Podocarpus* sp., *Taxodium distichum*, *Hibiscus rosa-sinensis*, *Terminalia arjuna*, *Wollemia nobilis,* and *Torreya grandifolia*. These recorded results demonstrate that endophytic fungi will be considered as promising alternative resources for the production of paclitaxel.

The supply of taxol from the stem bark of Pacific yew tree (*Taxus brevifolia* Nutt.) (*Taxaceae*) is limited (Wheeler et al. 1992); as this plant does not abundantly exist in nature (Cragg et al. 1993), and it grows slowly (Flores and Sgrignoli 1991); in addition, it contains trace amounts of paclitaxel (Banerjee et al. 1996). Taxol has become widely used as an anticancerous drug for the treatments of lung (Ettinger 1992), neck and head (Forastiere et al. 1993), prostrate, renal, colon, gastric, pancreatic, and cervix cancers (Brown et al. 1993). Furthermore, Taxol has also demonstrated effectiveness against noncancerous conditions such as polycystic kidney diseases (Woo et al. 1994). On the contrary to the other anti-microtubular agents, such as colchicine; podophyllotoxin, combretastatin, and vinca alkaloids, which act through inhibiting the microtubule assembly, Taxol stabilizes the microtubules against depolymerization. Through this mechanism of action, Taxol blocks the cancer cells capacity to disassemble the mitotic spindle during division, thus the cells become blocked in the G2\M phase of their cycle (Schiff et al. 1978), and leads finally to cells death.

5.9 Camptothecin (CPT)

A pentacyclic quinoline alkaloid termed Camptothecin (CPT) has been initially isolated from the wood of *Camptotheca acuminate*, and acts as an antineoplastic agent. The primary mode of action of CPT is through inhibiting the intranuclear enzyme topoisomerase-1, which is requested during the molecular events of DNA replication and transcription (Selvakumar and Panneerselvam 2018).

Camptothecin and its analogue10-hydroxycamptothecin are two of the potent antineoplastic agents. Sirikantaramas et al. (2007) reported that Camtostar (irinotecan) and Hycamtin (topotecan) are two of the effective CPT semi-synthetic drugs, which are being used against the ovarian, small lung, and refractory ovarian cancers. An endophytic fungus termed *Entrophospora infrequens* recovered from *Nothapodytes foetida* has been first reported by Puri et al. (2005), which has the capacity to produce Camptothecin.

5.10 Podophyllotoxin (PDT)

Podophyllotoxin (PDT) mainly exists in several genera of *Sabina* (Juniperus); Diphylleia, Sinopodophyllum (Podophyllum), and Dysosma (Cao et al. 2007). About 6 endophytic fungi recovered from *Dysosma veitchii*, *Sinopodophyllum hexandrum,* and *Diphylleia sinensis* has been first recorded by Yang et al. (2003), which have the capacity to produce PDT. Furthermore, Lu et al. (2006) later reported that *Alternaria* sp., which is an endophytic fungus recovered from *Sabina vulgaris* is able also to produce Podophyllotoxin. This aryltetralin lignan has potent antiviral; antibacterial, anticancer, immunostimulation, anti-rheumatic, and antioxidant activities. Kour et al. (2008) added that PDT has been used as a precursor for the chemical synthesis of several anticancer drugs, including etoposide, etopophose phosphate, and teniposide. These drugs are commonly used in the treatment of testicular cancer, lung cancer, and various other solid tumors, in addition to leukemias (Majumder and Jha 2009).

Podophyllotoxin is commercially extracted from the rhizomes and roots of *Podophyllum peltatum* L. (the American *Podophyllum*) and *Podophyllum hexandrum* Royle (the Indian *Podophyllum*), which belong to the family of *Berberidaceae*. However, agricultural production of PDT is difficult, as growth of this plant needs proper climatic conditions (Lee and Xiao 2003). Accordingly, production of PDT through several endophytic fungi, such as *P. peltatum*; *P. hexandrm*, *Juniperus recurva* L. *Horstmann,* and *J. communis*, are being extensively explored as alternative sources of PDT (Chandra 2012).

6 Bio-applications of the Endofungal Metabolites

The endophytic fungal metabolites have potent bioactivities including;

6.1 Antibacterial Potential

The recent study conducted by Nischitha and Shivanna (2022) demonstrated that some of the major compounds detected in the endophyte *Chaetomium subaffine* and in *Heteropogon contortus* as its host grass, include 2,3-dichloro-1-hexanol, phytosphingosine, and hexadecasphinganine, in addition to 11 major peak compounds. Out of the 14 major studied bioactive compounds, 4 antibacterial drugs including andrographolide; phytosphingosine, schaftoside, and hexadecasphinganine, have presented good binding affinity towards 5 proteins, which are related to the inhibition of bacterial DNA, protein, and cell wall synthesis.

The ethyl acetate extract of about 70 endophytic fungal strains recovered from the leaves of *Laguncularia racemosa* (L.) Gaertn plant demonstrated antibacterial efficacy against several bacterial genera; mainly *B. subtilis*, *E. faecalis*, *E. coli*, *Staphylococcus aureus*, *P. aeruginosa,* and *Micrococcus luteus* Furthermore, results of screening for in vitro antibacterial potency of the crude extracts of *T. reesei* and *T. viride* on CYS80 medium, showed effectiveness against several tested bacterial spp., such as *Staphylococcus agalactiae*, *E. coli*, *S. aureus*, *Streptococcus pyogenes*, *S. pneumoniae*, methicillin-resistant *Staphylococcus aureus*, *E. faecalis*, *K. pneumoniae*, *P. mirabilis*, *P. aeruginosa,* and *S. sonnei* (Selvakumar and Panneerselvam 2018).

A new isocoumarin derivative named Pestalotiopisorin B (1) has been extracted from *Pestalotiopsis* sp.; the endophytic fungus associated with *Rhizophora stylosa* that is a mangrove plant collected from China. This pestalotiopisorin B compound expressed moderate antibacterial potential against *P. aeruginosa* and *E. coli*, recording MIC values of 50 and 12.5 mg\ml, respectively (Xu et al. 2018). An anthraquinone; emodin (31) (Fig. 8), has been obtained from *Eurotium chevalieri* KUFA 0006, an endophytic fungus associated with *Rhizophora mucronata* Poir collected from Thailand. This compound showed antibacterial efficacy against *E. faecalis* and *S. aureus,* exhibiting MIC values of 64 and 32 mg\ml, respectively (Zin et al. 2017).

Asperphenone A and B (42, 43) (Fig. 8) are 2 phenone derivatives, which have been obtained from *Aspergillus* sp. YHZ-1 that inhabits unknown mangrove plants from China. They presented mild antibacterial potency against 4 bacterial spp., including *S. pyogenes* ATCC19615, *Staphylococcus. aureus* CMCC(B) 26003, *M. luteus,* and *B. subtilis* CICC 10283, recording MIC values in the range of 0.33–21.6 mg\ml (Guo et al. 2018). Penibenzophenone A, is a new compound that has been recovered from *Penicillium citrinum* HL-5126; an endophytic fungus obtained from *Bruguiera sexangula* var. *rhynchopetala*; which is a mangrove plant collected from the South China Sea. This new compound exhibited antibacterial efficacy against *S. aureus* recording MIC value of 20 mg\ml (Zheng et al. 2018).

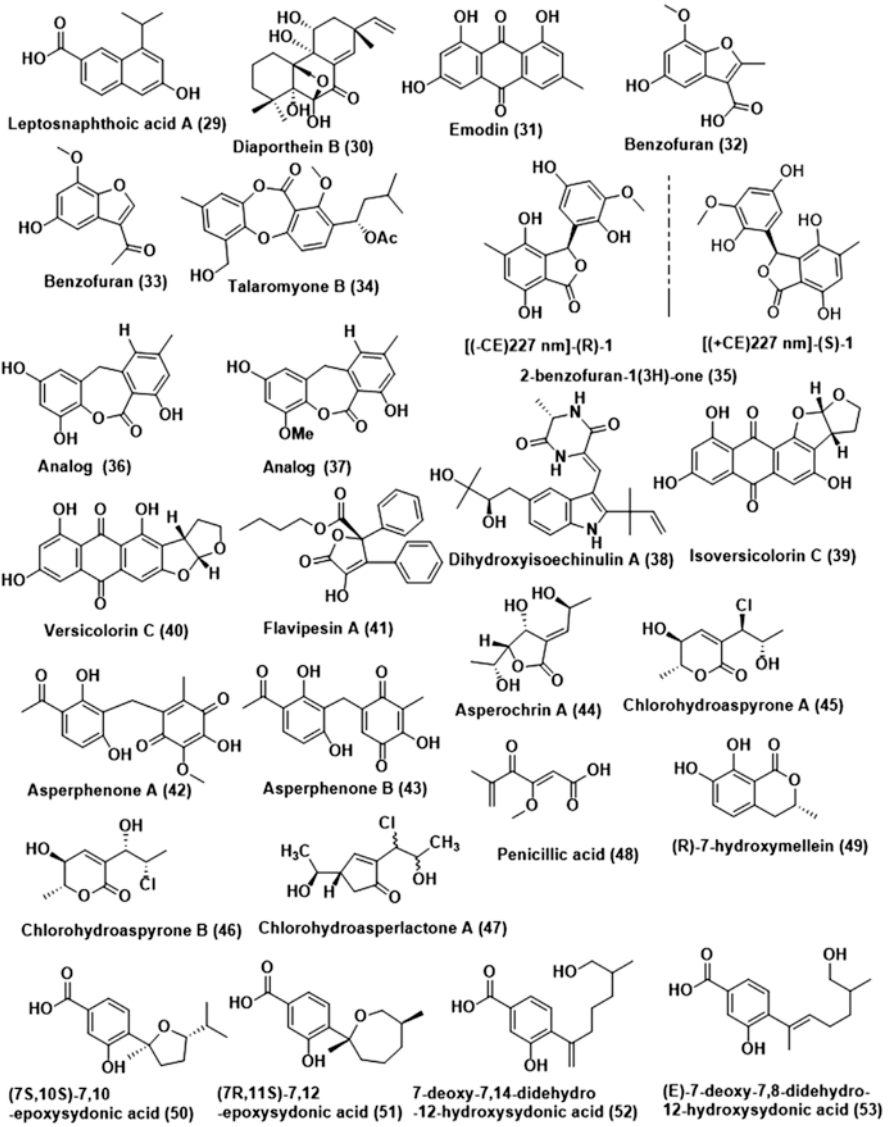


Fig. 8 Chemical structures of several bioactive compounds recovered from mangrove endophytic fungi that have demonstrated antibacterial potential (Deshmukh et al. 2020)

A novel isoprenylisoindole alkaloid termed Diaporisoindole A, together with its precursor named tenellone C have been isolated from *Diaporthe* sp. SYSU-HQ3; an endophytic fungus isolated from a mangrove plant named *Acanthus ilicifolius* that has been collected from China. Both compounds demonstrated inhibitory potential against the protein tyrosine phosphatase B (MptpB) of *M. tuberculosis,* recording IC_{50} values of 1.77 and 2.2 mg\ml, respectively (Cui et al. 2017).

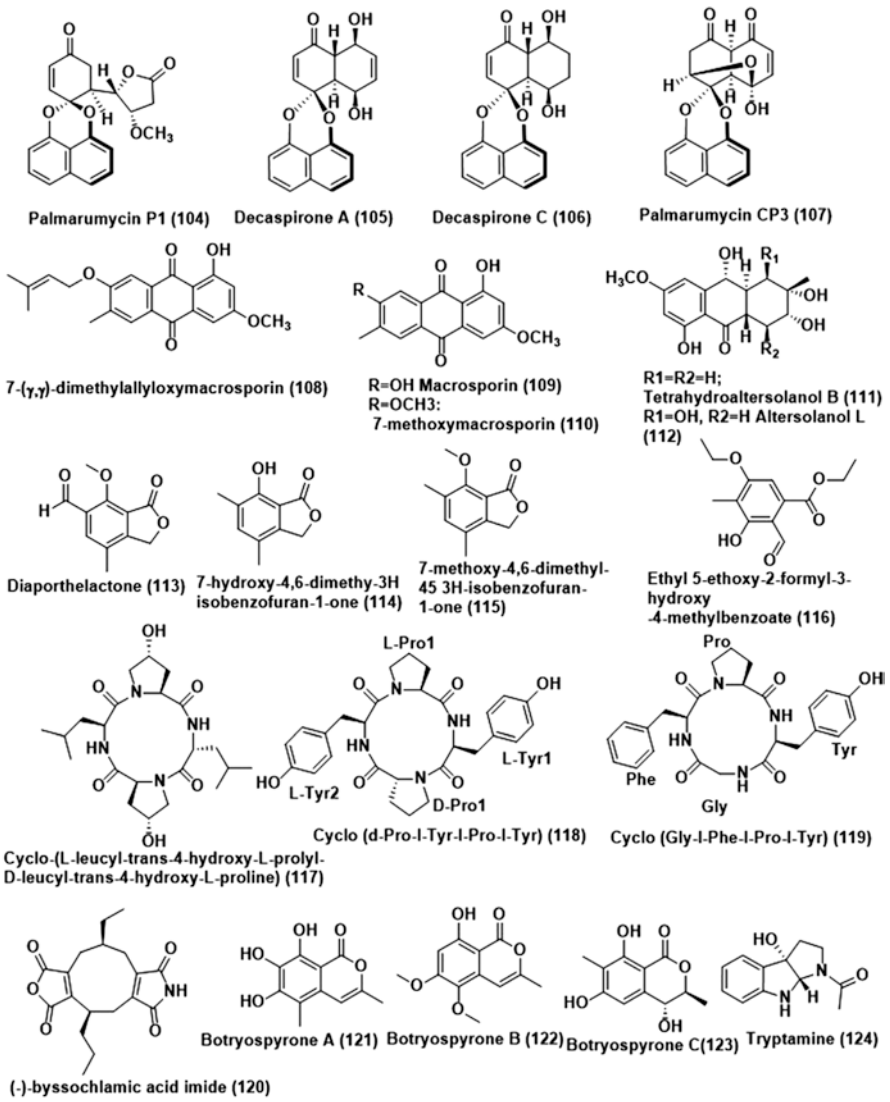


Fig. 9 Chemical structures of some metabolites recovered from mangrove endophytic fungi presenting anti-mycobacterial potency (104–107) and antifungal efficacy (108–124). (Adopted by Deshmukh et al. 2020)

Several compounds belonging to spirodioxynaphthalenes group, including palmarumycin CP3 (107) and palmarumycin P1 (104), in addition to decaspirones A (105) and C (106) (Fig. 9), have been extracted from the fungus BCC 25093 that is recovered from an unidentified mangrove wood of Thailand. These compounds expressed anti-tuberculosis potential against *Mycobacterium tuberculosis* H37Ra, recording MIC values of 3.13 mg\ml for palmarumycin CP3 (107) and decaspirone

C (106), and 1.56 mg\ml for decaspirone A (105) and Palmarumycin P1 (104) compounds (Bunyapaiboonsri et al. 2015).

During the previous study conducted by Qadri et al. (2013), about 4 endohytic fungi have been isolated from the medicinal plants of Western Himalayas; mainly *Alternaria* sp., *Fusarium* sp., *Chaetomium* sp., and *Penicillium* sp., which have suppressed the growth of *E. coli* and *S. aureus*, whereas *Fusarium* sp. has inhibited the growth of *Staphylococcus aureus*.

6.2 Antifungal Efficacy

The study conducted by Wu et al. (2019) reported that Botryospyrones A (121), B (122), C (123); new derivatives of isocoumarin, and (3aS, 8aS)-1-acetyl-1, 2, 3, 3a, 8, 8a-hexahydropyrrolo [2,3b] indol-3a-ol (124); a new tryptamine (Fig. 8), have been isolated from *Botryosphaeria ramosa* L29; an endophyte associated with *Myoporum bontioides* leaves collected from China. Botryospyrone A (121) has been active against *F. oxysporum* recording MIC of 25.11 mg\ml, and has expressed weak antifungal potency towards *F. graminearum,* recording MIC of 200.75 mg\ml. Meanwhile, Botryospyrone B (122) has expressed moderate antifungal potential against *F. graminearum*, *F. oxysporum,* and *P. italicum;* recording MIC values of 50.18, 25.0, 50.18 mg\ml, respectively. Botryospyrone C (123) has shown antifungal efficacy against *F. graminearum* and *F. oxysporum*, recording MIC value of 50.1 mg\ml. Finally, (3aS, 8aS)-1-acetyl-1, 2, 3, 3a, 8, 8a-hexahydropyrrolo [2,3b] indol-3a-ol (124) compound has expressed antifungal potential against *F. graminearum*, *F. oxysporum*, and *P. italicum*, with MIC values of 6.26, 6.26 and 12.5 mg\mL, respectively.

Fusarihexin A and fusarihexin B are two novel cyclic hexadepsipeptides, in addition to a known compound named cyclo-(L-Leu-L-Leu-DLeu-L-Leu-L-Val), have been extracted from *Fusarium* sp. R5; a semi-mangrove fungus that resides within the *Myoporum bontioides* plant collected from China (Zhu et al. 2018). A bioactive compound termed Fusarihexin A showed promising antifungal potency against 3 phytopathogens, including *F. oxysporum* Schlecht f. sp. *lycopersici* that causes fruit rot and *Fusarium* wilt in tomatoes, *Colletotrichum musae* that causes crown rot and anthracnose in bananas, and *Colletotrichum gloeosporioides*, the fungal causal agent of anthracnose in different vegetables, recording MIC values of 7.73, 19.96, and 12.43 mg\ml, respectively. Similarly, Fusarihexin B presented antifungal efficacy against *C. musae*, *C. gloeosporioides*, and *F. oxysporum,* exhibiting MIC values of 12.3, 12.3, and 24.7 mg\ml, respectively. Finally, cyclo (LLeu-L-Leu-D-Leu-L-Leu-L-Val) bioactive compound expressed moderate antifungal potential against *F. oxysporum*, *C. musae,* and *C. gloeosporioides*, expressing MIC values of 12.7, 24.85, and 50.2 mg\ml, respectively.

The previous study conducted by Huang et al. (2017) reported that 7-(g,g)-dimethylallyloxymacrosporin (108); a new anthraquinone, along with 7-methoxymacrosporin (110), macrosporin (109), altersolanol L (112), and

tetrahydroaltersolanol B (111) (Fig. 9), have been recovered from *Phoma* sp. L28 endophyte that has been isolated from a mangrove plant collected from China. These compounds demonstrated significant antifungal potential against *F. graminearum*, *C. musae*, *Penicillium italicum*, *C. gloeosporioides*, *Rhizoctonia solani,* and *F. oxysporum* f. sp. *lycopersici*, recording MIC values that ranged from 3.75 mg\ml to 100 mg\ml. Furthermore, Altersolanol L (112) expressed antifungal efficacy against *R. solani* and *P. italicum;* expressing MIC values of 50 and 35 mg\ml, respectively. Meanwhile, tetrahydroaltersolanol B (111) has been effective against *P. italicum* only recording MIC of 80 mg\ml. On the other hand, Altersolanol L (112) has demonstrated weak efficacy against *C. gloeosporioides* and *F. graminearum;* recording MIC values of 200 and 100 mg\ml, respectively.

The antifungal metabolite Ergokonin A, which has been isolated from *T. longibrachiatum*, has expressed very broad antifungal activity against *S. cerevisiae*, *Candida* sp., and several other filamentous fungi (Vicente et al. 2011).

The marine genus of *Trichoderma* produces several bioactive metabolites, including (a) the anti-mycobacterial compounds such as trichoderins and aminolipopeptids (Pruksakorn et al. 2010), (b) the antifungal, (c) the cytotoxic dipeptide, and (d) the trichodermamide B ketone (Garo et al. 2003), in addition to the antibacterial metabolites; mainly the tetra hydroanthraquinone and xanthone derivatives. Moreover, two pyridines including Trichodin A and Trichodin B, in addition to a known Pyridoxatin compound, have been extracted from the mycelia and culture broth of the same marine fungus. *Trichoderma* metabolites are effective against Gram-positive bacteria (i.e. *Staphylococcus aureus* and *B. subtilis*), and against the yeast fungus *C. albicans*. On the other hand, pyridoxatin has been effective against *Staphylococcus aureus*, *Staphylococcus epidermis*, *B. subtilis*, *Trichophyton rubrum,* and *C. albicans* (Wu et al. 2014).

6.3 Antiviral Potency

A new naphthalene derivative named Vaccinal A (159) (Fig. 10), has been isolated from *Pestalotiopsis vaccinii* (cgmcc3.9199); an endophyte recovered from a branch of *Kandelia. candel* that is widely distributed in China. This compound has showed in vitro anti-Enterovirus 71 (EV71) activity, with an IC_{50} of 3.88 mg\mL (Wang et al. 2014). Vaccinol J, is a new salicyloid derivative that has been also recovered from *Pestalotiopsis vaccinii* (cgmcc3.9199). Vaccinol J expresses in vitro anti-Enterovirus 7 l (EV71) potential with an IC_{50} of 8.36 mg\ml; in addition, this manifested inhibitory potential has been stronger than the positive control Ribavirin, which recorded IC_{50} of 43.22 mg\ml (Wang et al. 2017).

An unprecedented meroterpenoid termed Simpterpenoid A has been recovered from *Penicillium simplicissimum* MA-332 fungus, which inhabits the rhizosphere soil of *Bruguiera sexangula* var. *rhynchopetala*; a mangrove plant collected from the South China Sea. Simpterpenoid A bioactive compound has shown promising antiviral potency against Influenza neuraminidase virus recording an IC_{50} of

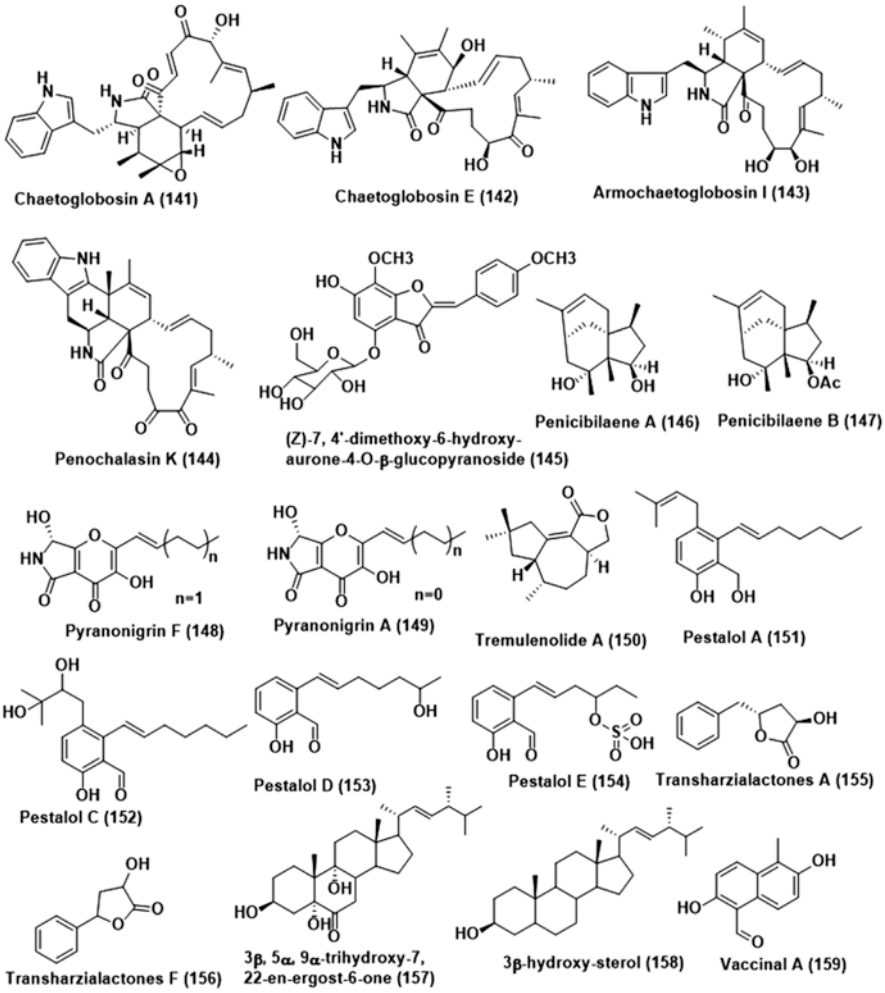


Fig. 10 Chemical structures of some bioactive metabolites that have been recovered from mangrove endophytic fungi; expressing antifungal (141–150) and antiviral activities (151–159) (Deshmukh et al. 2020)

0.003 mg\ml, whereas Oseltamivir (positive control) demonstrated antiviral efficacy with an IC_{50} of 0.00099 mg\ml (Li et al. 2018). The new brefeldins E1E5 (174178), in addition to the known brefeldins A 7-O-acetate; brefeldin A, 30-hydroxyalternar iol-5-O-methyl ether, alternariol-5-O-methyl ether, and mangrovamides A, have been obtained from *Penicillium* sp.; an endophytic fungus inhabiting the root of *Panax notoginseng* collected from China. The bioactive compounds, including Mangrovamides A; Brefeldin E1E5 (174178), 30-hydroxyalternariol-5-O-methyl ether, and alternariol-5-O-methyl ether, have expressed weak antiviral potency. On the other hand, the compounds brefeldin A 7-O-acetate and brefeldin A have shown

significant antiviral potential against HCV and HBV viruses, recording ID_{50} values in the range from 4.03 mg\ml to 7.09 mg\ml, respectively (Xie et al. 2017).

During the previous study reported by Yu et al. (2015), several potent bioactive compounds; named Fumiquinazoline alkaloids and Neosartoryadins A and B, have been recovered from *Neosartorya udagawae* HDN13-313, which is an endophytic fungus. Neosartoryadins A and B have manifested anti-influenza virus A (H1N1) potential; recording IC_{50} of 32.11 and 29.14 mg\ml; respectively, whereas Ribavirin as a positive control exhibited an IC_{50} of 22.95 mg\ml.

6.4 Anti-Cancerous Activity

Epothilones are secondary metabolites produced by *Sorangium cellulosum* plant with powerful anti-proliferative potential against the tumor cells; through arresting their cellular division at the G2-M phase and stabilizing their microtubule arrays. However, epothilone is produced by this plant in low yield. As an endophyte of *Catharanthus roseus* plant, *Aspergillus fumigatus* EFBL is a potent alternative epothilone producer, yielding about 21.5 μg\g biomass. Epothilone B metabolite produced by *A. fumigatus* has demonstrated significant anti-proliferative potency against MCF-7, LS174, and HepG-2 T cell lines, recording IC_{50} values of 8.7, 10.21 and 6.4 μM, respectively. The recent study conducted by El-Sayed et al. (2021) has explored for the first time the feasibility of using an endophytic fungus for epothilone production, thus *A. fumigatus* could be considered as a novel source for the production of this anticancerous metabolite on the industrial scale.

Sclerotiorin metabolite is recovered from the endophytic fungus *Cephalotheca faveolata*, and has demonstrated effective anti-proliferative activity against various cancer cells. This metabolite causes apoptosis in the colon cancer cells (i.e. HCT-116); through activation of the BAX and down regulation of the BCL-2. In addition, it stimulates the dissected caspase-3 leading to apoptosis of the cancer cells (Giridharan et al. 2012).

6.5 Cerebral Stimulant and Vasodilator

The cardiovascular disease (CVD) is one of the major causes of human deaths worldwide. Statins are a group of drugs that decreases the cholesterol level in the blood, which include lovastatin and compactin (Barrios-González and Miranda 2010). Lovastatin is a polyketide metabolite that is known as 'Merck's Mevacor', which is an anti-cholesterol agent. This metabolite is produced by several fungal endophytes; mainly *Aspergillus niger*, *Aspergillus flavus*, *Aspergillus terreus*, *Monascus ruber*, *Trichoderma viride*, *Penicillium* sp., *Monascus* sp., Cinnamomum sp., and *Pleurotuso streatus* (Amin-Hanjani et al. 2001). Lovastatin acts through inhibiting the level of a rate-limiting enzyme that is known as

3-hydroxy-3-methyl-glutaryl-CoA (HMG-CoA) reductase, which converts HMG CoA to mevalonate and participates in the cholesterol biosynthesis (Rai et al. 2021).

Similar to its host plant *Garcinia macrophylla*; the created endophytic fungal strain QJ18 produces a biometric compound known as gentiopicrin. In addition, the medicinal plant *Vinca minor* produces the alkaline vincamine, which is used as a cerebral catalyst and as a vasodilator. Vincamine; as a bioactive constituent, is extracted from the endophytic fungus (Vm-J2) and from its host plant (Yin and Sun 2011).

6.6 Endophytes as Promoters of Plant Growth

The endofungi are capable of promoting the host plant growth and increasing the production of several bioactive secondary metabolites in the medicinal plants in a sustainable and ecofriendly manner (Chen et al. 2021).

Some endophytic fungi improve the growth of their host plants through the secretion of siderophores; to chelate the Fe^{+3} ion from the environment, solubilize the phosphorus and\or potassium in the soil, fix the atmospheric nitrogen, and provide nutrients for their host plants (Turbat et al. 2020). The endofungi that can exist with their hosts for a long time affect their hosts metabolism (Kusari et al. 2012). Colonization of the host plants by the endophytic fungi triggers their defense responses (Sabra et al. 2018). These responses include accumulation of secondary metabolites that antagonise the pathogens and overexpression of the defense enzymes, in addition to changes in the plant cell wall structures (Schulz and Boyle 2005). Furthermore, the endophytes produce fungal elicitors, which trigger the plant defenses; leading thus to the accumulation of bioactive secondary metabolites (Zhai et al. 2017).

Recently, Domka et al. (2019) added that the endophytic fungi are capable of protecting their host plants against the various pathogens, in addition to promoting their growth; leading thus to much higher yield and to an increase in the host resistance to the various biotic and abiotic stresses. The fungal endophytes produce several secondary metabolites that can be used as ecofriendly products for promoting the plant growth, including the siderophores, phytohormones, hydrogen cyanide, hydrolytic enzymes, and phosphate solubilizing agents (Rana et al. 2020). As endophytes, *Fusarium proliferatum* BRL1and *Aspergillus fumigatus* TS1, can produce the gibberellins phytohormone, in addition to regulating the plant endogenous hormones as well (Bilal et al. 2018).

Manipulation of the plant growth promoting (PGP) endophytes as biofertilizers in the agricultural sector has shown significant promise in providing an eco-friendly and effective method that ensures food security (Glick 2014).

7 Approach's Employed to Enhance the Production of Endofungal Secondary Metabolites

Microorganisms produce bioactive compounds in low quantities as a defence mechanism against the various biotic and abiotic stresses. Several techniques are often used to place the microorganism under stress to enhance the production of secondary metabolites, such as strain improvement; optimization, epigenetic modulation, and one strain many compounds (OSMAC) (Deshmukh et al. 2020).

Co-cultivation of two or more microorganisms together in the laboratory is used to create competition amongst these species and to activate the silent biosynthetic genes, which remain silent in the normal conditions. On co-cultivation, the microorganisms antagonise each other's and\or compete for the limited resources, which activate their defence mechanisms for survival, thus lead to the production of bioactive secondary metabolites. In addition, co-cultivation significantly enhances the production of bioactive compounds that are not produced in single culture of a producing strain (Marmann et al. 2014).

Pestalone is an example of an antimicrobial compound that is produced on mixed cultures of a fungus and a bacterium (Cueto et al. 2001). Similarly, aspergicin, ergosterol, and neoaspergillic acid; are compounds produced on using co-culture of a mangrove epiphyte, which express significant antibacterial potential against certain selected Gram-positive bacteria (Zhu et al. 2011).

A previous study conducted on a fungal genome has confirmed the presence of silent gene clusters, which are responsible for production of the secondary metabolites (Brakhage and Schroeckh 2011). Epigenetics regulate the action of these silent gene clusters (Cichewicz 2010). The epigenetic modulators can induce these silent genes in the endophytes, which results in the production of more and new bioactive compounds (Fischer et al. 2016). Recently, Pfannenstiel and Keller (2019) added that in order to enhance the production of secondary metabolites; the chemical inhibitors are used to induce the expression of cryptic genes of the fungal genome. The chemical inhibitors such as sodium butyrate and suberoylanilide hydroxamic acid (SAHA) that modulate the histone deacetylase (HDAC) activity; are commonly used for activation of the biosynthetic pathways involved in biosynthesis of the fungal secondary metabolites, which remain silent under the normal laboratory conditions (Cichewicz 2010 and Demers et al. 2018).

8 Conclusion

The fungal endophytes live symbiotically within their host plants without causing any harm; as most of them are non-parasitic, at least in their host plants. They are promising producers of novel natural bioactive compounds, which present significant activities in both of the medical and agricultural sectors worldwide. Accordingly, the endofungi can be manipulated as natural sources of drugs for treatment of the

multidrug resistant microorganisms and tumor diseases, and can be applied also as potent microbicides and biofertilizers to promote the plant growth. The endofungi produce these bioactive compounds in different and\or similar pathways as their respective host plants; however, these compounds can not be produced chemically. Finally, it is recommended to place these endophytic fungi under stress conditions such as growth in dual cultures; to induce the silent biosynthetic genes, which results in the production of more and novel bioactive compounds.

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References

Abreu-Tarazi MF, Navarrete AA, Andreote FD, Almeida CV, Tsai SM, Almeida M (2010) Endophytic bacteria in long-term in vitro cultivated axenic pineapple microplants revealed by PCRDGGE. World J Microbiol Biotechnol 26:555–560. https://doi.org/10.1007/s11274-009-0191-3

Amin-Hanjani S, Stagliano NE, Yamada M, Huang PL, Liao JK, Moskowitz MA (2001) Mevastatin, an HMGCoA reductase inhibitor reduces stroke damage and upregulates endothelial nitric oxide synthase in mice. Stroke 32:980–986

Ancheeva E, Daletos G, Proksch P (2019) Bioactive secondary metabolites from endophytic fungi. Curr Med Chem 26(11). https://doi.org/10.2174/0929867326666190916144709

Ansari P, Häubl G (2016) Determination of cyclopiazonic acid in white mould cheese by liquid chromatography-tandem mass spectrometry (HPLC-MS/MS) using a novel internal standard. Food Chem 211:978–982

Anupama N, Murali M, Jogaiah S, Amruthesh KN (2014) Crude oligosaccharides from *Alternaria solani* with *Bacillus subtilis* enhance defensive activity against early blight disease of tomato. Asian J Sci Tech 5:412–416

Baba MS, Zin NM, Hassan ZA, Latip J, Pethick F, Hunter IS, Edrada-Ebel R, Herron PR (2015) *In vivo* antimalarial activity of the endophytic actinobacteria, *Streptomyces* SUK 10. J Microbiol 53(12):847–855

Babu AN, Jogaiah S, Ito S, Amruthesh KN, Tran LSP (2015) Improvement of growth, fruit weight and early blight disease protection of tomato plants by rhizosphere bacteria is correlated with their beneficial traits and induced biosynthesis of antioxidant peroxidase and polyphenol oxidase. Plant Sci 231:62–73

Bamisile BS, Dash CK, Akutse KS, Keppanan R, Wang L (2018) Fungal endophytes: beyond herbivore management. Front Microbiol 9:544

Banerjee S, Upadhyay N, Kukreja AK, Ahuja PS, Kumar S, Saha GC, Sharma RP, Chattopadhyay SK (1996) Taxanes from in vitro cultures of the Himalayan Yew *Taxus wallichiana*. Planta Med 62:333–335

Barnett CJ, Cullinan GJ, Gerzon K, Hoying RC, Jones WE, Newlon WM, Poore GA, Robison RL, Sweeney MJ, Todd GC, Dyke RW, Nelson RL (1978) Structure-activity relationships of dimeric Catharanthus alkaloids 1. Deacetyl vinblastine amide (vindesine sulfate). J Med Chem 21:88

Barrios-González J, Miran da RU (2010) Biotechnological production and applications of statins. Appl Microbiol Biotechnol 85:869

Barros FAP, Rodrigues-Filho E (2005) Four spiroquinazoline alkaloids from *Eupenicillium* sp. isolated as an endophytic fungus from leaves of *Murraya paniculata* (*Rutaceae*). Biochem Syst Ecol 33(3):257–268

Bérdy J (2005) Bioactive microbial metabolites: a personal view. J Antibiot 58:1–26
Bilal L, Sajjad A, Hamayun M, Gul H, Iqbal A, Ullah I, Lee IJ, Hussain A (2018) Plant growth promoting endophytic fungi *Aspergillus fumigatus* TS1 and *Fusarium proliferatum* BRL1 produce gibberellins and regulate plant endogenous hormones. Symbiosis 76:117–127. https://doi.org/10.1007/s13199-018-0545-4
Brader G, Compant S, Vescio K, Mitter B, Trognitz F, Ma LJ, Sessitsch A (2017) Ecology and genomic insights into plant-pathogenic and plant-nonpathogenic endophytes. Annu Rev Phytopathol 55:61–83
Brakhage AA, Schroeckh V (2011) Fungal secondary metabolites_strategies to activate silent gene clusters. Fungal Genet Biol 48(1):15–22
Bridgford JL, Xie SC, Cobbold SA, Pasaje CF, Herrmann S, Yang T, Gillett DL, Dick LR, Ralph SA, Dogovski C et al (2018) Artemisinin kills malaria parasites by damaging proteins and inhibiting the proteasome. Nat Commun 9:1–9
Brown T, Tangen C, Flemming T, Macdonald J (1993) A phase II trial of taxol and granulocyte colony stimulating factor (G-CSF) in patients with adenocarcinoma of pancreas. Proc Am Soc Clin Onco 12:200
Bunyapaiboonsri T, Yoiprommarat S, Nopgason R, Intereya K, Suvannakad R, Sakayaroj J (2015) Palmarumycins from the mangrove fungus bcc 25093. Tetrahedron 71:5572–5578
Cao L, Huang J, Li J (2007) Fermentation conditions of *Sinopodophyllum hexandrum* endophytic fungus on production of podophyllotoxin. Food and Fermentation Industries 33:28–32
Caruso M, Colombo AL, Fedeli L, Pavesi A, Quaroni S, Saracchi M, Ventrella G (2000) Isolation of endophytic fungi and actinomycetes taxane producers. Ann Microbiol 50(1):3–14
Chandra S (2012) Endophytic fungi: novel sources of anticancer lead molecules. Appl Microbiol Biotechnol 95:47–59
Chatterjee S, Ghosh R, Mandal NC (2019) Production of bioactive compounds with bactericidal and antioxidant potential by endophytic fungus *Alternaria alternata* AE1 isolated from *Azadirachta indica* A. Juss. PLoS One 14(4):e0214744. https://doi.org/10.1371/journal.pone0214744
Chen M, Yang L, Li Q, Shen Y, Shao A, Lin S, Huang L (2011) Volatile metabolites analysis and molecular identification of endophytic fungi bn12 from *Cinnamomum camphora* var. *borneol*. China J Chin Materia Med 36(23):3217–3221
Chen J, Li L, Tian P, Xiang W, Lu X, Huang R, Li L (2021) Fungal endophytes from medicinal plant *Bletilla striata* (Thunb.) Reichb. F. promot the host plant growth and phenolic accumulation. S Afr J Bot 143:25–32
Chetia H, Kabiraj D, Bharali B, Ojha S, BarkatakiMP SD, Singh T, Mosahari PV, Sharma P, Bora U (2019) Exploring the benefits of endophytic fungi via omics. In: Singh BP (ed) Advances in endophytic fungal research. Springer, New York, pp 51–81. https://doi.org/10.1007/978-3-030-03589-1_4
Chithra S, Jasim B, Sachidanandan P, Jyothis M, Radhakrishnan EK (2014) Piperine production by endophytic fungus *Colletotrichum gloeosporioides* isolated from *Piper nigrum*. Phytomedicine 21:534–540
Christensen MJ, Bennett RJ, Schmid J (2002) Growth of *Epichloe/Neotyphodium* and endophytes in leaves of *Lolium* and *Festuca* grasses. Mycol Res 106(1):93–106. https://doi.org/10.1017/S095375620100510X
Chutulo EC, Chalannavar RK (2018) Endophytic mycoflora and their bioactive compounds from *Azadirachta indica*: a comprehensive review. J Fungi 4:42
Cichewicz RH (2010) Epigenome manipulation as a pathway to new natural product scaffolds and their congeners. Nat Prod Rep 27(1):11–22
Cragg GM, Boyd MR, Cardellina JH II, Grever MR, Schepartz S, Snader KM, Suffness M (1993) The search for new pharmaceutical crops. In: Janick J, Simon JE (eds) Drug discovery and development at the national cancer institute: new crops. Wiley, New York, pp 61–167
Creasey WA (1979) The vinca alkaloids. In: Hahn FE (ed) Antibiotics, 5th edn. Springer, New York, pp 414–438

Croteau R, Kutchan TM, Lewis NG (2000) Natural products (secondary metabolites). In: Buchanan B, Gruissem W, Jones R (eds) Biochemistry & molecular biology of plants. American Society of Plant Physiologists, Chichester, pp 1250–1318

Crown J, O'Leary M (2000) The taxanes: an update. Lancet 355(9210):1176–1178. https://doi.org/10.1016/S0140-6736(00)02074-2

Cueto M, Jensen PR, Kauffman C, Fenical W, Lobkovsky E, Clardy J (2001) Pestalone, new antibiotic produced by a marine fungus in response to bacterial challenge. J Nat Prod 64(11):1444–1446

Cui R, Wang YZ, Wang L, Li GM, Lan K, Altmeyer R, Zou G (2016) Cyclopiazonic acid, an inhibitor of calcium-dependent ATPases with antiviral activity against human respiratory syncytial virus. Antivir Res 132:38–45

Cui H, Lin Y, Luo M, Lu Y, Huang X, She Z (2017) Diaporisoindoles A_C: three isoprenylisoindole alkaloid derivatives from the mangrove endophytic fungus *Diaporthe* sp. SYSU-HQ3. Org Lett 19:5621–5624

Das AK (2015) Anticancer effect of antimalarial artemisinin compounds. Ann Med Health Sci Res 5:93–102

de Carvalhoa CR, Maiaa MQ, Sobral M, Pereirac GMD, da Silvad K, Vitalc MJS, Zillie JE, Rosaa CA, Rosaa LH (2021) Diversity and antimicrobial activity of culturable endophytic fungi associated with the neotropical ethnomedicinal plants *Copaifera langsdorffii* and *Copaifera pubiflora*. S Afr J Bot 142:305–315

De Souza JJ, Vieira IJ, Rodrigues-Filho E, Braz-Filho R (2011) Terpenoids from endophytic fungi. Mol Ther 16:10604–10618

Demers D, Knestrick M, Fleeman R, Tawfik R, Azhari A, Souza A et al (2018) Exploitation of mangrove endophytic fungi for infectious disease drug discovery. Mar Drugs 16(10):376

Deshmukh SK, Verekar SA, Bhave SV (2015) Endophytic fungi: a reservoir of antibacterials. Front Microbiol 5(715):1–43

Deshmukh SK, Agrawal S, Prakash V, Gupta MK, Reddy MS (2020) Anti-infectives from mangrove endophytic fungi. S Afr J Bot 134:237–263

Dewi RT, Tachibana S, Fajriah S, d Hanafi M (2015) A-glucosidase inhibitor compounds from *Aspergillus terreus* RCC1 and their antioxidant activity. Med Chem Res 24:737–774

Domka AM, Rozpaadek P, Turnau K (2019) Are fungal endophytes merely mycorrhizal copycats? The role of fungal endophytes in the adaptation of plants to metal toxicity. Front Microbiol 10:371. https://doi.org/10.3389/fmicb.2019.00371

Duan L, Liwei G, Hong Y (2009) Isolation and identification of producing endophytic fungi of berberine from the plant *Phellodendron amurense*. J Anhui Agric Sci 22(7):10340

Eaton CJ, Cox MP, Scott B (2011) What triggers grass endophytes to switch from mutualism to pathogenism? Plant Sci 180(2):190–195. https://doi.org/10.1016/j.plantsci.2010.10.002

Ebada SS, Eze P, Okoye FB, Esimone CO, Proksch P (2016) The fungal endophyte Nigrosporaoryzae produces quercetin monoglycosides previously known only from plants. Chem Select 16:2767–2771

El-Sayed ASA, Shindia AA, Ali GS, Yassin MA, Hussein H, Awad SA, Ammar HA (2021) Production and bioprocess optimization of antitumor Epothilone B analogue from *Aspergillus fumigatus*, endophyte of *Catharanthus roseus*, with response surface methodology. Enzym Microb Technol 143:109718

Ettinger DS (1992) Taxol in the treatment of lung cancer. In: Abstracts of second National Cancer Institute workshop on taxol and taxus, Alexandria, pp 23–24

Fadiji AE, Babalola OO (2020) Exploring the potentialities of beneficial endophytes for improved plant growth. Saudi Journal of Biological Sciences 27:3622–3633

Feng Y, Liu W, Li M, Ouyang Y, Yuan T (2021) Cladosporitides A–C, three polyketides from an endophytic fungi *Cladosporium tenuissimum*. Tetrahedron Lett 85:153492

Fischer J, Schroeckh V, Brakhage AA (2016) Awakening of fungal secondary metabolite gene clusters. In: Schmoll M, Dattenbock C (eds) Gene expression systems in fungi: advancements and applications, pp 253–273. https://doi.org/10.1007/978-3-319-27951-0_11

Flores HE, Sgrignoli PJ (1991) In vitro culture and precocious germination of Taxus embryos. In Vitro Cell Dev Biol 27:139–142

Forastiere AA, Neuberg D, Taylor SG, DeConti R, Adams G (1993) Phase II evaluation of taxol in advanced head and neck cancer: an Eastern Cooperative Oncology Group Trial. J Natl Cancer Inst Monogr 15:181–184

Franken P (2012) The plant strengthening root endophyte *Piroformospora indica*: potential application and the biology behind. Appl Microbiol Biotechnol 96(6):1455–1464. https://doi.org/10.1007/s00253-012-4506-1

Gangadevi V, Muthumary J (2008) Isolation of *Colletotrichum gloeosporioides*: a novel endophytic taxol-producing fungus from the leaves of a medicinal plant, *Justicia gendarussa*. Mycol Balc 5:1–4

Garo E, Starks CM, Jensen PR, Fenical W, Lobkovsky E, Clardy J (2003) Trichodermamides A and B, cytotoxic modified dipeptides from the marine – derived fungus Trichoderma virens. J Nat Prod 66:423–426

Geetanjali (2017) Exploring the endophytic fungi for bioactive metabolites: an emerging paradigm. IJARSE 6(12):1815–1822

Giridharan P, Verekar SA, Khanna A, Mishra PD, Deshmukh SK (2012) Anticancer activity of sclerotiorin, isolated from an endophytic fungus *Cephalotheca faveolata* Yaguchi, Nishim. & Udagawa. Indian J Exp Biol 50(7):464–468

Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol Res 169(1):30–39

Gouda S, Das G, Sen SK, Shin H-S, Patra JK (2016) Endophytes: a treasure house of bioactive compounds of medicinal importance. Front Microbiol 7:1538. https://doi.org/10.3389/fmicb.2016.01538

Guo B, Li H, Zhang L (1998) Isolation of the fungus producting vinbrastine. J Yunnan Univ (Nat Sci Ed) 20(3):214–215

Guo ZK, Zhou YQ, Han H, Wang W, Xiang L, Deng XZ et al (2018) New antibacterial phenone derivatives asperphenone A_C from mangrove-derived fungus *Aspergillus* sp. YHZ-1. Mar Drugs 16:45

Gupta S, Chaturvedi P, Kulkarni MG, Van Staden J (2020) A critical review on exploiting the pharmaceutical potential of plant endophytic fungi. Biotechnol Adv 39:107462. https://doi.org/10.1016/j.biotechadv.2019.107462

Hardoim P, van-Overbeek L, van-Elsas J (2008) Properties of bacterial endophytes and their proposed role in plant growth. Trends Microbiol 16:463–471. https://doi.org/10.1016/j.tim.2008.07.008

Hardoim PR, Van Overbeek LS, Berg G, Pirttilä AM, Compant S, Campisano A, Döring M, Sessitsch A (2015) The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. Microbiol Mol Biol Rev 79(3):293–320. https://doi.org/10.1128/MMBR.00050-14

Hassan ES (2017) Plant growth-promoting activities for bacterial and fungal endophytes isolated from medicinal plant of *Teucrium polium* L. J Adv Res 8:687–695

Higgins KL, Arnold AE, Coley P, Kursar T (2014) Communities of fungal endophyte in tropical forest grasses: highly diverse host and habitat generalists characterized by strong spatial structure. Fungal Ecol 8:1–11. https://doi.org/10.1016/j.funeco.2013.12.005

Huang H, Liu T, Wu X, Guo J, Lan X, Zhu Q et al (2017) A new antibacterial chromone derivative from mangrove-derived fungus *Penicillium aculeatum* (No. 9EB). Nat Prod Res 31:2593–2598

Hussein RA, El-Anssary AA (2018) Plants secondary metabolites: the key drivers of the pharmacological actions of medicinal plants. Intech, London. https://doi.org/10.5772/intechopen.76139

Jain D, Phurailatpam L, Mishra S (2020) Microbes-mediated mitigation of drought stress in plants: recent trends and future challenges. In: Yadav A, Rastegari A, Yadav N, Kour D (eds) Advances in plant microbiome and sustainable agriculture, Microorganisms for sustainability, vol 20. Springer, Singapore, pp 199–218

Jennewein S, Rithner CD, Williams RM, Croteau RB (2001) Taxol biosynthesis: taxane 13-hydroxylase is a cytochrome P450-dependent monooxygenase. PNAS 98:13595–13600

Jia M, Ming QL, Zhang QY, Chen Y, Cheng N, Wu WW, Han T, Qin LP (2014) *Gibberella moniliformis* AH13 with antitumor activity, an endophytic fungus strain producing triolein isolated from Adlay (Coix lacryma-jobi: Poaceae). Curr Microbiol 69(3):381–387

Jinfeng EC, Rafi MIM, Hoon KC, Lian HK, Kqueen CY (2017) Analysis of chemical constituents, antimicrobial and anticancer activities of dichloromethane extracts of *Sordariomycetes* sp. endophytic fungi isolated from *Strobilanthes crispus*. World J Microbiol Biotechnol 33(1):5

Jogaiah S, Abdelrahman M, Tran LSP, Ito SI (2018) Different mechanisms of *Trichoderma virens*-mediated resistance in tomato against *Fusarium* wilt involve the jasmonic and salicylic acid pathways. Mol Plant Pathol 19:870–882

Joseph B, Priya RM (2011) Bioactive compounds from endophytes and their potential in pharmaceutical effect: a review. Am J Biochem Mol Bio 1:291–309. https://doi.org/10.3923/ajbmb.2011.291.309

Jung HJ, Kim Y, Lee HB, Kwon HJ (2015) Antiangiogenic activity of the lipophilic antimicrobial peptides from an endophytic bacterial strain isolated from red pepper leaf. Mol Cells 38(3):273–278

Khalil ZG (2014) Lipopolysaccharide (LPS) stimulation of fungal secondary metabolism. Mycology 5:168–178

Khan AL, Al-Harrasi A, Al-Rawahi A, Al-Farsi Z, Al-Mamari A, Waqas M, Asaf S, Elyassi A, Mabood F, Shin J-H (2016) Endophytic fungi from Frankincense tree improves host growth and produces extracellular enzymes and indole acetic acid. PLoS One 11(6):e0158207. https://doi.org/10.1371/journal.pone.0158207

Kloepper JW, McInroy JA, Liu K, Hu CH (2013) Symptoms of Fern distortion syndrome resulting from inoculation with opportunistic endophytic fluorescent *Pseudomonas* spp. PLoS One 8(3):e58531

Kour A, Shawl AS, Rehman S, Sultan P, Qazi PH, Suden P, Khajuria RK, Verma V (2008) Isolation and identification of an endophytic strain of *Fusarium oxysporum* producing podophyllotoxin from *Juniperus recurva*. World J Microbiol Biotechnol 24(7):1115–1121

Kusari S, Hertweck C, Spiteller M (2012) Chemical ecology of endophytic fungi: origins of secondary metabolites. Chem Biol 19:792–798. https://doi.org/10.1016/jchembiol.2012.06.004

Kusari S, Lamshoft M, Kusari P, Gottfried S, Zuhlke S, Louven K, Hentschel U, Kayser O, Spiteller M (2014) Endophytes are hidden producers of maytansine in *Putterlickia* roots. J Nat Prod 77(12):2577–2584. https://doi.org/10.1021/np500219a

Lee KH, Xiao Z (2003) Lignans in treatment of cancer and other diseases. Phytochem Rev 2:341–362

Li TX, Yang MH, Wang Y, Wang XB, Luo J, Luo JG, Kong LY (2016) Unusual dimeric tetrahydroxanthone derivatives from *Aspergillus lentulus* and the determination of their axial chiralities. Sci Rep:1–10

Li HL, Xu R, Li XM, Yang SQ, Meng LH, Wang BG (2018) Simpterpenoid A, a meroterpenoid with a highly functionalized cyclohexadiene moiety featuring gem-propane-1,2-dione and methylformate groups, from the mangrove-derived *Penicillium simplicissimum* MA-332. Org Lett 20:1465–1468

Li F, He X, Sun Y, Zhang X, Tang X, Li Y, Yi Y (2019) Distinct endophytes are used by diverse plants for adaptation to karst regions. Sci Rep 9:5246. https://doi.org/10.1038/s41598-019-41802-0

Liang WL (2014) Exploring the chemodiversity and biological activities of the secondary metabolites from the marine fungus *Neosartorya pseudofischeri*. Mar Drugs 12:5657–5676

Li-Li T, Ren H, Xi JM, Fang J, Zhang JZ, Wu QX (2021) Diverse anti-inflammation and anti-cancer polyketides isolated from the endophytic fungi *Alternaria* sp. MG1. Fitoterapia 153:105000. https://doi.org/10.1016/j.fitote.2021.105000

Lin L, Xu X (2013) Indole-3-acetic acid production by endophytic *Streptomyces* sp. En-1 isolated from medicinal plants. Curr Microbiol 67:209–217

Liu L (2018) Asperorydines A-M: prenylated tryptophan-derived alkaloids with neurotrophic effects from *Aspergillus oryzae*. J Organomet Chem 83:812–822

Lu L, He J, Yu X, Li G, Zhang X (2006) Studies on isolation and identification of endophytic fungi strain SC13 from harmaceutical plant *Sabina vulgaris* Ant. and metabolites. Acta Agric Bor Sin 15:85–89

Mahmud SMN, Sohrab MH, Begumc MN, Rony SR, Sharmin S, Moni F, Akhter S, Mohiuddin AKM, Afroz F (2020) Cytotoxicity, antioxidant, antimicrobial studies and phytochemical screening of endophytic fungi isolated from *Justicia gendarussa*. Ann Agric Sci 65:225–232

Majumder A, Jha S (2009) Biotechnological approaches for the production of potential anticancer leads podophyllotoxin and paclitaxel: an overview. J Bio Sci 1:46–69

Manganyi MC, Tchatchouang CDK, Regnier T, Bezuidenhout CC, Ateba CN (2019) Bioactive compound produced by endophytic fungi isolated from *Pelargonium sidoides* against selected bacteria of clinical importance. Mycobiology 47(3):335–339

Mapook A (2020) Polyketide-derived secondary metabolites from a dothideomycetes fungus, *Pseudopalawania siamensis* gen. et sp. nov., (Muyocopronales) with antimicrobial and cytotoxic activities. Biomol Ther 10:569

Marmann A, Aly AH, Lin W, Wang B, Proksch P (2014) Co-cultivation-A powerful emerging tool for enhancing the chemical diversity of microorganisms. Mar Drugs 12:1043–1065

Mathur P, Mehtani P, Sharma C (2021) Leaf endophytes and their bioactive compounds. In: Symbiotic soil microorganisms. Springer, Cham, pp 147–159

Matsuoka H, Akiyama M, Kobayashi K, Yamaji K (2013) Fe and P solubilization under limiting conditions by bacteria isolated from *Carex kobomugi* roots at the Hasaki coast. Curr Microbiol 66:314–321

Mishra S, Bhattacharjee A, Sharma S (2021) An ecological insight into the multifaceted world of plant-endophyte association. CRC Crit Rev Plant Sci 40(2):127–146. https://doi.org/10.1080/07352689.2021.1901044

Mondal A (2019) Alkaloids for cancer prevention and therapy: current progress and future perspectives. Eur J Clin Pharmacol 858:172472

Murali M, Amruthesh KN, Jogaiah S, Shetty HS (2012) Screening of plant growth promoting fungi and their ability for growth promotion and induction of resistance in pearl millet against downy mildew disease. J Phytology 4:30–36

Nair DN, Padmavathy S (2014) Impact of endophytic microorganisms on plants, environment and humans. Sci World J 22:1–11. https://doi.org/10.1155/2014/250693

Nischitha R, Shivanna MB (2022) Diversity and in silico docking of antibacterial potent compounds in endophytic fungus *Chaetomium subaffine* Sergeeva and host *Heteropogon contortus* (L.) P. Beauv. Process Biochem 112:124–138

Paramanantham P, Pattnaik S, Siddhardha B (2019) Natural products from endophytic fungi: synthesis and applications. In: Singh B (ed) Advances in endophytic fungal research. Springer, Cham, pp 83–103

Parthasarathi S, Sathya S, Bupesh G, Samy DR, Mohan MR, Selva GK et al (2012) Isolation and characterization of antimicrobial compound from marine *Streptomyces hygroscopicus* BDUS49. World J Fish Mar Sci 4:268–277

Petrini O (1991) Fungal endophytes of tree leaves. In: Andrews JH, Hirano SS (eds) Microbial ecology of leaves. Springer, New York, pp 179–197

Pfannenstiel BT, Keller NP (2019) On top of biosynthetic gene clusters: how epigenetic machinery influences secondary metabolism in fungi. Biotechnol Adv 37(6). https://doi.org/10.1016/j.biotechadv.2019.02.001

Phurailatpam L, Mishra S (2020) Role of plant endophytes in conferring abiotic stress tolerance. In: Hasanuzzaman M (ed) Plant ecophysiology and adaptation under climate change: mechanisms and perspectives II. Springer, Singapore, pp 603–628. https://doi.org/10.1007/978-981-15-2172-0_22

Pimentel MR, Molina G, Dionisio AP, Maróstica MR, Pastore GM (2011) Use of endophytes to obtain bioactive compounds and their application in biotransformation process. Biotechnol Res Int:576286. https://doi.org/10.4061/2011/576286

Pretsch A, Nagl M, Schwendinger K, Kreiseder B, Wiederstein M, Pretsch D, Genov M, Hollaus R, Zinssmeister D, Debbab A, Hundsberger H, Eger A, Proksch P, Wiesner C (2014) Antimicrobial and anti-inflammatory activities of endophytic fungi Talaromyces wortmannii extracts against acne-inducing bacteria. PLoS ONE 9(6):e97929. https://doi.org/10.1371/journal.pone.0097929

Pruksakorn P, Arai M, Kotoku N, Vilcheze C, Baughn AD, Moodley P, Jacobs WR, Kobayashi M (2010) Tricoderins, novel aminolipopeptiides from a marine sponge-derived *Trichoderma* sp., are active against dormant mycobacteria. Bioorg Med Chem Lett 20(12):3658–3663

Puri SC, Verma V, Amna T, Qazi GN, Spiteller M (2005) An endophytic fungus from *Nothapodytes foetida* that produces camptothecin. J Nat Prod 68:1717–1719

Puri SC, Amna T, Khajuria A, Gupta A, Arora R, Spiteller M, Qazi GN (2007) Immunomodulatory activity of an extract of the novel fungal endophyte *Entrophospora infrequens* isolated from *Nothapodytes foetida* (Wight) Sleumer. Acta Microbiol Immunol Hung 54(3):237–260

Qadri M, Johri S, Shah BA, Khajuria A, Sidiq T, Lattoo SK, Abdin MZ, Hassan UISR (2013) Identification and bioactive potential of endophytic fungi isolated from selected plants of the western Himalayas. Springer Plus 2(8):2–14

Qiu M, Xie R, Shi Y, Zhang H, Chen H (2010) Isolation and identification of two flavonoid-producing endophytic fungi from Ginkgo biloba L. Ann Microbiol 60(1):143–150

Rai N, Morales LO, Aphalo PJ (2021) Perception of solar UV radiation by plants: photoreceptors and mechanisms. Plant Physiol 186(3):1382–1396. https://doi.org/10.1093/plphys/kiab162

Rana KL, Kour D, Kaur T, Devi R, Yadav AN, Yadav N, Saxena AK (2020) Endophytic microbes: biodiversity, plant growth-promoting mechanisms and potential applications for agricultural sustainability. Antonie Van Leeuwenhoek 113:1075–1107. https://doi.org/10.1007/s10482-020-01429-y

Rosenblueth M, Martínez-Romero E (2006) Bacterial endophytes and their interactions with hosts. Mol Plant-Microbe Interact 19:827–837. https://doi.org/10.1094/MPMI-19-0827

Sabra M, Aboulnasr A, Franken P, Perreca E, Wright LP, Camehl I (2018) Beneficial root endophytic fungi increase growth and quality parameters of sweet basil in heavy metal contaminated soil. Front Plant Sci 9:1726. https://doi.org/10.3389/fpls.2018.01726

Sahu PK, Singh S, Gupta A, Singh UB, Brahmaprakash GP, Saxena AK (2019) Antagonistic potential of bacterial endophytes and induction of systemic resistance against collar rot pathogen *Sclerotium rolfsii* in tomato. Biol Control 137:104014. https://doi.org/10.1016/j.biocontrol.2019.104014

Sahu PK, Thomas P, Singh S, Gupta A (2020) Taxonomic and functional diversity of cultivable endophytes with respect to the fitness of cultivars against *Ralstonia solanacearum*. J Plant Dis Prot 127:667–676. https://doi.org/10.1007/s41348-020-00320-2

Salendra L, Luo X, Lin X, Liao S, Wang JZ, Yang X (2018) Bioactive novel indole alkaloids and steroids from deep sea-derived fungus *Aspergillus fumigatus* SCSIO 41012. Molecules 23:2379

Santos IP, Silva NL, Silva MV, Araujo JM, Cavalcant MSI, Lima VM (2015) Antibacterial activity of endophytic fungi from leaves of *Indigofera suffruticosa* Miller (*Fabaceae*). Front Microbiol 6(350):1–7

Satheesan J, Sabu KK (2020) Endophytic fungi for a sustainable production of major plant bioactive compounds. In: Swamy M (ed) Plant-derived Bioactives. Springer, Singapore, pp 195–207

Saunders M, Kohn LM (2009) Evidence for alteration of fungal endophyte community assembly by host defense compounds. New Phytol 182:229–238

Schiff PB, Fant J, Auster LA, Horowitz SB (1978) Effects of taxol on cell growth and in vitro microtubule assembly. J Supramol Struct Suppl 8:328

Schouten A (2019) Saving resources: the exploitation of endophytes by plants for the biosynthesis of multifunctional defence compounds. In: Schouten A (ed) Endophyte biotechnology: potential for agriculture and pharmacology. London, CABI International, pp 122–144

Schulz B, Boyle C (2005) The endophytic continuum. Mycol Res 109:661–686. https://doi.org/10.1017/S095375620500273X

Schulz B, Boyle C, Draeger S, Rommert AK, Krohn K (2002) Endophytic fungi: a source of novel biologically active secondary metabolites. Mycol Res 106:996–1004

Selvakumar V, Panneerselvam A (2018) Bioactive compounds from endophytic fungi. In: Gehlot P, Singh J (eds) Fungi and their role in sustainable development: current perspectives. Springer, Singapore, pp 699–717. https://doi.org/10.1007/978-981-13-0393-7_36

Shwab EK, Keller NP (2008) Regulation of secondary metabolite production in filamentous ascomycetes. Mycol Res 112(2):225–230. https://doi.org/10.1016/j.mycres.2007.08.021

Singh R, Dubey AK (2015) Endophytic actinomycetes as emerging source for therapeutic compounds. Indo Global J Pharm Sci 5:106–116

Singh SK, Strobel GA, Knighton B, Geary B, Sears J, Ezra D (2011) An endophytic *Phomopsis* sp. possessing bioactivity and fuel potential with its volatile organic compounds. Microb Ecol 61(4):729–739

Singh B, Sharma P, Kumar A, Chadha P, Kaur R, Kaur A (2016) Antioxidant and in vivo genoprotective effects of phenolic compounds identified from an endophytic *Cladosporium velox* and their relationship with its host plant *Tinospora cordifolia*. J Ethnopharmacol 194:450–456

Singh A, Singh DK, Kharwar RN, White JF, Gond SK (2021) Fungal endophytes as efficient sources of plant-derived bioactive compounds and their prospective applications in natural product drug discovery: insights, avenues, and challenges. Microorganisms 9:197. https://doi.org/10.3390/microorganisms9010197

Sirikantaramas S, Asano T, Sudo H, Yamazaki M, Saito K (2007) Camptothecin: therapeutic potential and biotechnology. Curr Pharm Biotechnol 8:196–202

Song FH (2012) Quinazolin-4-one coupled with pyrrolidin-2-iminium alkaloids from marine-derived fungus *Penicillium aurantiogriseum*. Mar Drugs 10:1297–1306

Specian V, Sarragiotto MH, Pamphile JA, Clemente E (2012) Chemical characterization of bioactive compounds from the endophytic fungus *Diaporthe helianthi* isolated from *Luehea divaricata*. Braz J Microbiol 43:1174–1182. https://doi.org/10.1590/S1517-83822012000300045

Stepniewska Z, Kuzniar A (2013) Endophytic microorganisms-promising applications in bioremediation of greenhouse gases. Appl Microbiol Biotechnol 97:9589–9596. https://doi.org/10.1007/s00253-013-5235-9

Strobel GA (2003) Endophytes as sources of bioactive products. Microbes Infect 5:535–544

Strobel G, Daisy B (2003) Bioprospecting for microbial endophytes and their natural products. Microbiol Mol Biol Rev 67:491–502

Strobel G, Hess WM, Li JY, Ford E, Sears J, Sidhu RS, Summerell B (1997) *Pestalotiopsis guepinii*, a taxol producing endophyte of the *Wollemi pine*, *Wollemia nobilis*. Aust J Bot 45(6):1073–1082

Subban K, Subramani R, Johnpaul M (2013) A novel antibacterial and antifungal phenolic compound from the endophytic fungus *Pestalotiopsis mangiferae*. Nat Prod Res 27(16):1445–1449. https://doi.org/10.1080/14786419.2012.722091

Subbulakshmi GK, Thalavaipandian A, Bagyalakshmi RV, Rajendran A (2012) Bioactive endophytic fungal isolates of *Biotaorientalis* (L) Endl., *Pinus excelsa* Wall. and *Thujaoccidentalis* L. Int J Adv Life Sci 4:9–15

Tan RX, Zou WX (2001) Endophytes: a rich source of functional metabolites. Nat Prod Rep 18(4):448–459

Tian Y, Amand S, Buisson D, Kunz C, Hachette F, Dupont J, Nay B, Prado S (2014) The fungal leaf endophyte *Paraconiothyrium variabile* specifically metabolizes the host-plant metabolome for its own benefit. Phytochemistry 108:95101

Turbat A, Rakk D, Vigneshwari A, Kocsube S, Thu H, Szepesi A, Bakacsy LD, Skrbic BD, Jigjiddorj EA, Vagvolgyi C, Szekeres A (2020) Characterization of the plant growth-promoting activities of endophytic fungi isolated from *Sophora flavescens*. Microorganisms 8:683. https://doi.org/10.3390/microorganisms8050683

Uche-Okereafor N, Sebola T, Tapfuma K, Mekuto L, Green E, Mavumengwana V.2019) Antibacterial activities of crude secondary metabolite extracts from *Pantoea* species obtained from the stem of *Solanum mauritianum* and their effects on two cancer cell lines. Int J Environ Res Publ Health 16(4): 602 https://doi.org/10.3390/ijerph16040602

Vicente MF, Cabello A, Platas G, Basilio A, Díez MT, Dreikorn S, Giacobbe RA, Onishi JC, Meinz M, Kurtz MB, Rosenbach M, Thompson J, Abruzzo G, Flattery A, Kong L, Tsipouras A, Wilson KE, Peláez F (2011) Antimicrobial activity of ergokonin A from *Trichoderma longibrachiatum*. J Appl Microbiol 91(5):806–813

Wang Y, Dai CC (2011) Endophytes: a potential resource for biosynthesis, biotransformation, and biodegradation. Ann Microbiol 61:207–215

Wang LG, Liu XM, Kreis W, Budman DR (1999) The effect of antimicrotubule agents on signal transduction pathways of apoptosis: a review. Cancer Chemother Pharmacol 44:355–361

Wang LW, Zhang YL, Lin FC, Hu YZ, Zhang CL (2011) Natural products with antitumor activity from endophytic fungi. Mini Rev Med Chem 11(12):1056–1074. https://doi.org/10.2174/138955711797247716

Wang J, Wei X, Lu X, Xu F, Wan J, Lin X et al (2014) Eight new polyketide metabolites from the fungus *Pestalotiopsis vaccinii* endogenous with the mangrove plant *Kandelia candel* (L.) druce. Tetrahedron 70:9695–9701

Wang JF, Liang R, Liao SR, Yang B, Tu ZC, Lin XP et al (2017) Vaccinols J_S, ten new salicyloid derivatives from the marine mangrove-derived endophytic fungus *Pestalotiopsis vaccinii*. Fitoterapia 120:164–170

Wang YN, Meng LH, Wang BG (2020) Progress in research on bioactive secondary metabolites from deep-sea derived microorganisms. Mar Drugs 18:614

Wang Z, Jiang Y, Xin X, An F (2021) Bioactive indole alkaloids from insect derived endophytic *Aspergillus lentulus*. Fitoterapia 153:104973

Wani ZA, Ashraf N, Mohiuddin T, Riyaz-Ul-Hassan S (2015) Plant endophyte symbiosis: an ecological perspective. Appl Microbiol Biotechnol 99(7):2955–2965. https://doi.org/10.1007/s00253-015-6487-3

Waqas M, Khan AL, Kamran M, Hamayun M, Kang S-M, Kim Y-H, Lee I-J (2012) Endophytic fungi produce gibberellins and indoleacetic acid and promotes host-plant growth during stress. Molecules 17(9):10754–10773. https://doi.org/10.3390/molecules170910754

Wheeler NC, Jech K, Masters S (1992) Effects of genetic, epigenetic and environmental factors on taxol content in *Taxus brevifolia* and related species. J Nat Prod 55:432–440

Woo DD, Miao SYP, Pelayo JC, Woolf AS (1994) Taxol inhibits progression of congenital polycystic kidney disease. Nature 368:750–753

Woodrow CJ, Haynes RK, Krishna S (2005) Artemisinins. Postgrad. Med J 81:71–78

Wu B, Oesker V, Wiese J, Schmalijohann R, Imhoff JF (2014) Two new antibiotic pyridines produced by a marine fungus, *Trichoderma* sp. strain MF106. Mar Drugs 12:1208–1219

Wu Z, Chen J, Zhang X, Chen Z, Li T, She Z et al (2019) Four new isocoumarins and a new natural tryptamine with antifungal activities from a mangrove endophytic fungus *Botryosphaeria ramosa* L29. Mar Drugs 17:88

Xie J, Wu YY, Zhang TY, Zhang MY, Zhu WW, Gullen EA et al (2017) New and bioactive natural products from an endophyte of *Panax notoginseng*. RSC Adv 7:38100–38109

Xing YM, Chen J, Cui JL, Chen XM, Guo SX (2011) Antimicrobial activity and biodiversity of endophytic fungi in *Dendrobium devonianum* and *Dendrobium thyrsiflorum* from Vietnam. Curr Microbiol 62(4):1218–1224

Xu Z, Wu X, Li G, Feng Z, Xu J (2018) Pestalotiopisorin B, a new isocoumarin derivative from the mangrove endophytic fungus *Pestalotiopsis* sp. HHL101. Nat Prod Res 34(7):1002–1007

Yan Y, Liu Q, Jacobsen SE, Tang Y (2018) The impact and prospect of natural product discovery in agriculture. EMBO Rep 19:e46824

Yang X, Guo S, Zhang L, Shao H (2003) Selection of producing podophyllotoxin endophytic fungi from podophyllin plant. Nat Prod Res Dev 15:419–422

Yang K, Liang J, Li Q, Kong X, Chen R, Jin Y (2013) *Cladosporium cladosporioides* XJ-AC03, an aconitine-producing endophytic fungus isolated from *Aconitum leucostomum*. World J Microbiol Biotechnol 29:933–938

Yin H, Sun YH (2011) Vincamine-producing endophytic fungus isolated from *Vinca minor*. Phytomedicine 18:802–805

Yu G, Zhou G, Zhu M, Wang W, Zhu T, Gu Q et al (2015) Neosartoryadins a and B, fumiquinazoline alkaloids from a mangrove-derived fungus *Neosartorya udagawae* HDN13-313. Org Lett 18:244–247

Ze-Hong WU, Dong LIU, Ying XU, Jian-Liang CHEN, Wen-Han LIN (2018) Antioxidant xanthones and anthraquinones isolated from a marine derived fungus *Aspergillus versicolor*. Chin J Nat Med 16:219–224

Zhai X, Jia M, Chen L, Zheng CJ, Rahman K, Han T, Qing LP (2017) The regulatory mechanism of fungal elicitor-induced secondary metabolite biosynthesis in medical plants. Crit Rev Microbiol 43(2):238–261. https://doi.org/10.1080/1040841X.2016.1201041

Zhao J, Zhou L, Wang J, Shan T, Zhong L, Liu X, Gao X (2010) Endophytic fungi for producing bioactive compounds originally from their host plants. In: Current research, technology and education topics in applied microbiology and microbial biotechnology, 1st edn. Formatex Research Center, Badajoz, pp 567–576

Zheng CJ, Liao HX, Mei RQ, Huang GL, Yang LJ, Zhou XM et al (2018) Two new benzophenones and one new natural amide alkaloid isolated from a mangrovederived fungus Penicillium citrinum. Natl Prod Res 33(8):1127–1134. https://doi.org/10.1080/14786419.2018.1460832

Zhu F, Chen G, Chen X, Huang M, Wan X (2011) Aspergicin, a new antibacterial alkaloid produced by mixed fermentation of two marine-derived mangrove epiphytic fungi. Chem Nat Compd 47(5):767–769

Zhu X, Zhong Y, Xie Z, Wu M, Hu Z, Ding W et al (2018) Fusarihexins a and B: novel cyclic hexadepsipeptides from the mangrove endophytic fungus *Fusarium* sp. R5 with antifungal activities. Planta Med 84:1355–1362

Zin WWM, Buttachon S, Dethoup T, Pereira JA, Gales L, Inacio A et al (2017) Antibacterial and antibiofilm activities of the metabolites isolated from the culture of the mangrove-derived endophytic fungus *Eurotium chevalieri* KUFA 0006. Phytochemistry 141:86–97

Symbiotic Relationships with Fungi: From Mutualism to Parasitism

Mohammad Magdy El-Metwally, Amal Ahmed Ibrahim Mekawey, Yasser El-Halmouch, and Nourhan Gaber Naga

1 Introduction

Fungi are a dynamic population with a great impact in the plant, animal, and human body. In the case of a plant, they are associated to the whole plant especially roots and rhizospheres with remarked effect on the fitness and productivity of the plant (Vicente et al. 2013; Vandenkoornhuyse et al. 2015).

This collection of fungi is termed mycobiome "a characteristic fungal community inhibiting a generally well-defined habitat which has distinct physical and chemical properties" (Dridi et al. 2011; Mendes et al. 2011). The combination of the plant and its mycobiome leads to environmental adaptation in plants which is essential for maintaining the function of terrestrial ecosystems (Chialva et al. 2018; Cavicchioli et al. 2019). Soil mycobiome have many effects on plant growth and development and inhibition of plant diseases by imposing physiological restrictions on pathogens establishing and infecting plant tissues (Kumar et al. 2012). They give the rhizosphere system some resistance to invaders (Van Elsas et al. 2012). They also provide nutrients, which play a crucial role in some processes such as

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phosphorus solubilization and nitrogen fixation. These processes support the nutrients uptake from the soil and promote plant protection by hindering agents of plant stresses, such as infection by pathogens and pests (Mendes et al. 2013; Quecine et al. 2014). All living microorganisms; microbiota live associated with each other or with other organisms in different types of relationships like synergism, amensalism, antagonism, parasitism, predation, and competition (Fig. 1).

In general, these types are divided into two large groups according to the degree of benefit and harm of the two partners of the relationship. Positive interactions such as commensalism or mutualism or synergism among microbial members are more prevalent. They can significantly affect the productivity of the bioprocess in industrial production (Hernandez et al. 2019). Contrary to that, the negative interactions exclude one organism from the community structure, such as parasitism, predation, or amensalism (Ghosh et al. 2016). In an asymmetric contact called amensalism, one species suffers harm or even dies while the other is untouched (Willey et al. 2011).

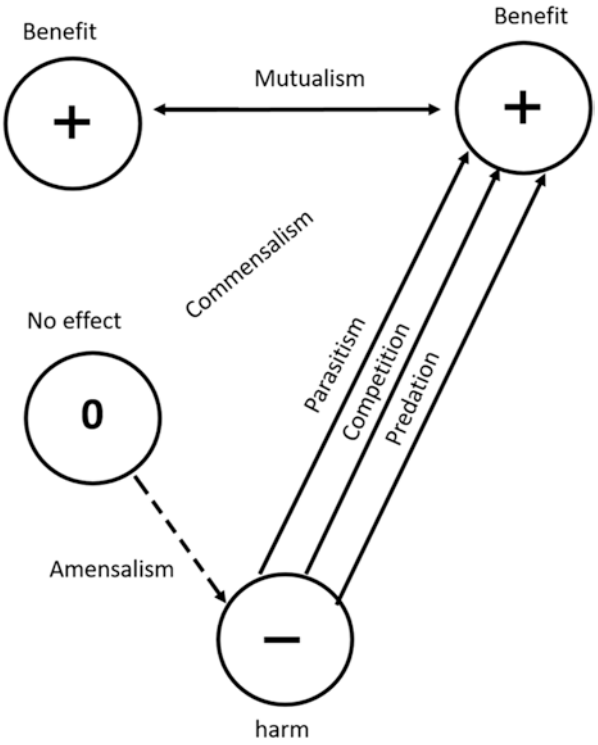

Fig. 1 The six different types of symbiotic relationships between the species. The dark black arrow mentions the direction of benefaction. Interrupted arrow mentions the harmful direction

2 Mutualism in Plant Fungi Symbiosis

The sassily of plants derived it to make multitrophic interactions with other organisms, mainly microorganisms, which are diversely localized and have remarkable functional lifestyles. Mutualism implies 'relative benefits' in associations involving two or more different organisms. Mutualism is an obligatory or highly specific interaction between two populations in which both of them benefit from each other. It usually required a close physical connection in which both partners may act as if they are one. When they exist separately, the physical tolerance and metabolic activities will be different for every single symbiont (Leung and Poulin 2008).

Mutualisms are everywhere in the biosphere and are fundamentally important in evolution and ecology (Bronstein 2015). The fungal plant mutualism is beneficial to host plants by conferring fitness benefits on hosts. It promotes plant growth and production (Yuan et al. 2019), improves resistance to herbivores e.g. insects (Estrada et al. 2013), enhances tolerance to biotic stress (Khare et al. 2018). It also increases the accumulation of useful secondary metabolites (Gupta and Chaturvedi 2019; Yuan et al. 2019) and confers tolerance to abiotic stress (Sabra et al. 2018). Mutualism includes plant-symbiotic nitrogen fixation, plant–Mycorrhizae and plant–endophyte associations. The first two associations have been discussed in other parts in this edition so we add some light in plant endophytes association.

Summary of mutulism types (Selim and Zayed 2017)

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

2.1 Plant–Endophyte Association

Endophytic fungi are obligate mutualists in plants and they introduce essential thermotolerance to the symbiosis (Redman et al. 2002). Endophytes have been identified in growing plants in all types of environments and represent a large taxonomic diversity of fungi. This suggests the convergent and redundant appearance of endophytism in different times and spaces during the co-evolution of plants and fungi.

Plant-mycoendophyte interactions are symbiotic. This symbiotic relationships are ranging from mutualism through commensalism to parasitism (Rodriguez and Redman 2008; Aly et al. 2011). Actually, endophytes can shift their lifestyle, being latent saprotrophs, pathogens, temporary residents, mutualists, or commensals (Suryanarayanan 2013). Some endophytes can survive as decomposers on leaves after the death of plant tissues, suggesting that mutualism could derive from saprophytism (Suryanarayanan 2013).

Host and mycoendophyte specific factors as well as external environmental factors play significant roles in shaping plant-mycoendophyte interactions. Such as host and fungal species (Jia et al. 2016; Fesel and Zuccaro 2016; Wang et al. 2019), growth and plant age (Jia et al. 2016), communication pattern (Fesel and Zuccaro 2016), and physiological stress (Rodriguez and Redman 2008). External factors such as light conditions and other abiotic stressors (Bacon et al. 2008; Alvarez-Loayza et al. 2011). In plant, mycoendophyte phytohormones form a part of the host's released metabolites which function as signal molecules that facilitate host-endophyte crosstalk and in turn determine the success of endophyte interactions and colonization (Lubna et al. 2018; Xu et al. 2018). Many genera of fungi are endophytes such as *Trichoderma* spp., *Epicoccum* spp., *Penicillium* spp., *Alternaria* spp., *Cladosporium* spp., *Fusarium* spp., *Chaetomium* spp., *Cladosporium* spp., *Aspergillus* spp., *Curvularia* spp., *Gilmaniella* spp., *Arthrobotrys* spp., *Acremonium* spp., *Colletotrichum* spp., *Fusarium* spp., *Saccharomyces* spp., *Beauveria* spp., and *paecilomyces* spp. (Zakaria et al. 2010; Oldroyd et al. 2011; Paul et al. 2012; Fávaro et al. 2012; Ek-Ramos et al. 2013; Sharma et al. 2019). One endophyte fungal species may be associated with many plant species, and vice versa many species of endophytes may be present in the same species (Rana et al. 2019).

Some fungal endophytes as *A. niger* CSR3, *Phoma glomerata* LWL2, and *Penicillium* sp. LWL3, have been reported to produce and degrade phytohormones like auxin, cytokinins, and gibberellins. They enable them to manipulate host defense responses to infection and facilitate the successful interaction and colonization (Lubna et al. 2018). Furthermore, a significant number of miRNAs induced in the host during endophyte infection and colonization target hormone-response pathways (Formey et al. 2014). Strigolactones are phytohormones which are known to be involved in plant-microorganism interactions in the rhizosphere (Xie et al. 2010). Experimental reports have shown that strigolactones have a role in mediating and shaping plant-fungi interactions including mycoendophytes (Foo et al. 2013).

3 Commensalism in Plant Fungi Symbiosis

The commensal relationship is often between a larger host (unaffected) and a smaller commensal. In this relation, commensals may obtain nutrients, support, shelter, or locomotion from the host species. For success, the commensal species may show great morphological adaptation. This relationship can be contrasted with mutualism, in which both species benefit (Alvarez-Loayza et al. 2011).

In Plant–fungal interaction commensalism is the undisturbed existence of fungus inside the plant tissue without affecting the host. It neither provides any benefit or support to plant growth in the form of nutrients or secondary metabolites nor causes any disease (Ko and Helariutta 2017). But this relationship can affect the plant immune responses. For example, commensal root microbiota members triggered an immune response in distant shoot organs and modulate resistance against a wide range of microbial pathogens and herbivores (Berendsen et al. 2018; Chialva et al. 2020). These responses include commensal-triggered induced systemic resistance (ISR) and pathogen-triggered systemic acquired resistance (SAR). Some recent evidences indicated that the accumulation of azelaic acid SAR component (AzA) in tomato leaves occurred in response to rhizosphere microbial commensals (Chialva et al. 2020). Additionally, there are 116 metabolites in distant shoot organs were modulated by the local rhizosphere microbiome. In contrast to SAR, initiation of ISR by beneficial root-colonizing microbes primes aboveground plant parts for an accelerated defense response upon pathogen or insect attack. This phenomenon has been extensively described by *Pseudomonas simiae* root colonization of *A. thaliana* via transcription factor MYB72, which also regulates the secretion of coumarins in the rhizosphere. These coumarins have a role in selecting beneficial over non-beneficial ISR and has a function in growth-promoting strains exist in the rhizosphere as it acts in concert with the root microbiota to improve iron nutrition (Ota et al. 2020). Although experimental evidence is lacking, coumarins might also travel from root to shoot and might contribute to the onset of ISR (Harbort et al. 2020).

Soil conditioning by plant residence time, plant species and mutants, or plant pathogen pressure resulted in host-induced shifts in rhizosphere microbial community composition that are directly linked with the plant's ability to resist aboveground pests and pathogens. This made the belowground microbial community composition and aboveground systemic immune outputs more tightly connected (Pineda et al. 2020). Commensal root microbiota members alleviate plant growth deficiency induced by aboveground changes in temperature or light conditions. It might influence the energetic status of aboveground shoot organs, thereby driving investment into growth when aboveground environmental conditions are suboptimal. Systemic defense responses in leaves are induced also by root microbiota members (Hou et al. 2020).

Prioritization of microbiota-induced growth in the context of aboveground abiotic stresses is associated with the down-regulation of microbiota-induced defense responses. Examples supporting this hypothesis in *A. thaliana* indicated that: (1) priority to shade avoidance responses occur at the expense of defense, (2) light and phytochrome photo perception mechanisms induced by SAR, and (3) root microbiota-induced growth under suboptimal light coincides with transcriptional repression of systemic leaf immune responses and increased susceptibility to microbial leaf pathogens (Liu et al. 2020).

Plant commensal microbes have evolved a variety of strategies to interfere with or bypass microbial-triggered immunity (MTI) to establish symbiosis (Teixeira et al. 2021). In nature, plants are colonized by different types of microorganisms from their habitats, including commensal microbes and pathogens (Fitzpatrick et al.

2020). The innate immune system of plants suppresses the invasion of pathogenic microbes. The defense is based on a series of immune responses, such as fungal chitin, peptidoglycan, flagellin 22 (flg22), and elongation factor Tu (EF-Tu) (Boller and Felix 2009). Moreover, symbiotic microbial communities promote mutualism by suppressing immunity (Buscaill and van der Hoorn 2021). Studies on plants have so far focused on single microorganisms, and the specific immunomodulatory effects of different strains have not been integrated into the context of complex communities.

On the other hand, aboveground biotic and abiotic stresses can modulate root microbiota assembly, and conversely, root commensals can promote host tolerance to biotic and abiotic stresses. It remains difficult to experimentally test whether these two responses are part of a microbiota-root-shoot circuit that promotes stress resistance in plants. Biotic stresses such as leaf pathogen inoculation can trigger selective host recruitment of beneficial root commensals that modulate aboveground pathogen growth through commensal-induced modulation of the host immune system. Beneficial root commensals were selectively stimulated through the combined action of commensal-mediated pathogen growth suppression and commensal-induced immune system modulation. Disease-induced re-assembly of beneficial root commensals is not limited to infection by microbial pathogens but has been also reported during herbivory. For example, compositional shifts in the root microbiome of maize mutants deficient in benzoxazinoids were correlated with changes in plant defense, growth, and herbivore resistance of the next plant generation (Liu et al. 2020). Complementation experiments with the benzoxazinoid; breakdown product of 6-methoxy-benzoxazolin-2-one (MBOA) indicated that MBOA induced the shift of rhizosphere microbiota, rather than MBOA itself (Hu et al. 2018). Therefore, modulation of benzoxazinoids exudation in the first generation and conditioning of the rhizosphere microbiota is the key to orchestrating leaf defense responses and suppression of herbivore growth in the second plant generation. These data suggest a general model in which recognition of aboveground pests in leaves can signal along the shoot–root axis to modulate rhizosphere microbiota assembly, thereby leaving a microbial footprint in soil that promotes offspring health.

4 Parasitism in Plant Fungi Symbiosis

An interactive association known as parasitism occurs when two biologically and phylogenetically distinct species coexist for an extended length of time. In this kind of interaction, the “host” suffers while the “parasite,” which typically benefits does not. The ability of an organism to cause a disease or pathogenicity is connected with parasitism. Many recent data suggest that oomycetes evolved plant parasitism several times and independently of other eukaryotic pathogens (Meng et al. 2009; Thines 2014).

In general, in the parasitism relationship at least one (the pathogen) benefits. There are some other cases; both host and pathogen alternate the benefits.

For instance, bacterial nodules in the roots of legume plants and the mycorrhizal infection of feeder roots of most flowering plants. Both biotic and abiotic agents have an impact on a number of crucial physiological and metabolic processes in the host that are involved. For example, growth including the production of chlorophyll, photosynthesis, transpiration, cell wall metabolism, the balance of growth regulators, seed germination, and nutrient uptake (Rizwan et al. 2016; Pandey et al. 2017; Cohen and Leach 2019; Ganie and Ahammed 2021). In many instances, parasitism is closely linked to pathogenicity, i.e., the ability of a pathogen to cause disease.

The amount of damage occurred to plants is often much greater than would be expected. This damage is caused by substances released by the parasite or made by the host in response to parasite resistance. In many plant-pathogen interactions, an arsenal of chemicals known as effectors is released by pathogens to aid in infection (Oliva et al. 2010). These effectors modify plant physiology to suppress plant defense responses. These effectors either exist in the interaction zone between the fungal hyphae and the host surface or are transferred inside the plant cells (Lo Presti et al. 2015). Some of these effectors are recognized directly or indirectly by resistance (R) proteins from the plant and then modulate the innate immunity of the plant. These R proteins are called avirulence (Avr) proteins. The presence of the 'R' gene and the corresponding 'Avr' gene leads to the recognition of the pathogen by the host cell which activates resistance against the pathogen (Patel et al. 2020). These proteins trigger a set of immune responses termed Effector-Triggered Immunity (ETI), which frequently lead to a rapid hypersensitive response (HR). Certain genetic changes such as complete deletion, inactivation, or down-regulation of the AVR gene, as well as point mutations, allow the recognition between the pathogen and plant cell to be evaded (Guttman et al. 2014).

Avr genes which are recognized by several *R* genes were reported in the pathosystems: *Leptosphaeria maculans*/oilseed rape (Rouxel and Balesdent 2017), *Magnaporthe oryzae*/rice (Kanzaki et al. 2012; Cesari et al. 2013), *Fusarium oxysporum*. lycopersici/tomato (Houterman et al. 2008; Houterman et al. 2009) and both the fungal pathogen *Cladosporium fulvum* and the nematode *Globodera rostochiensis*/tomato. R protein recognized Avr proteins as they render the pathogen avirulent on plants that carry the suitable receptor (Lozano-Torres et al. 2012).

4.1 Hyperparasitism

It is a phenomenon that occurs when pathogens are attacked and killed by a biocontrol agent. There are four categories of hyperparasites: obligate bacterial pathogens, mycoviruses as hypovirulence factors, facultative parasites, and predators. According to a study carried out by Latz et al. 2016 *Actinomyces*, *Pseudomonas*, and *Bacillus* rhizosphere bacteria were responsible for *Rhizoctonia solani* suppression in potato plants. Endophytic bacteria stimulate plant growth due to their good properties such as nitrogen fixation (Ladha and Reddy 2003), and synthesis of plant hormones such as IAA (Bal et al. 2013). Also, they play a role in phosphate

solubilization (Prakash 2011), inhibition of plant diseases (Sayyed et al. 2013), and production of some secondary substances such as siderophore. Recent work by (Do 2022) reported that strains of rice root endophytic bacteria; *Bacillus velezensis* and *Pseudomonas putida* can control the *Magnaporthe oryzae*; the causal agent of blast disease in rice. *Trichoderma* species have been reported to be effective against many plant pathogenic fungi, especially members of oomycetes (Verma et al. 2007). *Trichoderma* spp. has a multifaceted mode of approach including competition for nutrients (Elad 2000), mycoparasitism (Troian et al. 2014), secretion of antimicrobial compounds (Xiao-Yan et al. 2006), induction of the plant resistance and the host growth promotion (Martínez-Medina et al. 2014). *Trichoderma* has a successful antagonistic effect against various important plant pathogens, such as *Pythium* (Tchameni et al. 2020), *Phytophthora* sp. (Bae et al. 2016), *Botrytis* (You et al. 2016), *Fusarium* sp. (Saravanakumar et al. 2016; Sreenayana et al. 2022), *Sclerotinia sclerotiorum* (Sumida et al. 2018), *Sclerotium rolfsii* (Islam et al. 2017), *Macrophomina* (Pastrana et al. 2016) and *Rhizoctonia solani* (Daryaei et al. 2016).

4.2 Types of Parasitism

Parasites can be differentiated based on their life cycles into two categories:

4.2.1 Obligatory

The obligate parasitic fungi cannot complete their life cycle without exploiting a suitable host. If an obligate parasite cannot obtain a host, it will fail to reproduce. All obligatory and some non-obligate parasites must either penetrate living cells or come into close contact with them to obtain nourishment. The two most significant biotrophic fungi which cause powdery mildew and rust belong to the biggest category of plant pathogenic fungi, which harm numerous economically crucial crops and significantly reduce yields (Hückelhoven 2005; Jakupović et al. 2006; Micali et al. 2008; Yin et al. 2009). Rust and powdery mildew are caused by many fungi that can create specialized infective structures called haustoria. These haustoria have been identified as a fungal structure with a key role in disease establishment and have been implicated in essential processes like nutrient uptake and effector delivery.

4.2.2 Nonobligatory (Facultative)

Certain saprophytic fungi and bacteria can live on live, dead host tissues and various nutrient media. These parasites as necrotrophs grow saprophytically, but under specific circumstances, they attack live plants and cause disease. The nonobligatory parasites vary in their pathogenicity. They are more resilient and include many

common fungi such as *Rhizoctonia* sp., *Alternaria* sp., *Cercospora* sp., and *Sclerotium* sp. These pathogens have a highly diverse spectrum of hosts. Vascular wilts, which are frequently caused by *Fusarium*, *Verticillium*, *Ceratocystis*, and *Cephalosporium*, occupy a unique position among plant diseases since during the critical stages of pathogenesis, the fungus is confined within non-living xylem elements of the host. Most nonobligatory parasites primarily invade and infect plants by degrading the plant cell wall using lysozymes as one of their primary mechanisms (Nühse 2012; Davidsson et al. 2013).

Parasitic fungi-infected plants are classified generally based on their strategies into two categories, ectoparasitism, and endoparasitism. Most genera of *Erysiphaceae* are ectoparasites. Out of the 17 genera of the *Erysiphaceae*, only four genera, *Phyllactinia*, *Leveillula*, *Queirozia*, and *Pleochaeta* exhibit endoparasitism (Takamatsu et al. 2016). Mycorrhizas are commonly divided into ectomycorrhizas and endomycorrhizas. Ectomycorrhizal hyphae penetrate the root cortex with a web of closely intertwined fungus hyphae (Favre-Godal et al. 2020). The ectomycorrhizas hyphae remain apoplastic outside the protoplasts of the root cells. In other cases, hyphae may be invasive then representing ectomycorrhizae.

On the other hand, endomycorrhizae and fungal hyphae form coils for the exchange of metabolites and minerals within the root cells while still staying enveloped by a phagocytotic pocket. The hyphal coils may eventually be digested by the root cells. Endomycorrhiza includes arbuscular, ericoid, and orchid mycorrhiza (Brundrett 2004).

4.3 Factors Affecting Parasitism

It has been shown that the composition of the rhizosphere microbial community is influenced by many environmental factors such as temperature (Brooks et al. 2014), water content (Abdul Rahman et al. 2021), pH (Javed et al. 2002) (Aydi Ben Aydi-Ben-Abdallah et al. 2020), CO_2 concentration, O_2 levels (Abdul Rahman et al. 2021), EC (Aydi-Ben-Abdallah et al. 2020) and the biochemical composition of root exudates (Bais et al. 2008).

Exogenous environmental factors have a critical role in the predisposition of plants to infection and disease spread in the host after infection by fungi. The host damages ranging from small outbreaks to an epidemic-level scale depend mostly on some climatic, chemical, physical, and biological conditions that can interact with one another to induce the onset of disease (Thompson et al. 2014). The host-microbe interaction and the pathogenicity are varied according to the pathogen, the host, the environment, and the interference of human factors (Fig. 2). The host plant's development and resistance, as well as the pathogen's development or sporulation and level of virulence, may be affected by environmental and human variables.

Many pathogenic fungi create one or more protein elicitors during plant-microbe interactions, which can cause the induction of defense responses in plants (Peng et al. 2011). The mechanisms induced by microbial elicitors include many defense

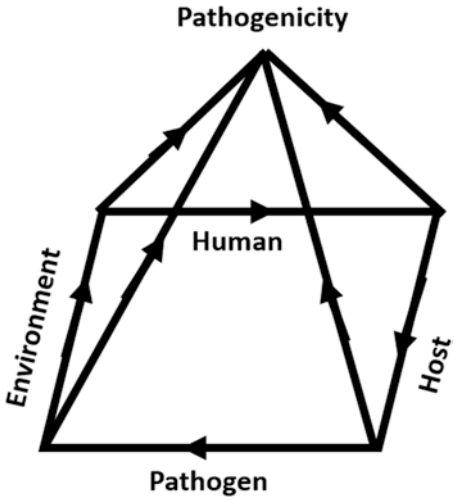

Fig. 2 Diagram illustrating the main factors affecting the pathogenicity

reactions like hypersensitive reaction (Allen et al. 2004; Rowland et al. 2005), systemic acquired resistance (Durrant and Dong 2004), reactive oxygen species (Glazebrook 2005), and biosynthesis of phytoalexins and pathogenesis-related protein (Silipo et al. 2010). Elicitors are signaling molecules that trigger secondary metabolites formation in a plant cell by inducing plant defense, hypersensitive response, and/or pathogenesis-related proteins (Yu et al. 2016). They fall into two categories: biotic and abiotic. The biotic elicitors are derived from the biological origin and include proteins, polysaccharides, glycoproteins, or cell-wall fragments derived from fungi, bacteria, and even plants (Ramirez-Estrada et al. 2016; Ochoa-Meza et al. 2021). Many physical and chemical factors are effective abiotic elicitors (Sák et al. 2021). These include ultraviolet irradiation, partial freezing, Ozone, salts of heavy metals, free radicals, and DNA-intercalating compounds.

Upon the abiotic or biotic elicitor treatment, many metabolic reactions may take place. For example, the accumulation of many toxic substances such as salicylic acid and jasmonate (Shinya et al. 2022) and activation of defense enzymes like peroxidase, oxidase, superoxidase, catalase, superoxide dismutase, chitinase and PR-proteins like β-1–3 glucanase. Also, the production of secondary metabolites was increased like phytoalexin (Shinya et al. 2022), cytokinins, ethylene, salicylic and abscisic acids (Morimoto et al. 2018), phenols, and lignin content (Patel et al. 2020). In addition to promoting disease resistance, fungal elicitors also play a significant role in inducing plant growth and development (Patel et al. 2020).

Some fungal spores have adhesive materials on their surfaces that enable them to adhere to different surfaces. Once the spore germinates, it often secretes more enzymes that presumably soften or dissolve the contact cell wall and make its penetration easier. When a pathogen attacks a host plant, the genes of the pathogen are activated, produced, and release all their chemical weapons of attack against the

host cell. The primary groups of chemicals generated by plant pathogens that are thought to be involved in the direct or indirect development of disease are enzymes, poisons, growth regulators, and polysaccharides (Komon-Zelazowska et al. 2007; Druzhinina et al. 2011). The toxicity of these chemicals varies widely, and their relative relevance may differ from one disease to another.

Nematophagous fungus; *Arthrobotrys oligospora* produces not only chemotaxis (Bargmann 2006) that trapped nematodes but also produces a sticky substance that fixes the pathogen to the prey. These sugars coat the nematode's surface and are involved in the interconnectivity caused by pectin and chemotaxis (Hsueh et al. 2013, 2017).

Pathogenic fungi have the ability to live off the substances manufactured by the host plants, and some other pathogens depend on these substances for survival. Additionally, many plant pathogens elaborate phytotoxic compounds when attacking the host which produces a variety of symptoms in sensitive plants. These toxins are mandatory for the pathogenicity of the sensitive host plant. The development of plant disease symptoms, such as leaf spots, chlorosis, wilting, necrosis, and growth inhibition and promotion is significantly influenced by fungus toxins (de Moraes Pontes et al. 2020; Chen et al. 2020). Most pathogenic fungi especially oomycetes secrete a plethora of effectors into the extra-haustorial space which is then seeped into the host cytoplasm (Oliva et al. 2010; Oliver and Solomon 2010). In the pathogenesis of the majority of plant diseases, toxins play a significant role. It has been demonstrated that a number of toxic substances produced by phytopathogenic fungi have been shown to produce all or part of the disease syndrome on the host plant and on other species of plants that are not normally invaded by these pathogens in nature. These toxins are called nonhost-specific toxins and affect the virulence of the pathogen, but they are not necessary to cause disease.

Many reviews reported that the phytotoxins are produced by one fungal genus (McLean 1996; Kim and Chen 2019) or one fungal species (Chen et al. 2019). Others stated that fungal interactions with a single plant species or plant group resulted in the production of phytotoxins (Masi et al. 2018). There are at least 545 fungal phytotoxic secondary metabolites identified to date, including 207 polyketides, 46 phenols, and phenolic acids, 135 terpenoids, 146 nitrogen-containing metabolites, and 11 other compounds (Xu et al. 2021).

For example, *Alternaria* is a well-known genus for the production of a variety of about 70 toxic metabolites (Logrieco et al. 2009; Pavón Moreno et al. 2012). Some of these metabolites are; altenuene, dibenzo-αpyrones alternariol, tentoxin, alternariol monomethyl ether, and a derivate of both tenuazonic acid and tetramic acid (Logrieco et al. 2003; Ostry 2008; Noelting et al. 2016; Escrivá et al. 2017; Topi et al. 2019; Crudo et al. 2019). Tentoxin is produced by *Alternaria alternata* fungus, which causes leaf spots and chlorosis in many plants (Noelting et al. 2022). Tentoxin is a cyclic tetrapeptide that inactivates a protein (chloroplast-coupling factor) involved in energy transfer into chloroplasts (Durbin and Uchytil 1977; Mochimaru and Sakurai 1997). This inhibits the light-dependent phosphorylation of ADP to ATP, in comparison to species that are not sensitive to the toxin, these all-inhibition

effects are substantially more pronounced in plant species susceptible to chlorosis after tentoxin treatment. *Alternaria* species create a lot of toxic substances like alternariol and alternariol monomethyl ether (Pero et al. 1973). Additionally, it produced non-specific toxins in culture filtrates, according to (Anand et al. 2008), which decreased cotton seedling vigor, root length, shoot length, and seed germination.

Cercosporin is a photosensitizing perylenequinone which is produced by the fungus *Cercospora* (Newman and Townsend 2016). It reacts with lipids, proteins, and nucleic acids of the host cells thereby enhancing the virulence of the pathogen. Another example of toxins produced by fungi is the fumaric acid which is produced by *Rhizopus* spp. in rot disease. Also, oxalic acid toxin which is produced by *Sclerotinia sclerotiorum* (Zhou and Boland 1999; Cessna et al. 2000) and *Cryphonectria parasitica* (Heiniger and Rigling 1994; Rigling and Prospero 2018). In various plants, ophiobolins are produced by *Cochliobolus* sp. (Tian et al. 2017); ceratoulmin is produced by *Ophiostoma ulmi* in Dutch elm disease (Temple et al. 1997); fusicoccin is produced by *Phomopsis amygdali* in the twig blight disease of peach (Marra et al. 2021); pyricularin is produced by *Pyricularia grisea* in rice blast disease (Valent and Chumley 1991); fusaric acid and lycomarasmin are produced by *Fusarium oxysporum* in barley wilt; and many others (Liu et al. 2016).

A host-specific is a substance produced by a pathogenic microorganism that is toxic only to the susceptible hosts of that pathogen and shows little or no toxicity against the non-susceptible plants (Meena and Samal 2019). It has been established that certain fungi, including *Helminthosporium*, *Alternaria*, *Periconia*, *Colletotrichum*, *Phyllosticta*, *Corynespora*, and *Hypoxylon*, produce these toxins (Xu et al. 2021).

Among such host-specific toxins produced by fungi are Victorin which are produced by *Helminthosporium victoria* (Rines and Luke 1985) in oat leaf blight. T toxin is produced by race T of *Cochliobolus heterostrophus* in southern corn leaf blight (Xiaodong et al. 2018); HC Toxin Race 1 of *Cochliobolus carbonum* causes northern leaf spot and ear rot disease in maize(Xiaodong et al. 2018). CCT toxin is produced by *Corynespora cassiicola* in tomato (Oka et al. 2006); peritoxin is produced by *Periconia circinate* which causes sorghum root rot disease (Macko et al. 1992); and many others.

Plant pathogens frequently disrupt the hormonal balance of the plant and induce irregular growth responses that are incompatible with a plant's healthy development. Pathogens may cause disease by affecting the growth regulatory systems of the infected plant through the secretion of growth regulators in the infected plant. This disturbance in plant growth regulatory systems may lead to abnormal plant growth responses which cause abnormal symptoms, such as overgrowths, stunting, rosetting, excessive root branching, stem malformation, leaf epinasty, defoliation, and suppression of bud growth. Some pathogenic fungi as *Fusarium oxysporum* in banana wilt can produce IAA on their own in addition to increasing the levels in their respective hosts. High concentrations of IAA can suppress the expression of plant defense genes (Shinshi et al. 1987) and may inhibit the hypersensitive response

(Jouanneau et al. 1991). Rice seedlings infected with *Fusarium fujikuroi* grow rapidly and become much taller than healthy plants (Hedden and Sponsel 2015). This observation is referred as gibberellin secretion by the pathogen.

Many studies showed that the microbial community in the plant rhizosphere depends on the plant species and ecotype (Lundberg et al. 2012; Peiffer et al. 2013; Lebeis 2014). Some fungal pathogens are restricted to a single plant species, others to one genus, and others have a wide range of hosts belonging to many families of higher plants. *Fusarium oxysporum* attacks only tomatoes to cause tomato wilt disease. Similarly, *Venturia inaequalis*, which causes apple scab, affects only apples, whereas *Puccinia graminis* which causes stem rust of wheat, attacks only wheat.

Most smut fungi attack the ovaries of monocot spikes and develop in them. Dematiaceous fungi cause wilt to invade susceptible plants through the roots and basal wounds to reach the vascular bundles. Depending on the cropping season, cultivar type, and stage of plant development, the microbial community in the rhizosphere of potato plants might vary (da Silva et al. 2003). Also, the plant growth stage had a greater impact on fungal community composition than bacterial community composition (Schlemper et al. 2018).

Many studies showed that the microbial population in the plant rhizosphere is influenced at least in part by the species and ecotype of the plant (Bulgarelli et al. 2012; Lundberg et al. 2012; Peiffer et al. 2013; Lebeis 2014). Plants can control soil microbial population through their root exudates serving as nutrient sources, chemical stimulants, or inhibitors for associated microorganisms. Chemical analysis of the *Arabidopsis thaliana* root exudates shows many variations between ecotypes, suggesting a way by which the plant controls the assembly of the community (Micallef et al. 2009). The chemical components which are found in *A. thaliana* root exudates, as well as the rhizosphere microbiome, change as the plant develops. This finding shows that *A. thaliana* sends out growth-stage-specific signals that influence the microbiome of its roots (Chaparro et al. 2014).

In addition, it has been noted that the microbial communities associated with potato cultivars are varied at different growth stages (İnceoğlu et al. 2010). Recent studies on maize (Hou et al. 2018) and wheat (Simonin et al. 2020) rhizosphere microbial communities have demonstrated that the plant types change the microbial community under stable environmental conditions. Finally, the physiological state of the plant also influences its microbiome. Susceptible plants that have specific receptors for certain pathogens become diseased (Bhaskar et al. 2021). While plants that lack such receptors remain resistant to pathogens and develop no symptoms. Plants species or varieties that do not produce one of the substances essential for the survival of an obligate parasite, or for its development would be resistant to this pathogen. Most plants and activities of the pathogen may partially or almost totally defend themselves with the aid of various combinations of naturally occurring or induced chemical compounds or defense structures.

Many pathogens that succeed to enter nonhost plants naturally fail to cause infection. This suggests that the resistance to infection displayed by plants against some pathogens is the result of chemical defense mechanisms rather than

structural ones. Plants release a range of chemicals through the surface of their shoots and roots that have a pathogen-inhibiting effect. For instance, fungi toxic exudates on the leaves of some plants, e.g., sugar beet and tomato inhibit the germination of spores of fungi *Cercospora* and *Botrytis* respectively.

Root exudates play an important role in understanding the relationships between plants and soil microorganisms, ranging from mutualistic to pathogenic. Recent research employing rRNA gene pyrosequencing showed that root exudate changes are mostly controlled by molecular cross -talk between plants and soil microorganisms (Chaparro et al. 2014; Sugiyama et al. 2014). It was observed that the root exudates are the first step toward colonization for many rhizosphere bacteria (Tan et al. 2013). They stimulate spore germination for root parasitic fungi (Harrison 1998; Clocchiatti et al. 2021), seed germination for flowering parasitic plants (El-Halmouch et al. 2006), and cyst hatching of nematodes (Turner and Subbotin 2013). In addition, root exudates can act as specific stimulatory compounds and antimicrobials which have a considerable toxic effect on the rhizosphere microflora. Root exudates are a complex mixture of high and low molecular-weight chemicals, many of which can trigger plant growth-pmoting rhizobacteria (PGPR) responses (Bais et al. 2008; Broeckling et al. 2008; Liu et al. 2017; Feng et al. 2018; Sharma et al. 2020). It was demonstrated that tiny sugars, polysaccharides, amino acids, aromatic chemicals, phenolics, and small organic acids are thought to be key drivers of bacterial and/or fungal attraction in the rhizosphere (de Weert et al. 2002; Ling et al. 2011; Neal et al. 2012; Zhang et al. 2020).

The compounds present in *A. thaliana* root exudates vary with the plant's developmental stages. For example, *A. thaliana* sends out growth-stage-specific signals that influence the microbiome of its roots (Chaparro et al. 2014). Also, some other evidence indicated that the microbiome of the soil can be shaped by the composition of root exudates that are released by host plants (Shi et al. 2011). Moreover, it was concluded that the host growth stage affects root physiology and changes the quality and amount of root exudates. As a result, these changes select root-associated microbiota during various growth stages (Dunfield and Germida 2003; Sugiyama et al. 2014). The secretion composition varies along the root length and this results in distinct bacterial communities along the root length (Ofek et al. 2011).

Zoospores of *Phytophthora* sp. may be attracted by the root and/or exudates of their hosts (Zentmyer 1961; Chepsergon et al. 2020; Bassani et al. 2020). *Pythium* species depend on seed and seedling exudates for either oospore germination (Stanghellini and Burr 1973; Martin and Loper 1999; Nzungize et al. 2012), sporangial germination (Nelson 1991), or zoospore attraction towards the host (Heungens and Parke 2000; Zhang et al. 2020). Contrary, maize root exudates inhibit the zoospore activity, cyst germination, and mycelial growth of *Phytophthora sojae* (Zhang et al. 2019, 2022).

5 Signaling and Quorum Sensing in Plant Symbiotic Relationships with Fungi

A large number of endophytes can colonize the plants; as a consequence, particular balancing mechanisms are required for their survival. This is a sophisticated process; quorum sensing (QS) plays a pivotal role in this communication. QS can be defined as a cell-to-cell communication system and it is a cell density-dependent microbial communication that controls gene expression by forming freely diffusible compounds called autoinducers (AIs) or quorum sensing molecules (QSMs) (Fuqua et al. 2001; Williams et al. 2007; Cornforth et al. 2014; Naga et al. 2021). These AIs synchronize responses across a density population to achieve crosstalk and inhibit the chemical defense of other organisms (Teplitski et al. 2011). QS is critical in microbe-microbe and plant-microbe crosstalks in all ecological niches (Safari et al. 2014). Since its discovery in the luminescent marine bacteria *Vibrio fischeri* (Nealson and Hastings 1979), it has been identified in a wide range of bacteria. QS regulates cell-cell communication, virulence factors, motility, competence, biofilm formation, antibiotic production, and sporulation (Miller and Bassler 2001). Through modulation of virulence factors, it allows environmental adaptation to microbial interactions with plants (Antunes et al. 2010). For decades, QS was thought to be limited to bacterial systems, eukaryotic QS gained attraction after the revolutionary discovery of farnesol compound as the QSM in the pathogenic fungus *Candida albicans* (Hornby et al. 2001) and some other fungal species were reported to have QS mechanisms and produce AIs (Table 1). QS regulates the expression of virulence genes in a variety of microorganisms, in addition to mediating a variety of functions (Antunes et al. 2010). Other growth of microorganisms has been reported to be inhibited or slowed by certain QSMs. For example, farnesol could inhibit the growth of *Saccharomyces cerevisiae* by lowering the level of diacylglycerol (DAG), effectively suppressing the G1 stage of the cell cycle (Machida et al. 1999). Astonishingly, cross-kingdom signaling was reported to be mediated by both bacterial and fungal QSMs. For example, eukaryotes signaling could approve an efficacy to interfere with bacterial quorum signals (Ismail et al. 2016) and similarly, bacteria could influence fungal QS (Martín-Rodríguez et al. 2014). In addition, endophytes exhibited a communication system network mediated by QS to control the expression of many genes among their confined populations, maintain their colonization in host plants, and counteract phytopathogens (Venkatesh Kumar et al. 2019). Qs allows for complex cross-talks between diverse endophytic microorganisms communities in *planta*. A pioneering study recently revealed the role of autoinducer-2 (AI-2) in endophytic fungi and bacteria inter-kingdom signaling systems (Tourneroche et al. 2019).

Surprisingly, plants also showed efficacy to synthesize QS-like molecules (Hartmann et al. 2014). N-acylated homoserine lactones (AHLs) serve as the most widely AI used in *proteobacteria*. QSMs that mimic AHL have been detected in some plants as *Oryza sativa* (rice) and *Phaseolus vulgaris* (bean) (Pérez-Montaño et al. 2013). These biomolecule analogs can bind to bacterial receptors and inhibit

Table 1 Some fungal QS molecules and the mediated processes

Fungi strain	QSMs	Mediated processes	Reference
Candida albicans	Farnesol	Morphogenesis, pathogenicity	Hornby et al. (2001)
	Tryptophol		Chen et al. (2004)
	Tyrosol		Chen et al. (2004)
	Phenylethanol		Chen et al. (2004)
	Farnesoic acid		Hogan (2006)
Saccharomyces cerevisiae	Tryptophol	Adhesion, invasive growth, morphogenesis	Hogan (2006)
	Tyrosol		Chen et al. (2004)
	Phenylethanol		Chen et al. (2004)
Aspergillus terreus	Butyrolactone I	Secondary metabolite synthesis	Raina et al. (2012)
A. nidulans	γ-hepatolactone	Secondary metabolite synthesis	Williams et al. (2012)
A. flavus	Oxylipins	Sporulation, mycotoxin production	Affeldt et al. (2012)
Penicillium sclerotiorum	γ-butyrolactone	Phospholipase A2 inhibitory activity	Raina et al. (2010)
Neurospora crassa	Unknown	Conidial anastomosis	Roca et al. (2005)
Cryptococcus neoformans	Amino acid peptides	Virulence	Lee et al. (2007)
Debaryomyces hansenii	Ammonia	Adhesion	Gori et al. (2011)
Penicillium decumbens	Farnesol	Cell wall biogenesis	Guo et al. (2011)
P. sclerotiorum	γ-butyrolactone	Phospholipase A2 inhibitory activity	Raina et al. (2010)
Ophiostoma floccosum	Cyclic sesquiterpenes	Yeast-mycellium dimorphism	Berrocal et al. (2014)

QS-based biofilm development in *Pantoea ananatis* and *Sinorhizobium fredii* (Pérez-Montaño et al. 2013). As a result, QS is more than a communication system used by microbes; it represents a more complex interactive phenomenon used by competing ecological niches like bacteria, fungi, and plants. Plants harbor a variety of microbes in their endospheric, rhizospheric, and phyllospheric microbiomes possibly coinciding with their origin. Hence, it is clear that co-evolutionary forces have endowed plants with the ability to produce signaling molecules to mimic microbial AIs (Teplitski et al. 2011; Hartmann et al. 2014). Research in agriculture and biotechnology today puts a great deal of attention on the complex interactions between plants and bacteria.

In a natural microbial community, a microbe's virulence is not only controlled by QS but can also be modified by other members of the community that occupy the same niche (Brader et al. 2017). Certain microorganisms can inhibit QS, this phenomenon is named by quorum quenching (QQ) and it mediates inter and intra-kingdom cross-talks (Dong et al. 2007). QQ can be achieved by inhibiting auto-inducer synthesis, preventing auto-inducer binding to their receptors, or by degrading them (Natrah et al. 2011). A variety of endophytic fungi was reported to exhibit QQ in artificial cultures, making them a potential source of alternative medicine against pathogenic microbes that utilize QS for virulence (Table 2).

Some endophytic bacteria and fungi use the QQ as antivirulence strategy (Kusari et al. 2014, 2015). In general, some QQ enzymes were reported to mediate the disruption of AIs (Hong et al. 2012). For example, lactonase and acylase enzymes can degrade AHL in Gram-negative bacteria by inactivating the lactone ring (Whitehead et al. 2001) (Fig. 3). Oxidoreductase enzyme can interfere with bacterial communication by reducing or oxidizing the acyl chain of AHLs rather than breaking them down (Hong et al. 2012).

AHL is composed of a homoserine lactone moiety and a variable-length acyl chain. Lactonase enzyme hydrolyses AHL lactone bonds, making it incapable of binding the target transcriptional factors required to synthesize virulence proteins. Lactonase was discovered in Endophytic *Enterobacter* that was isolated from the woody plant climber; *Ventilago madraspatana* (Rajesh and Rai 2014). Interestingly, lactonase enzyme from *Enterobacter* sp. CS66 isolated from another medicinal plant had a lower degrading AHL activity. However, it significantly inhibited

Table 2 Fungal endophytes have anti-quorum sensing potential

Endophytic fungi	Source	Test strain	Reference
Penicillium restrictum	*Silybum marianum*	Hybrid of bacterial strains AH2759	Figueroa et al. (2014)
Khuskia (LAEE21)	Marine plants	*Chromobacterium violaceum CVO26*	Martín-Rodríguez et al. (2014)
Fusarium (LAEE13)			
Sarocladium (LAEE06)			
Lasiodiplodia sp.			
Epicoccum (LAEE14)			
Fusarium graminearum	*Ventilago madraspatana*	*Chromobacterium violaceum CVO26*	Rajesh and Rai (2013)
Aspergillus sp.	Agricultural field	*Pseudomonas aeruginosa*	Dawande et al. (2019)
Penicillium sp.			
Fusarium sp.			
Phoma sp.			
Alternaria alternata	*Carica papaya*	*Pseudomonas aeruginosa*	Rashmi et al. (2018)
Phomopsis tersa	*Carica papaya*	*Pseudomonas aeruginosa*	Meena et al. (2020)

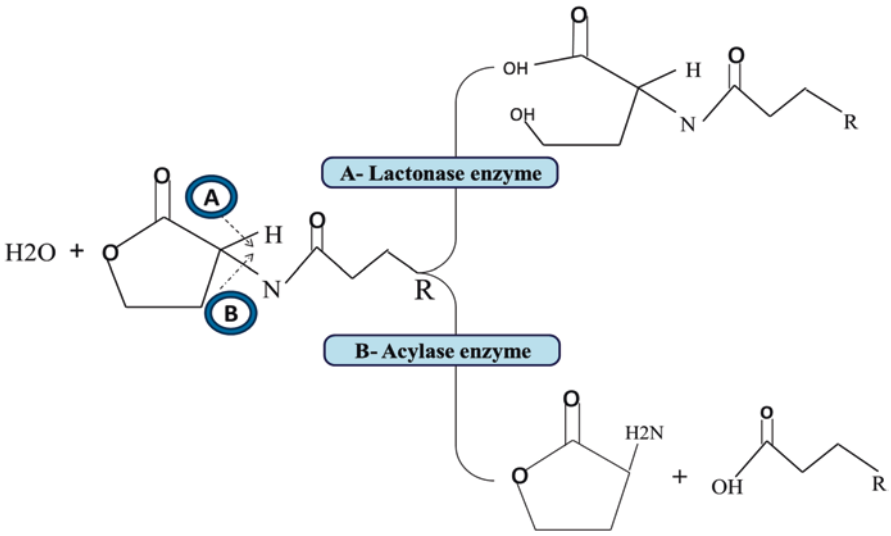

Fig. 3 QQ enzymes; lactonase enzyme (**a**) and acylase enzyme (**b**)

QS-dependent virulence factors production of *Pectobacterium atrosepticum* (Shastry et al. 2018). It suggests that various endophytic QQ enzymes evolved modifications, and their primary activity is to disrupt the virulence factors of surrounding microorganisms. *Phomopsis tersa* is an endophytic fungus isolated from *Carica papaya* that was recently discovered to reduce *Pseudomonas aeruginosa* QS-regulated virulence factors (Meena et al. 2020). As a result, it is clear that endophytes use QS and QQ to regulate the virulence and other related phenomena of resident and invading microorganisms, allowing them to survive inside plant tissues.

Many plants and their products exhibited anti-quorum sensing properties (Koh and Tham 2011; Kim and Park 2013; LaSarre and Federle 2013; Peter et al. 2019; Naga et al. 2022). Plants have been observed to disrupt QSMs through increased phytohormones production such as cytokinins and auxins, reactive oxygen species (ROS) generation, and the genes related to plant immune responses expression (von Rad et al. 2008; Bai et al. 2012; Schenk et al. 2012). They produce antivirulence quorum sensing inhibitors (QSIs), for example, *glycyrrhiza glabra* flavonoids reduced the virulence of *Acinetobacter baumannii* (Bhargava et al. 2015). Similarly, soft rot in potato is caused by *Pectobacterium* and depends on QS to synchronize its virulence factor and the plant cell wall degrading enzymes interfere with plant phenolic volatiles and disrupt its QS (Joshi et al. 2016). Furthermore, the reduction in AHL accumulation following treatment with plant volatiles indicating a direct interaction with N-acyl homoserine lactone synthase or regulatory protein (Joshi et al. 2016).

As a result, it is clear that plants are highly dependent on QQ and QS to sustain their endophytic microbiome for their growth, virulence, and sporulation. In light of this, the plant endospheric microbiome offers a favorable environment for endophytic microorganisms to compete in.

5.1 Endophytism Interactions

Endophytic behavior varies greatly and ranges from pathogenism, mutualism, and saprophytism (Saikkonen et al. 1998; Schulza and Boyle 2005). In physiological adaptation to fluctuating habitats, the transition between various lifestyles serves as an evolutionary determinant, providing phenotypic diversity to fungi. After colonizing several plants, the endophytic fungi may have a range of lifestyles depend on the transmission mode, infection pattern, the age of the plant, climate changes, and the genotype of the endophyte and host (Saikkonen et al. 1998; Freeman et al. 2001). One microbial species may have strains that are mutualistic, pathogenic, or commensal (Sheibani-Tezerji et al. 2015). Microbes from various strains share some genomes due to intra-specific existence, which allows the plant defense system to attack them identically. Comparative genomic research of endophytes and pathogens showed that their virulence factors are analogous. But, some endophytes lacked the essential virulence factors that act as a defining characteristic (Lòpez-Fernàndez et al. 2015). It is noteworthy to mention that a colonized fungus can change its lifestyle from pathogenism to endophytism or vice-versa. This relies on the metabolic and/or genetic condition of its interacting partners as well as environmental conditions (Márquez et al. 2007; Redman et al. 2001; Unterseher and Schnittler 2010). However, the genetic bases of switching in endophytic lifestyles is not understood (Redman et al. 2001; Unterseher and Schnittler 2010).

For instance, it was observed that the mutualistic endophyte; *Epichloe festucae* benefits its host plant; *Lolium perenne* by enhancing the acquisition of nutrients and this increased the biotic stressors resistance (Schardl 2001). *E. festucae* NoxA mutant strain which causes a change from parasitism to mutualism was isolated to pinpoint the symbiotic genes of *E. festucae* (Tanaka et al. 2006). NoxA gene in *E. festucae* and the symbiosis regulation was activated by GTPase RacA (Tanaka et al. 2008). ROS are released by the *E. festucae* NoxA gene, which encodes NADPH oxidase that caused a significant infection, loss of apical dominance, premature senescence, and ultimately death in the *L. perenne* plant. Further molecular information about this interaction provided detailed insight into the endophyte's intricate regulatory processes displayed by *E. festucae* within the host *L. perenne* (Bharadwaj et al. 2020) (Fig. 4). The most intriguing aspect of this interaction is the endophytes efforts to sustain themselves inside the host by trying to limit its growth in the intercellular spaces of the host. This autoregulation example shows that balanced antagonisms as well as other antagonism-independent methods may also help endophytes survive in a mutualistic and a symptomatic manner. Many endophytes particularly systemic ones that spread vertically are perpetually present in the host plant and never develop into pathogenic organisms. Some endophytes were evolved in close association with a specific host such that antagonism is not displayed against them, and they may have acquired alternative methods of endophytism maintenance.

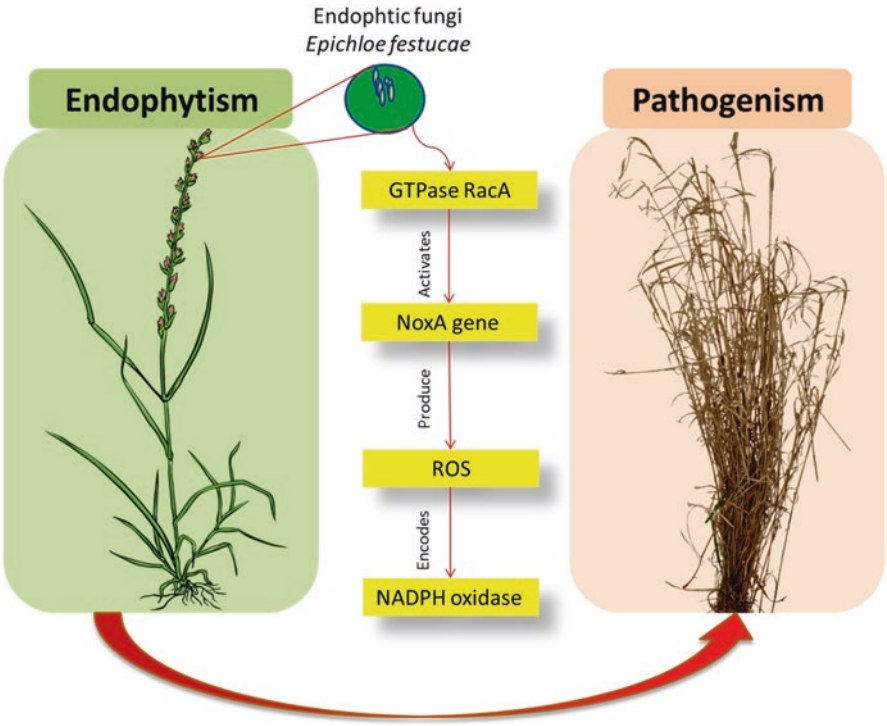

Fig. 4 Conversion the endophytic fungi *E. festucae from* endophytism to pathogenism in *L. perenne*

Similarly, saprophyte-endophyte shift was reported, but nothing is understood about the triggers that cause these shifts. For instance, *Phomopsis liquidambari* B3 fungi can form a mutualistic relationship with some host plants such as *Bischofia polycarpa* plant and revealed to exude a variety of enzymes in a saprophytic state including cellulase, laccase, and polyphenol oxidase (Chuan-Chao et al. 2010; Zhou et al. 2014). The colonization strategy used by *P. liquidambari* B3 in these plants is host adapted. They exhibit various growth promotions that are influenced by nitrogen (N_2) availability according to observations of colonization dynamics and promoting of plant growth evaluation as in *Oryza sativa* and *Arabidopsis thaliana*. By studying the genes connected with the saprophytic-endophytic transition, it was revealed that the most notable genes in *P. liquidambari* B3 participate in protein synthesis, ribosome biogenesis, and MAPK signaling and most of which are up-regulated in the endophyte (Zhou et al. 2017).

In addition, endophytic fungi exhibit a shift towards the pathogenic side of the spectrum with the aging of the leaves (Saikkonen et al. 1998). Age increases the prevalence of endophytic fungi which result in more visible outer infections. For instance, endophytic fungus colonized older *Pinus densiflora* and *Pinus thunbergia*

needles more than younger needles (Hata and Futai 1993). Similar to this, *Citrus lemon* older seedlings that have the endophytic *Metarhizium anisopliae* and *Beauveria bassiana* strains showed the best survival rate. Consequently, plant aging has an impact on endophytic lifestyle as it is distinguished by a deficiency of critical nutrients (Bamisile et al. 2020).

Also, it was evaluated that fungal community may be altered from stage to another according to the developmental stage of plant and this is important in the change from parasitic to mutualistic. For example, joshua trees relationship with arbuscular mycorrhizal fungi (AMF) (Harrower and Gilbert 2021). Furthermore, environmental factors can have an impact on the endophytic fungus symbiotic lifestyle. Under certain conditions, the symptomatic endophyte *Diplodia mutila* of *Iriartea deltoidea* plant becomes parasitic (Alvarez-Loayza et al. 2011). The impact of irradiance on the endophytic transition was also investigated; *I. deltoidea* was reported to favor the shaded parts while intense light causes the associated endophyte to become pathogenic. On the contrary, endophytic fungi *Periconia macrospinos* changes from a mutualistic lifestyle to an extreme pathogenic if the shade increased (Mandyam and Jumpponen 2015). Salinity was shown to increase *Fusarium solani* pathogenicity (Eydoux and Farrer 2020).

To retain the mutualism, there must be a balance between balancing strategies and antagonisms and in case of any disorder occurrence, disease symptoms may manifest and the host immune system will reject the fungus (Rai and Agarkar 2016). The relationship between genetic regulation of the pathways variables and the processes is yet unclear. Additionally, systemic endophytes tend to exhibit mutualism more whereas transitory endophytes are very dynamic. Thus, the above- mentioned variables may be modifying the balancing tactics to upset the endophytic lifestyle, pushing the fungus to the maximum pathogenicity.

Endophytes use QQ and QS as anti-pathogenic strategies against invader and resident microbes, any disruption in these communicating pathways influence and destabilize the mutualistic symbiosis. Microbial QSIs can regulate the virulence, proliferation, and sporulation of a particular target microbe. However, when the regulating mechanism becomes unstable owing to any intrinsic or external reason, the target microbe becomes harmful. Additionally, it is possible that plant QSIs balance the pathogenicity of endophytes in the microecosystem of plant whereas nutritional imbalances may make it unstable. For instance, the fungus *E. festucae* is mutualistic and asexually reproducing endophyte of *L. perenne* that has been extensively investigated (Schardl 2001). Nevertheless, the start of flowering in the host plant triggers the sexual life cycle in some *Epichloe* spp., which changes the fungi mutualism to antagonism because resources are being pushed towards flowering (Schardl et al. 2004). It implies that plants devote the entirety of their energy to flowering rather than the virulence resistance of endophytic microorganisms which leads to changing their lifestyle. Even though these methods of disruption cannot fully explain this complex phenomenon, their involvement could not be disregarded. Therefore, uncovering the complex interaction of numerous elements that underlies endophytic dynamism would require extensive research.

Organisms have evolved some complex strategies to interact and tolerate the environmental changes (Bouyahya et al. 2017). So, they may alter their metabolism to resist various intrinsic and/or extrinsic stress situations for improved survival in the changed surroundings (van't Padje et al. 2016). The fundamental cross-talks between endophytes and plants are based on secondary metabolites (Huang et al. 2019; Jacoby et al. 2021). The host metabolism is typically induced by endophyte (Ludwig-Müller 2015). While endophytes supply many metabolites to assist the host plants in surviving with diverse stress circumstances, plants can produce some compounds which are essential for their self-defense and the endophytes growth (Guo et al. 2008). Endophytes can produce secondary metabolites in axenic cultures, and they are being used to make well-known and innovative medicines with antimalarial, antioxidant, antiviral, and anti-cancerous properties (Kusari et al. 2012). Natural bioactive compounds generated from endophytes come into many structural classes including steroids, flavonoids, phenolics, alkaloids, phenylpropanoids, terpenoids, quinones, volatile organic and aliphatic compounds (Schulz et al. 2002).

It is noteworthy to mention that the endophytes influence not just the host plant metabolism, but also the metabolism of any resident endophytes. It is clear from the fact the large number of secondary metabolites remain equivocal (Lim et al. 2012). It was reported that microbial interactions are crucial in stimulating the secondary metabolites production. For example, culturing *Streptomyces hygroscopicus* with *Aspergillus nidulans* enabled polyketide biosynthetic gene cluster activation (Schroeckh et al. 2009). Also, methyl esters and polyketides production was induced by culturing *Bacillus subtilis* bacteria with the endophytic fungus *Chaetomiun* sp. (Akone et al. 2016).

In addition, some plant extracts have been reported to act as inhibitors of the epigenetic modification-related enzymes, hence activating specific quiet biosynthesis pathways of secondary metabolites. For instance, the endophytic fungus *Colletotrichum gloeosporioides* isolated from *Syzygium aromaticum* generated some metabolites after the addition of the epigenetic modulators curcumin and resveratrol from grape and turmeric extracts, respectively (Sharma et al. 2017). Similarly, *Eupenicillium* sp. LG41 (fungal endophyte) of *Xanthium sibricum* when treated with nicotinamide produced the two recognized metabolites; eupenicinicol A and eujavanicol A (Li et al. 2017). In a similar manner, treatment of the endophytic fungus *Hypoxylon anthochroum* of *Carica papaya* with the curry leaf extract and garlic led to the stimulation of cryptic bioactive metabolites (Mishra et al. 2020). Diallyl disulfide and allyl mercaptan; the two main ingredients of organosulfur compounds known for inhibiting histone deacetylases, are reported to be produced by garlic leaves. Curry leaves also contain mahanine, which repress DNA methyltransferase. These relationships are based on small diffusible signaling molecules that can activate normally silent biosynthetic pathways, such as QSMs (Hughes and Sperandio 2008; Scherlach and Hertweck 2009).

Endophytes are endosymbionts that persist for at least a portion of their life cycle inside of plants without causing any diseases (Hallmann et al. 1997). They are frequently bacteria or fungi which are stabilized by chemically mediated interactions

(Wang 2016). For example, hexacyclopeptides antimicrobial was produced by the endophytic fungi *Fusarium solani* and bacteria *Achromobacter xylosoxidans* on *Narcissus tazetta* (Wang et al. 2015; Haryani et al. 2020). Hence, it is clear to note that endophytes developed complex communication strategies due to their sharing ecosystems and not all these interactions are inherently antagonism-based cross-talks (Mattoo and Nonzom 2021). Intriguingly, the outcome of this cross-kingdom symbiosis is shaped by the diverse interactions between endophytic microorganisms and the plant (Rodriguez and Roossinck 2012). For instance, thermotolerance ability of *Dichanthelium lanuginosum* was believed to be caused by endophytic fungus *Curvularia protuberata* but actually it was caused by the double-stranded virus carried by the symbiont fungus (Márquez et al. 2007; Rodriguez and Roossinck 2012).

Few endophytic fungi were reported by harboring bacteria that could change how they interact with their host plants in some ways (MacDonald and Chandler 1981; Bonfante and Anca 2009; Kobayashi and Crouch 2009). For example, *Burkholderia* spp. that thrive within the *Gigaspora decipiens* fungi could inhibit the germination of spores (Levy et al. 2003). Numerous endohyphal bacteria have an impact on endophytic fungi ability to produce metabolites. For instance, after hosting *Luteibacter* sp. bacteria, the endophytic fungi *Pestalotiopsis neglecta* produced indole-3-acetic acid at a considerably higher rate (Hoffman et al. 2013). Additionally, it was discovered that the *Phyllosticta capitalensis* fungus which is an endophyte of *Buxus sinica* produced two novel lactamfused-4-pyrones by harboring *Herbaspirillum* sp. bacteria (Wang 2016). Also, it was reported that *Cupressus sempervirens* endophytic fungi that contain endohyphal bacteria as *Bacillus subtilis*, *B. pumilus*, and *Sphingomonas paucimobilis* which could produce organic volatile compounds which have antibacterial activity against many pathogens (Pakvaz and Soltani 2016). Additionally, endohyphal bacteria were shown to trigger phytohormones, which control the host reproductive system and protect host fungi from harsh conditions (Arora and Riyaz-Ul-Hassan 2019).

Endosymbiotic bacteria may be facultative or obligatory partners on the fungi (Bastías et al. 2020). Obligate symbionts reproduce vertically with the fungal host, but facultative symbionts more closely resemble the free-living members hence have the capacity to invade fungal hosts (Baltrus et al. 2017). Numerous facultative nonpathogenic bacteria can colonize plant tissues on their own independent of the fungal hosts (Glaeser et al. 2016). For instance, endoglucanases and endobetaxylanases enzymes assist the endohyphal bacteria *Rhizobium radiobacter* F4 to colonize several plants roots on their own (Guo et al. 2018).

Ectosymbiotic bacteria were observed to influence the fitness of their associated fungi as well as endosymbiotic counterparts. Numerous microbial interactions benefit their partners development and defense in various ways (Schelkle and Peterson 1997; Oh et al. 2018). For instance, *Rhizophagus irregularis* fungi and *Rahnella aquatilis* bacteria exchange of phosphorus, calcium, and carbon was reported to be essential for their interaction (Zhang et al. 2018). It is interesting to observe that the AMF fructose exudation was approved to enhance the bacterial genes expression that code for the enzyme phosphatase which dissolves phosphate (Mattoo and

Nonzom 2021). Various endophytes cooperate to support host growth and biocontrol mechanisms. For example, inoculation of nitrogen-fixing endophytic strains derived from *Phaseolus vulgaris* with *Rhizobium tropici* and nodule endophytic strains such as *Burkholderia*, *Bacillus*, *Pseudomonas*, and *Paenibacillus* enhanced disease resistance against *Rhizoctonia solani* (Ferreira et al. 2020). In conclusion, some endophytes that are closely symbiotic with their partners assist in the successful colonization of their partners while exhibiting antagonistic behavior toward some other endophytes and diseases. Therefore, it would appear that balanced antagonism is not always a necessary condition for maintaining endophytism. Theoretically, it can be one of the methods or a part of the complex plan the endophytes utilize to survive inside the host plants.

References

Abdul Rahman NSN, Abdul Hamid NW, Nadarajah K (2021) Effects of abiotic stress on soil microbiome. Int J Mol Sci 22:9036

Affeldt KJ, Brodhagen M, Keller NP (2012) Aspergillus oxylipin signaling and quorum sensing pathways depend on G protein-coupled receptors. Toxins (Basel) 4:695–717

Akone SH, Mándi A, Kurtán T, Hartmann R, Lin W, Daletos G, Proksch P (2016) Inducing secondary metabolite production by the endophytic fungus Chaetomium sp. through fungal–bacterial co-culture and epigenetic modification. Tetrahedron 72:6340–6347

Allen RL, Bittner-Eddy PD, Grenville-Briggs LJ, Meitz JC, Rehmany AP, Rose LE, Beynon JL (2004) Host-parasite coevolutionary conflict between Arabidopsis and downy mildew. Science (80–) 306:1957–1960

Alvarez-Loayza P, White JF Jr, Torres MS, Balslev H, Kristiansen T, Svenning J-C, Gil N (2011) Light converts endosymbiotic fungus to pathogen, influencing seedling survival and niche-space filling of a common tropical tree, Iriartea deltoidea. PLoS One 6:e16386

Aly AH, Debbab A, Proksch P (2011) Fungal endophytes: unique plant inhabitants with great promises. Appl Microbiol Biotechnol 90:1829–1845

Anand T, Bhaskaran R, Karthikeyan TG, Rajesh M, Senthilraja G (2008) Production of cell wall degrading enzymes and toxins by Colletotrichum capsici and Alternaria alternata causing fruit rot of chillies. J Plant Prot Res 48:437–451

Antunes LCM, Ferreira RBR, Buckner MMC, Finlay BB (2010) Quorum sensing in bacterial virulence. Microbiology 156:2271–2282

Arora P, Riyaz-Ul-Hassan S (2019) Endohyphal bacteria; the prokaryotic modulators of host fungal biology. Fungal Biol Rev 33:72–81

Aydi-Ben-Abdallah R, Jabnoun-Khiareddine H, Daami-Remadi M (2020) Variation in the composition of the microbial community in the rhizosphere of potato plants depending on cropping season, cultivar type, and plant development stage. Int J Agri Env Food Sci 4(3):319–333. https://doi.org/10.31015/jaefs.2020.3.11

Bacon CW, Glenn AE, Yates IE (2008) Fusarium verticillioides: managing the endophytic association with maize for reduced fumonisins accumulation. Toxin Rev 27:411–446

Bae S-J, Mohanta TK, Chung JY, Ryu M, Park G, Shim S, Hong S-B, Seo H, Bae D-W, Bae I (2016) Trichoderma metabolites as biological control agents against Phytophthora pathogens. Biol Control 92:128–138

Bai X, Todd CD, Desikan R, Yang Y, Hu X (2012) N-3-oxo-decanoyl-L-homoserine-lactone activates auxin-induced adventitious root formation via hydrogen peroxide-and nitric oxide-dependent cyclic GMP signaling in mung bean. Plant Physiol 158:725–736

Bais HP, Broeckling CD, Vivanco JM (2008) Root exudates modulate plant–microbe interactions in the rhizosphere. In: Secondary metabolites in soil ecology. Springer, pp 241–252
Bal HB, Nayak L, Das S, Adhya TK (2013) Isolation of ACC deaminase producing PGPR from rice rhizosphere and evaluating their plant growth promoting activity under salt stress. Plant Soil 366:93–105
Baltrus DA, Dougherty K, Arendt KR, Huntemann M, Clum A, Pillay M, Palaniappan K, Varghese N, Mikhailova N, Stamatis D (2017) Absence of genome reduction in diverse, facultative endohyphal bacteria. Microb Genomics 3
Bamisile BS, Senyo Akutse K, Dash CK, Qasim M, Ramos Aguila LC, Ashraf HJ, Huang W, Hussain M, Chen S, Wang L (2020) Effects of seedling age on colonization patterns of Citrus limon plants by endophytic Beauveria bassiana and Metarhizium anisopliae and their influence on seedlings growth. J Fungi 6:29
Bargmann CI (2006) Chemosensation in C. elegans. WormBook: The online review of C. elegans biology [Internet].
Bassani I, Larousse M, Tran QD, Attard A, Galiana E (2020) Phytophthora zoospores: from perception of environmental signals to inoculum formation on the host-root surface. Comput Struct Biotechnol J 18:3766–3773
Bastías DA, Johnson LJ, Card SD (2020) Symbiotic bacteria of plant-associated fungi: friends or foes? Curr Opin Plant Biol 56:1–8
Berendsen RL, Vismans G, Yu K, Song Y, de Jonge R, Burgman WP, Burmølle M, Herschend J, Bakker PAHM, Pieterse CMJ (2018) Disease-induced assemblage of a plant-beneficial bacterial consortium. ISME J 12:1496–1507
Berrocal A, Oviedo C, Nickerson KW, Navarrete J (2014) Quorum sensing activity and control of yeast-mycelium dimorphism in Ophiostoma floccosum. Biotechnol Lett 36:1503–1513
Bharadwaj R, Jagadeesan H, Kumar SR, Ramalingam S (2020) Molecular mechanisms in grass-Epichloë interactions: towards endophyte driven farming to improve plant fitness and immunity. World J Microbiol Biotechnol 36:1–28
Bhargava N, Singh SP, Sharma A, Sharma P, Capalash N (2015) Attenuation of quorum sensing-mediated virulence of Acinetobacter baumannii by Glycyrrhiza glabra flavonoids. Future Microbiol 10:1953–1968
Bhaskar R, Xavier LSE, Udayakumaran G, Kumar DS, Venkatesh R, Nagella P (2021) Biotic elicitors: a boon for the in-vitro production of plant secondary metabolites. Plant Cell Tissue Organ Cult:1–18
Boller T, Felix G (2009) A renaissance of elicitors: perception of Microbe–associated molecular patterns and danger signals by pattern-recognition. Ann Rev Plant Biol 60:379–406
Bonfante P, Anca I-A (2009) Plants, mycorrhizal fungi, and bacteria: a network of interactions. Annu Rev Microbiol 63:363–383
Bouyahya A, Dakka N, Et-Touys A, Abrini J, Bakri Y (2017) Medicinal plant products targeting quorum sensing for combating bacterial infections. Asian Pac J Trop Med 10:729–743
Brader G, Compant S, Vescio K, Mitter B, Trognitz F, Ma L-J, Sessitsch A (2017) Ecology and genomic insights into plant-pathogenic and plant-nonpathogenic endophytes. Annu Rev Phytopathol 55
Broeckling CD, Broz AK, Bergelson J, Manter DK, Vivanco JM (2008) Root exudates regulate soil fungal community composition and diversity. Appl Environ Microbiol 74:738–744
Bronstein JL (2015) Mutualism. Oxford University Press, Oxford
Brooks DR, Hoberg EP, Boeger WA, Gardner SL, Galbreath KE, Herczeg D, Mejía-Madrid HH, Rácz SE, Dursahinhan AT (2014) Finding them before they find us: informatics, parasites, and environments in accelerating climate change. Comp Parasitol 81:155–164
Brundrett M (2004) Diversity and classification of mycorrhizal associations. Biol Rev 79:473–495
Bulgarelli D, Rott M, Schlaeppi K, Ver Loren Van Themaat E, Ahmadinejad N, Assenza F, Rauf P, Huettel B, Reinhardt R, Schmelzer E (2012) Revealing structure and assembly cues for Arabidopsis root-inhabiting bacterial microbiota. Nature 488:91–95

Buscaill P, van der Hoorn RAL (2021) Defeated by the nines: nine extracellular strategies to avoid microbe-associated molecular patterns recognition in plants. Plant Cell 33:2116–2130

Cavicchioli R, Ripple WJ, Timmis KN, Azam F, Bakken LR, Baylis M, Behrenfeld MJ, Boetius A, Boyd PW, Classen AT (2019) Scientists' warning to humanity: microorganisms and climate change. Nat Rev Microbiol 17:569–586

Cesari S, Thilliez G, Ribot C, Chalvon V, Michel C, Jauneau A, Rivas S, Alaux L, Kanzaki H, Okuyama Y (2013) The rice resistance protein pair RGA4/RGA5 recognizes the Magnaporthe oryzae effectors AVR-Pia and AVR1-CO39 by direct binding. Plant Cell 25:1463–1481

Cessna SG, Sears VE, Dickman MB, Low PS (2000) Oxalic acid, a pathogenicity factor for Sclerotinia sclerotiorum, suppresses the oxidative burst of the host plant. Plant Cell 12:2191–2199

Chaparro JM, Badri DV, Vivanco JM (2014) Rhizosphere microbiome assemblage is affected by plant development. ISME J 8:790–803

Chen H, Fujita M, Feng Q, Clardy J, Fink GR (2004) Tyrosol is a quorum-sensing molecule in Candida albicans. Proc Natl Acad Sci 101:5048–5052

Chen Y, Kistler HC, Ma Z (2019) Fusarium graminearum trichothecene mycotoxins: biosynthesis, regulation, and management. Annu Rev Phytopathol 57:15–39

Chen J, Ullah C, Reichelt M, Beran F, Yang Z-L, Gershenzon J, Hammerbacher A, Vassão DG (2020) The phytopathogenic fungus Sclerotinia sclerotiorum detoxifies plant glucosinolate hydrolysis products via an isothiocyanate hydrolase. Nat Commun 11:1–12

Chepsergon J, Motaung TE, Bellieny-Rabelo D, Moleleki LN (2020) Organize, don't agonize: strategic success of Phytophthora species. Microorganisms 8:917

Chialva M, Salvioli di Fossalunga A, Daghino S, Ghignone S, Bagnaresi P, Chiapello M, Novero M, Spadaro D, Perotto S, Bonfante P (2018) Native soils with their microbiotas elicit a state of alert in tomato plants. New Phytol 220:1296–1308

Chialva M, Ghignone S, Cozzi P, Lazzari B, Bonfante P, Abbruscato P, Lumini E (2020) Water management and phenology influence the root-associated rice field microbiota. FEMS Microbiol Ecol 96:fiaa146

Chuan-Chao D, Yan C, Lin-shuang T, Yang S (2010) Correlation between invasion by endophytic fungus Phomopsis sp. and enzyme production. Afr J Agric Res 5:1324–1340

Clocchiatti A, Hannula SE, Van den Berg M, Hundscheid MPJ, De Boer W (2021) Evaluation of phenolic root exudates as stimulants of saptrophic fungi in the rhizosphere. Front Microbiol 12:644046

Cohen SP, Leach JE (2019) Abiotic and biotic stresses induce a core transcriptome response in rice. Sci Rep 9:1–11

Cornforth DM, Popat R, McNally L, Gurney J, Scott-Phillips TC, Ivens A, Diggle SP, Brown SP (2014) Combinatorial quorum sensing allows bacteria to resolve their social and physical environment. Proc Natl Acad Sci 111:4280–4284

Crudo F, Varga E, Aichinger G, Galaverna G, Marko D, Dall'Asta C, Dellafiora L (2019) Co-occurrence and combinatory effects of Alternaria mycotoxins and other xenobiotics of food origin: current scenario and future perspectives. Toxins (Basel) 11:640

da Silva KRA, Salles JF, Seldin L, van Elsas JD (2003) Application of a novel Paenibacillus-specific PCR-DGGE method and sequence analysis to assess the diversity of Paenibacillus spp. in the maize rhizosphere. J Microbiol Methods 54:213–231

de Moraes Pontes JG, Fernandes LS, Dos Santos RV, Tasic L, Fill TP (2020) Virulence factors in the phytopathogen–host interactions: an overview. J Agric Food Chem 68:7555–7570

de Weert S, Vermeiren H, Mulders IHM, Kuiper I, Hendrickx N, Bloemberg GV, Vanderleyden J, De Mot R, Lugtenberg BJJ (2002) Flagella-driven chemotaxis towards exudate components is an important trait for tomato root colonization by Pseudomonas fluorescens. Mol Plant-Microbe Interact 15:1173–1180

Daryaei A, Jones EE, Glare TR, Falloon RE (2016) pH and water activity in culture media affect biological control activity of Trichoderma atroviride against Rhizoctonia solani. Biol Control 92:24–30

Davidsson PR, Kariola T, Niemi O, Palva ET (2013) Pathogenicity of and plant immunity to soft rot pectobacteria. Front Plant Sci 4:191

Dawande AY, Gajbhiye ND, Charde VN, Banginwar YS (2019) Assessment of endophytic fungal isolates for its Antibiofilm activity on Pseudomonas aeruginosa. Int J Sci Res Biol Sci Vol 6:3

Do QT (2022) Antagonistic activities of endophytic bacteria isolated from rice roots against the fungus Magnaporthe oryzae, a causal of rice blast disease. Egypt J Biol Pest Control 32:1–11

Dong Y-H, Wang L-H, Zhang L-H (2007) Quorum-quenching microbial infections: mechanisms and implications. Philos Trans R Soc B Biol Sci 362:1201–1211

Dridi B, Raoult D, Drancourt M (2011) Archaea as emerging organisms in complex human microbiomes. Anaerobe 17:56–63

Druzhinina IS, Seidl-Seiboth V, Herrera-Estrella A, Horwitz BA, Kenerley CM, Monte E, Mukherjee PK, Zeilinger S, Grigoriev IV, Kubicek CP (2011) Trichoderma: the genomics of opportunistic success. Nat Rev Microbiol 9:749–759

Dunfield KE, Germida JJ (2003) Seasonal changes in the rhizosphere microbial communities associated with field-grown genetically modified canola (Brassica napus). Appl Environ Microbiol 69:7310–7318

Durbin RD, Uchytil TF (1977) A survey of plant insensitivity to tentoxin. Phytopathology 67:602–603

Durrant WE, Dong X (2004) Systemic acquired resistance. Annu Rev Phytopathol 42:185–209

Ek-Ramos MJ, Zhou W, Valencia CU, Antwi JB, Kalns LL, Morgan GD, Kerns DL, Sword GA (2013) Spatial and temporal variation in fungal endophyte communities isolated from cultivated cotton (Gossypium hirsutum). PLoS One 8:e66049

Elad Y (2000) Biological control of foliar pathogens by means of Trichoderma harzianum and potential modes of action. Crop Prot 19:709–714

El-Halmouch Y, Benharrat H, Thalouarn P (2006) Effect of root exudates from different tomato genotypes on broomrape (O. aegyptiaca) seed germination and tubercle development. Crop Prot 25:501–507

Escrivá L, Oueslati S, Font G, Manyes L (2017) Alternaria mycotoxins in food and feed: an overview. J Food Qual 2017

Estrada C, Wcislo WT, Van Bael SA (2013) Symbiotic fungi alter plant chemistry that discourages leaf-cutting ants. New Phytol 198:241–251

Eydoux L, Farrer EC (2020) Does salinity affect lifestyle switching in the plant pathogen Fusarium solani? Access Microbiol 2

Fávaro LCDL, Sebastianes FLDS, Araújo WL (2012) Epicoccum nigrum P16, a sugarcane endophyte, produces antifungal compounds and induces root growth. PLoS One 7:e36826

Favre-Godal Q, Gourguillon L, Lordel-Madeleine S, Gindro K, Choisy P (2020) Orchids and their mycorrhizal fungi: an insufficiently explored relationship. Mycorrhiza 30:5–22

Feng H, Zhang N, Du W, Zhang H, Liu Y, Fu R, Shao J, Zhang G, Shen Q, Zhang R (2018) Identification of chemotaxis compounds in root exudates and their sensing chemoreceptors in plant-growth-promoting rhizobacteria Bacillus amyloliquefaciens SQR9. Mol Plant-Microbe Interact 31:995–1005

Ferreira LDEVM, De Carvalho F, Andrade JFC, Oliveira DP, De Medeiros FHV, Moreira FMDES (2020) Co-inoculation of selected nodule endophytic rhizobacterial strains with Rhizobium tropici promotes plant growth and controls damping off in common bean. Pedosphere 30:98–108

Fesel PH, Zuccaro A (2016) Dissecting endophytic lifestyle along the parasitism/mutualism continuum in Arabidopsis. Curr Opin Microbiol 32:103–112

Figueroa M, Jarmusch AK, Raja HA, El-Elimat T, Kavanaugh JS, Horswill AR, Cooks RG, Cech NB, Oberlies NH (2014) Polyhydroxyanthraquinones as quorum sensing inhibitors from the guttates of Penicillium restrictum and their analysis by desorption electrospray ionization mass spectrometry. J Nat Prod 77:1351–1358

Fitzpatrick CR, Salas-González I, Conway JM, Finkel OM, Gilbert S, Russ D, Teixeira PJPL, Dangl JL (2020) The plant microbiome: from ecology to reductionism and beyond. Annu Rev Microbiol 74:81–100

Foo E, Yoneyama K, Hugill CJ, Quittenden LJ, Reid JB (2013) Strigolactones and the regulation of pea symbioses in response to nitrate and phosphate deficiency. Mol Plant 6:76–87

Formey D, Sallet E, Lelandais-Brière C, Ben C, Bustos-Sanmamed P, Niebel A, Frugier F, Combier JP, Debellé F, Hartmann C (2014) The small RNA diversity from Medicago truncatularoots under biotic interactions evidences the environmental plasticity of the miRNAome. Genome Biol 15:1–21

Freeman S, Horowitz S, Sharon A (2001) Pathogenic and nonpathogenic lifestyles in Colletotrichum acutatum from strawberry and other plants. Phytopathology 91:986–992

Fuqua C, Parsek MR, Greenberg EP (2001) Regulation of gene expression by cell-to-cell communication: acyl-homoserine lactone quorum sensing. Annu Rev Genet 35:439

Ganie SA, Ahammed GJ (2021) Dynamics of cell wall structure and related genomic resources for drought tolerance in rice. Plant Cell Rep 40:437–459

Ghosh S, Chowdhury R, Bhattacharya P (2016) Mixed consortia in bioprocesses: role of microbial interactions. Appl Microbiol Biotechnol 100:4283–4295

Glaeser SP, Imani J, Alabid I, Guo H, Kumar N, Kämpfer P, Hardt M, Blom J, Goesmann A, Rothballer M (2016) Non-pathogenic Rhizobium radiobacter F4 deploys plant beneficial activity independent of its host Piriformospora indica. ISME J 10:871–884

Glazebrook J (2005) Contrasting mechanisms of defense against biotrophic and necrotrophic pathogens. Annu Rev Phytopathol 43:205

Gori K, Knudsen PB, Nielsen KF, Arneborg N, Jespersen L (2011) Alcohol-based quorum sensing plays a role in adhesion and sliding motility of the yeast D ebaryomyces hansenii. FEMS Yeast Res 11:643–652

Guo B, Wang Y, Sun X, Tang K (2008) Bioactive natural products from endophytes: a review. Appl Biochem Microbiol 44:136–142

Guo H, Ma A, Zhao G, Yun J, Liu X, Zhang H, Zhuang G (2011) Effect of farnesol on Penicillium decumbens's morphology and cellulase production. Bioresources 6:3252–3259

Guo Y, Matsuoka Y, Miura T, Nishizawa T, Ohta H, Narisawa K (2018) Complete genome sequence of Agrobacterium pusense VsBac-Y9, a bacterial symbiont of the dark septate endophytic fungus Veronaeopsis simplex Y34 with potential for improving fungal colonization in roots. J Biotechnol 284:31–36

Gupta S, Chaturvedi P (2019) Enhancing secondary metabolite production in medicinal plants using endophytic elicitors: a case study of Centella asiatica (Apiaceae) and asiaticoside. Endophytes Grow World:310–323

Guttman DS, McHardy AC, Schulze-Lefert P (2014) Microbial genome-enabled insights into plant–microorganism interactions. Nat Rev Genet 15:797–813

Hallmann J, Quadt-Hallmann A, Mahaffee WF, Kloepper JW (1997) Bacterial endophytes in agricultural crops. Can J Microbiol 43:895–914

Harbort CJ, Hashimoto M, Inoue H, Niu Y, Guan R, Rombolà AD, Kopriva S, Voges MJ, Sattely ES, Garrido-Oter R (2020) Root-secreted coumarins and the microbiota interact to improve iron nutrition in Arabidopsis. Cell Host Microbe 28:825–837

Harrison MJ (1998) Development of the arbuscular mycorrhizal symbiosis. Curr Opin Plant Biol 1:360–365

Harrower JT, Gilbert GS (2021) Parasitism to mutualism continuum for Joshua trees inoculated with different communities of arbuscular mycorrhizal fungi from a desert elevation gradient. PLoS One 16:e0256068

Hartmann A, Rothballer M, Hense BA, Schröder P (2014) Bacterial quorum sensing compounds are important modulators of microbe-plant interactions. Front Plant Sci 5:131

Haryani Y, Hilma R, Delfira N, Martalinda T, Puspita F, Friska A, Juwita D, Farniga A, Ardi F (2020) Antibacterial activity of Achromobacter sp. and Bacillus sp., bacterial endophytes derived from Mangrove Ceriops tagal (Perr.) CB Robb. In: IOP conference series: materials science and engineering. IOP Publishing, p 12013

Hata K, Futai K (1993) Effect of needle aging on the total colonization rates of endophytic fungi on Pinus thunbergii and Pinus densiflora needles. J Jpn For Soc 75:338–341

Hedden P, Sponsel V (2015) A century of gibberellin research. J Plant Growth Regul 34:740–760
Heiniger U, Rigling D (1994) Biological control of chestnut blight in Europe. Annu Rev Phytopathol 32:581–599
Hernandez D, Kiesewetter KN, Palakurty S, Stinchcombe JR, Afkhami ME (2019) Synergism and symbioses: unpacking complex mutualistic species interactions using transcriptomic approaches. Model Legum Medicago truncatula:1045–1054
Heungens K, Parke J (2000) Zoospore homing and infection events: effects of the biocontrol bacterium Burkholderia cepacia AMMDR1 on two oomycete pathogens of pea (Pisum sativum L.). Appl Environ Microbiol 66:5192–5200
Hoffman MT, Gunatilaka MK, Wijeratne K, Gunatilaka L, Arnold AE (2013) Endohyphal bacterium enhances production of indole-3-acetic acid by a foliar fungal endophyte. PLoS One 8:e73132
Hogan DA (2006) Quorum sensing: alcohols in a social situation. Curr Biol 16:R457–R458
Hong K-W, Koh C-L, Sam C-K, Yin W-F, Chan K-G (2012) Quorum quenching revisited – from signal decays to signalling confusion. Sensors 12:4661–4696
Hornby JM, Jensen EC, Lisec AD, Tasto JJ, Jahnke B, Shoemaker R, Dussault P, Nickerson KW (2001) Quorum sensing in the dimorphic fungus Candida albicans is mediated by farnesol. Appl Environ Microbiol 67:2982–2992
Hou D, Wang R, Gao X, Wang K, Lin Z, Ge J, Liu T, Wei S, Chen W, Xie R (2018) Cultivar-specific response of bacterial community to cadmium contamination in the rhizosphere of rice (Oryza sativa L.). Environ Pollut 241:63–73
Hou S, Thiergart T, Vannier N, Mesny F, Ziegler J, Pickel B, Hacquard S (2020) Microbiota-root-shoot axis modulation by MYC2 favours Arabidopsis growth over defence under suboptimal light. bioRxiv
Houterman PM, Cornelissen BJC, Rep M (2008) Suppression of plant resistance gene-based immunity by a fungal effector. PLoS Pathog 4:e1000061
Houterman PM, Ma L, Van Ooijen G, De Vroomen MJ, Cornelissen BJC, Takken FLW, Rep M (2009) The effector protein Avr2 of the xylem-colonizing fungus Fusarium oxysporum activates the tomato resistance protein I-2 intracellularly. Plant J 58:970–978
Hsueh Y-P, Mahanti P, Schroeder FC, Sternberg PW (2013) Nematode-trapping fungi eavesdrop on nematode pheromones. Curr Biol 23:83–86
Hsueh Y-P, Gronquist MR, Schwarz EM, Nath RD, Lee C-H, Gharib S, Schroeder FC, Sternberg PW (2017) Nematophagous fungus Arthrobotrys oligospora mimics olfactory cues of sex and food to lure its nematode prey. Elife 6
Hu L, Robert CAM, Cadot S, Zhang XI, Ye M, Li B, Manzo D, Chervet N, Steinger T, Van Der Heijden MGA (2018) Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. Nat Commun 9:1–13
Huang AC, Jiang T, Liu Y-X, Bai Y-C, Reed J, Qu B, Goossens A, Nützmann H-W, Bai Y, Osbourn A (2019) A specialized metabolic network selectively modulates Arabidopsis root microbiota. Science (80–) 364:eaau6389
Hückelhoven R (2005) Powdery mildew susceptibility and biotrophic infection strategies. FEMS Microbiol Lett 245:9–17
Hughes DT, Sperandio V (2008) Inter-kingdom signalling: communication between bacteria and their hosts. Nat Rev Microbiol 6:111–120
Islam MM, Hossain DM, Nonaka M, Harada N (2017) Biological control of tomato collar rot induced by Sclerotium rolfsii using Trichoderma species isolated in Bangladesh. Arch Phytopathol Plant Prot 50:109–116
Ismail AS, Valastyan JS, Bassler BL (2016) A host-produced autoinducer-2 mimic activates bacterial quorum sensing. Cell Host Microbe 19:470–480
İnceoğlu Ö, Salles JF, van Overbeek L, van Elsas JD (2010) Effects of plant genotype and growth stage on the betaproteobacterial communities associated with different potato cultivars in two fields. Appl Environ Microbiol 76:3675–3684

Jacoby RP, Koprivova A, Kopriva S (2021) Pinpointing secondary metabolites that shape the composition and function of the plant microbiome. J Exp Bot 72:57–69
Jakupović M, Heintz M, Reichmann P, Mendgen K, Hahn M (2006) Microarray analysis of expressed sequence tags from haustoria of the rust fungus Uromyces fabae. Fungal Genet Biol 43:8–19
Javed N, Khan HU, Hussain Z, Ashfaq M (2002) Effect of temperature, soil pH, agitation intervals and soil types on the spore attachment of Pasteuria penetrans to root knot nematodes, Meloidogyne javanica. Plant Pathol J
Jia M, Chen L, Xin H-L, Zheng C-J, Rahman K, Han T, Qin L-P (2016) A friendly relationship between endophytic fungi and medicinal plants: a systematic review. Front Microbiol 7:906
Joshi JR, Burdman S, Lipsky A, Yariv S, Yedidia I (2016) Plant phenolic acids affect the virulence of P ectobacterium aroidearum and P. carotovorum ssp. brasiliense via quorum sensing regulation. Mol Plant Pathol 17:487–500
Jouanneau J-P, Lapous D, Guern J (1991) In plant protoplasts, the spontaneous expression of defense reactions and the responsiveness to exogenous elicitors are under auxin control. Plant Physiol 96:459–466
Kanzaki H, Yoshida K, Saitoh H, Fujisaki K, Hirabuchi A, Alaux L, Fournier E, Tharreau D, Terauchi R (2012) Arms race co-evolution of Magnaporthe oryzae AVR-Pik and rice Pik genes driven by their physical interactions. Plant J 72:894–907
Khare E, Mishra J, Arora NK (2018) Multifaceted interactions between endophytes and plant: developments and prospects. Front Microbiol 9:2732
Kim W, Chen W (2019) Phytotoxic metabolites produced by legume-associated Ascochyta and its related genera in the Dothideomycetes. Toxins (Basel) 11:627
Kim H-S, Park H-D (2013) Ginger extract inhibits biofilm formation by Pseudomonas aeruginosa PA14. PLoS One 8:e76106
Ko D, Helariutta Y (2017) Shoot–root communication in flowering plants. Curr Biol 27:R973–R978
Kobayashi DY, Crouch JA (2009) Bacterial/fungal interactions: from pathogens to mutualistic endosymbionts. Annu Rev Phytopathol 47:63–82
Koh KH, Tham F-Y (2011) Screening of traditional Chinese medicinal plants for quorum-sensing inhibitors activity. J Microbiol Immunol Infect 44:144–148
Komon-Zelazowska M, Bissett J, Zafari D, Hatvani L, Manczinger L, Woo S, Lorito M, Kredics L, Kubicek CP, Druzhinina IS (2007) Genetically closely related but phenotypically divergent Trichoderma species cause green mold disease in oyster mushroom farms worldwide. Appl Environ Microbiol 73:7415–7426
Kumar AS, Lakshmanan V, Caplan JL, Powell D, Czymmek KJ, Levia DF, Bais HP (2012) Rhizobacteria Bacillus subtilis restricts foliar pathogen entry through stomata. Plant J 72:694–706
Kusari S, Hertweck C, Spiteller M (2012) Chemical ecology of endophytic fungi: origins of secondary metabolites. Chem Biol 19:792–798
Kusari P, Kusari S, Lamshöft M, Sezgin S, Spiteller M, Kayser O (2014) Quorum quenching is an antivirulence strategy employed by endophytic bacteria. Appl Microbiol Biotechnol 98:7173–7183
Kusari P, Kusari S, Spiteller M, Kayser O (2015) Implications of endophyte-plant crosstalk in light of quorum responses for plant biotechnology. Appl Microbiol Biotechnol 99:5383–5390
Ladha JK, Reddy PM (2003) Nitrogen fixation in rice systems: state of knowledge and future prospects. Plant Soil 252:151–167
LaSarre B, Federle MJ (2013) Exploiting quorum sensing to confuse bacterial pathogens. Microbiol Mol Biol Rev 77:73–111
Latz E, Eisenhauer N, Rall BC, Scheu S, Jousset A (2016) Unravelling linkages between plant community composition and the pathogen-suppressive potential of soils. Sci Rep 6:1–10
Lebeis SL (2014) The potential for give and take in plant–microbiome relationships. Front Plant Sci 5:287

Lee H, Chang YC, Nardone G, Kwon-Chung KJ (2007) TUP1 disruption in Cryptococcus neoformans uncovers a peptide-mediated density-dependent growth phenomenon that mimics quorum sensing. Mol Microbiol 64:591–601

Leung TLF, Poulin R (2008) Parasitism, commensalism, and mutualism: exploring the many shades of symbioses. Vie Milieu/Life Environ:107–115

Levy A, Chang BJ, Abbott LK, Kuo J, Harnett G, Inglis TJJ (2003) Invasion of spores of the arbuscular mycorrhizal fungus Gigaspora decipiens by Burkholderia spp. Appl Environ Microbiol 69:6250–6256

Li G, Kusari S, Golz C, Laatsch H, Strohmann C, Spiteller M (2017) Epigenetic modulation of endophytic Eupenicillium sp. LG41 by a histone deacetylase inhibitor for production of decalin-containing compounds. J Nat Prod 80:983–988

Lim FY, Sanchez JF, Wang CCC, Keller NP (2012) Toward awakening cryptic secondary metabolite gene clusters in filamentous fungi. In: Methods in enzymology. Elsevier, pp 303–324

Ling N, Raza W, Ma J, Huang Q, Shen Q (2011) Identification and role of organic acids in watermelon root exudates for recruiting Paenibacillus polymyxa SQR-21 in the rhizosphere. Eur J Soil Biol 47:374–379

Liu S, Dai H, Orfali RS, Lin W, Liu Z, Proksch P (2016) New fusaric acid derivatives from the endophytic fungus Fusarium oxysporum and their phytotoxicity to barley leaves. J Agric Food Chem 64:3127–3132

Liu Y, Chen L, Wu G, Feng H, Zhang G, Shen Q, Zhang R (2017) Identification of root-secreted compounds involved in the communication between cucumber, the beneficial Bacillus amyloliquefaciens, and the soil-borne pathogen Fusarium oxysporum. Mol Plant-Microbe Interact 30:53–62

Liu C, Atanasov KE, Arafaty N, Murillo E, Tiburcio AF, Zeier J, Alcázar R (2020) Putrescine elicits ROS-dependent activation of the salicylic acid pathway in Arabidopsis thaliana. Plant Cell Environ 43:2755–2768

Lo Presti L, Lanver D, Schweizer G, Tanaka S, Liang L, Tollot M, Zuccaro A, Reissmann S, Kahmann R (2015) Fungal effectors and plant susceptibility. Annu Rev Plant Biol 66:513–545

Logrieco A, Bottalico A, Mulé G, Moretti A, Perrone G (2003) Epidemiology of toxigenic fungi and their associated mycotoxins for some Mediterranean crops. In: Epidemiology of mycotoxin producing fungi. Springer, pp 645–667

Logrieco A, Moretti A, Solfrizzo M (2009) Alternaria toxins and plant diseases: an overview of origin, occurrence and risks. World Mycotoxin J 2:129–140

Lòpez-Fernàndez S, Sonego P, Moretto M, Pancher M, Engelen K, Pertot I, Campisano A (2015) Whole-genome comparative analysis of virulence genes unveils similarities and differences between endophytes and other symbiotic bacteria. Front Microbiol 6:419

Lozano-Torres JL, Wilbers RHP, Gawronski P, Boshoven JC, Finkers-Tomczak A, Cordewener JHG, America AHP, Overmars HA, Van 't Klooster JW, Baranowski L (2012) Dual disease resistance mediated by the immune receptor Cf-2 in tomato requires a common virulence target of a fungus and a nematode. Proc Natl Acad Sci 109:10119–10124

Lubna AS, Hamayun M, Gul H, Lee I-J, Hussain A (2018) Aspergillus niger CSR3 regulates plant endogenous hormones and secondary metabolites by producing gibberellins and indoleacetic acid. J Plant Interact 13:100–111

Ludwig-Müller J (2015) Plants and endophytes: equal partners in secondary metabolite production? Biotechnol Lett 37:1325–1334

Lundberg DS, Lebeis SL, Paredes SH, Yourstone S, Gehring J, Malfatti S, Tremblay J, Engelbrektson A, Kunin V, del Rio TG (2012) Defining the core Arabidopsis thaliana root microbiome. Nature 488:86–90

MacDonald RM, Chandler MR (1981) Bacterium-like organelles in the vesicular-arbuscular mycorrhizal fungus Glomus caledonius. New Phytol 89:241–246

Machida K, Tanaka T, Yano Y, Otani S, Taniguchi M (1999) Farnesol-induced growth inhibition in Saccharomyces cerevisiae by a cell cycle mechanism. Microbiology 145:293–299

Macko V, Stimmel MB, Wolpert TJ, Dunkle LD, Acklin W, Bänteli R, Jaun B, Arigoni D (1992) Structure of the host-specific toxins produced by the fungal pathogen Periconia circinata. Proc Natl Acad Sci 89:9574–9578

Mandyam KG, Jumpponen A (2015) Mutualism–parasitism paradigm synthesized from results of root-endophyte models. Front Microbiol 5:776

Márquez LM, Redman RS, Rodriguez RJ, Roossinck MJ (2007) A virus in a fungus in a plant: three-way symbiosis required for thermal tolerance. Science (80–) 315:513–515

Marra M, Camoni L, Visconti S, Fiorillo A, Evidente A (2021) The surprising story of fusicoccin: a wilt-inducing phytotoxin, a tool in plant physiology and a 14-3-3-targeted drug. Biomolecules 11:1393

Martin FN, Loper JE (1999) Soilborne plant diseases caused by Pythium spp.: ecology, epidemiology, and prospects for biological control. CRC Crit Rev Plant Sci 18:111–181

Martínez-Medina A, Del Mar AM, Pascual JA, Van Wees S (2014) Phytohormone profiles induced by Trichoderma isolates correspond with their biocontrol and plant growth-promoting activity on melon plants. J Chem Ecol 40:804–815

Martín-Rodríguez AJ, Reyes F, Martín J, Pérez-Yépez J, León-Barrios M, Couttolenc A, Espinoza C, Trigos Á, Martín VS, Norte M (2014) Inhibition of bacterial quorum sensing by extracts from aquatic fungi: first report from marine endophytes. Mar Drugs 12:5503–5526

Masi M, Cimmino A, Reveglia P, Mugnai L, Surico G, Evidente A (2018) Advances on fungal phytotoxins and their role in grapevine trunk diseases. J Agric Food Chem 66:5948–5958

Mattoo AJ, Nonzom S (2021) Endophytic fungi: understanding complex cross-talks. Symbiosis 83:237–264

McLean M (1996) The phytotoxicity ofFusarium metabolites: an update since 1989. Mycopathologia 133:163–179

Meena M, Samal S (2019) Alternaria host-specific (HSTs) toxins: an overview of chemical characterization, target sites, regulation and their toxic effects. Toxicol Rep 6:745–758

Meena H, Mishra R, Ranganathan S, Sarma VV, Ampasala DR, Kalia VC, Lee J-K, Siddhardha B (2020) Phomopsis tersa as inhibitor of quorum sensing system and biofilm forming ability of Pseudomonas aeruginosa. Indian J Microbiol 60:70–77

Mendes R, Kruijt M, De Bruijn I, Dekkers E, Van Der Voort M, Schneider JHM, Piceno YM, DeSantis TZ, Andersen GL, Bakker PAHM (2011) Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Science (80–) 332:1097–1100

Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiol Rev 37:634–663

Meng S, Torto-Alalibo T, Chibucos MC, Tyler BM, Dean RA (2009) Common processes in pathogenesis by fungal and oomycete plant pathogens, described with Gene Ontology terms. BMC Microbiol 9:1–11

Micali C, Göllner K, Humphry M, Consonni C, Panstruga R (2008) The powdery mildew disease of Arabidopsis: a paradigm for the interaction between plants and biotrophic fungi. Arab Book/Am Soc Plant Biol 6

Micallef SA, Shiaris MP, Colón-Carmona A (2009) Influence of Arabidopsis thaliana accessions on rhizobacterial communities and natural variation in root exudates. J Exp Bot 60:1729–1742

Miller MB, Bassler BL (2001) Quorum sensing in bacteria. Annu Rev Microbiol 55:165–199

Mishra R, Kushveer JS, Majumder D, Sarma VV (2020) Stimulation of secondary metabolite production in Hypoxylon anthochroum by naturally occurring epigenetic modifiers. J Food Meas Charact 14:946–962

Mochimaru M, Sakurai H (1997) Three kinds of binding site for tentoxin on isolated chloroplast coupling factor 1. FEBS Lett 419:23–26

Morimoto N, Ueno K, Teraishi M, Okumoto Y, Mori N, Ishihara A (2018) Induced phenylamide accumulation in response to pathogen infection and hormone treatment in rice (Oryza sativa). Biosci Biotechnol Biochem 82:407–416

Naga NG, El-Badan DE-S, Rateb HS, Ghanem KM, Shaaban MI (2021) Quorum sensing inhibiting activity of cefoperazone and its metallic derivatives on Pseudomonas aeruginosa. Front Cell Infect Microbiol 945

Naga NG, Zaki AA, El-Badan DE, Rateb HS, Ghanem KM, Shaaban MI (2022) Methoxyisoflavan derivative from Trigonella stellata inhibited quorum sensing and virulence factors of Pseudomonas aeruginosa. World J Microbiol Biotechnol 38:1–13

Natrah FMI, Defoirdt T, Sorgeloos P, Bossier P (2011) Disruption of bacterial cell-to-cell communication by marine organisms and its relevance to aquaculture. Mar Biotechnol 13:109–126

Neal AL, Ahmad S, Gordon-Weeks R, Ton J (2012) Benzoxazinoids in root exudates of maize attract Pseudomonas putida to the rhizosphere. PLoS One 7:e35498

Nealson KH, Hastings JW (1979) Bacterial bioluminescence: its control and ecological significance. Microbiol Rev 43:496–518

Nelson EB (1991) Exudate molecules initiating fungal responses to seeds and roots. In: The rhizosphere and plant growth. Springer, pp 197–209

Newman AG, Townsend CA (2016) Molecular characterization of the cercosporin biosynthetic pathway in the fungal plant pathogen Cercospora nicotianae. J Am Chem Soc 138:4219–4228

Noelting MC, Sisterna M, Lovisolo M, Molla-Kralj A, Lori G, Sandoval MC, Sulyok M, Molina MC (2016) Discoloured seeds of amaranth plant infected by Alternaria alternata: physiological, histopathological alterations and fungal secondary metabolites associated or registered. J Plant Prot Res 56:244–249

Noelting MC, Sisterna MN, Sulyok M, Abbiati NN, Molina MC (2022) Damage caused by Alternaria alternata to the quality and germination of amaranth seeds. Eur J Plant Pathol 163:193–202

Nühse TS (2012) Cell wall integrity signaling and innate immunity in plants. Front Plant Sci 3:280

Nzungize JR, Lyumugabe F, Busogoro J-P, Baudoin J-P (2012) Pythium root rot of common bean: biology and control methods. A review. Biotech Agron Soc Environ 16:405–413

Ochoa-Meza LC, Quintana-Obregón EA, Vargas-Arispuro I, Falcón-Rodríguez AB, Aispuro-Hernández E, Virgen-Ortiz JJ, Martínez-Téllez MÁ (2021) Oligosaccharins as elicitors of defense responses in wheat. Polymers (Basel) 13:3105

Ofek M, Hadar Y, Minz D (2011) Colonization of cucumber seeds by bacteria during germination. Environ Microbiol 13:2794–2807

Oh S-Y, Kim M, Eimes JA, Lim YW (2018) Effect of fruiting body bacteria on the growth of Tricholoma matsutake and its related molds. PLoS One 13:e0190948

Oka K, Okubo A, Kodama M, Otani H (2006) Detoxification of α-tomatine by tomato pathogens Alternaria alternata tomato pathotype and Corynespora cassiicola and its role in infection. J Gen plant Pathol 72:152–158

Oldroyd GED, Murray JD, Poole PS, Downie JA (2011) The rules of engagement in the legume-rhizobial symbiosis. Annu Rev Genet 45:119–144

Oliva R, Win J, Raffaele S, Boutemy L, Bozkurt TO, Chaparro-Garcia A, Segretin ME, Stam R, Schornack S, Cano LM (2010) Recent developments in effector biology of filamentous plant pathogens. Cell Microbiol 12:705–715

Oliver RP, Solomon PS (2010) New developments in pathogenicity and virulence of necrotrophs. Curr Opin Plant Biol 13:415–419

Ostry V (2008) Alternaria mycotoxins: an overview of chemical characterization, producers, toxicity, analysis and occurrence in foodstuffs. World Mycotoxin J 1:175–188

Ota R, Ohkubo Y, Yamashita Y, Ogawa-Ohnishi M, Matsubayashi Y (2020) Shoot-to-root mobile CEPD-like 2 integrates shoot nitrogen status to systemically regulate nitrate uptake in Arabidopsis. Nat Commun 11:1–9

Pakvaz S, Soltani J (2016) Endohyphal bacteria from fungal endophytes of the Mediterranean cypress (Cupressus sempervirens) exhibit in vitro bioactivity. For Pathol 46:569–581

Pandey P, Irulappan V, Bagavathiannan MV, Senthil-Kumar M (2017) Impact of combined abiotic and biotic stresses on plant growth and avenues for crop improvement by exploiting physio-morphological traits. Front Plant Sci 8:537

Pastrana AM, Basallote-Ureba MJ, Aguado A, Akdi K, Capote N (2016) Biological control of strawberry soil-borne pathogens Macrophomina phaseolina and Fusarium solani, using Trichoderma asperellum and Bacillus spp. Phytopathol Mediterr:109–120

Patel ZM, Mahapatra R, Jampala SSM (2020) Role of fungal elicitors in plant defense mechanism. In: Molecular aspects of plant beneficial microbes in agriculture. Elsevier, pp 143–158

Paul NC, Deng JX, Sang H-K, Choi Y-P, Yu S-H (2012) Distribution and antifungal activity of endophytic fungi in different growth stages of chili pepper (Capsicum annuum L.) in Korea. Plant Pathol J 28:10–19

Pavón Moreno MÁ, Alonso G, Martin de Santos R (2012) The importance of genus Alternaria in mycotoxins production and human diseases. Nutr Hosp 27:1772–1781

Peiffer JA, Spor A, Koren O, Jin Z, Tringe SG, Dangl JL, Buckler ES, Ley RE (2013) Diversity and heritability of the maize rhizosphere microbiome under field conditions. Proc Natl Acad Sci 110:6548–6553

Peng D-H, Qiu D-W, Ruan L-F, Zhou C-F, Sun M (2011) Protein elicitor PemG1 from Magnaporthe grisea induces systemic acquired resistance (SAR) in plants. Mol Plant-Microbe Interact 24:1239–1246

Pérez-Montaño F, Jiménez-Guerrero I, Sánchez-Matamoros RC, López-Baena FJ, Ollero FJ, Rodríguez-Carvajal MA, Bellogín RA, Espuny MR (2013) Rice and bean AHL-mimic quorum-sensing signals specifically interfere with the capacity to form biofilms by plant-associated bacteria. Res Microbiol 164:749–760

Pero RW, Harvan D, Blois MC (1973) Isolation of the toxin, altenuisol, from the fungus, Alternaria tenuis Auct. Tetrahedron Lett 14:945–948

Peter AE, Sudhakar P, Sandeep B V, Rao BG (2019) Antimicrobial and anti-quorum sensing activities of medicinal plants. In: Implication of quorum sensing and biofilm formation in medicine, agriculture and food industry. Springer, pp 189–217

Pineda A, Kaplan I, Hannula SE, Ghanem W, Bezemer TM (2020) Conditioning the soil microbiome through plant–soil feedbacks suppresses an aboveground insect pest. New Phytol 226:595–608

Prakash S (2011) Bio-control and plant growth promotion potential of siderophore producing endophytic Streptomyces from Azadirachta indica A. Juss. J Basic Microbiol 51(5):550–556

Quecine MC, de Araújo WL, Tsui S, Parra JRP, de Azevedo JL, Pizzirani-Kleiner AA (2014) Control of Diatraea saccharalis by the endophytic Pantoea agglomerans 33.1 expressing cry1Ac7. Arch Microbiol 196:227–234

Rai M, Agarkar G (2016) Plant–fungal interactions: what triggers the fungi to switch among lifestyles? Crit Rev Microbiol 42:428–438

Raina S, Odell M, Keshavarz T (2010) Quorum sensing as a method for improving sclerotiorin production in Penicillium sclerotiorum. J Biotechnol 148:91–98

Raina S, De Vizio D, Palonen EK, Odell M, Brandt AM, Soini JT, Keshavarz T (2012) Is quorum sensing involved in lovastatin production in the filamentous fungus Aspergillus terreus? Process Biochem 47:843–852

Rajesh PS, Rai VR (2013) Hydrolytic enzymes and quorum sensing inhibitors from endophytic fungi of Ventilago madraspatana Gaertn. Biocatal Agric Biotechnol 2:120–124

Rajesh PS, Rai VR (2014) Molecular identification of aiiA homologous gene from endophytic Enterobacter species and in silico analysis of putative tertiary structure of AHL-lactonase. Biochem Biophys Res Commun 443:290–295

Ramirez-Estrada K, Vidal-Limon H, Hidalgo D, Moyano E, Golenioswki M, Cusidó RM, Palazon J (2016) Elicitation, an effective strategy for the biotechnological production of bioactive high-added value compounds in plant cell factories. Molecules 21:182

Rana KL, Kour D, Sheikh I, Dhiman A, Yadav N, Yadav AN, Rastegari AA, Singh K, Saxena AK (2019) Endophytic fungi: biodiversity, ecological significance, and potential industrial applications. In: Recent advancement in white biotechnology through fungi. Springer, pp 1–62

Rashmi M, Meena H, Meena C, Kushveer JS, Busi S, Murali A, Sarma VV (2018) Anti-quorum sensing and antibiofilm potential of Alternaria alternata, a foliar endophyte of Carica papaya, evidenced by QS assays and in-silico analysis. Fungal Biol 122:998–1012

Redman RS, Dunigan DD, Rodriguez RJ (2001) Fungal symbiosis from mutualism to parasitism: who controls the outcome, host or invader? New Phytol 151:705–716
Redman RS, Sheehan KB, Stout RG, Rodriguez RJ, Henson JM (2002) Thermotolerance generated by plant/fungal symbiosis. Science (80–) 298:1581
Rigling D, Prospero S (2018) Cryphonectria parasitica, the causal agent of chestnut blight: invasion history, population biology and disease control. Mol Plant Pathol 19:7–20
Rines HW, Luke HH (1985) Selection and regeneration of toxin-insensitive plants from tissue cultures of oats (Avena sativa) susceptible to Helminthosporium victoriae. Theor Appl Genet 71:16–21
Rizwan M, Ali S, Adrees M, Rizvi H, Zia-ur-Rehman M, Hannan F, Qayyum MF, Hafeez F, Ok YS (2016) Cadmium stress in rice: toxic effects, tolerance mechanisms, and management: a critical review. Environ Sci Pollut Res 23:17859–17879
Roca MG, Arlt J, Jeffree CE, Read ND (2005) Cell biology of conidial anastomosis tubes in Neurospora crassa. Eukaryot Cell 4:911–919
Rodriguez R, Redman R (2008) More than 400 million years of evolution and some plants still can't make it on their own: plant stress tolerance via fungal symbiosis. J Exp Bot 59:1109–1114
Rodriguez RJ, Roossinck M (2012) Viruses, fungi and plants: cross-kingdom communication and mutualism. In: Biocommunication of fungi. Springer, pp 219–227
Rowland O, Ludwig AA, Merrick CJ, Baillieul F, Tracy FE, Durrant WE, Fritz-Laylin L, Nekrasov V, Sjölander K, Yoshioka H (2005) Functional analysis of Avr9/Cf-9 rapidly elicited genes identifies a protein kinase, ACIK1, that is essential for full Cf-9–dependent disease resistance in tomato. Plant Cell 17:295–310
Rouxel T, Balesdent MH (2017) Life, death and rebirth of avirulence effectors in a fungal pathogen of Brassica crops, L eptosphaeria maculans. New Phytologist, 214(2): 526–532
Sabra M, Aboulnasr A, Franken P, Perreca E, Wright LP, Camehl I (2018) Beneficial root endophytic fungi increase growth and quality parameters of sweet basil in heavy metal contaminated soil. Front Plant Sci 9:1726
Safari M, Amache R, Esmaeilishirazifard E, Keshavarz T (2014) Microbial metabolism of quorum-sensing molecules acyl-homoserine lactones, γ-heptalactone and other lactones. Appl Microbiol Biotechnol 98:3401–3412
Saikkonen K, Faeth SH, Helander M, Sullivan TJ (1998) Fungal endophytes: a continuum of interactions with host plants. Annu Rev Ecol Syst:319–343
Sák M, Dokupilová I, Kaňuková Š, Mrkvová M, Mihálik D, Hauptvogel P, Kraic J (2021) Biotic and abiotic elicitors of stilbenes production in Vitis vinifera L. cell culture. Plants 10:490
Saravanakumar K, Yu C, Dou K, Wang M, Li Y, Chen J (2016) Synergistic effect of Trichoderma-derived antifungal metabolites and cell wall degrading enzymes on enhanced biocontrol of Fusarium oxysporum f. sp. cucumerinum. Biol Control 94:37–46
Sayyed RZ, Chincholkar SB, Reddy MS, Gangurde NS, Patel PR (2013) Siderophore producing PGPR for crop nutrition and phytopathogen suppression. In: Bacteria in agrobiology: disease management. Springer, pp 449–471
Schardl CL (2001) Epichloë festucae and related mutualistic symbionts of grasses. Fungal Genet Biol 33:69–82
Schardl CL, Leuchtmann A, Spiering MJ (2004) Symbioses of grasses with seedborne fungal endophytes. Annu Rev Plant Biol 55:315–340
Schelkle M, Peterson RL (1997) Suppression of common root pathogens by helper bacteria and ectomycorrhizal fungi in vitro. Mycorrhiza 6:481–485
Schenk ST, Stein E, Kogel K-H, Schikora A (2012) Arabidopsis growth and defense are modulated by bacterial quorum sensing molecules. Plant Signal Behav 7:178–181
Scherlach K, Hertweck C (2009) Triggering cryptic natural product biosynthesis in microorganisms. Org Biomol Chem 7:1753–1760
Schlemper TR, van Veen JA, Kuramae EE (2018) Co-variation of bacterial and fungal communities in different sorghum cultivars and growth stages is soil dependent. Microb Ecol 76:205–214

Schroeckh V, Scherlach K, Nützmann H-W, Shelest E, Schmidt-Heck W, Schuemann J, Martin K, Hertweck C, Brakhage AA (2009) Intimate bacterial–fungal interaction triggers biosynthesis of archetypal polyketides in Aspergillus nidulans. Proc Natl Acad Sci 106:14558–14563

Schulz B, Boyle C, Draeger S, Römmert A-K, Krohn K (2002) Endophytic fungi: a source of novel biologically active secondary metabolites. Mycol Res 106:996–1004

Schulza B, Boyle C (2005) The endophyte continuum. Mycol Res 109:661–686

Selim SM, Zayed MS (2017) Microbial interactions and plant growth. In: Plant-microbe interactions in agro-ecological perspectives. Springer, pp 1–15

Sharma VK, Kumar J, Singh DK, Mishra A, Verma SK, Gond SK, Kumar A, Singh N, Kharwar RN (2017) Induction of cryptic and bioactive metabolites through natural dietary components in an endophytic fungus Colletotrichum gloeosporioides (Penz.) Sacc. Front Microbiol 8:1126

Sharma S, Kour D, Rana KL, Dhiman A, Thakur S, Thakur P, Thakur S, Thakur N, Sudheer S, Yadav N (2019) Trichoderma: biodiversity, ecological significances, and industrial applications. In: Recent advancement in white biotechnology through fungi. Springer, pp 85–120

Sharma M, Saleh D, Charron J-B, Jabaji S (2020) A crosstalk between Brachypodium root exudates, organic acids, and Bacillus velezensis B26, a growth promoting bacterium. Front Microbiol 11:575578

Shastry RP, Dolan SK, Abdelhamid Y, Vittal RR, Welch M (2018) Purification and characterisation of a quorum quenching AHL-lactonase from the endophytic bacterium Enterobacter sp. CS66. FEMS Microbiol Lett 365:fny054

Sheibani-Tezerji R, Naveed M, Jehl M-A, Sessitsch A, Rattei T, Mitter B (2015) The genomes of closely related Pantoea ananatis maize seed endophytes having different effects on the host plant differ in secretion system genes and mobile genetic elements. Front Microbiol 6:440

Shi S, Richardson AE, O'Callaghan M, DeAngelis KM, Jones EE, Stewart A, Firestone MK, Condron LM (2011) Effects of selected root exudate components on soil bacterial communities. FEMS Microbiol Ecol 77:600–610

Shinshi H, Mohnen D, Meins F Jr (1987) Regulation of a plant pathogenesis-related enzyme: inhibition of chitinase and chitinase mRNA accumulation in cultured tobacco tissues by auxin and cytokinin. Proc Natl Acad Sci 84:89–93

Shinya T, Miyamoto K, Uchida K, Hojo Y, Yumoto E, Okada K, Yamane H, Galis I (2022) Chitooligosaccharide elicitor and oxylipins synergistically elevate phytoalexin production in rice. Plant Mol Biol 109:595–609

Silipo A, Erbs G, Shinya T, Dow JM, Parrilli M, Lanzetta R, Shibuya N, Newman M-A, Molinaro A (2010) Glyco-conjugates as elicitors or suppressors of plant innate immunity. Glycobiology 20:406–419

Simonin M, Dasilva C, Terzi V, Ngonkeu ELM, Diouf D, Kane A, Béna G, Moulin L (2020) Influence of plant genotype and soil on the wheat rhizosphere microbiome: evidences for a core microbiome across eight African and European soils. FEMS Microbiol Ecol 96:fiaa067

Sreenayana B, Vinodkumar S, Nakkeeran S, Muthulakshmi P, Poornima K (2022) Multitudinous potential of Trichoderma species in imparting resistance against F. oxysporum f. sp. cucumerinum and Meloidogyne incognita disease complex. J Plant Growth Regul 41:1187–1206

Stanghellini ME, Burr TJ (1973) Germination in vivo of Pythium aphanidermatum oospores and sporangia. Phytopathology 63:1493–1496

Sugiyama A, Ueda Y, Zushi T, Takase H, Yazaki K (2014) Changes in the bacterial community of soybean rhizospheres during growth in the field. PLoS One 9:e100709

Sumida CH, Daniel JFS, Araujod APCS, Peitl DC, Abreu LM, Dekker RFH, Canteri MG (2018) Trichoderma asperelloides antagonism to nine Sclerotinia sclerotiorum strains and biological control of white mold disease in soybean plants. Biocontrol Sci Technol 28:142–156

Suryanarayanan TS (2013) Endophyte research: going beyond isolation and metabolite documentation. Fungal Ecol 6:561–568

Takamatsu S, Siahaan SAS, Moreno-Rico O, Cabrera de Álvarez MG, Braun U (2016) Early evolution of endoparasitic group in powdery mildews: molecular phylogeny suggests missing link between Phyllactinia and Leveillula. Mycologia 108:837–850

Tan S, Yang C, Mei X, Shen S, Raza W, Shen Q, Xu Y (2013) The effect of organic acids from tomato root exudates on rhizosphere colonization of Bacillus amyloliquefaciens T-5. Appl Soil Ecol 64:15–22

Tanaka A, Christensen MJ, Takemoto D, Park P, Scott B (2006) Reactive oxygen species play a role in regulating a fungus–perennial ryegrass mutualistic interaction. Plant Cell 18:1052–1066

Tanaka A, Takemoto D, Hyon G, Park P, Scott B (2008) NoxA activation by the small GTPase RacA is required to maintain a mutualistic symbiotic association between Epichloë festucae and perennial ryegrass. Mol Microbiol 68:1165–1178

Tchameni SN, Cotârleț M, Ghinea IO, Bedine MAB, Sameza ML, Borda D, Bahrim G, Dinică RM (2020) Involvement of lytic enzymes and secondary metabolites produced by Trichoderma spp. in the biological control of Pythium myriotylum. Int Microbiol 23:179–188

Teixeira PJPL, Colaianni NR, Law TF, Conway JM, Gilbert S, Li H, Salas-González I, Panda D, Del Risco NM, Finkel OM (2021) Specific modulation of the root immune system by a community of commensal bacteria. Proc Natl Acad Sci 118:e2100678118

Temple B, Horgen PA, Bernier L, Hintz WE (1997) Cerato-ulmin, a hydrophobin secreted by the causal agents of Dutch elm disease, is a parasitic fitness factor. Fungal Genet Biol 22:39–53

Teplitski M, Mathesius U, Rumbaugh KP (2011) Perception and degradation of N-acyl homoserine lactone quorum sensing signals by mammalian and plant cells. Chem Rev 111:100–116

Thines M (2014) Phylogeny and evolution of plant pathogenic oomycetes – a global overview. Eur J Plant Pathol 138:431–447

Thompson SE, Levin S, Rodriguez-Iturbe I (2014) Rainfall and temperatures changes have confounding impacts on P hytophthora cinnamomi occurrence risk in the southwestern USA under climate change scenarios. Glob Chang Biol 20:1299–1312

Tian W, Deng Z, Hong K (2017) The biological activities of sesterterpenoid-type ophiobolins. Mar Drugs 15:229

Topi D, Tavčar-Kalcher G, Pavšič-Vrtač K, Babič J, Jakovac-Strajn B (2019) Alternaria mycotoxins in grains from Albania: alternariol, alternariol monomethyl ether, tenuazonic acid and tentoxin. World Mycotoxin J 12:89–99

Tourneroche A, Lami R, Hubas C, Blanchet E, Vallet M, Escoubeyrou K, Paris A, Prado S (2019) Bacterial–fungal interactions in the kelp endomicrobiota drive autoinducer-2 quorum sensing. Front Microbiol 10:1693

Troian RF, Steindorff AS, Ramada MHS, Arruda W, Ulhoa CJ (2014) Mycoparasitism studies of Trichoderma harzianum against Sclerotinia sclerotiorum: evaluation of antagonism and expression of cell wall-degrading enzymes genes. Biotechnol Lett 36:2095–2101

Turner SJ, Subbotin SA (2013) Cyst nematodes. Plant Nematol:109–143

Unterseher M, Schnittler M (2010) Species richness analysis and ITS rDNA phylogeny revealed the majority of cultivable foliar endophytes from beech (Fagus sylvatica). Fungal Ecol 3:366–378

van't Padje A, Whiteside MD, Kiers ET (2016) Signals and cues in the evolution of plant–microbe communication. Curr Opin Plant Biol 32:47–52

von Rad U, Klein I, Dobrev PI, Kottova J, Zazimalova E, Fekete A, Hartmann A, Schmitt-Kopplin P, Durner J (2008) Response of Arabidopsis thaliana to N-hexanoyl-DL-homoserine-lactone, a bacterial quorum sensing molecule produced in the rhizosphere. Planta 229:73–85

Valent B, Chumley FG (1991) Molecular genetic analysis of the rice blast fungus, Magnaporthe grisea. Annu Rev Phytopathol 29:443–467

Van Elsas JD, Chiurazzi M, Mallon CA, Elhottovā D, Krištůfek V, Salles JF (2012) Microbial diversity determines the invasion of soil by a bacterial pathogen. Proc Natl Acad Sci 109:1159–1164

Vandenkoornhuyse P, Quaiser A, Duhamel M, Le Van A, Dufresne A (2015) The importance of the microbiome of the plant holobiont. New Phytol 206:1196–1206

Venkatesh Kumar R, Singh RP, Mishra P (2019) Endophytes as emphatic communication barriers of quorum sensing in Gram-positive and Gram-negative bacteria – a review. Environ Sustain 2:455–468

Verma M, Brar SK, Tyagi RD, Surampalli RY, Valero JR (2007) Antagonistic fungi, Trichoderma spp.: panoply of biological control. Biochem Eng J 37:1–20

Vicente CSL, Ikuyo Y, Mota M, Hasegawa K (2013) Pinewood nematode-associated bacteria contribute to oxidative stress resistance of Bursaphelenchus xylophilus. BMC Microbiol 13:1–8
Wang W-X (2016) Crosstalk and antibacterial molecules from endophytes harbored in Narcissus tazetta and Buxus sinica
Wang W-X, Kusari S, Sezgin S, Lamshöft M, Kusari P, Kayser O, Spiteller M (2015) Hexacyclopeptides secreted by an endophytic fungus Fusarium solani N06 act as crosstalk molecules in Narcissus tazetta. Appl Microbiol Biotechnol 99:7651–7662
Wang L, Ren L, Li C, Gao C, Liu X, Wang M, Luo Y (2019) Effects of endophytic fungi diversity in different coniferous species on the colonization of Sirex noctilio (Hymenoptera: Siricidae). Sci Rep 9:1–11
Whitehead NA, Barnard AML, Slater H, Simpson NJL, Salmond GPC (2001) Quorum-sensing in Gram-negative bacteria. FEMS Microbiol Rev 25:365–404
Willey JM, Sherwood L, Woolverton CJ (2011) Prescott's microbiology. McGraw-Hill, New York
Williams P, Winzer K, Chan WC, Camara M (2007) Look who's talking: communication and quorum sensing in the bacterial world. Philos Trans R Soc B Biol Sci 362:1119–1134
Williams HE, Steele JCP, Clements MO, Keshavarz T (2012) γ-Heptalactone is an endogenously produced quorum-sensing molecule regulating growth and secondary metabolite production by Aspergillus nidulans. Appl Microbiol Biotechnol 96:773–781
Xiaodong X, Olukolu B, Yang Q, Balint-Kurti P (2018) Identification of a locus in maize controlling response to a host-selective toxin derived from Cochliobolus heterostrophus, causal agent of southern leaf blight. Theor Appl Genet 131:2601–2612
Xiao-Yan S, Qing-Tao S, Shu-Tao X, Xiu-Lan C, Cai-Yun S, Yu-Zhong Z (2006) Broad-spectrum antimicrobial activity and high stability of Trichokonins from Trichoderma koningii SMF2 against plant pathogens. FEMS Microbiol Lett 260:119–125
Xie X, Yoneyama K, Yoneyama K (2010) The strigolactone story. Annu Rev Phytopathol 48:93–117
Xu G, Yang S, Meng L, Wang B-G (2018) The plant hormone abscisic acid regulates the growth and metabolism of endophytic fungus Aspergillus nidulans. Sci Rep 8:1–9
Xu D, Xue M, Shen Z, Jia X, Hou X, Lai D, Zhou L (2021) Phytotoxic secondary metabolites from fungi. Toxins (Basel) 13:261
Yin C, Chen X, Wang X, Han Q, Kang Z, Hulbert SH (2009) Generation and analysis of expression sequence tags from haustoria of the wheat stripe rust fungus Puccinia striiformis f. sp. tritici. BMC Genomics 10:1–9
You J, Zhang J, Wu M, Yang L, Chen W, Li G (2016) Multiple criteria-based screening of Trichoderma isolates for biological control of Botrytis cinerea on tomato. Biol Control 101:31–38
Yu X, Bi Y, Yan L, Liu X, Wang Y, Shen K, Li Y (2016) Activation of phenylpropanoid pathway and PR of potato tuber against Fusarium sulphureum by fungal elicitor from Trichothecium roseum. World J Microbiol Biotechnol 32:1–12
Yuan J, Zhang W, Sun K, Tang M-J, Chen P-X, Li X, Dai C-C (2019) Comparative transcriptomics and proteomics of Atractylodes lancea in response to endophytic fungus Gilmaniella sp. AL12 reveals regulation in plant metabolism. Front Microbiol 10:1208
Zakaria L, Yaakop AS, Salleh B, Zakaria M (2010) Endophytic fungi from paddy. Trop Life Sci Res 21:101
Zentmyer GA (1961) Chemotaxis of zoospores for root exudates. Science (80–) 133:1595–1596
Zhang L, Feng G, Declerck S (2018) Signal beyond nutrient, fructose, exuded by an arbuscular mycorrhizal fungus triggers phytate mineralization by a phosphate solubilizing bacterium. ISME J 12:2339–2351
Zhang H, He Y, Wu J, Yang Y, Zheng K, Yang M, Zhu S, He X, Zhu Y, Liu Y (2019) Inhibitory activity of antifungal substances in maize root exudates against Phytophthora sojae. Plant Prot 45:124–130
Zhang H, Yang Y, Mei X, Li Y, Wu J, Li Y, Wang H, Huang H, Yang M, He X (2020) Phenolic acids released in maize rhizosphere during maize-soybean intercropping inhibit Phytophthora blight of soybean. Front Plant Sci 11:886

Zhang Z, Zhao Y, An T, Yu H, Bi X, Liu H, Xu Y, Yang Z, Chen Y, Wen J (2022) Maize and common bean seed exudates mediate part of nonhost resistance to Phytophthora sojae prior to infection. Phytopathology® 112:335–344

Zhou T, Boland GJ (1999) Mycelial growth and production of oxalic acid by virulent and hypovirulent isolates of Sclerotinia sclerotiorum. Can J Plant Pathol 21:93–99

Zhou J, Yang T, Mei Y-Z, Kang L, Dai C-C (2014) Laccase production by Phomopsis liquidambari B3 cultured with food waste and wheat straw as the main nitrogen and carbon sources. J Air Waste Manag Assoc 64:1154–1163

Zhou L, Zhang L-H, Cámara M, He Y-W (2017) The DSF family of quorum sensing signals: diversity, biosynthesis, and turnover. Trends Microbiol 25:293–303

Roles and Benefits of Mycorrhiza

Younes M. Rashad, Tarek A. A. Moussa, and Sara A. Abdalla

1 Introduction

Soil microbiome comprises a diverse set of microbial species, including bacteria, fungi, and archaea. There are around one thousand microbial cells per gram of a soil sample, with a variety up to hundred species (Tecon and Or 2017), and 10% of them live in the plant-influenced zones (Spence and Bais 2013). Utilizing microbial soil ecosystems is therefore the most effective method for achieving sustained and healthy crop production. Even under severe conditions, they may sustain the biosphere by enhancing not just plant nutrition and health but also soil quality. Arbuscular mycorrhizal fungi (AMF) are among the most important biotrophic root colonizing fungi, which belong to phylum: Mucoromycota, subphylum: Glomeromycotina (Spatafora et al. 2016). They live with plant roots in a mutualistic association, where both partners benefit each other. Mycorrhizal associations with the plants are grouped into four basic categories based on their structure and function into; endomycorrhiza or arbuscular mycorrhiza (AM), ectomycorrhiza (EM), orchid mycorrhiza, and ericoid mycorrhiza (Smith and Read 2008). AM can colonize 74% of the terrestrial plants, while, orchid mycorrhiza (9%) and ectomycorrhiza (2%). Ericoid mycorrhiza interacts with a variety of host plants at various hierarchical levels, including temperate and tropical herbaceous plants, bushes, and trees (Brundrett and Tedersoo 2018). In an ecosystem, AMF play many roles and serve as a valuable instrument for establishment, diversification, productivity, and sustainability of the ecosystem. Moreover, AMF represent a crucial factor in the

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afforestation programs, assisting in sustainable agriculture, landscape restoration, and horticulture (Castillo et al. 2016).

In AM association, the plant partner provides the fungus with the assimilated carbon as a photosynthesis product through the passive diffusion, while the fungus partner benefits the host with many advantages such as uptake of water and nutrients from soil via extraradical mycelial network that extend in the soil deeper than the plant roots can do. More than half of AM's fungal biomass can be detected below 30 cm. Therefore, AMF communities of the subsurface differ from those of the topsoil. Fungal hyphae are much thinner (10 μm in diameter) than the plant roots and can therefore compete with soil microorganisms for nutrient uptake more effectively than the plant roots (Allen 2011). In the same time, AMF colonize the root cortex and form arbuscules, which serve as exchange sites between the host and the mycorrhizal fungus. However, the mycorrhizal association is more complicated than just exchange of water and nutrients. Vangelisti et al. (2018) reported that once the AM association was established in the plant root, a highly complicated genetic reprogramming is occurred in the host plant leading to a diverse array of metabolic modulations and elicitation of innate and adaptive plant responses. However, the intensity and type of modulation depend on other factors such as the host plant, the colonizing fungus, the colonization phase, and soil and environmental conditions (Jung et al. 2012). AM colonization simultaneously primes the plat growth and induces its defense and adaptive responses to various biotic and abiotic stresses such as pathogen invasion, drought, salinity, heat and chilling conditions and heavy metal toxicity (Bücking and Kafle 2015). In this chapter, we will highlight different roles and mechanisms utilized by AMF in their association with the host plants.

2 Roles and Mechanisms of AMF in Water and Nutrients Acquisition

2.1 Water Acquisition

AMF have the potential to actively and passively improve the plant water acquisition in different ways. AM extraradical hyphae represent an additive and facilitated water absorbing system to the host plant. Length of these dichotomously branched hyphae may reach 100 m occupied in 1 cm^3 of the soil forming absorbing networks. Such absorptive tubes can extend more than 10 cm deeper than the roots (Jansa et al. 2003). When compared to the individual plant roots, these absorbing networks can enhance the absorbing surface area by twofold (Raven and Edwards 2001). Mycorrhizal hyphae are generally very smaller in diameter than the plant root, they can reach soil pores that are not reachable by the roots (Allen 2007), and so utilize available resources there. Because the roots grow into moist soil and the hyphae obtain water via small pores physically unreachable to the roots, these highly branched hyphae would facilitate water acquisition over short distances.

Furthermore, the runner hyphae can help as highways for water uptake, successfully increasing plants' reach even to far-off groundwater sources (Drew et al. 2003). Absorbing hyphae may play an important role in the water uptake by plants in isolated moist regions. This technique could be suitable for long-distance water transportation. However, despite the fact that the support of water discharge to plants via AM hyphae has been widely reported, the idea remains disputed (Smith et al. 2010). In contrary, other researchers have found that the rate of water absorption via AM hyphae in a plant is negligible in comparison to its transpiration demands. Because the inner diameter of hyphae is very tiny, water will have to flow through the hyphae at excessively high speeds to be relevant for the plant (George et al. 1992). Moreover, once the real quantity of water accessible from tiny pores is evaluated and contrasted to the amount from large size pores, the benefits linked with AM hyphae's ability to penetrate small pores become disputed (Allen 2007). In a recent study, Püschel et al. (2020) studied water uptake via AMF in *Medicago truncatula* planted in two-compartment rhizoboxes using isotope tracing with deuterium. Despite AM colonization increased labelled water uptake in the mycorrhizal plants more than twofold than non-mycorrhizal plants, but water uptake due to mycorrhizal fungi was less than the plant transpiration demand.

However, AM colonization can improve plants water uptake via another passive way, which is may be more important than its active water transfer. It has been found that the presence of AM fungus improves soil hydraulic conductivity (Bitterlich et al. 2018a, b). The degree of water transfer mediated by the AM fungi in the soil is not affected only by the soil water content but also the soil hydraulic parameters, which are influenced by the size and distribution of the pore spaces. In case of soil pores of large diameter are water-filled, AM mediated water transport is expected to be insignificant (Allen 2007). When the soil desiccates, the large pores get air-filled and water becomes progressively confined in microscopic pores that are well spaced from one to another. As a result, the continuity between water filled pores decreases, the texture of the soil to root route increases, and the hydraulic conductivity of the soil decreases (Rowell 2001). In certain cases, the hyphae may serve as links connecting water-filled pores to plant roots through air-filled pores (Miller and Jastrow 2000).

2.2 AMF-Mediated Induction of Tolerance Responses to Drought

One of the most important expected impacts of climate change is the acceleration of droughts conditions, which negatively affect the crops production causing up to 50% reduction in their yields. Drought stress can limit water and nutrient acquisition leading to a reduction in the transpiration rate, cell permeability, metabolic reactions, physiological processes, and plant development in general (Fernández-Lizarazo and Moreno-Fonseca 2016). Therefore, drought is considered the most effective abiotic stress limiting the global agriculture in the future (Yang et al. 2008).

AMF have been reported to improve drought tolerant in different plant species, and represent a sustainable mitigation way to drought stress (Aroca 2012). However, this improvement depends on the species of AMF and the plant partner and on the intensity of the drought stress. The potential mechanisms driving the tolerance responses triggered by AMF colonization include:

2.2.1 Induction of Phytohormones

Abscisic acid, strigolactones, and jasmonic acid (JA) signaling pathways have been widely reported to be induced in the host plant due to the mycorrhizal colonization, especially under drought stress, which indicates their roles and complexity of interactions in the tolerance responses against the drought stress. Induction of these signaling pathways regulates different drought-related genes enhancing the plant tolerance to the drought stress.

2.2.2 Improving Plant Water Uptake

Mycorrhizal colonization has been found to enhance the water-uptake efficiency by improving the level of transpiration, stomatal and hydraulic conductivity, and water potential. Improving water uptake in the plant leads to increment in the photosynthesis due to the increment in stomatal conductance increases diffusion of CO_2 (Boldt et al. 2011).

2.2.3 Enhancing the Hydraulic Conductivity

AMF extraradical hyphal network magnifys the absorbing surface area in the soil resulting in enhancing the relative water content, water absorbing efficiency, and rate of plant transpiration. In addition, AMF can improve the soil structure by soil particles aggregation via production of a glycoproteins (glomalin) that connects the soil particles with each other leading to an improvement of the soil texture and the water holding capacity.

2.2.4 Osmoprotectants Production

One of the most important drought tolerance responses induced in mycorrhizal plants is the production of the osmolytes such as proline that adjusts the cellular osmotic pressure to increase tolerance to drought stress. Osmotic adjustment has a potential role in reducing water from the plant cells under drought condition (Santander et al. 2017).

2.2.5 Induction of Antioxidant Activity

Reduction of the oxidative free radicals generation due to drought stress is one of the crucial benefits of mycorrhizal colonization of plants (Fernández-Lizarazo and Moreno-Fonseca 2016). In addition, enhancement of enzymatic and non-enzymatic antioxidant systems due to plant mycorrhization is also reported under drought conditions (Amiri et al. 2015).

2.2.6 Improvement of the Photosynthesis Efficiency

Drought stress reduces the photosynthesis rate due to the oxidative damaging resulted by the free radicals that attack the photosynthetic apparatus (Abbaspour et al. 2012). Increased photosynthetic rate in mycorrhizal plants under drought stress is due to the increment in the photosynthetic pigments content, which prevents the inhibition and destruction in the photosynthetic apparatus, compared with the non-mycorrhizal plants (Asrar and Elhindi 2011).

2.3 Nutrients Acquisition

Root colonization by AMF enhances the root surface area available for the nutrient acquisition via extension several centimeters into the soil and secretion of the hydrolyzing enzymes and organic acids to utilize the nutrients (Kakouridis et al. 2022). The increment in the nitrogen (N), phosphorus (P), potassium (K), sulfur, and magnesium (Mg) absorption, as well as the trace elements has been observed as a result of AMF extraradical hyphae mediated root system expansion (Bücking and Kafle 2015). This wide nutrient absorbing system surrounds the roots and spreads outside the rhizosphere's nutritional zones, enabling AMF to acquire a wider amount of soil than non-mycorrhizal roots. Significance of the AM symbiosis to plant nutrition is widely reported, nevertheless, the involvement of AMF in their host's nitrogen nutrition has received more attention (Bücking and Kafle 2015). Furthermore, when compared to the data on symbiotic phosphorus and nitrogen uptake in plants, the significance of AM symbiosis in plant potassium (K^+) acquisition is far less well understood (Liu et al. 2019; Haro and Benito 2019).

2.3.1 Nitrogen

Nitrogen element is found in the form of $NO3^-$ in the majority of cultivated fields, meanwhile $NH4^+$ is found in unmodified or acidified soils as it is less transportable and more common. Although $NH3^-/NH4^+$ is the predominant form of nitrogen

produced by the fungus and absorbed by the plant, AMF may absorb both forms of nitrogen (Bücking and Kafle 2015). Plants can get up to 42% of their nitrogen from the AMF symbiotic (Walder et al. 2012). AMF has a greater affinity for $NH4^+$ than plant roots, therefore it helps plants obtain nitrogen even in the low-nitrogen soils (Pérez-Tienda et al. 2011). AMF hyphae utilize hydrolytic enzymes like phosphatases, pectinases, cellulases, xylanases, and chitinases to transport nitrogen from organic regions to the host plant (Leigh et al. 2009). Unlike phosphorus, nitrogen is only acquired from mineral resources by AM hyphae to a maximum of 20%, depending on a variety of parameters such as soil moisture, pH, and type (Hodge and Fitter 2010). When soils have poor mineral nitrogen supply, plants and AMF compete for soil nitrogen uptake, resulting in mycorrhizal plants' being able to take up less nitrogen from nitrogen-deficient soils than non-mycorrhizal plants. Mycorrhizal plant may improve nitrogen acquisition via better P acquisition and/or N intake from organic nitrogen sources, particularly in organic soils (Püschel et al. 2016).

When natural additions like organic manure, plant litter, yeast biomass, chitin, biomolecules, or proteins are applied to soil substrate, they have been found to improve AMF development and spore densities (Jansa et al. 2019). The production of organic nitrogen, particularly in the form of $NH4^+$, from these supplements during AMF growth and spore development is responsible for this positive response during AMF growth and spore formation (Nuccio et al. 2013). Phosphorus and $NH4^+$ carriers are required not only for the transport of nutrient elements but also for the survival of arbuscules and mycorrhization in the root system (Breuillin-Sessoms et al. 2015). Despite the fact that the fungal arbuscules are loaded with nutrients, just the required amount is delivered by a transporter inside the host plant's root cortex cell. Plants can use the nutrient-dependent AMF colonization as a feedback mechanism to either encourage or inhibit fungal growth (Nouri et al. 2015). AMF colonize root systems of plants with N_2 fixing bacteria in high numbers (>70–80%), primarily in *Fabaceae* species, which act as mycorrhizal helper bacteria, supporting AMF in raising the number of spores and mycorrhization (Muleta 2010). The enrichment of the soil nitrogen by microbiological grazers such as protists and nematodes can make the nitrogen easily accessible for AMF hyphae to take up and then use or transmit to the host plants (Bukovská et al. 2018).

2.3.2 Phosphorus

Phosphorus (P) can be found in the natural soils as inorganic orthophosphates including iron phosphate ($FePO_4$), aluminum phosphate ($AlPO_4$), and calcium phosphate ($CaPO_4$), as well as organic molecules such as lecithin and phytate, which can make up to 50% of the total available organic phosphate. Because phosphorus is very insoluble in soils, its acquisition by roots causes a deficiency zone around the root hairs in the rhizosphere as a result of interactions with soil bivalent and trivalent

cations, primarily Ca_2^+, Fe_3^+, and Al_3^+ (Thangavel et al. 2022). Plants have evolved several phosphorus uptake methods that either boost the effectiveness of phosphorus acquisition via rapid root growth, root hairs, and AM colonization, or release phosphorus from recalcitrant sources through ecto- and ericoid-mycorrhiza. It was found that length of mycorrhizal hyphae is influenced by nutrient levels, particularly soil phosphorus levels. Several plant parameters, including root length, root diameter, root surface area, shoot-to-root ratio, and root hair density, length, and diameter, have also been thought to be essential for nutrient uptake, particularly in low mobile phosphorous conditions (Richardson et al. 2011). The small hyphae of AMF, on the other hand, may be more efficient than plant root hairs in absorbing minerals from the soil. Phosphatases may be used in the AMF colonization to hydrolyze phosphate from organic phosphate molecules (Joner and Johansen 2000). In sunflower shoots and roots, mycorrhiza-associated plants had higher nutritional content, including Mg_2^+, K^+, and P_3^+ (Nafady et al. 2019). Phosphorus and organic acids produced by AMF or organic acids produced by plant development microorganisms may be involved in AMF-mediated increases in phosphorus uptake, which leach the cations linked to phosphate and improve phosphorus availability in soil (Rosier et al. 2018). Through AMF, phosphorus can be transmitted from the failing roots of one plant to the intact roots of a recipient or neighboring plant (Giovannetti et al. 2015). Extraradical hyphae of AMF have been documented to stay active and colonies surrounding plants for up to 5 months after their plant hosts have died and no longer have functional roots (Pepe et al. 2018). Absorption and transport of other nutrients in the soil and in plants are influenced by soil macronutrients, particularly N, P, and K. For this purpose, Zhang et al. (2016) found that phosphorus fertilizer had a significant impact on root Zn absorption in the upper soil layer but had a lesser impact in the deeper soil layer. The hyphal height frequency was shown to decrease dramatically as soil depth increased, with the greatest hyphal length concentration values obtained in the soil surface layer (0–20 cm) (Hou et al. 2021).

2.3.3 Potassium

Despite the amount of potassium (K) in the soil, plants have limited access to it, limiting their development and productivity (Garcia and Zimmermann 2014). Mycorrhization has been shown to promote plant potassium uptake, especially in potassium-deficient environments. Nevertheless, the relationship between soil potassium and AMF is incompletely understood. AMF-induced increases in potassium intake in plants were found to be variety dependent (Priyadharsini and Muthukumar 2016). There are two potassium transmission methods: one of them is potassium selective and effective in lower potassium levels, and the other is less sensitive to potassium and effective in greater soil potassium levels (Zare-Maivan et al. 2017). The second method effectively facilitates calcium permeability through the cell membrane with higher cation levels in the rhizosphere, limiting potassium

uptake in the procedure. It was believed to be associated with potassium absorption in plants when soil calcium levels are too high. AMF can assist plants in absorbing potassium under abiotic stress conditions such as salt and drought (Garcia and Zimmermann 2014). In numerous cases, the AM connection improved plant salt stress by modifying the potassium nitrogen ratio under salt stress through the AMF (Estrada et al. 2013). The AM symbiosis increased plants' growth during a water deficit by increasing potassium absorption, which is essential for osmotic correction (Garcia and Zimmermann 2014).

3 Roles and Mechanisms of AMF in Plant Growth

The growth enhancing influence of AMF has been widely reported on different plant species (Rashad et al. 2020b; El-Sharkawy et al. 2022). Different modes of action have been discussed in this regard, including accumulation of a set of growth regulators suc as cytokinins, gibberellins, and auxins. Pons et al. (2020) recorded an accumulation of isopentenyl adenosine, indole-acetic acid, gibberellin A4, and ethylene by the germinated spores of *Rhizophagus irregularis.* These phytohormones play an important role in enhancing the plant growth, activation of various metabolic reactions, and upregulation of different growth-related genes in the plant. Induction of photosynthesis pigments and performance was reported also by AMF (Rashad et al. 2022). Priming water and nutrient uptake is another mode of action by which AMF can promote the host growth. Forming an extra radical hyphal network by AMF, which extends in the soil, improves water and nutrients acquisition for the host and connect roots of neighboring plants with each other. This hyphal network plays a vital role in translocation of nutrients and water between the neighboring plants (Muneer et al. 2020). Furthermore, AMF can produce organic acids, which improve availability of different nutrients in soil, particularly acid and alkaline phosphatases (Sato et al. 2019).

Many species of plants exhibited up to a 47-fold increase in the root absorption area as a result of AMF colonization in their cortex, which allowed plants to absorb water and mineral nutrients from underground ecosystems (Valverde-Barrantes et al. 2018). Since the sensitivity of crop species to AMF differs among species, where it was found to be high in maize and low in wheat and barley, many studies have showed that plants grew more quickly in response to AMF inoculation (Smith and Smith 2011). Onion plants (*Allium cepa* L.) grown in mineral soil with AMF colonized bulbs had higher biomass, a marketed size bulb (>25 mm in diameter), and a 22% increase in yield, compared to non-colonized plants (Charron et al. 2001). According to Surendirakumar et al. (2019) AMF-colonized pepper plants showed an enhanced growth rate and yield. In addition, pepper plants can sustain membrane growth and stability through mycorrhizal colonization, which may be linked to phosphorus supplementation (Beltrano et al. 2013).

4 Roles and Mechanisms of AMF in Plant Protection

AMF colonization results in a vast genetic reprogramming in the host cells, leading to some physiological alterations that activate the plant responses (Vangelisti et al. 2018). These physiological modulations include triggering of many innate and adaptive defense responses against the attacking pathogens. However, these modifications vary in their acuity depending on species of both partners, colonization stage, and the environmental conditions. Different defense mechanisms have been reported to be activated due to AMF colonization including overexpression of defense related genes. In a recent study, Rashad et al. (2020a) recorded upregulation of multi genes regulating the polyphenol biosynthetic pathway in sunflower plants in response to their colonization with AMF. Cell wall lignification and accumulation of antifungal phenolic compounds were the main mechanisms in this case. Ultrastructural alterations including granulated cytoplasm and programmed cell death were also recorded in AMF colonization (Abdel-Fattah et al. 2011). In addition, activation of enzymatic and non-enzymatic antioxidant systems as well as antifungal proteins were also reported. El-Sharkawy et al. (2022) reported an increment in the activities of the antioxidant enzymes peroxidase and polyphenol oxidase in pea plants in colonized with *R. irregularis* against infection with Fusarium Wilt.

Mycorrhiza induced resistance (MIR), a defense provided by AMF symbiosis in hosts, provides systemic defense against a variety of invading pathogens (Nguvo and Gao 2019). MIR combines traits of both systemic acquired resistance (SAR), which develops after a plant is infected with a pathogen, and induced systemic resistance (ISR), which develops after non-pathogenic rhizobacteria colonize a plant roots (Cameron et al. 2013). MIR is a result of plant-accumulated reactions to mycorrhizal colonization, and it can protect against biotrophic and necrotrophic fungi, viruses, nematodes, and insects (Dey and Ghosh 2022). Salicylic acid (SA), JA, and their metabolites are produced as a result of MIR, which is activated after AMF is established in the host (Fiorilli et al. 2018). MIR is also responsible for the production of chitinases, glucanases, and pathogenesis-related (PR) proteins (Pozo De La Hoz et al. 2021). AMF colonization resulted in activation of JA dependent signaling pathway in its host plant, leading to rapid and intense induction of numerous cellular defensive responses when exposed to pathogens or abiotic stress (Dey and Ghosh 2022). In order to control plant immunological homeostasis, two important defense hormones; SA and JA construct a complicated regulatory network (Yu et al. 2022).

In addition, the host plant responds to AM colonization by producing a variety of novel proteins (endomycorrhizins), new polypeptides and the disappearance of others (Bigeard et al. 2015). The early stages of AM production do not reveal phytoalexins, low-molecular-weight, toxic substances that are typically accumulated with pathogen attack and discharged at the sites of infection, but they can be later determined in the symbiosis (Poltronieri et al. 2019). For instance, the primary phytoalexin of soybeans, glyceollin, was not detectable for the first 30 days following AM

inoculation, while roots infection with *Rhizoctonia solani* showed a clear rise in this substance (Boutaj et al. 2022). Level of the phytoalexin medicarpin in *M. truncatula* increased during the early stages of AM colonization but declined to relatively low levels during the latter phases of symbiotic formation (Finkel et al. 2017). Directly or indirectly, AMF can inhibit both necrotrophic and biotrophic pathogens (Veresoglou and Rillig 2012). Furthermore, AMF colonization induce plant resistance against plant viruses (Aseel et al. 2019). AMF can protect the host plant against parasitic nematode infections (Koffi et al. 2013). Different mechanisms may be discussed including (i) increased microbial functioning and competition in the rhizosphere; (ii) accumulation of actinomycetes at AMF-associated roots; (iii) a more efficient trade-off in the root's mechanism for absorbing nutrients; and (iv) changes in the amount and nature of chemical products produced by the host plant's roots (Devi et al. 2021). In addition to producing volatile compounds and controlling soil and seed-borne phytopathogens (Bell et al. 2015), it has been shown to protect plants and reduce the growth of plant-destructive microbes.

5 Role and Mechanism of Arbuscular Mycorrhizal Fungi in Plant Tolerance to Salinity

Plant productivity is frequently hampered by salt of the soil in both agricultural and natural contexts. AMF symbionts can control plant stress responses by improving salinity tolerance, but less focus has been placed on evaluating these effects across plant-AMF investigations, posing a serious danger to global food security. Soil salinization is a growing environmental issue. It is well recognized that salinity stress inhibits plant growth by reducing the vegetative development and net assimilation rate, which results in lower yield productivity (Ahanger et al. 2017a). In addition, it encourages the overproduction of reactive oxygen species (Ahanger et al. 2017b, 2018). There are efforts underway to investigate potential strategies for improving agricultural productivity in salt-affected soils. One such promising method is the careful use of AMF to reduce the harmful effects of salinity on plants (Santander et al. 2019). Numerous studies have documented the effectiveness of AMF in promoting plant growth and yield under salt stress (Talaat and Shawky 2014). Accordingly, AMF improved the Antirrhinum majus plants' growth rate, leaf water potential, and water use efficiency (El-Nashar 2017). The positive impacts of AMF symbiosis on physiological variables as photosynthetic rate, stomatal conductance, and leaf water relations under saline regimes have recently been described (Ait-El-Mokhtar et al. 2019). AMF greatly reduced the negative effects of salt stress on photosynthesis (Sheng et al. 2011). Under saline conditions, mycorrhizal inoculation significantly increased the photosynthetic rate, as well as other gas exchange features, chlorophyll content, leaf area index and fresh, dry biomass and water usage efficiency (Elhindi et al. 2017). Mycorrhizal inoculation under moderately

salinity circumstances significantly improved fresh and dry weights as well as N concentration of shoot and root (Wang et al. 2018).

Synthesis of salicylic acid, jasmonic acid, and several other crucial inorganic nutrients is improved in plants with AMF. For instance, under salt stress conditions, AMF-treated plants had increased amounts of total P, Ca^{2+}, N, Mg^{2+}, and K^{+} compared to untreated plants. Under saline conditions, mycorrhizal inoculation of resulted in increased chlorophyll contents, Mg^{2+} and N uptake, and decreased Na^{+} transport (Çekiç et al. 2012). Furthermore, using lettuce that mycorrhizal plants produced more biomass, increased proline synthesis, increased N uptake, and noticed changes in ionic relations, particularly decreased Na^{+} accumulation, than non-mycorrhizal plants did under stress (Santander et al. 2019). Key growth regulator levels can be efficiently controlled by AMF inoculation. For instance, under salt stress, an AMF-mediated increase in cytokinin concentration led to a noticeable photosynthate translocation was found (Talaat and Shawky 2014). In addition, it was determined that the altered polyamine pool was the cause of the AMF-mediated growth promotion under salt stress. Furthermore, how salt impacts on lettuce plants were significantly reduced by increased strigolactone in AMF-treated plants was demonstrated (Aroca et al. 2013). By inhibiting lipid membrane peroxidation in response to salinity stress, AMF-colonized plants can reduce oxidative stress (Talaat and Shawky 2014). In addition, it was found that the inoculation of AMF increased the accumulation of several organic acids, which in turn increased the osmoregulation process in plants grown under saline stress. For instance, the indirect involvement of AMF in plant osmoregulation under salt stress by seeing increased synthesis/accumulation of certain organic acids in maize plants growing in saline soil and inducing higher production of betaine was confirmed (Sheng et al. 2011).

A surplus of sodium chloride (NaCl) harms almost 20% of the 230 million acres of irrigated agricultural land worldwide (Munns and Tester 2008). Because of overabsorption, ion imbalance, and hyperosmotic stress (water shortage under highly negative water potential), higher concentrations of Na^{+} (>40 mM) have a detrimental effect on plant growth (Munns and Tester 2008).

AMF have been proven to enhance nutrient uptake from the soil, including nitrogen, phosphate, magnesium, and micronutrients. They have also been demonstrated to improve soil structure and increase plant tolerance to a variety of abiotic and biotic stresses. In addition, AMF supports root architecture and the provision of vital nutrients to the host plant under salt stress. Ion and membrane transport proteins that regulate the ion homeostasis of the host plants are heavily regulated by AMF (Ramos et al. 2011).

The concentrations of K^{+}, Ca^{2+}, and NO_3 in crop plants drop with increased salinity on irrigated agricultural land, whereas the concentrations of inorganic phosphate increase (P). However, if the concentration of Na^{+} and Cl^{-} ions rises, it can cause ionic damage as well as osmotic and nutritional imbalance (Bothe 2012). Maintaining ion balance in the cytoplasm is also thought to benefit from having a healthy K/Na ratio (Tomar and Agarwal 2013).

Compared to non-AMF plants, plants inoculated with AMF absorb more K^+ ions and less Na^+ ions, showing that AMF causes preferential loading of K^+ rather than Na^+ into the root (Tomar and Agarwal 2013). Phosphorus (P) uptake in plants is influenced by an increase in AMF colonization, suggesting that alkaline phosphatases are likely involved in P acquisition. In addition, there is a chance that more than one acid phosphatase may be in charge of transporting P, which would result in an increase in P uptake under salt stress conditions. The amount of P accumulated largely determines how well the plant can withstand stress (Reichert et al. 2022).

Salt stress may reduce plants capacity for photosynthetic activity and cause physiological dryness, which lowers food production. By controlling the physiological and biochemical processes of plants, AMF are known to survive disturbed soil, contribute to plant growth and development, and improve plant tolerance against biotic and abiotic stresses (Ma et al. 2020).

The amount of chlorophyll pigments declines when affected by salinity stress. This reduced chlorophyll content caused by salinity stress was confirmed in some plants (Datta and Kulkarni 2014). Reduced chlorophyll contents under stress are attributed to increased activity of chlorophyllase causing degradation of pigments and hence resulting in reduced photosynthesis and affect growth. AMF-inoculated plants maintained increased contents of chlorophyll pigments compared to stressed plants. The fact that many plants' chlorophyll content was greatly boosted by AMF colonization. The increase in chlorophyll pigments brought on by AMF is the result of increased mineral intake, particularly magnesium, a crucial part of the chlorophyll molecule (Sheng et al. 2008). In plants inoculated with AMF, higher chlorophyll concentrations promote better photosynthetic activity, which supports maintenance of normal growth. Therefore, it is evident that AMF inoculation increases chlorophyll concentrations and partially offsets the detrimental effects of salt (Sheng et al. 2008).

Along with increasing soil salinity, an imbalance in nutrients and ions results from the rise in salt content in soil solution. This ion and nutritional imbalance cause a significant rise in ROS formation within the plant. Understanding the many processes that allow plants to withstand salt-induced stress and growth is crucial because salinity impairs plant health. In order to combat salt stress, plants produce more osmolytes and antioxidant enzymes that guard against oxidative damage (Rai et al. 2011). In order to defend themselves against oxidants, plants have developed specialized defense mechanisms involving enzymes and antioxidant compounds (Nunez et al. 2003). When pathogens assault a plant, the plant responds by activating its defence mechanisms, such as POD and CAT, which help to reinforce the cell wall or by acting as antioxidants (Kaur et al. 2022). The fundamental antioxidant enzyme known as superoxide dismutase (SOD) transforms superoxide to oxygen and hydrogen peroxide (H_2O_2) (Alscher et al. 2002).

The level of antioxidant enzyme activity varied between different AMF fungus species in the maize crop. The plant under salinity stress displayed an increase in SOD activity in the root rather than the shoot. SOD activity was higher in mycorrhizal plants than in non-mycorrhizal maize crops (Dastogeer et al. 2020).

The mycorrhizal maize crop's increased SOD activity aids in reducing oxidative stress. The absence of CAT activity in maize plants under salt stress conditions suggests that the AMF symbiosis has no effect on CAT activity in these circumstances (Dastogeer et al. 2020).

The most prevalent osmolyte in plants, proline, is essential for enhancing a plant's capacity to adapt to salinity stress. It is one among the organic solutes that plants produce in response to salinity and drought stress, and it is crucial for maintaining the osmotic balance of cells to lessen the effects of salt stress. Pyronine-5 carboxylate synthase (P-5 Cs) and pyronine-5 carboxylate reductase (P-5 Cr) are two enzymes that produce proline (Ondrasek et al. 2022). An essential organic substance called proline plays a role in osmotic adjustment under abiotic stress circumstances (Ondrasek et al. 2022).

AMF cause plants under drought stress to accumulate more proline (Chun et al. 2018). Proline is one of the osmolytes that builds up in species that are less tolerant to salinity. It modulates salt stress through osmotic adjustment, plays a variety of roles in plant stress tolerance, safeguards macromolecules during dehydration (Raja et al. 2022), and acts as a hydroxyl radical scavenger (Chun et al. 2018). AMF are therefore thought to improve saline soils biologically (Raja et al. 2022).

6 Role and Mechanism of Arbuscular Mycorrhizal Fungi in Plant Tolerance to Drought

One of the main abiotic stresses, drought stress, has a significant impact on agricultural output and threatens global food security (Zhang et al. 2018). Plants use morphological, physiological, and molecular responses as part of their drought avoidance and/or tolerance mechanisms to adapt to drought deficient conditions (Zhang 2016). Numerous elements of plant physiology are significantly impacted by water deficiency (Batool et al. 2019). For example, it disrupts the structure of enzymes, uncouples photosynthesis, and lowers nutrient uptake and/or transport to the shoot, which causes a hormonal and nutritional imbalance in the plant (Xie et al. 2018). In addition, osmotic stress brought on by drought stress can result in turgor loss, which can limit plant growth and development. Reactive oxygen species (ROS) are produced as a result of drought stress, which causes oxidative damage to carbohydrates, protein synthesis, and lipid metabolisms. ROS can also result in membrane damage and cell death in plant tissues (Ahanger et al. 2017a, b).

In comparison to normal soils, it has been discovered that AMF species are less common in soils deficient in water, with Glomeraceae being distributed as the "global family." These AMF species exhibit opportunistic behaviour because they focus most of their efforts on producing offspring. AMF species have additionally developed traits that are useful in dry conditions (Sýkorová et al. 2007). Some AMF isolates or specific species are widely dispersed and can withstand drought stress (Stahl and Christensen 1991). After extensive periods of adaptation to soils with

severe features, native AMF ecotypes have emerged (Bethlenfalvay and Barea 1994). Numerous studies have shown that Glomus species are common in semi-arid Mediterranean habitats and can thrive when there is a water shortage (Tian et al. 2009).

However, there is compelling evidence that AMF reduces the effects of drought stress in a variety of crops, including wheat, barley, maize, soybean, strawberries, and onions (Yooyongwech et al. 2016; Moradtalab et al. 2019). The extensive area of soil that plant roots can access, and the extra-radical hyphae of fungi may be the main causes of plant tolerance to drought (Zhang et al. 2017).

A variety of physio-biochemical processes in plants are thought to be regulated by such a symbiotic relationship, including increased osmotic adjustment (Wahab et al. 2022; Yan et al. 2022), stomatal regulation by regulating ABA metabolism (Muhammad Aslam et al. 2022; Mildaziene et al. 2022), enhanced proline accumulation (Yooyongwech et al. 2016; Begum et al. 2019), or increased glutathione (Begum et al. 2019). Under immediate drought conditions, a symbiotic association between diverse plants and AMF may eventually boost root size and efficiency, leaf area index, and biomass (Begum et al. 2019). In addition, AMF and the host plant they interact with help protect plants from harsh environmental circumstances.

AMF represent a viable way to enhance next-generation agriculture and regulate multiple pathways to minimize oxidative damage under drought stress (Chitarra et al. 2016). The emergence of AMF-mediated processes in response to drought stress involves alterations in the concentration of plant hormones including strigolactones, jasmonic acid (JA), and abscisic acid (ABA), as well as an improvement in plant water status through an increase in hydraulic conductivity (Fernández-Lizarazo and Moreno-Fonseca 2016).

Different methods that enable plants to avoid stress and/or improve their tolerance to drought are adopted in response to drought stress in plants. Although most plant species find these alterations to be critically important, they have not been proven to be a typical response in host plant species with various evolutionary histories (Grabherr et al. 2011). By maintaining a greater water status, these plant adaptation methods enable the plant to endure water-limiting situations. AMF can modify the extremely plastic features of plant roots to increase water uptake and/or reduce water loss. When the leaf water potential is low, continuous physiological adjustments help the leaves' capacity to withstand dehydration (Zou et al. 2017). This dehydration tolerance is related to survival. Fascinatingly, most plants instantly request AMF assistance when they sense drought stress by secreting rhizosphere signalling molecules, or so-called "strigolactone" (a type of phytohormones) (Oldroyd 2013). The use of AMF inoculation to reduce the effects of drought stress has recently attracted a lot of interest (Kumar and Verma 2018). A thorough assessment of the literature reveals that leaf water potential was not static in certain tests, and that mycorrhizal interaction with host plants improves the hydration status overall, as measured by leaf relative water content (LRWC) (Wu et al. 2017; Barros et al. 2018) (Table 1). Several concerns still need to be answered, despite the fact that the AMF colonization-mediated adaptation processes in plants have been well documented.

Table 1 Drought stress effects on morphological, physiological, and biochemical differences in different experimental set-ups and plant species, adopted from (Bahadur et al. 2019)

Plant species	AMF species	AMF variables	Plant variables			References
			Morphological	Physiological	Biochemical	
Calotropis procera Ait	*Glomus intraradices*	Col%$^{\uparrow}$		N$^{\uparrow}$, K$^{\uparrow}$	CAT$^{\uparrow}$, POD$^{\uparrow}$, APX$^{\uparrow}$, SOD$^{\uparrow}$	Bahmani et al. (2018)
Cynophala flexuosa L.	AMF	Col% ^{ns}		LRWC$^{\uparrow}$, PEUE$^{\uparrow}$ (Cycle 2), leaf construction cost$^{\uparrow}$ (Cycle 2), SLA$^{\uparrow}$ (Cycle 1)		Barros et al. (2018)
Glycine max L.	AMF	Col%$^{\uparrow}$	Soil moisture (%)$^{\uparrow}$, LAI$^{\uparrow}$, growth performance$^{\uparrow}$	Pn$^{\uparrow}$, Leaf proline concentration$^{\downarrow}$		Pavithra and Yapa (2018)
Glycyrrhiza uralensis Fisch. ex DC.	*Rhizophagus irregularis*	Col%$^{\uparrow}$, A%$^{\downarrow}$		Leaf proline concentrations$^{\uparrow}$, P$^{\uparrow}$, C:N$^{\uparrow}$, Pn$^{\uparrow}$, WUE$^{\uparrow}$, C:P$^{\downarrow}$, N:P$^{\downarrow}$	Root ABA$^{\downarrow}$	Xie et al. (2018)
Ipomoea batatas (L.) Lam.	Commercial inoculum containing *Glomus sp.* and *Acaulospora sp.*		Plant growth$^{\uparrow}$, tubers per plant$^{\uparrow}$, tuber fresh weight$^{\uparrow}$	P content$^{\uparrow}$, soluble sugars$^{\uparrow}$, leaf osmotic potential$^{\uparrow}$, chlorophyll degradation$^{\downarrow}$, photosynthetic pigments$^{\uparrow}$, maximum quantum yield of PSII (Fv/Fm)$^{\uparrow}$, photon yield of PSII (ΦPSII) $^{\uparrow}$, net photosynthetic rate$^{\uparrow}$	Proline$^{\uparrow}$	Yooyongwech et al. (2016)
Pelargonium graveolens (L.) Herit.	*Funneliformis mosseae*, *Rhizophagus irregularis*	Col%$^{\downarrow}$		Essential oil content$^{\uparrow}$, oil yield$^{\uparrow}$	MDA$^{\downarrow}$, $H_2O_2{}^{\downarrow}$, CAT$^{\uparrow}$, APX$^{\uparrow}$, SOD$^{\uparrow}$, GPX$^{\uparrow}$	Amiri et al. (2015)

(continued)

Table 1 (continued)

Plant species	AMF species	AMF variables	Plant variables			References
			Morphological	Physiological	Biochemical	
Phoenix dactylifera L.	*Funneliformis monosporum*, *Rhizophagus clarus*, *Glomus deserticola* Δ		Plant growth performance$^{\uparrow}$	Nutrient absorption$^{\uparrow}$, RWC$^{\uparrow}$, water potential$^{\uparrow}$, stomatal resistance$^{\downarrow}$		Meddich et al. (2015)
Poncirus trifoliata (L.)	*Diversispora versiformis*	Col%$^{\downarrow}$, hyphal length$^{\downarrow}$	Plant growth performance$^{\uparrow}$, root morphology$^{\uparrow}$	LWP$^{\downarrow}$	IAA$^{\uparrow}$, MeJA$^{\uparrow}$, NO$^{\uparrow}$	Zou et al. (2017)
Poncirus trifoliata (L.)	*Funneliformis mosseae*	Col%$^{\downarrow}$	Shoot$^{\uparrow}$, root$^{\uparrow}$, total biomass$^{\uparrow}$, surface area of lateral roots$^{\uparrow}$		$O_2^{-\downarrow}$, $H_2O_2^{\downarrow}$, MDA$^{\downarrow}$	Huang et al. (2017)
Poncirus Trifoliata (L.)	*Funneliformis mosseae*, *Paraglomus occultum*	Col%$^{\downarrow}$	Plant height$^{\uparrow}$, stem diameter$^{\uparrow}$, leaf number$^{\uparrow}$, leaf, stem, and root dry weight$^{\uparrow}$	LRWC$^{\uparrow}$	Leaf sucrose$^{\uparrow}$, glucose$^{\uparrow}$, fructose$^{\uparrow}$, leaf proline concentration$^{\downarrow}$	Wu et al. (2017)
Poncirus trifoliate (L.)	*Funneliformis mosseae*	Col%$^{\downarrow}$	Plant height$^{\uparrow}$, shoot and root biomass$^{\uparrow}$, root hairs density$^{\uparrow}$, length$^{\uparrow}$, diameter$^{\uparrow}$		Root IAA$^{\uparrow}$	Chun-Yan et al. (2017)
Poncirus trifoliata (L.)	*Funneliformis mosseae*, *Paraglomus occultum*	Col%$^{\downarrow}$	Root biomass$^{\uparrow}$, taproot length$^{\uparrow}$, number of lateral roots$^{\uparrow}$		Root sucrose$^{\downarrow}$, glucose$^{\uparrow}$, fructose$^{\uparrow}$ root sucrose relevant enzymes$^{\uparrow}$, root proline$^{\downarrow}$	Zhang et al. (2018)
Solanum lycopersicum L. mutant notabilis and its wild-type	*Rhizophagus intraradices*	Col%$^{\uparrow}$, Col%$^{\downarrow}$	Shoot biomass$^{\uparrow}$	Shoot and root P concentrations$^{\uparrow}$, WUE$^{\uparrow}$, Tr$^{\uparrow}$	ABA$^{\downarrow}$	Xu et al. (2018)

Plant species	AMF species	AMF variables	Plant variables			References
			Morphological	Physiological	Biochemical	
Solanum lycopersicum L.	*Funneliformis mosseae*, *Rhizophagus intraradices*		Plant height$^{\uparrow}$, root fresh weight$^{\downarrow}$	Stomatal density$^{\uparrow}$, WUE$^{\uparrow}$, Tr$^{\uparrow}$	ABA$^{\downarrow}$, $H_2O_2{}^{\downarrow}$, proline$^{\uparrow}$	Chitarra et al. (2016)
Zea mays L.	*Rhizophagus irregularis*	Col%$^{\downarrow}$	Plant growth$^{\uparrow}$	P$^{\uparrow}$, WUE$^{\uparrow}$, rehydration rate$^{\uparrow}$, leaf moisture percentage$^{\uparrow}$	Proline$^{\uparrow}$, C:P$^{\downarrow}$, N:P$^{\downarrow}$, MDA$^{\downarrow}$	Zhao et al. (2015)
Zea mays L.	*Rhizophagus irregularis*	Col%^{ns}	Shoot dry weight$^{\uparrow}$, root dry weight$^{\uparrow}$	gs$^{\uparrow}$, Lpr$^{\uparrow}$, Lo$^{\uparrow}$	Root ABA$^{\uparrow}$	Quiroga et al. (2017)

$^{\uparrow}$ and $^{\downarrow}$ indicate increasing and decreasing responses. *AMF* arbuscular mycorrhizal fungi, *WUE* water use efficiency, *Tr* transpiration rate, *ABA* abscisic acid, *Col* AMF colonization, *P* phosphorus, *C:N* carbon: nitrogen, *Pn* photosynthetic rate, *C:P* carbon: phosphorus ratio, *N:P* nitrogen: phosphorus, *LAI* leaf area index, *LRWC* leaf relative water content, *PEUE* photosynthetic energy use efficiency, *SLA* specific leaf area, *CAT* catalase, *POD* peroxidase, *APX* ascorbate peroxidase, *SOD* superoxide dismutase, *N* nitrogen, *K* potassium, *gs* stomatal conductance, *Lpr* hydrostatic root hydraulic conductivity, *Lo* osmotic root hydraulic conductivity, *IAA* indoleacetic acid, O_2^- superoxide radical, H_2O_2 hydrogen peroxide, *MDA* malondialdehyde, *LWP* leaf water potential, *MeJA* methyl jasmonate, *NO* nitric oxide, *GPX* glutathione peroxidase, *ns* non-significant

7 Role and Mechanism of Arbuscular Mycorrhizal Fungi in Plant Tolerance to Heavy Metal Toxicity

Due to the usage of sludge, pesticides, fertilizers, emissions from municipal waste incinerators, car exhausts, residues from metalliferous mines, and smelting enterprises, heavy metals are among the most dangerous inorganic compounds that have contaminated significant areas of land (Alengebawy et al. 2021). Despite the fact that metal ions like copper (Cu), zinc (Zn), iron (Fe), manganese (Mn), and nickel (Ni) etc. participate in redox reactions, electron transfers, and a variety of enzyme-catalyzed reactions in various cellular metabolism at optimal concentrations, the toxic concentration of the same essential metals or the non-essential toxic ions of Cd, Hg, Pb, Ag, As, Al, etc. are strongly poisonous to metal-sensitive (Smethurst and Shcherbik 2021; Jomova et al. 2022). How do plants defend themselves from metal poisoning and control their metabolism in reaction to heavy metals? The key is to comprehend how plants detoxify and how they can withstand excessive metal stress (Hasan et al. 2017).

Because of their capacity to strengthen the defensive system of the AMF-mediated plants to promote growth and development, AMF is widely regarded to support plant establishment in soils contaminated with heavy metals. Food crops, fruits, vegetables, and soils may collect heavy metals, posing varied health risks (Yousaf et al. 2016). Under aluminium stress, a favourable interaction between wheat and AMF enhanced nutrient absorption (Aguilera et al. 2014). The growth of shoots and roots, leaf chlorosis, and even plant death are significantly suppressed in plants raised in soils enriched with Cd and Zn (Moghadam 2016). The effects of AMF on the accumulation of metals in plants have been the subject of numerous reports in the literature (Souza et al. 2013). By fixing heavy metals in the cell wall and storing them in the vacuole or by chelating with other compounds in the cytoplasm, fungal hyphae of internal and external origin can immobilize heavy metals, reducing their toxicity to plants (Ouziad et al. 2005). The ability of these fungi to increase morphological and physiological processes that increase plant biomass and, as a result, uptake of significant immovable nutrients like Cu, Zn, and P and consequently, reduced metal toxicity in the host plants, accounts for the majority of the strong effects of AMF on plant development and growth under severely stressful conditions (Miransari 2017). In addition, it is thought that chelation or improved development in the rhizosphere of the soil might dilute metals in plant tissues (Audet 2014). AMF are said to bind Cd and Zn in the mantle hyphae and cortical cells' cell walls, preventing them from being absorbed and enhancing growth, yield, and nutrient status (Garg and Chandel 2012).

Mycorrhizae can impede certain metals' uptake by plants from the rhizosphere and their passage from the root zone to the aerial regions (Li et al. 2016a; Ma et al. 2022). As a result, many AMFs exhibit substantial cation-exchange capacities and metal absorption in their mycelia (Joner et al. 2012). AMFs are considered to control the absorption and accumulation of some significant inorganic nutrients (Ho-Plágaro and García-Garrido 2022).

In soil that has been artificially polluted with various elements such as Cd, Ni, and Zn, metal non-adapted AMF settles the polluted soils and lowers uptake and accumulation of heavy metals (Begum et al. 2019; Riaz et al. 2021). Some important inorganic nutrients are thought to be regulated by AMFs in terms of absorption and accumulation. For instance, mycorrhiza-inoculated plants have been shown to have increased Si uptake (Etesami et al. 2021). In addition, significant Si absorption and transmission to the host roots were observed in *Rhizophagus irregularis* spores and hyphae (Hammer et al. 2011). It is important to note that AMF can also address poor Cd mobility and toxicity by raising soil pH, reintroducing Cd into extra-radical mycelium (Janoušková and Pavlíková 2010), and binding Cd to the glycoprotein glomalin. For instance, the Cd levels in the vacuoles and cell walls of rice were significantly reduced by AMF, resulting in Cd detoxification (Li et al. 2016b). The alteration of the chemical forms of Cd in various plant tissues may have contributed to AMF-mediated increased Cd tolerance in alfalfa (*Medicago sativa* L.) (Wang et al. 2012). Immobilization/restriction of metal compounds, granulation of polyphosphate in the soil, and adsorption to fungal cell walls are some of the actions that are carried out by the AMF (Begum et al. 2019).

8 Role and Mechanism of Common Mycorrhizal Networks

Shared or common mycorrhizal networks (CMNs), which serve as channels for the exchange of resources among plants, can connect plant roots. All significant terrestrial ecosystems have mycorrhizal networks, which are defined as a shared mycorrhizal mycelium connecting the roots of at least two plants (Figueiredo et al. 2021).

In natural communities, CMNs which serve as channels for the exchange of resources between plants frequently connect the plant roots (Figueiredo et al. 2021). Such networks can create "guilds of mutual aid" between nearby plants of the same or different species or shift nutrients along traditional source-sink gradients from resource-rich (source) to resource-poor plants (Simard et al. 2015). There have been recorded net carbon, nitrogen, and phosphorus translocations between plants connected by CMNs (Gorzelak et al. 2015). It has been suggested that CMNs are fundamental agents in ecosystems because they provide significant pathways for a variety of ecological interaction processes (Torrecillas et al. 2014). Information on the structure of CMNs is now becoming available (Simard et al. 2015).

The AMF may associate with most plant species and has almost limitless host ranges (Smith and Read 2010). Compared to perennial plant species, annual plant species have higher AMF diversity, and half of the AMF species now recognized are specialized to a single plant species (Torrecillas et al. 2012). The AMF species and the related plant species both affect the length of intact extraradical mycelium. CMNs can be formed by the extraradical mycelium of one AMF or the hyphal fusion of separate mycelia (Walder et al. 2012). These networks can connect nearby plants of the same or different species within a community (Gorzelak et al. 2015).

The ectomycorrhizal fungi (EMF) class is the other important mycorrhizal class. In contrast to AMF, fewer plant species have been discovered to form symbioses with EMF; nonetheless, these hosts tend to be more numerous, plentiful, and dominant in their assemblages (Rasmussen et al. 2017). The majority of coniferous trees (including Pinaceae), the majority of woody shrub species in temperate and boreal forests, and the Dipterocarpaceae, for instance, are hosts for EMF. As a result, EMF is also frequent in tropical forests (Brearley 2012). Root tips harbouring EMF can be identified by macroscopic characteristics such as I the mantle, a fungal sheath that surrounds a colonised root tip, and (ii) extramatrical mycelium (diffuse hyphae that extend out into the surrounding soil). EMF species, mostly from the phylum Basidiomycota and Ascomycota, produce either epigeous mushrooms or hypogeous truffles. Up to 66 instances of ectomycorrhizal fungi have been discovered thus far from phylogenetic evidence, suggesting that they may have originated individually in several plant families (Tedersoo et al. 2010). Some remarkable plant groups and genera have the capacity to simultaneously generate healthy symbioses with EMF and AMF. AMF systems have recently been shown to have lower soil C: N ratios than those dominated by EMF, indicating fundamentally different nutrient cycle regimes, resulting in more carbon trapped in EMF forests. This has large-scale implications for resource availability (Averill et al. 2014).

There is evidence that both EMF and AMF fungus can create networks. The contrasts between them are emphasized, and it is also underlined that despite these differences, both appear to be able to influence changes in plant behaviour through the construction of networks. As this topic is covered elsewhere (Barto et al. 2012).

CMNs have several advantages for their host plants, and they can carry information back and forth between them with a net flux in favour of one plant (Selosse et al. 2006). By facilitating plant-to-plant communication, CMNs can enhance interplant nutrition, interplant nutrition and growth, impact plant and microorganism community compositions, and increase seedling establishment (Gorzelak et al. 2015; He et al. 2019). In addition, through a variety of phytohormones like jasmonic acid, methyl jasmonate, and zeatin riboside, CMNs can stimulate plant defense responses (defense enzyme activity and defense-related gene expression) and plant communication (Song et al. 2010).

By changing the distribution of population size classes, which is a functional feature representing symmetrical or asymmetrical competition (Weremijewicz et al. 2016, 2018) between young and adult trees, CMNs increase intraspecific competition (Merrild et al. 2013). After germination, population distributions are often symmetrical, but as plants age, they become more asymmetrical, reflecting the predominance of large individuals who receive an excessive share of a finite resource. Plants with intact CMNs displayed asymmetrical competition, whereas plants with severed CMNs displayed symmetrical competition (Weremijewicz et al. 2016, 2018). This suggests that intact CMNs may provide nutrients such as N to large individuals that are highly photosynthetically active and provide the most C to their associated AMF (Merrild et al. 2013). The pace of nutrient exchange between

the host plant and the fungus could determine this reciprocal benefit (Kiers et al. 2011). Other factors, such as host sink strength, intraspecies size hierarchy, and interspecies interactions, may affect the dynamics of nutrients in CMNs (Walder and Van Der Heijden 2015). However, in a CMN between sorghum and flax, the reciprocal reward does not appear to represent a general occurrence (Walder et al. 2012, 2015). This suggests that biological market dynamics governs the flow of resources in AM symbiosis, and there is evidence that the cost-benefit ratio of nutrients differs among various host plant species (Walder et al. 2012, 2015).

As opposed to waiting for AMF spore germination, the effects of CMNs on seedling recruitment may be advantageous. For the growth of the intraradical and extraradical mycelia, for instance, AMF spore germination implies a C cost for the growing seedlings that is larger for Gigasporaceae species than for Glomus species (Chagnon et al. 2013). In addition, seedlings' P resources may be restricted, and the results of interactions between one plant and various AMF species are not always predictable in terms of net advantages (Hoeksema et al. 2010; Kiers et al. 2011). On the other hand, when seedlings are entrapped in the already-existing CMN, the effects of CMNs on plant germination (growth and chances of establishment) are favorable (Walder and Van Der Heijden 2015). Depending on plant photosynthetic rates or the intensity of sources and sinks, CMNs may promote faster mycorrhiza development, restrict seedling investment in hyphal network construction expenses, provide access to mineral nutrients and water, and transport carbon from one plant to another.

Plant-plant communication may help ensure food security by lowering crop losses brought on by pests. AMF can influence rivals through allelopathy (Barto et al. 2012). Following a caterpillar attack (Song et al. 2010) or necrotrophic fungal attack (Babikova et al. 2013), the CMN might operate quickly (between 24 and 50 h) (Song et al. 2010). The CMN alters leaf volatile organic compounds or assists in extending the bioactive zone of allelochemicals in the soil (Barto et al. 2012; Babikova et al. 2013). As a result, CMNs offer a significant opportunity for crop pest management via this underground plant-plant transmission pathway (Babikova et al. 2014). The frequency and speed of pest attacks, the number of attacked crop plants, the signal travelling over long distances (Babikova et al. 2013), the putative relay of the signals among plants, and the putative transfer to other CMNs will all affect the reliability of CMNs in agroecosystems and their ability to play a direct, rapid, and realistic role in pest control. But in order for CMNs to be effective and beneficial in crop pest control, they must first be alerted to attacks and then maintain their physical integrity. Tilling most cropped soils probably breaks up CMNs. Tillage intensity increases reduce plant mycorrhizal colonization (Sommermann et al. 2018). By favoring more tolerant AMF species and having an effect on CMNs' capacity to transmit defense signals, tillage may alter the composition of the AMF population (Brigido et al. 2017). Together, these results demonstrate the significance of CMNs and the urgent need for additional study into their purpose and function, particularly in relation to agroecological management.

References

Abbaspour H, Saeidi-Sar S, Afshari H, Abdel-Wahhab MA (2012) Tolerance of Mycorrhiza infected Pistachio (Pistacia vera L.) seedling to drought stress under glasshouse conditions. J Plant Physiol 169:704–709. https://doi.org/10.1016/j.jplph.2012.01.014

Abdel-Fattah GM, El-Haddad SA, Hafez EE, Rashad YM (2011) Induction of defense responses in common bean plants by arbuscular mycorrhizal fungi. Microbiol Res 166:268–281. https://doi.org/10.1016/j.micres.2010.04.004

Aguilera P, Cornejo P, Borie F et al (2014) Diversity of arbuscular mycorrhizal fungi associated with Triticum aestivum L. plants growing in an Andosol with high aluminum level. Agric Ecosyst Environ 186:178–184

Ahanger MA, Tittal M, Mir RA, Agarwal R (2017a) Alleviation of water and osmotic stress-induced changes in nitrogen metabolizing enzymes in Triticum aestivum L. cultivars by potassium. Protoplasma 254:1953–1963. https://doi.org/10.1007/s00709-017-1086-z

Ahanger MA, Tomar NS, Tittal M et al (2017b) Plant growth under water/salt stress: ROS production; antioxidants and significance of added potassium under such conditions. Physiol Mol Biol Plants 23:731–744

Ahanger MA, Alyemeni MN, Wijaya L et al (2018) Potential of exogenously sourced kinetin in protecting Solanum lycopersicum from NaCl-induced oxidative stress through up-regulation of the antioxidant system, ascorbate-glutathione cycle and glyoxalase system. PLoS One 13:e0202175

Ait-El-Mokhtar M, Ben LR, Anli M et al (2019) Use of mycorrhizal fungi in improving tolerance of the date palm (Phoenix dactylifera L.) seedlings to salt stress. Sci Hortic (Amsterdam) 253:429–438

Alengebawy A, Abdelkhalek ST, Qureshi SR, Wang M-Q (2021) Heavy metals and pesticides toxicity in agricultural soil and plants: ecological risks and human health implications. Toxics 9. https://doi.org/10.3390/toxics9030042

Allen MF (2007) Mycorrhizal fungi: highways for water and nutrients in arid soils. Vadose Zone J 6:291–297. https://doi.org/10.2136/vzj2006.0068

Allen MF (2011) Linking water and nutrients through the vadose zone: a fungal interface between the soil and plant systems. J Arid Land 3:155–163

Alscher RG, Erturk N, Heath LS (2002) Role of superoxide dismutases (SODs) in controlling oxidative stress in plants. J Exp Bot 53:1331–1341

Amiri R, Nikbakht A, Etemadi N (2015) Alleviation of drought stress on rose geranium [Pelargonium graveolens (L.) Herit.] in terms of antioxidant activity and secondary metabolites by mycorrhizal inoculation. Sci Hortic (Amsterdam) 197:373–380. https://doi.org/10.1016/j.scienta.2015.09.062

Aroca, R (ed.) (2012) Plant responses to drought stress: frommorphological to molecular features. Springer-Verlag Berlin;GmbH & Co. K, Heidelberg, Germany

Aroca R, Ruiz-Lozano JM, Zamarreño ÁM et al (2013) Arbuscular mycorrhizal symbiosis influences strigolactone production under salinity and alleviates salt stress in lettuce plants. J Plant Physiol 170:47–55

Aseel DG, Rashad YM, Hammad SM (2019) Arbuscular mycorrhizal fungi trigger transcriptional expression of flavonoid and chlorogenic acid biosynthetic pathways genes in tomato against tomato mosaic virus. Sci Rep 9: 9692. https://doi.org/10.1038/s41598-019-46281-x

Asrar AWA, Elhindi KM (2011) Alleviation of drought stress of marigold (Tagetes erecta) plants by using arbuscular mycorrhizal fungi. Saudi J Biol Sci 18:93–98. https://doi.org/10.1016/j.sjbs.2010.06.007

Audet P (2014) Arbuscular mycorrhizal fungi and metal phytoremediation: ecophysiological complementarity in relation to environmental stress. In: Emerging technologies and management of crop stress tolerance. Elsevier, pp 133–160

Averill C, Turner BL, Finzi AC (2014) Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. Nature 505:543–545

Babikova Z, Gilbert L, Bruce TJA et al (2013) Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. Ecol Lett 16:835–843
Babikova Z, Gilbert L, Randall KC et al (2014) Increasing phosphorus supply is not the mechanism by which arbuscular mycorrhiza increase attractiveness of bean (Vicia faba) to aphids. J Exp Bot 65:5231–5241
Bahadur A, Batool A, Nasir F et al (2019) Mechanistic insights into arbuscular mycorrhizal fungi-mediated drought stress tolerance in plants. Int J Mol Sci 20. https://doi.org/10.3390/ijms20174199
Bahmani M, Naghdi R, Kartoolinejad D (2018) Milkweed seedlings tolerance against water stress: comparison of inoculations with Rhizophagus irregularis and Pseudomonas putida. Environ Technol Innov 10:111–121
Barros V, Frosi G, Santos M et al (2018) Arbuscular mycorrhizal fungi improve photosynthetic energy use efficiency and decrease foliar construction cost under recurrent water deficit in woody evergreen species. Plant Physiol Biochem 127:469–477
Barto EK, Weidenhamer JD, Cipollini D, Rillig MC (2012) Fungal superhighways: do common mycorrhizal networks enhance below ground communication? Trends Plant Sci 17:633–637
Batool A, Akram NA, Cheng Z-G et al (2019) Physiological and biochemical responses of two spring wheat genotypes to non-hydraulic root-to-shoot signalling of partial and full root-zone drought stress. Plant Physiol Biochem 139:11–20
Begum N, Qin C, Ahanger MA et al (2019) Role of arbuscular mycorrhizal fungi in plant growth regulation: implications in abiotic stress tolerance. Front Plant Sci 10:1068
Bell CW, Asao S, Calderon F et al (2015) Plant nitrogen uptake drives rhizosphere bacterial community assembly during plant growth. Soil Biol Biochem 85:170–182. https://doi.org/10.1016/j.soilbio.2015.03.006
Beltrano J, Ruscitti M, Arango MC, Ronco M (2013) Effects of arbuscular mycorrhiza inoculation on plant growth, biological and physiological parameters and mineral nutrition in pepper grown under different salinity and p levels. J Soil Sci Plant Nutr 13:123–141
Bethlenfalvay GJ, Barea J-M (1994) Mycorrhizae in sustainable agriculture. I. Effects on seed yield and soil aggregation. Am J Altern Agric 9:157–161
Bigeard J, Colcombet J, Hirt H (2015) Signaling mechanisms in pattern-triggered immunity (PTI). Mol Plant 8:521–539. https://doi.org/10.1016/j.molp.2014.12.022
Bitterlich M, Franken P, Graefe J (2018a) Arbuscular mycorrhiza improves substrate hydraulic conductivity in the plant available moisture range under root growth exclusion. Front Plant Sci 9:301
Bitterlich M, Sandmann M, Graefe J (2018b) Arbuscular mycorrhiza alleviates restrictions to substrate water flow and delays transpiration limitation to stronger drought in tomato. Front Plant Sci 9:154. https://doi.org/10.3389/fpls.2018.00154
Boldt K, Pörs Y, Haupt B, Bitterlich M, Kühn C, Grimm B, Franken P (2011) Photochemical processes, carbon assimilationand RNA accumulation of sucrose transporter genes in tomatoarbuscular mycorrhiza. J Plant Physiol 168:1256–1263. https://doi.org/10.1016/j.jplph.2011.01.026
Bothe H (2012) Arbuscular mycorrhiza and salt tolerance of plants. Symbiosis 58:7–16
Boutaj H, Meddich A, Roche J et al (2022) The effects of mycorrhizal fungi on vascular wilt diseases. Crop Prot 155:105938. https://doi.org/10.1016/j.cropro.2022.105938
Brearley F (2012) Ectomycorrhizal associations of the dipterocarpaceae. Biotropica 44:637–648. https://doi.org/10.2307/23273034
Breuillin-Sessoms F, Floss DS, Karen Gomez S et al (2015) Suppression of arbuscule degeneration in Medicago truncatula phosphate transporter4 mutants is dependent on the ammonium transporter 2 family protein AMT2;3. Plant Cell 27:1352–1366. https://doi.org/10.1105/tpc.114.131144
Brigido C, Van Tuinen D, Brito I et al (2017) Management of the biological diversity of AM fungi by combination of host plant succession and integrity of extraradical mycelium. Soil Biol Biochem 112:237–247

Brundrett MC, Tedersoo L (2018) Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytol 220:1108–1115. https://doi.org/10.1111/nph.14976
Bücking H, Kafle A (2015) Role of arbuscular mycorrhizal fungi in the nitrogen uptake of plants: current knowledge and research gaps. Agronomy 5:587–612
Bukovská P, Bonkowski M, Konvalinková T et al (2018) Utilization of organic nitrogen by arbuscular mycorrhizal fungi – is there a specific role for protists and ammonia oxidizers? Mycorrhiza 28:269–283. https://doi.org/10.1007/s00572-018-0825-0
Cameron DD, Neal AL, van Wees SCM, Ton J (2013) Mycorrhiza-induced resistance: more than the sum of its parts? Trends Plant Sci 18:539–545. https://doi.org/10.1016/j.tplants.2013.06.004
Castillo CG, Oehl F, Sieverding E (2016) Arbuscular mycorrhizal fungal diversity in wheat agroecosystems in Southern Chile and effects of seed treatment with natural products. J Soil Sci Plant Nutr 16:967–978
Çekiç FÖ, Ünyayar S, Ortaş İ (2012) Effects of arbuscular mycorrhizal inoculation on biochemical parameters in Capsicum annuum grown under long term salt stress. Turk J Bot 36:63–72
Chagnon P-L, Bradley RL, Maherali H, Klironomos JN (2013) A trait-based framework to understand life history of mycorrhizal fungi. Trends Plant Sci 18:484–491
Charron G, Furlan V, Bernier-Cardou M, Doyon G (2001) Response of onion plants to arbuscular mycorrhizae 2. Effects of nitrogen fertilization on biomass and bulb firmness. Mycorrhiza 11:145–150. https://doi.org/10.1007/s005720100122
Chitarra W, Pagliarani C, Maserti B et al (2016) Insights on the impact of arbuscular mycorrhizal symbiosis on tomato tolerance to water stress. Plant Physiol 171:1009–1023
Chun SC, Paramasivan M, Chandrasekaran M (2018) Proline accumulation influenced by osmotic stress in arbuscular mycorrhizal symbiotic plants. Front Microbiol 9:2525. https://doi.org/10.3389/fmicb.2018.02525
Chun-Yan LIU, Srivastava AK, Qiang-Sheng WU (2017) Mycorrhizal fungi regulate root responses and leaf physiological activities in trifoliate orange. Not Bot Hortic Agrobot Cluj-Napoca 45:17–21
Dastogeer KMG, Zahan MI, Tahjib-Ul-Arif M et al (2020) Plant salinity tolerance conferred by arbuscular mycorrhizal fungi and associated mechanisms: a meta-analysis. Front Plant Sci 11:588550
Datta P, Kulkarni MV (2014) Arbuscular mycorrhizal colonization enhances biochemical status and mitigates adverse salt effect on two legumes. Not Sci Biol 6:381–393
Devi S, Bhupenchandra I, Sinyorita S et al (2021) Mycorrhizal fungi and sustainable agriculture. In: Bhupenchandra I (ed) Nitrogen in agriculture – physiological, agricultural and ecological aspects [working title]. IntechOpen, Rijeka, p Ch. 12
Dey M, Ghosh S (2022) Arbuscular mycorrhizae in plant immunity and crop pathogen control. Rhizosphere 22:100524. https://doi.org/10.1016/j.rhisph.2022.100524
Drew EA, Murray RS, Smith SE, Jakobsen I (2003) Beyond the rhizosphere: growth and function of arbuscular mycorrhizal external hyphae in sands of varying pore sizes. Plant Soil 251:105–114. https://doi.org/10.1023/A:1022932414788
Elhindi KM, El-Din AS, Elgorban AM (2017) The impact of arbuscular mycorrhizal fungi in mitigating salt-induced adverse effects in sweet basil (Ocimum basilicum L.). Saudi J Biol Sci 24:170–179. https://doi.org/10.1016/j.sjbs.2016.02.010
El-Nashar YI (2017) Response of snapdragon (Antirrhinum majus L.) to blended water irrigation and arbuscular mycorrhizal fungi inoculation: uptake of minerals and leaf water relations. Photosynthetica 55:201–209
El-Sharkawy HHA, Rashad YM, Elazab NT (2022) Synergism between Streptomyces viridosporus HH1 and Rhizophagus irregularis effectively induces defense responses to fusarium wilt of pea and improves plant growth and yield. J Fungi 8(7):683. https://doi.org/10.3390/jof8070683
Estrada B, Aroca R, Barea JM, Ruiz-Lozano JM (2013) Native arbuscular mycorrhizal fungi isolated from a saline habitat improved maize antioxidant systems and plant tolerance to salinity. Plant Sci 201–202:42–51. https://doi.org/10.1016/j.plantsci.2012.11.009

Etesami H, Jeong BR, Glick BR (2021) Contribution of arbuscular mycorrhizal fungi, phosphate-solubilizing bacteria, and silicon to P uptake by plant. Front Plant Sci 12:699618. https://doi.org/10.3389/fpls.2021.699618

Fernández-Lizarazo JC, Moreno-Fonseca LP (2016) Mechanisms for tolerance to water-deficit stress in plants inoculated with arbuscular mycorrhizal fungi. A review. Agron Colomb 34:179–189

Figueiredo AF, Boy J, Guggenberger G (2021) Common mycorrhizae network: a review of the theories and mechanisms behind underground interactions. Front Fungal Biol 2:735299

Finkel OM, Castrillo G, Herrera Paredes S et al (2017) Understanding and exploiting plant beneficial microbes. Curr Opin Plant Biol 38:155–163. https://doi.org/10.1016/j.pbi.2017.04.018

Fiorilli V, Vannini C, Ortolani F et al (2018) Omics approaches revealed how arbuscular mycorrhizal symbiosis enhances yield and resistance to leaf pathogen in wheat. Sci Rep 8:9625. https://doi.org/10.1038/s41598-018-27622-8

Garcia K, Zimmermann SD (2014) The role of mycorrhizal associations in plant potassium nutrition. Front Plant Sci 5:337. https://doi.org/10.3389/fpls.2014.00337

Garg N, Chandel S (2012) Role of arbuscular mycorrhizal (AM) fungi on growth, cadmium uptake, osmolyte, and phytochelatin synthesis in Cajanus cajan (L.) Millsp. under NaCl and Cd stresses. J Plant Growth Regul 31:292–308

George E, Häussler K-U, Vetterlein D et al (1992) Water and nutrient translocation by hyphae of Glomus mosseae. Can J Bot 70:2130–2137. https://doi.org/10.1139/b92-265

Giovannetti M, Avio L, Sbrana C (2015) Functional significance of anastomosis in arbuscular mycorrhizal networks. In: Horton TR (ed) Mycorrhizal networks, Ecological studies. Springer Netherlands, Dordrecht, pp 41–67

Gorzelak MA, Asay AK, Pickles BJ, Simard SW (2015) Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. AoB Plants 7. https://doi.org/10.1093/aobpla/plv050

Grabherr MG, Haas BJ, Yassour M et al (2011) Full-length transcriptome assembly from RNA-Seq data without a reference genome. Nat Biotechnol 29:644–652

Hammer EC, Nasr H, Pallon J et al (2011) Elemental composition of arbuscular mycorrhizal fungi at high salinity. Mycorrhiza 21:117–129

Haro R, Benito B (2019) The role of soil fungi in k+ plant nutrition. Int J Mol Sci 20. https://doi.org/10.3390/ijms20133169

Hasan MK, Cheng Y, Kanwar MK et al (2017) Responses of plant proteins to heavy metal stress – a review. Front Plant Sci 8:1492. https://doi.org/10.3389/fpls.2017.01492

He Y, Cornelissen JHC, Wang P et al (2019) Nitrogen transfer from one plant to another depends on plant biomass production between conspecific and heterospecific species via a common arbuscular mycorrhizal network. Environ Sci Pollut Res 26:8828–8837

Hodge A, Fitter AH (2010) Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. Proc Natl Acad Sci U S A 107:13754–13759. https://doi.org/10.1073/pnas.1005874107

Hoeksema JD, Chaudhary VB, Gehring CA et al (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecol Lett 13:394–407

Ho-Plágaro T, García-Garrido JM (2022) Molecular regulation of arbuscular mycorrhizal symbiosis. Int J Mol Sci 23:5960

Hou L, Zhang X, Feng G et al (2021) Arbuscular mycorrhizal enhancement of phosphorus uptake and yields of maize under high planting density in the black soil region of China. Sci Rep 11:1100. https://doi.org/10.1038/s41598-020-80074-x

Huang Y-M, Zou Y-N, Wu Q-S (2017) Alleviation of drought stress by mycorrhizas is related to increased root H(2)O(2) efflux in trifoliate orange. Sci Rep 7:42335. https://doi.org/10.1038/srep42335

Janoušková M, Pavlíková D (2010) Cadmium immobilization in the rhizosphere of arbuscular mycorrhizal plants by the fungal extraradical mycelium. Plant Soil 332:511–520

Jansa J, Mozafar A, Frossard E (2003) Long-distance transport of P and Zn through the hyphae of an arbuscular mycorrhizal fungus in symbiosis with maize. Agronomie 23:481–488. https://doi.org/10.1051/agro:2003013

Jansa J, Forczek ST, Rozmoš M et al (2019) Arbuscular mycorrhiza and soil organic nitrogen: network of players and interactions. Chem Biol Technol Agric 6:10. https://doi.org/10.1186/s40538-019-0147-2

Jomova K, Makova M, Alomar SY et al (2022) Essential metals in health and disease. Chem Biol Interact 367:110173. https://doi.org/10.1016/j.cbi.2022.110173

Joner EJ, Johansen A (2000) Phosphatase activity of external hyphae of two arbuscular mycorrhizal fungi. Mycol Res 104:81–86. https://doi.org/10.1017/S0953756299001240

Joner E, Briones-Gallardo R, Leyval C (2012) Metal-binding capacity of arbuscular mycorrhizal mycelium. Plant Soil 226:227–234. https://doi.org/10.1023/A:1026565701391

Jung SC, Martinez-Medina A, Lopez-Raez JA, Pozo MJ (2012) Mycorrhiza-induced resistance and priming of plant defenses. J Chem Ecol 38:651–664. https://doi.org/10.1007/s10886-012-0134-6

Kakouridis A, Hagen JA, Kan MP et al (2022) Routes to roots: direct evidence of water transport by arbuscular mycorrhizal fungi to host plants. New Phytol. https://doi.org/10.1111/nph.18281

Kaur S, Samota MK, Choudhary M et al (2022) How do plants defend themselves against pathogens-biochemical mechanisms and genetic interventions. Physiol Mol Biol Plants 28:485–504. https://doi.org/10.1007/s12298-022-01146-y

Kiers ET, Duhamel M, Beesetty Y et al (2011) Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science (80-) 333:880–882

Koffi MC, Vos C, Draye X, Declerck S (2013) Effects of Rhizophagus irregularis MUCL 41833 on the reproduction of Radopholus similis in banana plantlets grown under in vitro culture conditions. Mycorrhiza 23:279–288. https://doi.org/10.1007/s00572-012-0467-6

Kumar A, Verma JP (2018) Does plant – microbe interaction confer stress tolerance in plants: a review? Microbiol Res 207:41–52

Leigh J, Hodge A, Fitter AH (2009) Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. New Phytol 181:199–207. https://doi.org/10.1111/j.1469-8137.2008.02630.x

Li H, Chen XW, Wong MH (2016a) Arbuscular mycorrhizal fungi reduced the ratios of inorganic/organic arsenic in rice grains. Chemosphere 145:224–230

Li H, Luo N, Zhang LJ et al (2016b) Do arbuscular mycorrhizal fungi affect cadmium uptake kinetics, subcellular distribution and chemical forms in rice? Sci Total Environ 571:1183–1190

Liu J, Liu J, Liu J et al (2019) The potassium transporter slhak10 is involved in mycorrhizal potassium uptake. Plant Physiol 180:465–479. https://doi.org/10.1104/pp.18.01533

Ma Y, Dias MC, Freitas H (2020) Drought and salinity stress responses and microbe-induced tolerance in plants. Front Plant Sci 11:591911. https://doi.org/10.3389/fpls.2020.591911

Ma Y, Ankit TJ, Bauddh K (2022) Plant-mycorrhizal fungi interactions in phytoremediation of geogenic contaminated soils. Front Microbiol 13:843415. https://doi.org/10.3389/fmicb.2022.843415

Meddich A, Jaiti F, Bourzik W et al (2015) Use of mycorrhizal fungi as a strategy for improving the drought tolerance in date palm (Phoenix dactylifera). Sci Hortic (Amsterdam) 192:468–474

Merrild MP, Ambus P, Rosendahl S, Jakobsen I (2013) Common arbuscular mycorrhizal networks amplify competition for phosphorus between seedlings and established plants. New Phytol 200:229–240

Mildaziene V, Ivankov A, Sera B, Baniulis D (2022) Biochemical and physiological plant processes affected by seed treatment with non-thermal plasma. Plants (Basel, Switzerland) 11. https://doi.org/10.3390/plants11070856

Miller RM, Jastrow JD (2000) Mycorrhizal fungi influence soil structure. In: Kapulnik Y, Douds DD (eds) Arbuscular mycorrhizas: physiology and function. Springer Netherlands, Dordrecht, pp 3–18

Miransari M (2017) Arbuscular mycorrhizal fungi and heavy metal tolerance in plants. In: Arbuscular mycorrhizas and stress tolerance of plants. Springer, pp 147–161
Moghadam HRT (2016) Application of super absorbent polymer and ascorbic acid to mitigate deleterious effects of cadmium in wheat. Pesqui Agropecu Trop 46:9–18
Moradtalab N, Hajiboland R, Aliasgharzad N et al (2019) Silicon and the association with an arbuscular-mycorrhizal fungus (Rhizophagus clarus) mitigate the adverse effects of drought stress on strawberry. Agronomy 9:41
Muhammad Aslam M, Waseem M, Jakada BH et al (2022) Mechanisms of abscisic acid-mediated drought stress responses in plants. Int J Mol Sci 23:1084
Muleta D (2010) Legume responses to arbuscular mycorrhizal fungi inoculation in sustainable agriculture. In: Khan MS, Musarrat J, Zaidi A (eds) Microbes for legume improvement. Springer Vienna, Vienna, pp 293–323
Muneer MA, Wang P, Zaib-un-Nisa et al (2020) Potential role of common mycorrhizal networks in improving plant growth and soil physicochemical properties under varying nitrogen levels in a grassland ecosystem. Glob Ecol Conserv 24:e01352. https://doi.org/10.1016/j.gecco.2020.e01352
Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911
Nafady NA, Hashem M, Hassan EA et al (2019) The combined effect of arbuscular mycorrhizae and plant-growth-promoting yeast improves sunflower defense against Macrophomina phaseolina diseases. Biol Control 138:104049. https://doi.org/10.1016/j.biocontrol.2019.104049
Nguvo KJ, Gao X (2019) Weapons hidden underneath: bio-control agents and their potentials to activate plant induced systemic resistance in controlling crop Fusarium diseases. J Plant Dis Prot 126:177–190. https://doi.org/10.1007/s41348-019-00222-y
Nouri E, Breuillin-Sessoms F, Feller U, Reinhardt D (2015) Correction: phosphorus and nitrogen regulate arbuscular mycorrhizal symbiosis in Petunia hybrida. PLoS One 10:e90841. https://doi.org/10.1371/journal.pone.0127472
Nuccio EE, Hodge A, Pett-Ridge J et al (2013) An arbuscular mycorrhizal fungus significantly modifies the soil bacterial community and nitrogen cycling during litter decomposition. Environ Microbiol 15:1870–1881. https://doi.org/10.1111/1462-2920.12081
Nunez M, Mazzafera P, Mazorra LM et al (2003) Influence of a brassinosteroid analogue on antioxidant enzymes in rice grown in culture medium with NaCl. Biol Plant 47:67–70
Oldroyd GED (2013) Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. Nat Rev Microbiol 11:252–263
Ondrasek G, Rathod S, Manohara KK et al (2022) Salt stress in plants and mitigation approaches. Plants (Basel, Switzerland) 11. https://doi.org/10.3390/plants11060717
Ouziad F, Hildebrandt U, Schmelzer E, Bothe H (2005) Differential gene expressions in arbuscular mycorrhizal-colonized tomato grown under heavy metal stress. J Plant Physiol 162:634–649
Pavithra D, Yapa N (2018) Arbuscular mycorrhizal fungi inoculation enhances drought stress tolerance of plants. Groundw Sustain Dev 7:490–494
Pepe A, Giovannetti M, Sbrana C (2018) Lifespan and functionality of mycorrhizal fungal mycelium are uncoupled from host plant lifespan. Sci Rep 8:10235. https://doi.org/10.1038/s41598-018-28354-5
Pérez-Tienda J, Testillano PS, Balestrini R et al (2011) GintAMT2, a new member of the ammonium transporter family in the arbuscular mycorrhizal fungus Glomus intraradices. Fungal Genet Biol 48:1044–1055. https://doi.org/10.1016/j.fgb.2011.08.003
Poltronieri P, Brutus A, Reca IB et al (2019) Engineering plant leucine rich repeat-receptors for enhanced pattern-triggered immunity (PTI) and effector-triggered immunity (ETI). In: Applied plant biotechnology for improving resistance to biotic stress, pp 1–31
Pons S, Fournier S, Chervin C et al (2020) Phytohormone production by the arbuscular mycorrhizal fungus Rhizophagus irregularis. PLoS One 15:e0240886. https://doi.org/10.1371/journal.pone.0240886

Pozo De La Hoz J, Rivero J, Azcón-Aguilar C et al (2021) Mycorrhiza-induced resistance against foliar pathogens is uncoupled of nutritional effects under different lightintensities. J Fungi 7. https://doi.org/10.3390/jof7060402

Priyadharsini P, Muthukumar T (2016) Interactions between arbuscular mycorrhizal fungi and potassium-solubilizing microorganisms on agricultural productivity. In: Meena VS, Maurya BR, Verma JP, Meena RS (eds) Potassium solubilizing microorganisms for sustainable agriculture. Springer India, New Delhi, pp 111–125

Püschel D, Janoušková M, Hujslová M et al (2016) Plant–fungus competition for nitrogen erases mycorrhizal growth benefits of Andropogon gerardii under limited nitrogen supply. Ecol Evol 6:4332–4346. https://doi.org/10.1002/ece3.2207

Püschel D, Bitterlich M, Rydlová J, Jansa J (2020) Facilitation of plant water uptake by an arbuscular mycorrhizal fungus: a Gordian knot of roots and hyphae. Mycorrhiza 30:299–313. https://doi.org/10.1007/s00572-020-00949-9

Quiroga G, Erice G, Aroca R et al (2017) Enhanced drought stress tolerance by the arbuscular mycorrhizal symbiosis in a drought-sensitive maize cultivar is related to a broader and differential regulation of host plant aquaporins than in a drought-tolerant cultivar. Front Plant Sci 8:1056

Rai MK, Kalia RK, Singh R et al (2011) Developing stress tolerant plants through in vitro selection – an overview of the recent progress. Environ Exp Bot 71:89–98

Raja B-L, Soufian L, Salma T et al (2022) Use of biostimulants to improve salinity tolerance in cereals BT. In: Abdel Latef AAH (ed) Sustainable remedies for abiotic stress in cereals. Springer Nature Singapore, Singapore, pp 471–517

Ramos AC, Façanha AR, Palma LM et al (2011) An outlook on ion signaling and ionome of mycorrhizal symbiosis. Braz J Plant Physiol 23:79–89

Rashad Y, Aseel D, Hammad S, Elkelish A (2020a) Rhizophagus irregularis and Rhizoctonia solani differentially elicit systemic transcriptional expression of polyphenol biosynthetic pathways genes in sunflower. Biomol 10(3): 379.. https://doi.org/10.3390/biom10030379

Rashad YM, Abbas MA, Soliman HM et al (2020b) Synergy between endophytic Bacillus amyloliquefaciens GGA and arbuscular mycorrhizal fungi induces plant defense responses against white rot of garlic and improves host plant growth. Phytopathol Mediterr 59:169–186. https://doi.org/10.14601/Phyto-11019

Rashad YM, El-Sharkawy HHA, Elazab NT (2022) Ascophyllum nodosum extract and mycorrhizal colonization synergistically trigger immune responses in pea plants against rhizoctonia root rot, and enhance plant growth and productivity. J Fungi 8(3):268. https://doi.org/10.3390/jof8030268

Rasmussen AL, Busby RR, Hoeksema JD (2017) Host preference of ectomycorrhizal fungi in mixed pine–oak woodlands. Can J For Res 48:153–159. https://doi.org/10.1139/cjfr-2017-0227

Raven JA, Edwards D (2001) Roots: evolutionary origins and biogeochemical significance. J Exp Bot 52:381–401. https://doi.org/10.1093/jexbot/52.suppl_1.381

Reichert T, Rammig A, Fuchslueger L et al (2022) Plant phosphorus-use and -acquisition strategies in Amazonia. New Phytol 234:1126–1143. https://doi.org/10.1111/nph.17985

Riaz M, Kamran M, Fang Y et al (2021) Arbuscular mycorrhizal fungi-induced mitigation of heavy metal phytotoxicity in metal contaminated soils: a critical review. J Hazard Mater 402:123919. https://doi.org/10.1016/j.jhazmat.2020.123919

Richardson AE, Lynch JP, Ryan PR et al (2011) Plant and microbial strategies to improve the phosphorus efficiency of agriculture. Plant Soil 349:121–156. https://doi.org/10.1007/s11104-011-0950-4

Rosier A, Medeiros FHV, Bais HP (2018) Defining plant growth promoting rhizobacteria molecular and biochemical networks in beneficial plant-microbe interactions. Plant Soil 428:35–55. https://doi.org/10.1007/s11104-018-3679-5

Rowell DL (2001) Solute movement in the rhizosphere. Eur J Soil Sci 52:521–522. https://doi.org/10.1046/j.1365-2389.2001.00418-2.x

Santander C, Aroca R, Ruiz-Lozano JM, et al (2017) Arbuscular mycorrhiza effects on plant performance under osmotic stress. Mycorrhiza 27:639–657. https://doi.org/10.1007/s00572-017-0784-x

Santander C, Sanhueza M, Olave J et al (2019) Arbuscular mycorrhizal colonization promotes the tolerance to salt stress in lettuce plants through an efficient modification of ionic balance. J Soil Sci Plant Nutr 19:321–331

Sato T, Hachiya S, Inamura N et al (2019) Secretion of acid phosphatase from extraradical hyphae of the arbuscular mycorrhizal fungus Rhizophagus clarus is regulated in response to phosphate availability. Mycorrhiza 29:599–605. https://doi.org/10.1007/s00572-019-00923-0

Selosse M-A, Richard F, He X, Simard SW (2006) Mycorrhizal networks: des liaisons dangereuses? Trends Ecol Evol 21:621–628

Sheng M, Tang M, Chen H et al (2008) Influence of arbuscular mycorrhizae on photosynthesis and water status of maize plants under salt stress. Mycorrhiza 18:287–296

Sheng M, Tang M, Zhang F, Huang Y (2011) Influence of arbuscular mycorrhiza on organic solutes in maize leaves under salt stress. Mycorrhiza 21:423–430

Simard S, Asay A, Beiler K et al (2015) Resource transfer between plants through ectomycorrhizal fungal networks BT. In: Horton TR (ed) Mycorrhizal networks. Springer Netherlands, Dordrecht, pp 133–176

Smethurst DGJ, Shcherbik N (2021) Interchangeable utilization of metals: new perspectives on the impacts of metal ions employed in ancient and extant biomolecules. J Biol Chem 297:101374. https://doi.org/10.1016/j.jbc.2021.101374

Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic, London

Smith SE, Read DJ (2010) Mycorrhizal symbiosis, 3rd edn. Academic, London

Smith SE, Smith FA (2011) Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. Annu Rev Plant Biol 62:227–250. https://doi.org/10.1146/annurev-arplant-042110-103846

Smith SE, Facelli E, Pope S, Smith FA (2010) Plant performance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas. Plant Soil 326:3–20. https://doi.org/10.1007/s11104-009-9981-5

Sommermann L, Geistlinger J, Wibberg D et al (2018) Fungal community profiles in agricultural soils of a long-term field trial under different tillage, fertilization and crop rotation conditions analyzed by high-throughput ITS-amplicon sequencing. PLoS One 13:e0195345

Song YY, Sen ZR, Xu JF et al (2010) Interplant communication of tomato plants through underground common mycorrhizal networks. PLoS One 5:e13324

Souza LA, López Andrade SA, Ribeiro Souza SC, Schiavinato MA (2013) Evaluation of mycorrhizal influence on the development and phytoremediation potential of Canavalia gladiata in Pb-contaminated soils. Int J Phytoremediation 15:465–476

Spatafora JW, Chang Y, Benny GL et al (2016) A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. Mycologia 108:1028–1046. https://doi.org/10.3852/16-042

Spence C, Bais H (2013) Probiotics for plants: rhizospheric microbiome and plant fitness. Mol Microb Ecol Rhizosph 2:713–721

Stahl PD, Christensen M (1991) Population variation in the mycorrhizal fungus Glomus mosseae: breadth of environmental tolerance. Mycol Res 95:300–307

Surendirakumar K, Pandey RR, Muthukumar T (2019) Influence of indigenous arbuscular mycorrhizal fungus and bacterial bioinoculants on growth and yield of Capsicum chinense cultivated in non-sterilized soil. J Agric Sci 157:31–44. https://doi.org/10.1017/S0021859619000261

Sýkorová Z, Ineichen K, Wiemken A, Redecker D (2007) The cultivation bias: different communities of arbuscular mycorrhizal fungi detected in roots from the field, from bait plants transplanted to the field, and from a greenhouse trap experiment. Mycorrhiza 18:1–14

Talaat NB, Shawky BT (2014) Protective effects of arbuscular mycorrhizal fungi on wheat (Triticum aestivum L.) plants exposed to salinity. Environ Exp Bot 98:20–31

Tecon R, Or D (2017) Biophysical processes supporting the diversity of microbial life in soil. FEMS Microbiol Rev 41:599–623. https://doi.org/10.1093/femsre/fux039
Tedersoo L, May TW, Smith ME (2010) Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza 20:217–263
Thangavel P, Anjum NA, Muthukumar T et al (2022) Arbuscular mycorrhizae: natural modulators of plant–nutrient relation and growth in stressful environments. Arch Microbiol 204:264. https://doi.org/10.1007/s00203-022-02882-1
Tian H, Gai JP, Zhang JL et al (2009) Arbuscular mycorrhizal fungi associated with wild forage plants in typical steppe of eastern Inner Mongolia. Eur J Soil Biol 45:321–327
Tomar NS, Agarwal RM (2013) Influence of treatment of Jatropha curcas L. leachates and potassium on growth and phytochemical constituents of wheat (Triticum aestivum L.). Am J Plant Sci 4(5):1134–1150. https://doi.org/10.4236/ajps.2013.4514
Torrecillas E, del Mar Alguacil M, Roldán A (2012) Differences in the AMF diversity in soil and roots between two annual and perennial gramineous plants co-occurring in a Mediterranean, semiarid degraded area. Plant Soil 354:97–106
Torrecillas E, del Mar Alguacil M, Roldán A et al (2014) Modularity reveals the tendency of arbuscular mycorrhizal fungi to interact differently with generalist and specialist plant species in gypsum soils. Appl Environ Microbiol 80:5457–5466
Valverde-Barrantes OJ, Smemo KA, Feinstein LM et al (2018) Patterns in spatial distribution and root trait syndromes for ecto and arbuscular mycorrhizal temperate trees in a mixed broadleaf forest. Oecologia 186:731–741. https://doi.org/10.1007/s00442-017-4044-8
Vangelisti A, Natali L, Bernardi R et al (2018) Transcriptome changes induced by arbuscular mycorrhizal fungi in sunflower (Helianthus annuus L.) roots. Sci Rep 8:4. https://doi.org/10.1038/s41598-017-18445-0
Veresoglou SD, Rillig MC (2012) Suppression of fungal and nematode plant pathogens through arbuscular mycorrhizal fungi. Biol Lett 8:214–217. https://doi.org/10.1098/rsbl.2011.0874
Wahab A, Abdi G, Saleem MH et al (2022) Plants' physio-biochemical and phyto-hormonal responses to alleviate the adverse effects of drought stress: a comprehensive review. Plants (Basel, Switzerland) 11. https://doi.org/10.3390/plants11131620
Walder F, Van Der Heijden MGA (2015) Regulation of resource exchange in the arbuscular mycorrhizal symbiosis. Nat Plant 1:1–7
Walder F, Niemann H, Natarajan M et al (2012) Mycorrhizal networks: common goods of plants shared under unequal terms of trade. Plant Physiol 159:789–797. https://doi.org/10.1104/pp.112.195727
Walder F, Brulé D, Koegel S et al (2015) Plant phosphorus acquisition in a common mycorrhizal network: regulation of phosphate transporter genes of the Pht1 family in sorghum and flax. New Phytol 205:1632–1645
Wang Y, Huang J, Gao Y (2012) Arbuscular mycorrhizal colonization alters subcellular distribution and chemical forms of cadmium in Medicago sativa L. and resists cadmium toxicity. PLoS One 7:e48669
Wang Y, Wang M, Li Y et al (2018) Effects of arbuscular mycorrhizal fungi on growth and nitrogen uptake of Chrysanthemum morifolium under salt stress. PLoS One 13:e0196408
Weremijewicz J, Sternberg L da SLO, Janos DP (2016) Common mycorrhizal networks amplify competition by preferential mineral nutrient allocation to large host plants. New Phytol 212:461–471
Weremijewicz J, da Silveira Lobo O, Janos DP (2018) Arbuscular common mycorrhizal networks mediate intra-and interspecific interactions of two prairie grasses. Mycorrhiza 28:71–83
Wu H-H, Zou Y-N, Rahman MM et al (2017) Mycorrhizas alter sucrose and proline metabolism in trifoliate orange exposed to drought stress. Sci Rep 7:1–10
Xie W, Hao Z, Zhou X et al (2018) Arbuscular mycorrhiza facilitates the accumulation of glycyrrhizin and liquiritin in Glycyrrhiza uralensis under drought stress. Mycorrhiza 28:285–300
Xu L, Li T, Wu Z et al (2018) Arbuscular mycorrhiza enhances drought tolerance of tomato plants by regulating the 14-3-3 genes in the ABA signaling pathway. Appl Soil Ecol 125:213–221

Yan Q, Li X, Xiao X et al (2022) Arbuscular mycorrhizal fungi improve the growth and drought tolerance of Cinnamomum migao by enhancing physio-biochemical responses. Ecol Evol 12:e9091. https://doi.org/10.1002/ece3.9091

Yang Y, Han C, Liu Q, Lin B, Wang JW (2008) Effect of drought and low light on growth and enzymatic antioxidant system of Picea asperata seedlings. Acta Physiol Plant 30:433–440

Yooyongwech S, Samphumphuang T, Tisarum R et al (2016) Arbuscular mycorrhizal fungi (AMF) improved water deficit tolerance in two different sweet potato genotypes involves osmotic adjustments via soluble sugar and free proline. Sci Hortic (Amsterdam) 198:107–117

Yousaf B, Liu G, Wang R et al (2016) Bioavailability evaluation, uptake of heavy metals and potential health risks via dietary exposure in urban-industrial areas. Environ Sci Pollut Res 23:22443–22453

Yu L, Zhang H, Zhang W et al (2022) Cooperation between arbuscular mycorrhizal fungi and plant growth-promoting bacteria and their effects on plant growth and soil quality. PeerJ 10:e13080. https://doi.org/10.7717/peerj.13080

Zare-Maivan H, Khanpour-Ardestani N, Ghanati F (2017) Influence of mycorrhizal fungi on growth, chlorophyll content, and potassium and magnesium uptake in maize. J Plant Nutr 40:2026–2032. https://doi.org/10.1080/01904167.2017.1346119

Zhang B (2016) Small RNA and degradome deep sequencing reveals drought-and tissue-specific micrornas and their important roles in drought-sensitive and drought-tolerant tomato genotypes. Plant Biotechnol J 14(8):1727–1746

Zhang T, Yang X, Guo R, Guo J (2016) Response of AM fungi spore population to elevated temperature and nitrogen addition and their influence on the plant community composition and productivity. Sci Rep 6:24749. https://doi.org/10.1038/srep24749

Zhang X, Wang L, Ma F et al (2017) Effects of arbuscular mycorrhizal fungi inoculation on carbon and nitrogen distribution and grain yield and nutritional quality in rice (Oryza sativa L.). J Sci Food Agric 97:2919–2925

Zhang F, Zou Y-N, Wu Q-S (2018) Quantitative estimation of water uptake by mycorrhizal extraradical hyphae in citrus under drought stress. Sci Hortic (Amsterdam) 229:132–136

Zhao R, Guo W, Bi N et al (2015) Arbuscular mycorrhizal fungi affect the growth, nutrient uptake and water status of maize (Zea mays L.) grown in two types of coal mine spoils under drought stress. Appl Soil Ecol 88:41–49

Zou Y-N, Wang P, Liu C-Y et al (2017) Mycorrhizal trifoliate orange has greater root adaptation of morphology and phytohormones in response to drought stress. Sci Rep 7:1–10

Mycorrhizal Networks: A Secret Interplant Communication System

Mansoor Karimi-Jashni and Farzaneh Yazdanpanah

1 Introduction

In plant-fungal interactions, symbiosis has received special attention because of its role in driving microbial and plant communities. The word "symbiosis" was firstly applied by Frank at 1877 for coexistence of dissimilar organisms that help each other and do not imply parasitism (Sapp 2004). Over time, the term of "symbiosis" was more used by De Bary and others for beneficial associations and the term "parasitism" was used for pathogenesis of pathogens (Sapp 2010). Symbiosis was later defined for a broad range of association from parasitic relationship to commensalism and mutualism (Martin and Schwab 2012). Parasitism is a type of symbiotic relationship in which one species is parasite and benefits, while the other species is host and harm from the association. In Mutualism both species benefit from the symbiotic relationship. Commensalism is another type of symbiotic relationship in which one species benefits while the other species is not affected. Therefore, there is a continuum of associations from parasitic symbiosis of biotrophic fungi that cause rust and powdery mildews to mutualistic symbiosis of mycorrhizal fungi (Sapp 2010). Although, mycorrhizal fungi also represent a continuum of symbioses, the majority are beneficial. In this chapter, we focus on mycorrhiza with mutual interaction with their host partners. The word mycorrhiza is coming from the Greek terms "Myco" meaning the "fungus" and term "Rrhiza meaning the "root" describing the association of fungi with roots (Alizadeh 2011). Mycorrhizal fungi mainly

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create a wide network of hyphae in soil to offer an efficient horizontal transfer of compounds. This association includes interaction of plant-mycorrhiza as well as interplant communication via mycorrhizal fungal hyphae that link neighboring plants (Figueiredo et al. 2021). Even, the non-host plant species, which for any reason do not interact with these fungi, were found to connect with mycorrhizal fungi through mediated-host plants (Wang et al. 2022b). Mycorrhizal fungi together with plant roots and other partners create a brilliant underground community that benefit them from their cooperation.

2 Mycorrhiza in Rhizosphere

Rhizosphere is the zone of interaction between root and soil where root exudates effect the surrounding soil typically from millimeters to centimeter (Lettice 2018). Rhizosphere is a dynamic microenvironment zone containing plant roots, surrounding microorganisms, and soil components. Rhizosphere is an ecosystem crowded with combination of flora and fauna of beneficial microbes as well as pathogens for the plants (Velmourougane et al. 2017). Among this microbiome complex, plants need to recognize their friend and foes and properly respond them. Beyond this, plants need to interact with proper partners within beneficial microbes that can support them in unfavorable conditions. Beneficial microbes include some mycorrhizal fungi and nitrogen (N_2)-fixing bacteria that improve soil physicochemical properties and enhance plant development (Mendes et al. 2013). Mycorrhiza colonize roots of approximately 80% of plants (Brundrett 2009). During the growth of root, the distal elongation zone of root release exudates that attract mycorrhizal fungi of soil. These microorganisms colonize the root surface just behind the meristematic tissue and begin the mutualistic association. Fungal spores or residues released from previously colonized neighboring plants initiate colonization of root of the same or different plant species (Marschner 2012). Mycorrhizae increase the accessibility of plant roots to inaccessible soil spaces (Becquer et al. 2019; Hodge et al. 2010; Wipf et al. 2019). Majority of mycorrhizae colonizes and with their mycelium interconnect many plant species known as wood wide web (WWW) (Castro-Delgado 2020). WWW influences the whole life of connected plants as well as the composition of microbial community at the surroundings.

3 Taxonomy of Mycorrhizal Fungi

Mycorrhizal fungi based on their morphology and physiology, are classified into two main group of ectomycorrhiza and endomycorrhiza. Ectomycorrhizal fungi (EM) colonize the intercellular spaces of the root cells and form a network of hyphae that called as “hartig net”. The outer layer of EM includes external hyphal elements

that shape "mantle" to cover the plant root and extracardial appendages to connect with soil. The inner layer includes the hartig net, which mainly develop around the epidermal cell of host roots and do not often reach to the cortex (Anderson and Cairney 2007). EM often associate with roots of woody plants and contribute to produce humus in the forest. More than 2000 species of EM fungi have been identified worldwide, where the majority belong to fungal species Basidiomycotina, a few species belong to the Ascomycotina and Endogone genus in the Zygomycotina (Rinaldi et al. 2008). Various plant members belong to gymnosperms and angiosperms host these EM fungi. Species, such as Populus, Fagus, Eucalyptus, Betula, Shorea; respectively, from Pinaceae, Fagaceae, Betulaceae, and Diperocarpaceae are the main EM-associated plants in the forest ecosystems (Reddy and Saravanan 2013). Some EM mycorrhizal fungi are more specialized and penetrate more into the plant root reaching to intercellular space of four cells of cortex. These group was called ectoendomycorrhiza including members of the Ericales from ascomycotina that mainly colonizes conifer plants (Čatská 1997).

The other type of mycorrhiza includes Endomycorrhizal fungi. Endomycorrhiza include ericoid mycorrhizas, orchid mycorrhizas and the arbuscular mycorrhizae (AMs) (Brundrett 2009). In nature, orchid plants require the association with fungi for their growth and sometimes are very dependent to them that carry fungus in their seeds for early stages of their development. Orchid mycorrhizas produce highly coiled arbuscules called "peletons" in the cortical cells of host cell. These structures are the source of carbohydrate and nutrient supplies cellulose and pectin within the host cell and are released after the fungal death (Favre-Godal et al. 2020; Rasmussen and Rasmussen 2009). The other group of Endomycorrhizal fungi are Ericoid mycorrhiza that evolutionary were evolved with Ericaceae plants and have narrow to broad host range within this family. Based on the molecular studies, Ericoid mycorrhiza were diversified from saprobes, and apparently also from some lineages of ecto- and endomycota. Ericoids produce distinctive hyphal coils within root cells of Ericaceae (Vohník 2020) (Fig. 1).

AM fungi belong to phylum Glomeromycota, previously known as vascular arbuscular mycorrhizas (VAMs), and are the most common mycorrhizal fungi associated with plants (Kehri et al. 2018; Krüger et al. 2012; Schüßler and Walker 2011). Phylogenetic studies based on the sequence of three markers including small subunit rRNA (SSU) gene, large subunit (LSU) rRNA gene and the complete internal transcribed spacer (ITS) region of ribosome-encoding operon (rDNA) demonstrate a complex of AM communities consisting of various glomeromycotan lineages (Kehri et al. 2018; Kolaříková et al. 2021). AM fungi interact with wide range of angiosperms, gymnosperms, pteridophytes, and bryophytes (Hata et al. 2010). In their associations, plant partners provide carbon for arbuscular mycorrhiza and in turn, AMs mobilize N, S, and P and other mineral nutrients for plant. AMs are the most common mycorrhiza and more predominant in warm climates (Krüger et al. 2012). Mycorrhiza also participate in a number of beneficial interactions with various groups of soil microorganisms (Giovannini et al. 2020).

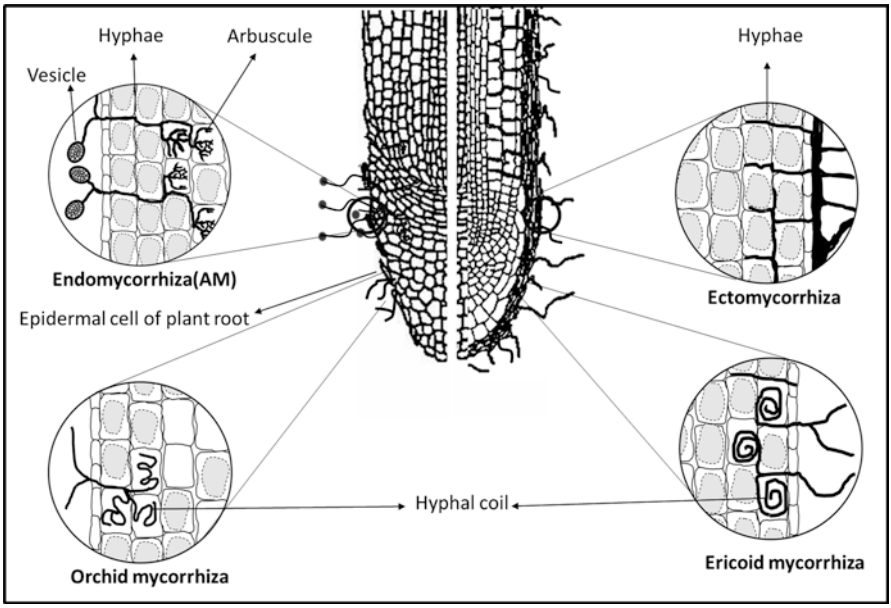

Fig. 1 Representative of the relationships between four common types of mycorrhiza and cells of plant root. Mycelium of endomycorrhiza penetrate into plant root and develop mycelium between cells of cortex and form arbuscules inside close to cell membranes for exchange of various compounds. Endomycorrhiza also produce vesicles containing fungal spores outside the root. Orchid and ericoid mycorrhiza also produce morphologically different hyphal coil in the root cell. Ectomycorrhiza produce hyphae between root cells below epidermal layer and do not penetrate into cells. (Figure is designed by author based on the references discussed in the chapter)

4 Plant-Mycorrhizal Association

Ectomycorrhizal and endomycorrhizal fungi are involved in building of plant-mycorrhiza network and together with other biological networks can shape the underground ecosystem (Oelmüller 2019). This connection facilitates the transfer of water, nutrients, defense signals or allelochemicals and leads to plenty changes in plant physiology and reprogramming of gene expressions and defense responses (Gorzelak et al. 2015). Apart from their own benefits, plant-mycorrhiza interaction facilitates the transfer of compounds from one plant to another via hyphal networks. Taking the temporal and environmental influences to account, EM fungi provide more protection against pathogens (Castro-Delgado 2020). Due to the development of structures outside the plant roots, EM to some extents are more efficient in the transfer of compounds and signals for plant development and the relationship between fungi and plants (Bennett et al. 2017).

Endomycorrhizal fungi are more widespread, however are restricted to the roots and do not colonize the aerial parts of plants, probably due to the presence of inhibitory barriers (Wang et al. 2018). These fungi penetrate the cell wall of roots and

colonize the inside of the cells to form branched intracellular structures called "arbuscules". To develop a successful interaction both fungus and plant secretes various molecules. Some of these molecules stimulate the growth of root system (Oldroyd 2013; Oldroyd and Downie 2008), while other molecules stimulate the fungal metabolism leading to development of arbuscules (Pozo et al. 2015). Arbuscules of AMs develop inside the root cells of host and actually produce a site to exchange various signals and nutrients with the symbiotic partners. At the later stages, fungus decompose arbuscules as the source of nutrients in the benefit of plant. AM fungi also develop an outer layer that includes the runner or extraradicular hyphae that increase the root surface and grow into the soil to absorb more water and nutrients (Barbosa et al. 2019). The interaction of extraradical mycelium that interconnect two neighboring during *in vitro* growth demonstrates the impact of host demand on nutrient transfer strategy of fungus (van't Padje et al. 2021). It seems Endomycorrhiza follow mainly the biological market theory as the bidirectional transfer of resources between partners show the rewards for the best rate of exchange (Kiers et al. 2011).

The interaction of plant and mycorrhiza has been evolved during evolution (Wang and Qiu 2006). It is a great question that how plant reach to the point of a stable relation with one or a few specific fungal species, despite the diversity of microbes with different capacity to offer benefits as well as the fluctuation in the availability of resources. For both plant and mycorrhizal fungi, it is more reliable to trade with multiple partners as a complex network (Heaton et al. 2012; Oelmüller 2019). It means that in the complex network multiple fungal species colonize an individual plant and an individual fungus interacts with multiple plant hosts and species, simultaneously (Wipf et al. 2019). Studies showed that symbiont actively colonize and share common mycorrhizal networks (CMNs) with various host plants with high and low carbon (C) source strength. Although mycorrhizal fungi discriminate the quality of host plants, they simultaneously provide multiple host plants with nutrients with phosphate and nitrogen to all plants not on an all-or-none basis (Fellbaum et al. 2014). It is expected that symbionts share CMN and preferentially allocated more nutrients to high-quality host plants, however the quality of host seem does not affect the quality of root colonization.

5 How Plants Recognize the Mycorrhizal Fungi as Friends

Plants roots live in close contact with large variety of microorganisms. These microorganisms include beneficial microbes as friends and parasitic pathogens foes. Under nutrient limitations, plants require to build the symbiosis interaction with beneficial microbes. The main question is that how plants discriminate beneficials from pathogens to enter into symbiosis (Fig. 2). Much studies discovered the involvement of molecules and mechanisms that enable plants to permit or ban these interactions (Zamioudis and Pieterse 2012). These mechanisms can be discussed in three levels: the first mechanism is called "METABOLIC GATING", where plants

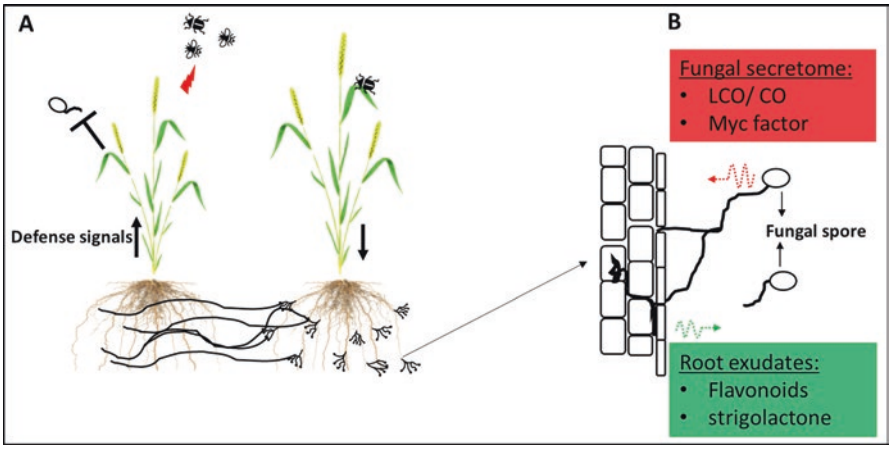

Fig. 2 Representation of signal transfer in plant–plant communication and molecules involved in connection of plant-mycorrhiza connection. (**a**) Transfer of defense signals from plant treated with pathogen/pest to the neighboring plant through common mycorrhizal network. Perception of signals from CMN induces receiver plant to produce defense related compounds against invading pest/pathogens. (**b**) Root exudates include strigolactones and flavonoids that trigger germination of fungal spores and branching of hyphae. Lipochito-oligosaccharides (LCO), Chito-oligosaccharides (CO) and other Myc factors promote colonization of root and development of arbuscules. (Figure is designed by author based on the references discussed in the chapter)

secrete molecules that select or restrict potential group of beneficials or pathogens. One type of these molecules are nutrients. Plant secretes a type of nutrient compounds that mainly beneficial microbes prefer to use. The second type are antimicrobial compounds that inhibit or expose toxicity to pathogens but not to beneficials. The third type include molecules present in root exudate that attract specific microbes. These molecules are also called as "branching factor" as they effect on spore germination and branching of hyphae when fungus reach to plant roots (Tamasloukht et al. 2003). One of the most documented molecules is strigolactone, a phytohormone that induce the mitosis and respiration of fungi (Rozpądek et al. 2018). Even after penetration into plant roots, Strigolactone stimulates the metabolism of fungal hyphae leading to development of arbuscules (Pozo et al. 2015). Other molecules like plant cutin monomers, which are normally present in aerial tissues, stimulate the mycorrhizal symbiosis in plant root (Murray et al. 2013). The second mechanism is called "Dual receptor recognition". Recognition of mycorrhiza follow similar principle explained for fungal pathogens (Jones and Dangl 2006; Kanyuka and Rudd 2019). Molecules called Microbe associated molecular patterns (MAMPs) like chitin is a common between these two types of microorganisms and its recognition by plant receptors can only inform that the invader is a fungus. However, beneficial mycorrhiza secrete additional molecules including lipochitooligosaccharides (LCOs) known as "Myc-factors" that the dual perception of these molecules triggers the initiation of symbiosis (Schmitz and Harrison 2014). There are two types of molecules that their recognition promotes signalling

pathways in plant cells leading to arbuscular mycorrhizal symbiosis. Signal molecules chitooligosaccharides (COs) and lipochitooligosaccharides (Myc-LCOs) in soil (Gobbato 2015) were shown to be involved in plant-mycorrhizal connection.

Plants LysM-receptors that are present in the membrane of root cells, recognize and trigger the symbiotic signalling pathway (CSSP) through calmodulin-dependent protein kinase (CCaMK), CYCLOPS and GRAS transcription factors (Camps et al. 2015). After recognition at molecular level, fungal hyphae penetrate the cortical cells of roots, and forms the arbuscules (Schmitz and Harrison 2014). The third mechanism is the integration of environmental signals with immune homeostasis to fine-tune decision making in symbiosis. For instance, in high phosphorous level plant do not produce strigolactone and as its consequence restrict the symbiosis, while secretion of strigolactone occurs mainly in P deficiency (Czarnecki et al. 2013). The integration of intrinsic and environmental signals affects the threshold immunity for or against symbiosis that eventually shape the microbiome community.

6 Role of Mycorrhiza in Exchange of Info-Chemical Molecules

The role of volatile molecules in the plant-plant communication is well documented (Arimura et al. 2000; Brilli et al. 2019; Naznin et al. 2014). Over 80% of plants are connected through underground systems with CMNs of mycorrhiza. CMNs were evidenced for their involvement in the transfer of info-chemicals from infected (donor) plants to healthy (receiver) plants. It is shown that pathogenesis related proteins like chitinase, b-1,3-glucanase, peroxidase, polyphenol oxidase, phenylalanine ammonia-lyase and lipoxygenase were induced in the healthy tomato interconnected with infected tomato inoculated with *Alternaria solani* (Song et al. 2010). With the same condition, healthy neighboring 'receiver' common bean (*Vicia fabae*) plants become less attractive to the aphid *Acyrthosiphon pisum* when interconnected with plants infested with aphids (Babikova et al. 2013). Comparing to airborne communication, communication through CMN is more reliable and stable and is away from environmental effects. Colonization of *Nicotiana attenuate* plants having roots interconnected with CMNs showed that fungal hyphae transmit herbivory-elicited defense signaling molecules among connected plants (Song et al. 2019). Methyl-salicylate and JA are two info-chemicals that are suggested to transfer via a CMN of the arbuscular mycorrhizal to activate defense responses in healthy neighboring receiver plants when they are connected to the donor plant fungus *Glomus mosseae* (Gorzelak et al. 2015; Song et al. 2019). These molecules are suggested to induce pathogenesis-related proteins peroxidase, polyphenol oxidase, chitinase, b-1,3-glucanase, phenylalanine ammonia-lyase, and lipoxygenase in healthy neighboring receiver plants (Gorzelak et al. 2015; Song et al. 2019). The transfer of info-chemical molecules was observed or experimentally documented in different ways including fungal cytoplasm, fungal apoplast, transport along with a biofilm or

through the fungal cell wall, and plasma membrane (Oelmüller 2019). Apparently, transfer of nutrients occurs through symplast from the cytoplasm of a plant cell via the symplast of the fungal mycelia to the cytoplasm of a connected plant cell. The info-chemicals and some nutrients released by plant cell transfer through apoplast of fungal hyphae. However transfer of hormone through symplast is not documented yet and it is possible that the message is converted into other signals that can travel through CMNs and induce defense response in the neighboring plant (Oelmüller 2019) (Fig. 2).

7 Role of Mycorrhiza in Exchange of Allelo-Chemical and Toxic Molecules

The role of CMNs by transferring allelochemicals between plants was also proved experimentally. It is shown that CMNs can increase transfer rates of the herbicide imazamox from treated to mock *Z. mays* grown in screen-divided pots with shared soil inoculated with a mixture of convenient arbuscular mycorrhizal fungi *Glomus mosseae* or *Funelliformis mossae*, without root contact (Achatz et al. 2014). Another group of allo-chemicals are toxic ions and radionuclides that accumulate in soil and get absorbed by plants and remain in food chain. Radiocesium is one of the major contaminant and its direct transfer to via the cytoplasm/protoplasm of the AM fungi between donor and receiver *Medicago truncatula* plants is demonstrated (Gyuricza et al. 2010). The established CMNs are able to transfer heavy metal cadmium (Cd) between plants of different species, maize (*Zea mays* L.) to soybean (*Glycine max* (Linn.) Merr.). Soil-borne AM are able to establish mutualistic symbiosis with many plants and this system can serve to collect toxic heavy metals from main food crops to heavy metal hyperaccumulators. It can also significantly improve plant performance and nutrient acquisition and increase resistance to Cd stress (Ding et al. 2022).

8 Resource Exchange in the Plant-Mycorrhizal Association

In the symbiotic relationship, the cost for developing root to shoot ratio often is reduced for plant. In this relation, fungus assist plant to absorb nutrients from soil, therefore plant does not expense carbon to develop its roots and in turn fungus receive its carbon from plant side (Corrêa et al. 2012). Apparently, under availability of nutrients, plant distribute carbon resources to associated fungi in non-directional way. However, under limitation of nutrients the cost and benefits of symbiosis differs and this condition influences on the normal relationship. For example, in the soils limited in nitrogen, interaction of plant-mycorrhiza always is not mutual and fungus suppresses the plant growth (Johnson et al. 2010). Influence of environmental factors strict the plants to develop an efficient and stable

symbiosis with a proper partner. In addition to plant-mycorrhiza connection, Mycorrhizal fungi develop CMNs that interconnect roots of neighboring plant species (Figueiredo et al. 2021; Walder et al. 2012; Weremijewicz et al. 2016). The presence of CMN influences plant community dynamics, through transfer of nutrients phosphorus, nitrogen, carbon, and other micronutrients (Philip 2006).

Phosphorus is the major macronutrient in soil, which predominantly is present as phosphate ion (Pi). Pi is crucial for plant growth and plant absorb it root from rhizosphere (Nussaume et al. 2011). However, under Pi limitation, mycorrhizal fungi increase root surface (100 times than root area) to transfer it from long distance of rhizosphere (Nussaume et al. 2011). The extraradical hyphae of AM release phosphatase enzymes probably to solubilize organic P of soil and transfer it (as poly P) to plant partner (Ezawa and Saito 2018). EM fungi also obtain phosphorus from the hyphae of a saprotrophic fungus and pass it to the associated plant (Cairney 2011).

Nitrogen is another macronutrient that is required for plant growth. Nitrogen is present in amino acids, chlorophyll and plant protoplasm. The most abundant molecule (about 78%) in air is nitrogen (N_2), however plants are not able to use them directly. Some free-living bacteria and algae are able to transform Nitrogen molecules (N_2) to ammonia (NH_3) and further into nitrites, nitrates, and organic acids and fix them in the soil and (Dos Santos et al. 2012). In Rhizobium-legume interaction, plant secretes metabolites flavonoids and iso-flavonoids that start a signaling event in the root epidermis. These signals induce Nod genes of symbiotic bacteria and at the presence of plant hormones form nodules, where fixation of nitrogen occurs (Oldroyd and Downie 2008). Non-N_2-fixing plants provide their nitrogen from fertilized soil and from nitrogen sources fixed by Leguminosae plants. It seems that transfer of nitrogen is greater among heterospecific plants growing adjacent to AM (Ingraffia et al. 2021). In systems with low nitrogen, plants compete for the small amounts N, but it is likely that competition between symbionts for N also occurs (Hodge et al. 2010; Hodge and Storer 2015). In this situation, it is not clear that symbiont is a mere extension of plant root or has competition with plant.

In turn to providing nutrients, plant support its symbionts with carbon (C) supply. During photosynthesis, plants use solar energy to produce starches and sugars from CO_2 and H_2O (Calvin 1974). These starches and sugars are the source of carbon. In the reverse direction, plant supply the symbiotic partner with these sources of carbon. AM take the amount for its need and through its extraradical hyphae transfer the rest to other microbes. AM and other microbes use these carbohydrates for their growth, development and reproduction (Finlay and Söderström 1992; Zhang et al. 2016). It is shown that for the AM, phosphate-solubilizing bacteria produce inorganic P from the organic phosphate of soil and in turn receive carbohydrates from plant through AM (Zhang et al. 2016).

To measure the mobility of nitrogen, phosphorus and carbon among interconnected plants, researchers apply isotopes for stable labeling of these elements and compare (He et al. 2009). Compared to non-radioisotope atoms, isotopes contain the same number of protons but different in the number of neutrons (Adelstein and Manning 1995). Stable radioisotope ^{15}N, ^{33}P supplied in soil and CO_2 containing ^{14}C for photosynthesis are common chemicals for isotope labelling studies. Researches

determined that AM actively mediate the nutrient uptake and transfer to plant and in reverse direction fungus acquire carbon products (Cruz-Paredes and Gavito 2020; Thirkell et al. 2019; Walder et al. 2012).

9 Models That Mycorrhiza Follow for Transfer of Nutrients Between Plants

To realize the dynamics and composition of the underground community, it is necessary to understand the behavior of plant communities and competition among the species involved in the CMN and as well as the forces driving these interactions (Simard et al. 2015). In contrast to the AM fungi, plant species are not obligately dependent to their partner; particularly, when nutrients are highly available. Moreover, some plants have no tendency to interact with symbionts. Studies show that plants transfer up to 20% of their photosynthetically fixed C to AM fungi. Evolutionary thinking, it is hard to explain how the mutual trade occurs specially when an individual plant is connected to many fungi and an individual fungus is connected to many plants. The next point is that how egotistic individuals that compete for more benefit do not ruin the many to many mutual interactions (Leigh 2010). The patterns for resource exchange are consistent with complex adaptive system models explained below.

In the source-sink model, the nutrient transfer occurs through CMNs from source that is abundant in nutrient to the sink where it is more necessary to use (Heaton et al. 2012). This theory is illustrated for C and N following a source-sink pattern that help survival and development of ecosystem. This pattern was found for transfer of these nutrients from trees having high photosynthesis rate to shaded trees or from defoliated and old trees with high nutrient sources to young seedling through connected ectomycorrhiza (Muneer et al. 2020; Teste et al. 2009). Common transfer occurs between older plants supporting young seedlings; however, there are also reports of reduced transfer of C within a CMN to sink (shaded, defoliated, seedling) plants, and even C transfer from sink (shaded) plants to source plants (Weremijewicz et al. 2016) (Fig. 3).

Another model that is observed between connected plants and mycorrhizal fungi is called the “Biological Market” theory. Based on this theory, both plant and fungi, adjust their resource allocation according to gains from the other sides (Fellbaum et al. 2014). This means the organism that contain a source of a nutrient like C, N or P allocates it in bidirectional way to the best rate it rewarded (Wang et al. 2016). This relation is evolutionary stable and plants cooperate with the best fungal partner that transfer more nutrient and fungus also provide the more nutrient to those roots providing more carbohydrates. It seems this relationship follows a reciprocal relation and a plant that needs more N or P should produce more C and provide it to its fungal partner (Kiers et al. 2011). In this theory the large flux of nutrient can be

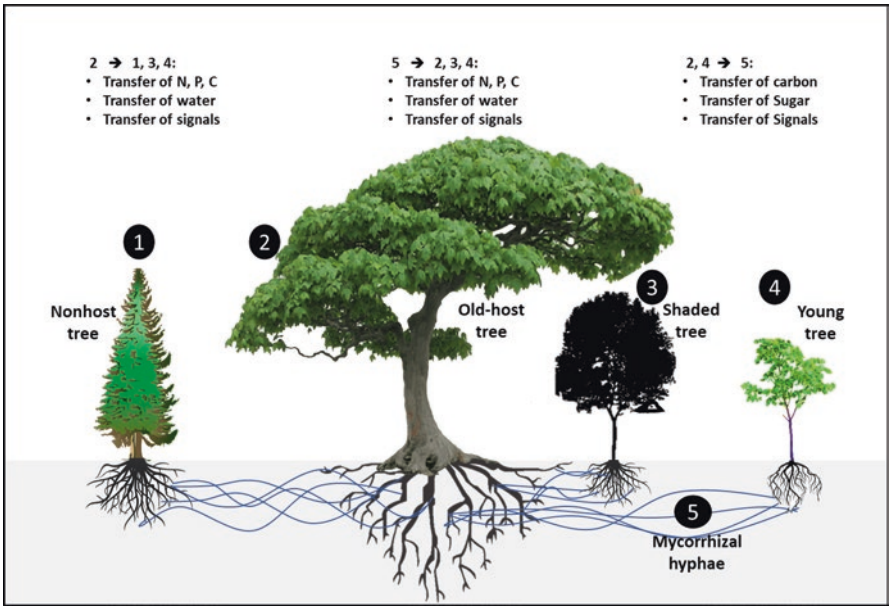

Fig. 3 Representative of the role of common mycorrhizal network (CMN) in the transfer of nutrients among trees; tree number 2 is an old and photosynthetic tree that can support nonhost (number 1), shaded (number 3) and young tree (number 4) with nutrients of nitrogen (N), Phosphorus (P), photosynthetically produced sugars/carbohydrates (C) and even water through fungal CMN. Plants 2 and 4 also can support mycorrhiza with nutrients as they have access to light for photosynthesis. (Figure is designed by author based on the information of references discussed in the chapter)

explained when a large tree obtains more N and P from fungal partner and in turn provide more C (Gorzelak et al. 2015).

In the mycorrhizal symbiosis, plant transfer the photosynthesized carbon to its fungal partner in a mutual interaction and in turn fungus facilitates the plant nutrition by uptake of mineral nutrients from the soil (Smith and Read 2010). In Mutualistic cooperation benefits often come at the cost paid for the interaction. There are over 500 non-photosynthetic plants called cheaters of which about half the total number are associated with AM fungi (Mycoheterotrophic) (Selosse and Cameron 2010). Cheaters established an adaptive strategy to subvert the biological market established between photosynthetic plants and mycorrhizal fungi and indirectly retrieve carbon by cheating of mycorrhizal symbiosis without paying the associated cost (Rasmussen and Rasmussen 2009). Factors such as autotrophic green host, interactions with reliance fungus, and soil nutrient availability can potentially contribute to the existence of mycoheterotrophic plants at a local scale (Merckx 2012). Although, cheaters have interaction with some specific mycorrhiza, it is considered as "functional constraints", forced through physiological or biochemical and regulation of interaction (Perez-Lamarque et al. 2020) than a species-specific interaction (Perez-Lamarque et al. 2020).

10 Impact of Mycorrhizas on Plant Immunity

Mycorrhizal fungi were found in symbiosis with various crops and trees in natural ecosystems. Mycorrhiza improve resistance of host plants in a plant genotype-specific manner against pathogens (Kumar and Verma 2018). There are several mechanisms that were proposed to enhance the resistance of host plants. First, mycorrhiza improve plant resistance by transferring more nutrients through their hyphae to plant roots. Second, mycorrhiza might also change the structure and the longevity of roots and by this it increases the plant ability to absorb more water and nutrients and enhances the photosynthesis. Third, mycorrhiza also colonizes niches in competition with pathogens that limits the progress of pathogens. Forth, mycorrhiza induces host defense mechanisms known as mycorrhiza-induced resistance (MIR). Pre-inoculation of tomato with AM fungus *Rhizophagus irregularis* reduced the disease caused by *Fusarium oxysporum* through jasmonate signaling pathway (Wang et al. 2022a). The role of mycorrhiza is highly documented in bioprotection of plants against fungi (Dey and Ghosh 2022; Goicoechea 2020; Hu et al. 2010; Shukla et al. 2015) and nematodes (Poveda et al. 2020; Schouteden et al. 2015), oomycetes (Gallou et al. 2011), Bacteria (Fujita et al. 2022) and viruses (Deja-Sikora et al. 2020). Mycorrhiza are not the only beneficial microbes in soil. Other soil microorganisms like growth promoting rhizobacteria also synergistically or alone affect the soil fertility through nutrient solubilization and enhance plant growth against biotic and abiotic stresses (Nanjundappa et al. 2019).

11 Application of Mycorrhizas in Agriculture, Horticulture and Forestry

Mycorrhizal symbiosis plays an important role in nature. The prevalence of their beneficial effects on plant can be used in agriculture (both agronomy and horticulture) or forestry systems (Smith and Read 2010). Worries about environment and growing demands for food are the main reasons to apply mycorrhiza in sustainable and organic agriculture. Mycorrhizal application has been successfully developed for both AM and EM fungi (Basiru et al. 2020). AM mainly were used for improvement of various agriculture and horticulture programs, and EM for forest production and replantation programs (Smith and Read 2010).

11.1 Arbuscular Mycorrhizas in Agriculture and Horticulture

There are several methods for formulation and application of AM as biological material. Different parts of fungus including resting spores, hyphae and root fragments colonized with desired AM are the source of fungal biomass. For formulation

of fungal biomass, carriers, surfactants and stabilizers are required to increase their efficiency on plant and durability in storage (Gianinazzi and Vosátka 2004). Arbuscular mycorrhiza can be formulated as capsules of fungal biomass (Plenchette and Strullu 2003). Application of AM requires adequate quality standards and ease of use for seed and seedlings inoculation (Gianinazzi and Vosátka 2004). Inoculation of seedlings is appropriate method for establishing selected fungi in roots at early stage before infection by soil-borne species (Smith and Read 2010). Many studies confirmed that crop productivity is improved by AM symbioses. Application of AM at the initial stage of plant development enhanced the AM symbiosis and improved the plant growth parameters both in the nursery and in the field (Wang et al. 2008). Inoculation of seedlings with mycorrhizal fungi significantly influenced the length of stems and roots in tomato (Jamiołkowska et al. 2019). In another study, the improved gaining of phosphate by mycorrhiza positively affected on tomato productivity (Subramanian et al. 2006). Furthermore, AM symbiosis enhanced the content of chlorophyll in maize leaves (Sheng et al. 2008; Zhu et al. 2012) and improved the photosynthesis parameters and drought tolerance in poplar (Liu et al. 2015). Comparison of the yield of mycorrhized tomato grown in artificial rockwool and natural soil, have determined that beneficial interaction of AM and tomato roots does not occur in artificial culture (Michałojć et al. 2015). The cost of application of AM products in large scales is much lower than using synthetic fertilizers in soils deficient in phosphorous (Igiehon and Babalola 2017).

11.2 Ectomycorrhizas and Forest Production

EM fungi play a critical role in carbon and N cycling, phosphorus uptake, and soil aggregation in many native ecosystems (Cairney 2011; Pandey et al. 2019; Rillig and Mummey 2006). The most important issues for application of mycorrhizas in agricultural environments are their effectiveness and persistence. In forestry ecosystems, this application might be less successful as natural selection over many generations has produced stable populations that limits the establishment of new species. Therefore, mycorrhizal associations should be considered as integral components of soil complexity in both agricultural and forestry ecosystems (Philippot et al. 2013).

Determining appropriate management strategies of mycorrhizal fungi and effective inoculation techniques should be established to maximize plants productivity (Smith and Read 2010). Ectomycorrhizas that were used in the nursery itself and after out-planting were significantly increased the timber (Mbora et al. 2008). Tree plants grown in ectotrophic forests had better growth in comparison with those in soils deficient in EM fungi. Application of EM fungi that physiologically and ecologically were corresponded to a specific planting area enhanced their crop performance as shown in Austria, Argentina and Australia (Marx et al. 1991). Inoculation with mycelium of EM at seedlings stage in nursery were found as the most effective types at the best growth stage (Sanchez-Zabala et al. 2013). Application of spores

also were used in different formulations such as inoculation of substrates with fungal spores or irrigation of substrates by suspension of spore before and after seed and seedling (Rincón et al. 2001). In tropical forests seedlings that are grown close to congeneric adult trees are colonized more rapidly and/or by a greater diversity of EM fungi (Jones et al. 2003). However, plants receive more benefits from ectomycorrhiza when are imposed by biotic and abiotic stress (Liu et al. 2017). This phenomenon is observed for drought and salt stresses as well (Chen et al. 2014).

12 Mycorrhiza Restore Human Activity and Climate Disturbance

Anthropic human activities directed to soil environment can negatively affect the abundance and richness of the mycorrhizal community in soil (Philippot et al. 2013; Pringle et al. 2009). Pesticides and agricultural fertilizers are two main sources that contaminate the soil and negatively affect the microbial community (Jamiołkowska et al. 2021). These pollutants also harm the human health through their toxicity and their contribution in physiological changes in plants (Saladin and Clément 2005). Mycorrhizae increase the absorption through fungal hyphae and plant roots and indirectly reduce the pollution of agrochemicals (Wang et al. 2020). Human activities and climate change also disturb soil structure leading to quick soil erosion. Fungal hyphae and AMs secrete protein glomalins that is known for its role in aggregating soil particles and improving the stability of soil structure (Muneer et al. 2020). Mycorrhizal fungi absorb heavy metals from the contaminated soils and store them in their vesicles. With this, metals are immobilized in the fungal and cannot inhibit nutrient uptake leading to enhancing tolerance to metals and crop quality of plants cells (Fester 2013; Wang et al. 2020). Although bioremediation seems very valuable, there are concerns for transfer of organic contaminant residues from the aboveground to belowground in plant roots (Wang et al. 2020). Molecules of glomalins and metallothionin also immobilize toxic metals that significantly reduces the toxicity of heavy metals (copper, cadmium, zinc) in the soil (Bano and Ashfaq 2013). The other point is that mycorrhiza reduces the mobility of P in repacked soil columns in favor of plant growth in low P soils and restrict its losses to streams and groundwater (Asghari et al. 2005).

13 Conclusion

In this chapter, we focused on the most relevant issues on the plant-mycorrhiza interaction. We know that beneficial microbes created an outstanding network underground that bring all individuals into community, directly or indirectly. This network transfers sympathy of all fortune and worries and share nutrients among the

community. Like that of human beings, there are collaborations and competitions among individuals described by several models of trades. In this community, individuals reduce the risk of life by connecting with many other collaborators. During the last two decades, much attention is paid to mycorrhizal fungi due to their relevance in sustainable agriculture. Due to manmade environmental situations, we need to listen and back to nature, where both endo- and ectomycorrhiza have been evolved with plants. These fungi have potential to be used in agriculture, horticulture and forestry. There are several concerns on the direction of studies on mycorrhiza that needs more attention. The first issue is that the majority of publications, reviews and studies repetitively describe these microbes, while scientists should grow-up this field experimentally. Second, with lots of variables affecting plant-mycorrhiza interactions, studies should fundamentally determine all parameters that can affect their interaction. Third, to replace biofertilizers of mycorrhiza with synthetic fertilizers, studies should discover effective species of fungus with clear effect on soil fertility and plant health. Forth, advanced technologies should support the outstanding ideas and cutting-edge studies to elucidate several dark points present during interactors in soil. It is not clear what is the effect of climate change, wealth or wanes of nutrients, presence of cheaters and pathogens on interaction of mycorrhiza-plant and at which condition this collaboration comes to competition?. Technologies like metagenomics, transcriptomics and proteomics can produce valuable data for laboratory experiments to benefit human from natural ecosystem.

References

Achatz M, Morris EK, Müller F, Hilker M, Rillig MC (2014) Soil hypha-mediated movement of allelochemicals: arbuscular mycorrhizae extend the bioactive zone of juglone. Funct Ecol 28:1020–1029

Adelstein SJ, Manning FJ (1995) Isotopes for medicine and the life sciences. National Academies Press, Washington, DC

Alizadeh O (2011) Mycorrhizal symbiosis. Adv Stud Biol 6:273–281

Anderson IC, Cairney JWG (2007) Ectomycorrhizal fungi: exploring the mycelial frontier. FEMS Microbiol Rev 31:388–406

Arimura G, Ozawa R, Shimoda T, Nishioka T, Boland W, Takabayashi J (2000) Herbivory-induced volatiles elicit defence genes in lima bean leaves. Nature 406:512–515

Asghari H, Marschner P, Smith S, Smith F (2005) Growth response of Atriplex nummularia to inoculation with arbuscular mycorrhizal fungi at different salinity levels. Plant Soil 273:245–256

Babikova Z, Gilbert L, Bruce TJA, Birkett M, Caulfield JC, Woodcock C, Pickett JA, Johnson D (2013) Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. Ecol Lett 16:835–843

Bano SA, Ashfaq D (2013) Role of mycorrhiza to reduce heavy metal stress. Nat Sci 5:16–20

Barbosa MV, Pedroso DF, Curi N, Carneiro MAC (2019) Do different arbuscular mycorrhizal fungi affect the formation and stability of soil aggregates? Ciênc Agrotecnol 43. https://doi.org/10.1590/1413-7054201943003519

Basiru S, Mwanza HP, Hijri M (2020) Analysis of arbuscular mycorrhizal fungal inoculant benchmarks. Microorganisms 9:81

Becquer A, Guerrero-Galán C, Eibensteiner JL, Houdinet G, Bücking H, Zimmermann SD, Garcia K (2019) The ectomycorrhizal contribution to tree nutrition. Adv Bot Res (Elsevier) 89:77–126
Bennett JA, Maherali H, Reinhart KO, Lekberg Y, Hart MM, Klironomos J (2017) Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. Science 355:181–184
Brilli F, Loreto F, Baccelli I (2019) Exploiting plant volatile organic compounds (VOCs) in agriculture to improve sustainable defense strategies and productivity of crops. Front Plant Sci 10:264
Brundrett MC (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320:37–77
Cairney JW (2011) Ectomycorrhizal fungi: the symbiotic route to the root for phosphorus in forest soils. Plant Soil 344:51–71
Calvin M (1974) Solar energy by photosynthesis. Science 184:375–381
Camps C, Jardinaud MF, Rengel D, Carrère S, Hervé C, Debellé F, Gamas P, Bensmihen S, Gough C (2015) Combined genetic and transcriptomic analysis reveals three major signalling pathways activated by Myc-LCOs in Medicago truncatula. New Phytol 208:224–240
Castro-Delgado AL (2020) Wood wide web: communication through the mycorrhizal network. Tecnología en Marcha 33:114–125
Čatská V (1997) Smith, S.E., Read, D.J.: Mycorrhizal symbiosis. Biol Plant 40:154–154
Chen S, Hawighorst P, Sun J, Polle A (2014) Salt tolerance in Populus: significance of stress signaling networks, mycorrhization, and soil amendments for cellular and whole-plant nutrition. Environ Exp Bot 107:113–124
Corrêa A, Gurevitch J, Martins-Loução MA, Cruz C (2012) C allocation to the fungus is not a cost to the plant in ectomycorrhizae. Oikos 121:449–463
Cruz-Paredes C, Gavito ME (2020) Isotope labeling to study phosphorus uptake in the arbuscular mycorrhizal symbiosis. Methods Mol Biol 2146:213–222
Czarnecki O, Yang J, Weston DJ, Tuskan GA, Chen J-G (2013) A dual role of strigolactones in phosphate acquisition and utilization in plants. Int J Mol Sci 14:7681–7701
Deja-Sikora E, Kowalczyk A, Trejgell A, Szmidt-Jaworska A, Baum C, Mercy L, Hrynkiewicz K (2020) Arbuscular mycorrhiza changes the impact of potato virus Y on growth and stress tolerance of Solanum tuberosum L. in vitro. Front Microbiol 10:2971
Dey M, Ghosh S (2022) Arbuscular mycorrhizae in plant immunity and crop pathogen control. Rhizosphere 22:100524
Ding C, Zhao Y, Zhang Q, Lin Y, Xue R, Chen C, Zeng R, Chen D, Song Y (2022) Cadmium transfer between maize and soybean plants via common mycorrhizal networks. Ecotoxicol Environ Saf 232:113273
Dos Santos PC, Fang Z, Mason SW, Setubal JC, Dixon R (2012) Distribution of nitrogen fixation and nitrogenase-like sequences amongst microbial genomes. BMC Genomics 13:162
Ezawa T, Saito K (2018) How do arbuscular mycorrhizal fungi handle phosphate? New insight into fine-tuning of phosphate metabolism. New Phytol 220:1116–1121
Favre-Godal Q, Gourguillon L, Lordel-Madeleine S, Gindro K, Choisy P (2020) Orchids and their mycorrhizal fungi: an insufficiently explored relationship. Mycorrhiza 30:5–22
Fellbaum CR, Mensah JA, Cloos AJ, Strahan GE, Pfeffer PE, Kiers ET, Bücking H (2014) Fungal nutrient allocation in common mycorrhizal networks is regulated by the carbon source strength of individual host plants. New Phytol 203:646–656
Fester T (2013) Arbuscular mycorrhizal fungi in a wetland constructed for benzene-, methyl tert-butyl ether-and ammonia-contaminated groundwater bioremediation. Microb Biotechnol 6:80–84
Figueiredo AF, Boy J, Guggenberger G (2021) Common mycorrhizae network: a review of the theories and mechanisms behind underground interactions. Front Fungal Biol 2:735299
Finlay R, Söderström B (1992) Mycorrhiza and carbon flow to the soil. In: Mycorrhizal functioning. Chapman & Hall, New York, pp 134–160

Fujita M, Kusajima M, Fukagawa M, Okumura Y, Nakajima M, Akiyama K, Asami T, Yoneyama K, Kato H, Nakashita H (2022) Response of tomatoes primed by mycorrhizal colonization to virulent and avirulent bacterial pathogens. Sci Rep 12:1–12

Gallou A, Lucero Mosquera HP, Cranenbrouck S, Suárez JP, Declerck S (2011) Mycorrhiza induced resistance in potato plantlets challenged by Phytophthora infestans. Physiol Mol Plant Pathol 76:20–26

Gianinazzi S, Vosátka M (2004) Inoculum of arbuscular mycorrhizal fungi for production systems: science meets business. Can J Bot 82:1264–1271

Giovannini L, Palla M, Agnolucci M, Avio L, Sbrana C, Turrini A, Giovannetti M (2020) Arbuscular mycorrhizal fungi and associated microbiota as plant biostimulants: research strategies for the selection of the best performing Inocula. Agronomy 10:106

Gobbato E (2015) Recent developments in arbuscular mycorrhizal signaling. Curr Opin Plant Biol 26:1–7

Goicoechea N (2020) Mycorrhizal fungi as bioprotectors of crops against verticillium wilt—A hypothetical scenario under changing environmental conditions. Plan Theory 9:1468

Gorzelak MA, Asay AK, Pickles BJ, Simard SW (2015) Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. AoB Plants 7:plv050

Gyuricza V, Thiry Y, Wannijn J, Declerck S, Dupré de Boulois H (2010) Radiocesium transfer between Medicago truncatula plants via a common mycorrhizal network. Environ Microbiol 12:2180–2189

Hata S, Kobae Y, Banba M (2010) Interactions between plants and arbuscular mycorrhizal fungi. Int Rev Cell Mol Biol 281:1–48

He X, Xu M, Qiu GY, Zhou J (2009) Use of 15N stable isotope to quantify nitrogen transfer between mycorrhizal plants. J Plant Ecol 2:107–118

Heaton L, Obara B, Grau V, Jones N, Nakagaki T, Boddy L, Fricker MD (2012) Analysis of fungal networks. Fungal Biol Rev 26:12–29

Hodge A, Storer K (2015) Arbuscular mycorrhiza and nitrogen: implications for individual plants through to ecosystems. Plant Soil 386:1–19

Hodge A, Helgason T, Fitter A (2010) Nutritional ecology of arbuscular mycorrhizal fungi. Fungal Ecol 3:267–273

Hu J-L, Lin X-G, Wang J-H, Shen W-S, Wu S, Peng S-P, Mao T-T (2010) Arbuscular mycorrhizal fungal inoculation enhances suppression of cucumber fusarium wilt in greenhouse soils. Pedosphere 20:586–593

Igiehon NO, Babalola OO (2017) Biofertilizers and sustainable agriculture: exploring arbuscular mycorrhizal fungi. Appl Microbiol Biotechnol 101:4871–4881

Ingraffia R, Giambalvo D, Frenda AS, Roma E, Ruisi P, Amato G (2021) Mycorrhizae differentially influence the transfer of nitrogen among associated plants and their competitive relationships. Appl Soil Ecol 168:104127

Jamiołkowska A, Skwaryło-Bednarz B, Michałek W (2019) Response of tomato seedlings inoculated with mycorrhizal fungi on the photosynthetic activity, growth, and health status of plants after infection with the fungus Colletotrichum coccodes. Acta Agrobot 72:1785

Jamiołkowska A, Skwaryło-Bednarz B, Thanoon AH, Kursa W (2021) Contribution of mycorrhizae to sustainable and ecological agriculture: a review. Int Agrophys 35:331–341

Johnson NC, Wilson GWT, Bowker MA, Wilson JA, Miller RM (2010) Resource limitation is a driver of local adaptation in mycorrhizal symbioses. PNAS 107:2093–2098

Jones JD, Dangl JL (2006) The plant immune system. Nature 444:323–329

Jones MD, Durall DM, Cairney JW (2003) Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging. New Phytol 157:399–422

Kanyuka K, Rudd JJ (2019) Cell surface immune receptors: the guardians of the plant's extracellular spaces. Curr Opin Plant Biol 50:1–8

Kehri HK, Akhtar O, Zoomi I, Pandey D (2018) Arbuscular mycorrhizal fungi: taxonomy and its systematics. Int J Life Sci Res 6:58–71

Kiers ET, Duhamel M, Beesetty Y, Mensah JA, Franken O, Verbruggen E, Fellbaum CR, Kowalchuk GA, Hart MM, Bago A, Palmer TM, West SA, Vandenkoornhuyse P, Jansa J, Bücking H (2011) Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science 333:880–882

Kolaříková Z, Slavíková R, Krüger C, Krüger M, Kohout P (2021) PacBio sequencing of Glomeromycota rDNA: a novel amplicon covering all widely used ribosomal barcoding regions and its applicability in taxonomy and ecology of arbuscular mycorrhizal fungi. New Phytol 231:490–499

Krüger M, Krüger C, Walker C, Stockinger H, Schüßler A (2012) Phylogenetic reference data for systematics and phylotaxonomy of arbuscular mycorrhizal fungi from phylum to species level. New Phytol 193:970–984

Kumar A, Verma JP (2018) Does plant-microbe interaction confer stress tolerance in plants: a review? Microbiol Res 207:41–52

Leigh EG Jr (2010) The evolution of mutualism. J Evol Biol 23:2507–2528

Lettice EP (2018) The rhizosphere: measuring the zone of interaction. Ann Plant Rev Online 2:219–236

Liu T, Sheng M, Wang C, Chen H, Li Z, Tang M (2015) Impact of arbuscular mycorrhizal fungi on the growth, water status, and photosynthesis of hybrid poplar under drought stress and recovery. Photosynthetica 53:250–258

Liu S-H, Zeng G-M, Niu Q-Y, Liu Y, Zhou L, Jiang L-H, Tan X-F, Xu P, Zhang C, Cheng M (2017) Bioremediation mechanisms of combined pollution of PAHs and heavy metals by bacteria and fungi: a mini review. Bioresour Technol 224:25–33

Marschner P (2012) Chapter 15: Rhizosphere biology. In: Marschner P (ed) Marschner's mineral nutrition of higher plants, 3rd edn. Academic, San Diego, pp 369–388

Martin BD, Schwab E (2012) Symbiosis: "living together" in chaos. Stud Hist Biol 4:7–25

Marx D, Ruehle J, Cordell C (1991) 17 methods for studying nursery and field response of trees to specific Ectomycorrhiza. In: Methods in microbiology. Elsevier, pp 383–411

Mbora A, Lillesø J-PB, Jamnadass R (2008) Good nursery practices: a simple guide. World Agroforestry Centre, Nairobi

Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiol Rev 37:634–663

Merckx V (2012) Mycoheterotrophy: the biology of plants living on fungi. Springer Science & Business Media, New York

Michałojć Z, Jarosz Z, Pitura K, Dzida K (2015) Effect of mycorrhizal colonization and nutrient solutions concentration on the yielding and chemical composition of tomato grown in rockwool and straw medium. Acta Scientiarum Polonorum-Hortorum Cultus 14:15–27

Muneer MA, Wang P, Zaib un N, Lin C, Ji B (2020) Potential role of common mycorrhizal networks in improving plant growth and soil physicochemical properties under varying nitrogen levels in a grassland ecosystem. Glob Ecol Conserv 24:e01352

Murray JD, Cousins DR, Jackson KJ, Liu C (2013) Signaling at the root surface: the role of cutin monomers in mycorrhization. Mol Plant 6:1381–1383

Nanjundappa A, Bagyaraj DJ, Saxena AK, Kumar M, Chakdar H (2019) Interaction between arbuscular mycorrhizal fungi and Bacillus spp. in soil enhancing growth of crop plants. Fungal Biol Biotechnol 6:23

Naznin HA, Kiyohara D, Kimura M, Miyazawa M, Shimizu M, Hyakumachi M (2014) Systemic resistance induced by volatile organic compounds emitted by plant growth-promoting fungi in Arabidopsis thaliana. PLoS One 9:e86882

Nussaume L, Kanno S, Javot H, Marin E, Nakanishi TM, Thibaud M-C (2011) Phosphate import in plants: focus on the PHT1 transporters. Front Plant Sci 2:83

Oelmüller R (2019) Interplant communication via hyphal networks. Plant Physiol Rep 24:463–473

Oldroyd GED (2013) Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. Nat Rev Microbiol 11:252–263

Oldroyd GED, Downie JA (2008) Coordinating nodule morphogenesis with Rhizobial infection in legumes. Annu Rev Plant Biol 59:519–546
Pandey D, Kehri HK, Zoomi I, Akhtar O, Singh AK (2019) Mycorrhizal fungi: biodiversity, ecological significance, and industrial applications. In: Recent advancement in white biotechnology through fungi. Springer, Cham, pp 181–199
Perez-Lamarque B, Selosse M-A, Öpik M, Morlon H, Martos F (2020) Cheating in arbuscular mycorrhizal mutualism: a network and phylogenetic analysis of mycoheterotrophy. New Phytol 226:1822–1835
Philip LJ (2006) The role of ectomycorrhizal fungi in carbon transfer within common mycorrhizal networks. University of British Columbia
Philippot L, Raaijmakers JM, Lemanceau P, Van Der Putten WH (2013) Going back to the roots: the microbial ecology of the rhizosphere. Nat Rev Microbiol 11:789–799
Plenchette C, Strullu DG (2003) Long-term viability and infectivity of intraradical forms of Glomus intraradices vesicles encapsulated in alginate beads. Mycol Res 107:614–616
Poveda J, Abril-Urias P, Escobar C (2020) Biological control of plant-parasitic nematodes by filamentous fungi inducers of resistance: Trichoderma, mycorrhizal and endophytic fungi. Front Microbiol 11:992
Pozo MJ, López-Ráez JA, Azcón-Aguilar C, García-Garrido JM (2015) Phytohormones as integrators of environmental signals in the regulation of mycorrhizal symbioses. New Phytol 205:1431–1436
Pringle A, Bever JD, Gardes M, Parrent JL, Rillig MC, Klironomos JN (2009) Mycorrhizal symbioses and plant invasions. Annu Rev Ecol Evol Syst 40:699–715
Rasmussen HN, Rasmussen FN (2009) Orchid mycorrhiza: implications of a Mycophagous life style. Oikos 118:334–345
Reddy CA, Saravanan RS (2013) Chapter 3: Polymicrobial multi-functional approach for enhancement of crop productivity. In: Sariaslani S, Gadd GM (eds). Academic, Advances in applied microbiology, pp 53–113
Rillig MC, Mummey DL (2006) Mycorrhizas and soil structure. New Phytol 171:41–53
Rinaldi AC, Comandini O, Kuyper TW (2008) Ectomycorrhizal fungal diversity: seperating the wheat from the chaff. Fungal Divers 33:1–45
Rincón A, Alvarez IF, Pera J (2001) Inoculation of containerized Pinus pinea L. seedlings with seven ectomycorrhizal fungi. Mycorrhiza 11:265–271
Rozpądek P, Domka AM, Nosek M, Ważny R, Jędrzejczyk RJ, Wiciarz M, Turnau K (2018) The role of strigolactone in the cross-talk between *Arabidopsis thaliana* and the endophytic fungus Mucor sp. Front Microbiol 9:441
Saladin G, Clément C (2005) Physiological side effects of pesticides on non-target plants. In: Agriculture and soil pollution: new research. Nova Science Publishers, Inc, pp 53–86
Sanchez-Zabala J, Majada J, Martín-Rodrigues N, Gonzalez-Murua C, Ortega U, Alonso-Graña M, Arana O, Duñabeitia MK (2013) Physiological aspects underlying the improved outplanting performance of Pinus pinaster Ait. seedlings associated with ectomycorrhizal inoculation. Mycorrhiza 23:627–640
Sapp J (2004) The dynamics of symbiosis: an historical overview. Can J Bot 82:1046–1056
Sapp J (2010) On the origin of symbiosis. In: Symbioses and stress. Springer, pp 3–18
Schmitz AM, Harrison MJ (2014) Signaling events during initiation of arbuscular mycorrhizal symbiosis. J Integr Plant Biol 56:250–261
Schouteden N, De Waele D, Panis B, Vos CM (2015) Arbuscular mycorrhizal fungi for the biocontrol of plant-parasitic nematodes: a review of the mechanisms involved. Front Microbiol 6:1280
Schüßler A, Walker C (2011) Evolution of the 'plant-symbiotic' fungal phylum, Glomeromycota. In: Pöggeler S, Wöstemeyer J (eds) Evolution of fungi and fungal-like organisms. Springer Berlin Heidelberg, Berlin/Heidelberg, pp 163–185
Selosse M-A, Cameron DD (2010) Introduction to a virtual special issue on mycoheterotrophy: new Phytologist sheds light on non-green plants. New Phytol 185:591–593

Sheng M, Tang M, Chen H, Yang B, Zhang F, Huang Y (2008) Influence of arbuscular mycorrhizae on photosynthesis and water status of maize plants under salt stress. Mycorrhiza 18:287–296

Shukla A, Dehariya K, Vyas D, Jha A (2015) Interactions between arbuscular mycorrhizae and Fusarium oxysporum f. sp. ciceris: effects on fungal development, seedling growth and wilt disease suppression in Cicer arietinum L. Arch Phytopathol Plant Prot 48:240–252

Simard SW, Asay A. Beiler KJ, Bingham MA, Deslippe JR, He, X, Philip LJ, Sony Y, Teste FP (2015) Resource transfer between plants through ectomycorrhizal fungal networks. In: Horton TR (ed), Mycorrhizal networks. (Ecological studies: Analysis and Synthesis). Springer, vol 224, pp 133–176. http://link.springer.com/book/10.1007/978-94-017-7395-9

Smith SE, Read DJ (2010) Mycorrhizal symbiosis. Academic, London

Song YY, Zeng RS, Xu JF, Li J, Shen X, Yihdego WG (2010) Interplant communication of tomato plants through underground common mycorrhizal networks. PLoS One 5:e13324

Song Y, Wang M, Zeng R, Groten K, Baldwin IT (2019) Priming and filtering of antiherbivore defences among Nicotiana attenuata plants connected by mycorrhizal networks. Plant Cell Environ 42:2945–2961

Subramanian K, Santhanakrishnan P, Balasubramanian P (2006) Responses of field grown tomato plants to arbuscular mycorrhizal fungal colonization under varying intensities of drought stress. Sci Hortic 107:245–253

Tamasloukht MB, Séjalon-Delmas N, Kluever A, Jauneau A, Roux C, Bécard G, Franken P (2003) Root factors induce mitochondrial-related gene expression and fungal respiration during the developmental switch from asymbiosis to presymbiosis in the arbuscular mycorrhizal fungus Gigaspora rosea. Plant Physiol 131:1468–1478

Teste FP, Simard SW, Durall DM, Guy RD, Jones MD, Schoonmaker AL (2009) Access to mycorrhizal networks and roots of trees: importance for seedling survival and resource transfer. Ecology 90:2808–2822

Thirkell T, Cameron D, Hodge A (2019) Contrasting nitrogen fertilisation rates Alter mycorrhizal contribution to barley nutrition in a field trial. Front Plant Sci 10:1312

van't Padje A, Oyarte Galvez L, Klein M, Hink MA, Postma M, Shimizu T, Kiers ET (2021) Temporal tracking of quantum-dot apatite across in vitro mycorrhizal networks shows how host demand can influence fungal nutrient transfer strategies. ISME J 15:435–449

Velmourougane K, Saxena G, Prasanna R (2017) Plant-microbe interactions in the rhizosphere: mechanisms and their ecological benefits. In: Plant-microbe interactions in agro-ecological perspectives. Springer, Singapore, pp 193–219

Vohník M (2020) Ericoid mycorrhizal symbiosis: theoretical background and methods for its comprehensive investigation. Mycorrhiza 30:671–695

Walder F, Niemann H, Natarajan M, Lehmann MF, Boller T, Wiemken A (2012) Mycorrhizal networks: common goods of plants shared under unequal terms of trade. Plant Physiol 159:789–797

Wang B, Qiu YL (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16:299–363

Wang C, Li X, Zhou J, Wang G, Dong Y (2008) Effects of arbuscular mycorrhizal fungi on growth and yield of cucumber plants. Commun Soil Sci Plant Anal 39:499–509

Wang G, Sheng L, Zhao D, Sheng J, Wang X, Liao H (2016) Allocation of nitrogen and carbon is regulated by nodulation and mycorrhizal networks in soybean/maize intercropping system. Front Plant Sci 7:1901

Wang M, Schäfer M, Li D, Halitschke R, Dong C, McGale E, Paetz C, Song Y, Li S, Dong J (2018) Blumenols as shoot markers of root symbiosis with arbuscular mycorrhizal fungi. elife 7:e37093

Wang F, Zhang X, Zhang S, Zhang S, Sun Y (2020) Interactions of microplastics and cadmium on plant growth and arbuscular mycorrhizal fungal communities in an agricultural soil. Chemosphere 254:126791

Wang H, Hao Z, Zhang X, Xie W, Chen B (2022a) Arbuscular mycorrhizal fungi induced plant resistance against fusarium wilt in Jasmonate biosynthesis defective mutant and wild type of tomato. J Fungi 8:422

Wang Y, He X, Yu F (2022b) Non-host plants: are they mycorrhizal networks players? Plant Divers 44:127–134

Weremijewicz J, Sternberg LSLOR, Janos DP (2016) Common mycorrhizal networks amplify competition by preferential mineral nutrient allocation to large host plants. New Phytol 212:461–471

Wipf D, Krajinski F, van Tuinen D, Recorbet G, Courty PE (2019) Trading on the arbuscular mycorrhiza market: from arbuscules to common mycorrhizal networks. New Phytol 223:1127–1142

Zamioudis C, Pieterse CM (2012) Modulation of host immunity by beneficial microbes. Mol Plant-Microbe Interact 25:139–150

Zhang L, Xu M, Liu Y, Zhang F, Hodge A, Feng G (2016) Carbon and phosphorus exchange may enable cooperation between an arbuscular mycorrhizal fungus and a phosphate-solubilizing bacterium. New Phytol 210:1022–1032

Zhu X, Song F, Liu S, Liu T, Zhou X (2012) Arbuscular mycorrhizae improves photosynthesis and water status of Zea mays L. under drought stress. Plant Soil Environ 58:186–191

Impacts of Climate Change on Plant Mycobiome

Abdelghafar M. Abu-Elsaoud and Walaa I. Saadeldin

1 Introduction

There is widespread agreement that climate change is a serious threat to the environment and one of the most pressing social issues of the century. More atmospheric carbon dioxide (CO_2) and, by extension, increased ultraviolet radiation (UVR) reaching Earth's surface owing to both rising temperatures and ozone depletion are two of the many phenomena associated to global climate change that have their roots in industrialization (Madronich et al. 1998). These climatic shifts may have both direct and indirect effects on organisms, altering their phenology and physiology (Beaugrand et al. 2003; Cloern et al. 2005) and impacting environmental parameters that regulate mortality and growth (Beardall et al. 2009). There is a chance that this might change the species' range, the composition of communities, and the ecosystem's ability to operate (Beaugrand et al. 2002).

The effects of ultraviolet radiation (UVR) on plants and fungi are not only dependent on the UVR's intensity and spectrum content, but also on the interaction of UVR exposure with other environmental factors such as nutrients (Marcoval et al. 2007), light acclimation history (van de Poll et al. 2006), and temperature (Villafañe

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et al. 2008). (Boyd et al. 2010). Biological processes including nutrition uptake, growth, species composition, and toxin generation might all be negatively impacted by UVR. Evidence from many studies (Beardall et al. 2009; Fu et al. 2012; Hogue et al. 2005) supports this notion. The community structure of phytoplankton might shift as a result of this since various species/groups react differently to UVR. As a result of affecting both the dark and light responses of photosynthesis at photosystem II, namely the enzyme RuBisCO (Vincent and Neale 2000), exposure to UVR can reduce photosynthetic rates. Significant UVR-induced damage on nucleic acids has also been observed (Boelen et al. 1999; Buma et al. 1996), leading to nucleotide damage and the production of photoproducts (Görner 1994). These photoproducts, such as pyrimidine dimers, can induce mutations and decrease the amount of free RNA polymerase, which affects transcription (Britt 1996). UVR exposure has been linked to an increase in reactive oxygen species (He and Häder 2002), which may damage macromolecules including lipids, DNA, and proteins, leading to oxidative damage and possibly even cell death.

The rise in atmospheric carbon dioxide concentrations since the start of the Industrial Revolution has had a significant impact on global warming. The increase in atmospheric CO_2 from 280 parts per million (before the start of the Industrial Revolution) to the present 410 parts per million is roughly proportional to the increase in average global temperature of about 1 °C since 1880. (Ciais et al. 2014). As long as CO_2 concentrations are on the increase, the Earth will continue to warm, but the extent to which this happens will rely on political will and human ability to limit carbon emissions as quickly as feasible. Therefore, increasing temperatures will lead to different climatic conditions in many places, which will affect the way species operate and their current geographic ranges. By taking in some of the carbon dioxide (CO_2) emitted into the air from burning fossil fuels, terrestrial plants have played an important role in mitigating climate change. Ciais et al. (2014) found that plants now absorb 30% of annual CO_2 emissions, hence slowing the pace at which the planet is warming. However, plants are adaptive, and some of them may adjust their optimal development temperature based on external conditions (see below). Because forests are responsible for a sizable proportion of global terrestrial production, knowing how they will respond to climate change is crucial for foreseeing the future. In order to assess how trees in a forest will react to rising temperatures, it is important to measure any potential changes in tree physiology. One of the major gaps in our knowledge of the carbon cycle and our capacity to forecast future increases in atmospheric CO_2 concentrations is how temperature influences the physiological changes of forest trees (Mercado et al. 2018). Since the greatest fluxes of carbon intake and loss occur during photosynthesis and respiration, respectively, the capacity of a species to physically modify its plant metabolism is a first line of defence for how they would adapt to rising temperatures. The topics of this chapter include global warming (temperature), UV radiation, and carbon dioxide emissions.

2 Effect of Climate Change on Plants and Mycobiota

2.1 Ultraviolet Radiations

2.1.1 Nature of Light

Light is an essential source of energy for virtually all organisms on Earth. Many different kinds of organisms are able to absorb and use the energy from light. Autotrophs and plants, for instance, are able to achieve this via photosynthesis. However, light has many other functions than providing energy for biological reactions. Its quality (the ratio of photons at different wavelengths), intensity (energy flux), and relationships to other environmental characteristics all reveal information about the condition of the environment right now. (Jones et al. 2013).

Relativity and quantum physics, the two dominant theories of the twentieth century, both focus on the behaviour of as light travels through space as well as interacts with matter. The study of this phenomenon is also crucial to our knowledge of how organisms behave and operate (Björn 2015).

Photomorphogenesis is described as an organism's developmental reaction to information in light, such as the amount of light, the quality of light in terms of wavelengths present, the direction of light, or the length of night and day and (photoperiod). Photoreceptors are molecules within cells that take in light and trigger a series of reactions in the organism when exposed to it (Jones et al. 2013). *Photostimulators* are a specific kind of light utilised in the process of *photostimulation*, which is the use of light to stimulate biological processes.

2.2 Electromagnetic Spectrum

For all forms of energy production that do not involve nuclear fission, the Sun is indispensable. Energy from the sun is the result of nuclear fusion, and each year the Earth absorbs around 5.62 × 1024 joules of solar radiation through its atmosphere, seas, and landmasses; of this amount, photosynthesis is responsible for capturing 3.16 × 1021 joules (Table 1). The electromagnetic spectrum includes not only visible light but also - and X-rays, and all the way to radio waves at the other end. Light is both a particle and a wave at the same time. As a simplified metaphor, think of it as waves made up of discrete packets of energy, or quanta. A photon is the quantization of light's energy. Lambda (λ), the Greek letter that represents wavelength, is often written in nanometers when referring to visible light (nm). Radiation with wavelengths between around 380 nm (violet) and 760 nm (far red) is known as the visible spectrum (Fig. 1). Equation 14.1 expresses the relationship between frequency (ν, Greek letter nu; units = s^{-1}), speed of light (c, units = m s^{-1}), and wavelength (in meters). There are two primary characteristics of light. Light has both particle and wave qualities, and they can be clearly seen in an adjusted version of Young's double-slit experiment (Jones 2013).

Table 1 The fate of solar energy reaching Earth (Jones 2013)

Global solar power balance	Amount in terawatts[a]
Solar power input[b]	178,000
Reflected to space immediately	53,000
Absorbed and then reflected as heat	82,000
Used to evaporate water	40,000
Captured by photosynthesis (net primary productivity)[c]	100
Total power used by human society	
In 2005	13
Projected use in 2100	46
Total used for food	0.6

[a]Power is measured in watts, and a watt is equal to one joule every second. Terawatts are measured in units of power equivalent to 1012 joules second^{-1}, or 1012 watts
[b]Solar energy input is 5.621012 terawatts (5.621024 joules)
[c]Photosynthetic organisms are responsible for harvesting an average of 3.16 × 109 terawatts (3.16 × 1021 joules) of solar energy every year

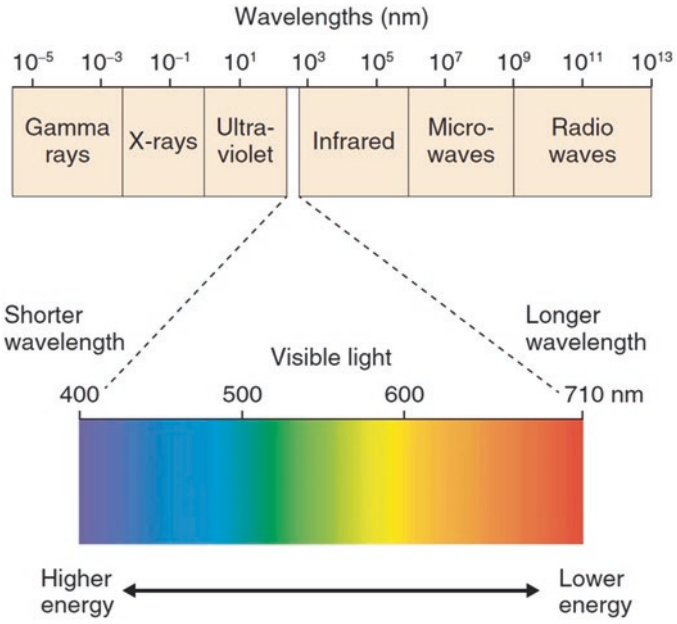

Fig. 1 The visible portion of the electromagnetic spectrum, from 400 to 710 nm, enlarged to display colour. The blue end of the spectrum (380 nm) and the red end of the spectrum (760 nm) are not the absolute limiting factors for human perceptual abilities. Keep in mind that the units of energy are J mol^{-1} (Jones 2013)

Equation 1 Relationship between light speed, frequency & wavelength

$$c = \upsilon\lambda$$

Equation 2 Energy as a function of electromagnetic radiation wavelength or frequency:

$$E = hc / \lambda$$

Where c = speed of light (approximately 300×10^6 m s^{-1}) and h = Planck's constant (4.14×10^{-15} eV.s).

2.3 Photobiology: Interaction of Light with Living Organisms

Photobiology is the study of how various wavelengths of light influence living organisms. Photoreceptors are light-absorbing molecules that trigger a series of reactions in living things when they detect light (Jones et al. 2013). Photostimulators are a specific kind of light utilised in the process of photostimulation, which is the use of light to stimulate biological processes. Photoreceptor molecules detect light and transmit that information to the cell so that the body may respond to changes in its environment.

Rhodopsin is found in the eyes of humans and other animals and functions as a photoreceptor. Photoreceptors are found in a wide variety of plant and microbial species. Phytochromes, cryptochromes, and phototropins are all examples of photosynthetic pigments. There is a unique spectrum of light that is taken in by each type of photoreceptor. Absorption of light by a photoreceptor causes a variety of reactions depending on the wavelength of the light. An action spectrum is the result of plotting the magnitude of a certain physiological reaction against the wavelengths that elicit that response. The photoreceptor responsible for a given reaction can be determined by measuring the spectrum of the associated action potential.

UV light with shorter wavelengths than the visible and infrared ranges display a greater number of quantum characteristics. We arbitrarily divide ultraviolet light into three bands, each with distinct biological consequences. Since it carries the least amount of energy, UV-A light is the least dangerous and most frequent kind of UV radiation. The ultraviolet-a (UV-A) spectrum of light is commonly referred to as "black light" because of its reputation for inducing visible light emission from fluorescent materials. UV-A lamps, the kind used in tanning salons and phototherapy, are the most common (Fig. 2).

Since UV-B has enough energy to destroy living tissues yet is not completely absorbed by the atmosphere, it is the most dangerous kind of UV radiation. Overexposure to UV-B rays has been linked to skin cancer. Given that the atmosphere blocks most of the UV-B radiation from space, even a little change in the

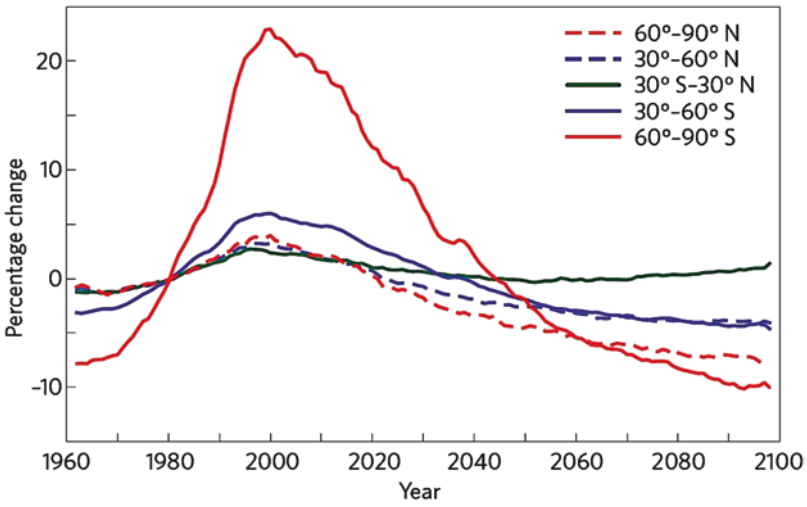

Fig. 2 Annual mean erythemal (skin-burning) clear-sky UV-B radiation at the Earth's surface, observed (before 2010) and anticipated (after 2010) compared to 1980 for different latitude bands (Bais et al. 2015; McKenzie et al. 2011; Williamson et al. 2014)

ozone layer might significantly increase the risk of skin cancer. While the sun's ultraviolet radiation (UV) is essential for life on Earth, it has the potential to damage living as well as non-living organisms. Conventionally, UV light has been separated into three wavelength bands: UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (200 nm) (100–280 nm). Potentially harmful ultraviolet (UV)-C radiation is blocked entirely by Earth's atmosphere before it reaches the planet's surface. Stratospheric ozone absorbs the most harmful short wavelength UV-B radiation, protecting Earth's surface from it. The majority of the sun's ultraviolet (UV) light reaching the ground is UV-A, which is mostly unimpeded by the Earth's atmosphere. UV-A radiation is mutagenic and suppresses the immune system in humans, but it also has essential impacts on tropospheric chemistry, air quality, aquatic and soil processes, and is typically less hazardous than UV-B radiation (Damian et al. 2011). Insect pests and harmful bacteria can be effectively repressed by plants' natural defence mechanisms, and solar UV light, especially UV-B, can be a positive regulator of these mechanisms (Williamson et al. 2014). Microorganisms can be affected positively or negatively by UV light, with UV-A and UV-B having the most dramatic impacts (Abu-Elsaoud and Abdel-Azeem 2020).

In an in vitro experiment, we determined how exposure to higher UV radiation levels, particularly UVA + UVB, affected certain aeromycobiota from the Ismailia region in Egypt (unpublished data). *Paecilomyces* sp. and *Drechslera* sp. were the two kinds of fungi examined. While both *Drechslera* sp. and *Paecilomyces* sp. showed an effect of UV-B and UV-A on biochemical consequences and conidial structure (size), UV-absorbing compound levels were found to be much higher in *Paecilomyces* following irradiation with both wavelengths compared to the control

group. Mycosporine-like amino acids (MAAs) were found in increased quantities (Abu-Elsaoud and Abdel-Azeem 2020). Table 2 Summarized selected studies on the effect of climate change in terms of Electromagnetic spectrum on microorganisms especially fungi (Figs. 3 and 4).

The majority of filamentous fungi finish their asexual life cycle by forming specialised structures known as conidia. They are critical to the proliferation of fungi as well as the survival of their habitats. They also play a role in pathogenic species identification and infection. Solar radiation can have a variety of effects on conidial production, survival, dispersal, germination, pathogenicity, and virulence, some of

Table 2 Some selected studies Effect of climate change in terms of Electromagnetic spectrum on microorganisms especially fungi

EM radiation	Wavelength (λ; nm)	Subject	Microorganism	Reference
UV-B	280–320	Growth, pigmentation, and spore generation in the phytopathogenic fungus Alternaria solani in response to ultraviolet B light	*Alternaria solani*	Fourtouni et al. (1998)
UV-B	280–320	Effect of UV-B irradiation on the antioxidant activity and content of the medicinal Caterpillar fungus, Cordyceps militaris (ascomycetes)	*Cordyceps militaris*	Huang et al. (2015)
		Serpula himantioides cultures exposed to UV-B radiation accumulate more xerocomic acid, which is found in the cell wall	*Serpula himantioides*	Torres et al. (2019)
		Physiological and molecular effects of environmental UV radiation on fungal conidia	*Magnaporthe grisea*, *Alternaria alternata*, *Colletotrichum lagenarium*, *Cochliobolus heterostrophus*, and *Aspergillus* spp.	Braga et al. (2015)
UV-A + UV-B	320–400	Conidial structure has been altered	*Fungi*: *Drechslera* sp. *Paecilomyces* sp.	Abu-Elsaoud and Abdel-Azeem (2020)
	280–320	UV-absorbing chemicals have been increased		
		Mycosporine-like-amino acids have increased (MAAs)		
He-Ne laser and UV		Endo-polysaccharide synthesis and antioxidant activity	*Phellinus igniarius*	Zhang et al. (2016)

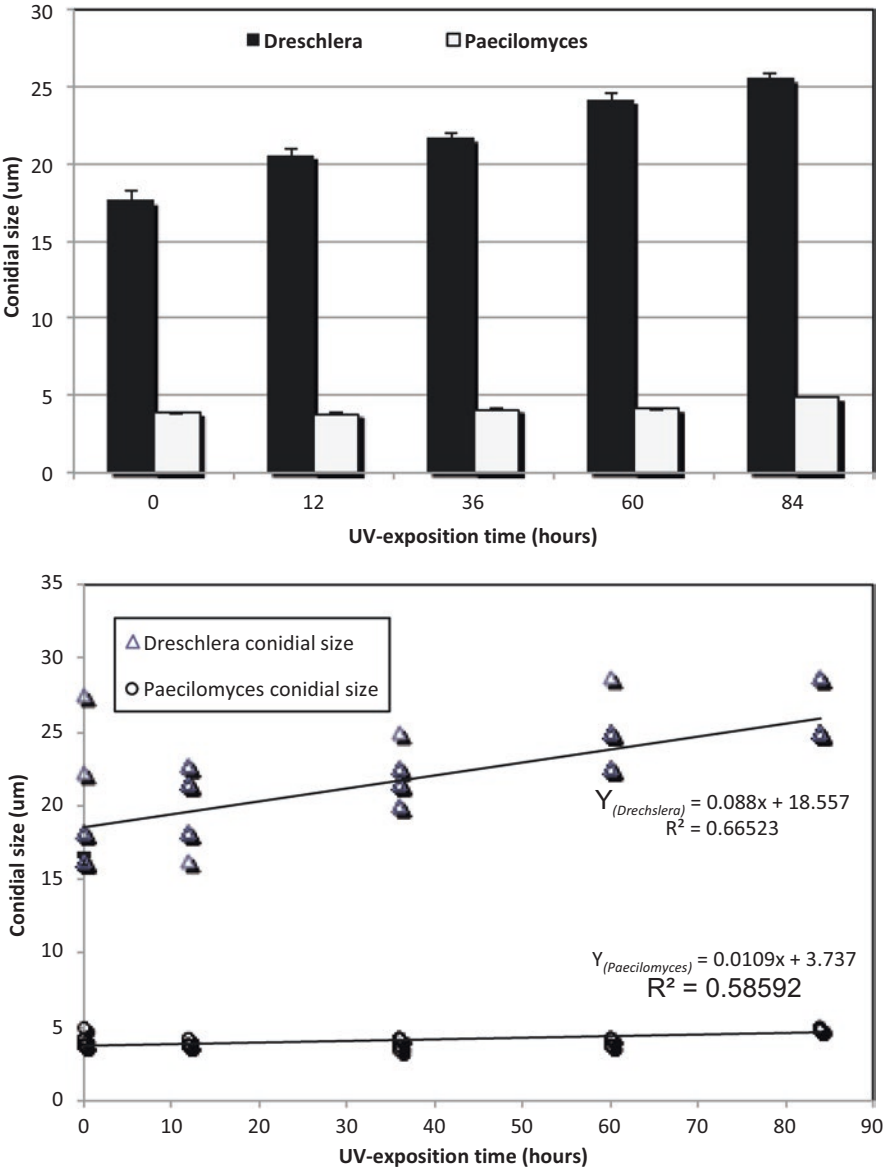

Fig. 3 The conidial size (m) of Paecilomyces spp. and *Dreschlera* spp. increases in response to increased ultraviolet radiations (UV-B, UV-A). (Abu-Elsaoud and Abdel-Azeem unpublished data)

which are species-specific. The ultraviolet (UV) spectrum of the sun's radiation is the most harmful and mutagenic. Most fungal conidia are susceptible to mortality when exposed to direct sunlight for a few hours. Conidia are killed by UV-A and UV-B rays from the sun. Sublethal UV light exposure can decrease the speed and

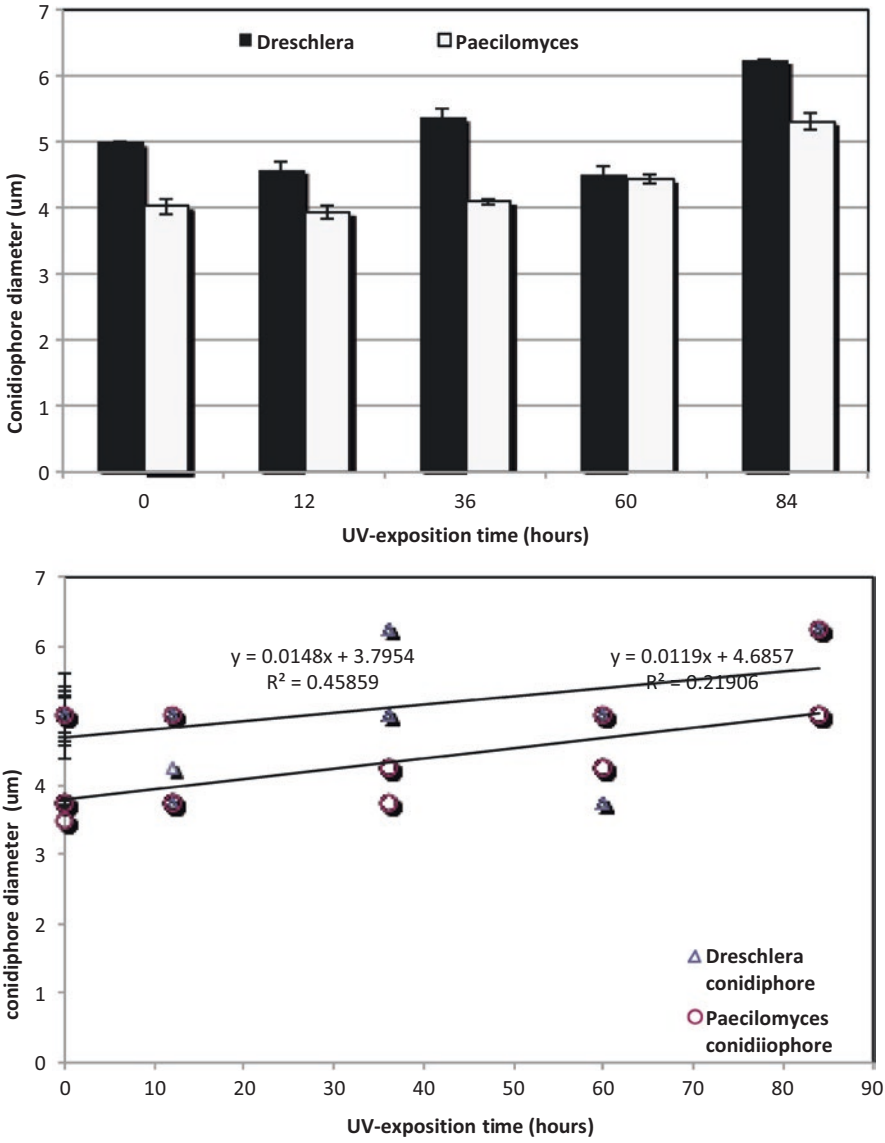

Fig. 4 The conidiophore diameter (m) of *Paecilomyces* sp. and *Dreschlera* sp. increases when exposed to higher amounts of ultraviolet radiations (UV-B, UV-A). (Abu-Elsaoud and Abdel-Azeem unpublished data)

pathogenicity of conidial germination as well as kill conidia, reducing the number and spread of the fungal population. This page attempts to provide readers with an overview of the key systems involved in UV radiation defence and healing, with a particular emphasis on how these mechanisms influence conidia. The methods used

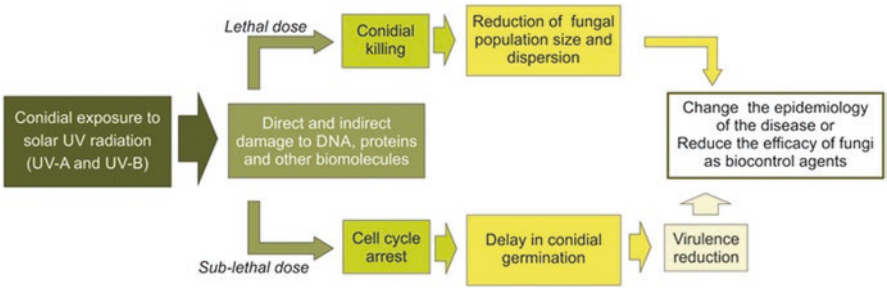

Fig. 5 The biological and molecular impacts of solar UV radiation on conidia and their ability to operate. (Source: Braga et al. 2015)

to create sun radiation-resistant strains of fungal species of interest, such as entomopathogens, will also be discussed. To further understand how solar UV radiation affects conidia on a molecular and physiological level, as well as how conidia respond functionally, refer to Fig. 5 (Braga et al. 2015).

3 Climate Warming

3.1 Plant Responses to Climate Warming

Tree growth and other physiological processes are very sensitive to temperature. A rise of 2–5 °C is forecast for this century, creating circumstances for numerous species that have never been seen before in evolutionary history. Sedentary and living for far longer periods of time than animals, plants, and especially trees, may require physiological adaptations to greater temperatures. But most plants can adjust to new conditions, and they typically do so in ways that maintain or even improve their carbon gain. Climate change has led to adaptations that increase carbon intake and growth, such as reduced respiration rates (Atkin and Tjoelker 2003), increased leaf areas (Way and Oren 2010), and even increased assimilation rates at warmer growth temperatures (Way and Sage 2008). In addition, most species may raise their thermal optimum of photosynthesis in response to rising temperatures (Crous et al. 2013; Way and Oren 2010) (Fig. 6). "Thermal acclimation" refers to the process by which a plant's physiology adapts to different temperatures used for growth. In most cases, the thermal ideal of photosynthesis will alter by a fraction of a degree for every degree that the growth temperature changes. By allowing plants to function at extremely high temperatures without a decrease in photosynthetic rates, raising the temperature ideal of photosynthesis has the potential to greatly mitigate the negative effects of warming (Fig. 6). Furthermore, in comparison to non-adaptive respiration rates, lower respiration rates with warming minimise carbon loss (Atkin et al. 2015). Large-scale changes in plant fluxes of respiration and photosynthesis will impact

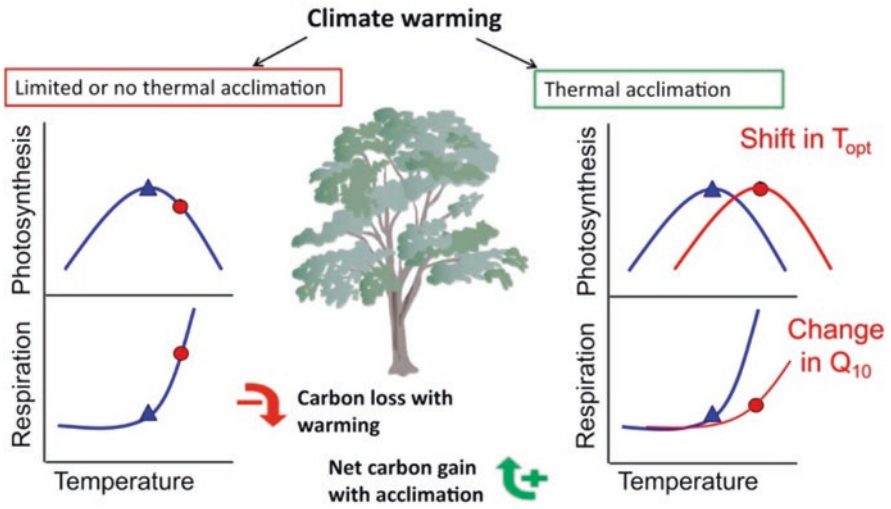

Fig. 6 Reduced complexity version of the physiological responses plants can make to rising temperatures throughout time (i.e., thermal acclimation). Temperature increases (red dots) and higher respiration (blue dots) relative to ambient conditions (left picture) both lead to lower rates of carbon uptake through photosynthesis. In reaction to rising temperatures, plants often move to a higher temperature optimum for photosynthesis (Shift in Topt), which allows them to keep their photosynthetic rates constant even as the temperature rises (compare red with blue lines in upper right panel). Consider the case when respiration is equal at the new growth temperature compared to ambient conditions, but with a lower slope, to see how thermal adaptation in respiration (Change in Q 10) can reduce carbon loss due to warming temperatures (compare red with blue lines in bottom right panel). (Source: Crous 2019)

the future degree of climate warming because plants affect global and regional temperature (Dusenge et al. 2019).

The climatic conditions to which a species is used have a role in determining how well it adapts to its new environment. When temperatures rise, many plant and animal species respond positively by increasing their rate of development and photosynthetic ability (Gunderson et al. 2009; Way and Sage 2008). On the other hand, research conducted in warmer climes showed that tree growth and carbon acquisition are lower in species native to warmer low-latitude conditions, as is the species' photosynthetic capability (Crous et al. 2013; Feeley et al. 2007). This data suggests that warmer-grown animals have a restricted physiological potential to adapt to higher temperatures. Species native to the equator, which experience relatively constant temperatures throughout the year, may be less able to adapt to rising global temperatures than those native to colder regions (higher latitudes), where seasonal temperature swings are more pronounced. Species that live at lower latitudes are also more likely to be operating at their thermal optimum (Crous et al. 2018; Doughty and Goulden 2008). As a result, the tropical rainforests, the most productive ecosystem on Earth, may lose some of their capacity to act as a carbon sink if the global average temperature continues to rise.

Plant responses to warming can be modulated by a number of other variables, including, but not limited to, increased (CO_2), nutrient availability, and changing precipitation patterns. Drought stress is anticipated to rise as a result of changes in rainfall patterns, the frequency of heatwaves, and the intensity of those heatwaves, all of which reinforce the negative impacts of higher temperatures. Warmer temperatures not only slow development, but also hinder seed generation and dissemination, which can ultimately lead to fewer seedling establishments and widespread forest dieback (Allen et al. 2010). Climate change has several consequences, including altered plant communities and decreased or modified distribution ranges of several plant species (Harsch and HilleRisLambers 2016).

3.2 Climate Affects Symbiotic Fungal Endophyte Diversity and Performance

The genetic diversity of endophytic fungi, which are microorganisms found on the surfaces of plants, is exceptionally great (Rodriguez et al. 2009). As a result, they can alter a plant's growth, offspring, and resistance to predators and adverse conditions (Cosme et al. 2016; Kivlin et al. 2013; Mayerhofer et al. 2013; Oberhofer et al. 2014; Rho et al. 2018; Rodriguez et al. 2008). Increased nitrogen absorption by host plants is one positive effect of endophytes (Afkhami and Strauss 2016; Aguilar-Trigueros and Rillig 2016; Behie and Bidochka 2014; Clay and Holah 1999; Rudgers et al. 2004, 2005) have all shown that endophytes have an impact on the overall structure and function of plant communities and the ecological webs that connect them (e.g. herbivores and their parasitoids; Omacini et al. 2001). The genus Neotyphodium and its asexual stage, Epichlo, have been used in a small number of experiments to teach us about fungal endophytes. It is not feasible to undertake randomised controlled trials to validate the ecological activities of most fungal endophytes due to their infamous difficulty to cultivate.

One of the most notable features of this important group of fungal endophytes is the wide host and geographic ranges of the species that make up the Serendipitaceae family, which is part of the order Sebacinales (Garnica et al. 2016; Weiß et al. 2011). Previous studies have demonstrated that Serendipita indica (Piriformospora indica) improves plant growth and modulates plant nutrition and tolerances to biotic and abiotic stresses, however these studies have mostly focused on S. indica (Achatz et al. 2010; Barazani et al. 2005; Gill et al. 2016; Waller et al. 2005). Tübingen coworkers and I have recently identified and cultured Serendipita herbamans, another member of the Serendipitaceae family that is widespread and associated with a wide range of host species and environmental conditions across Central Europe (Riess et al. 2014).

Soil microorganisms may have an impact on both plant growth and stress resistance, albeit how exactly they do so may differ from host to host. As a result, plant-microbe interactions aid in the development of plant communities, and there is

growing evidence that they play a role in the spread of invasive plant species (Callaway et al. 2004; Dawson and Schrama 2016; Inderjit and van der Putten 2010; Klironomos 2002). Plants may profit from or be harmed by the microorganisms that live on them (Bever et al. 2012; van der Putten et al. 2013). If exotics accumulate biota that has a net favourable effect on the plant, they may have an advantage over locals. This could happen if the imported region does not have the same natural illnesses as the exotic does (Callaway et al. 2011; Maron et al. 2014; Mitchell and Power 2003; Reinhart et al. 2003). It has been suggested that the introduction of exotic plants into an area can have a negative effect on the soil biota by either increasing the number of diseases that attack native plants (Mangla and Callaway 2008) or by disrupting the interactions between mutualists and native plants (Meinhardt and Gehring 2012; Stinson et al. 2006).

Many studies on plant-microbe interactions and plant invasion have focused on soil-borne microbes rather than endophytes, despite the fact that fungal endophytes are apparently widespread and diverse also in invasive plant populations (Clay et al. 2016; Shipunov et al. 2008). A remarkable set of research by Aschehoug et al. (2012, 2014) showed how the leaf endophyte Alternaria alternata causes the invasive knapweed (Centaurea stoebe) highly effective and allelopathic towards native North American grasses.

3.3 Climate Change and Fungal Pathogens

Growing evidence suggests environmental factors have a significant influence in the emergence and resurgence of infectious illnesses, notably those caused by fungus and other fungal infections (El-Sayed and Kamel 2020; Wu et al. 2016; Nnadi and Carter 2021). The United Nations Framework Convention on Climate Change defines climate change as "a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods," suggesting that climate change may lead to the emergence of new fungal diseases (Farber 2021). Reference: (Garcia-Solache and Casadevall 2010). The possible role of viruses and bacteria in epidemics and pandemics is well discussed, but fungus should not be overlooked. Fungi may grow saprotrophically, producing huge amounts of infectious spores, and infecting new hosts does not necessitate direct contact between them. Despite these challenges, no vaccines have been developed specifically for fungal infections (Casadevall 2019). To be sure, fungi appear to be the only organisms capable of triggering total host extinction (Fisher et al. 2012).

Most fungal species cannot infect animals and establish lifelong infections because they cannot tolerate high temperatures. While a rise in disease-causing organisms is possible as a result of climate change's sluggish adaptation to warming temperatures, fungi can be taught to gain thermotolerance (Casadevall 2020; de Crecy et al. 2009). Climate change also increases the likelihood that pathogenic

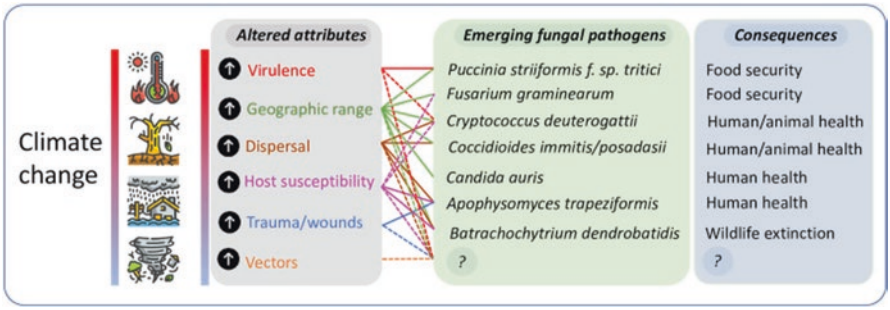

Fig. 7 Climate change's impact on the development of fungal diseases. Climate change modifies the characteristics of the fungus, its habitat, and its host, which can lead to the creation of novel, unusual, or adaptable fungal species, with repercussions for human health, biodiversity, and food security. On this diagram, solid lines between characteristics and fungal species represent associations supported by published research, whereas dashed lines represent associations that are likely but unconfirmed. "?" signifies the advent of as-yet-unidentified fungus species with unclear repercussions. (Source: Nnadi and Carter 2021)

organisms or the vectors that carry them may move to new locations, perhaps resulting in the emergence of diseases that have not been seen in those areas before (Casadevall 2020). Mold may be spread and aerosolized during climate-related environmental disruptions like floods, storms, and hurricanes, or it can be implanted via traumatic wounds and cause diseases from previously identified fungal species. Figure 7 depicts the potential consequences of climate change through the lens of emergent fungus and its effects, as well as the possibility that new and undiscovered species will emerge.

3.4 Climate Affects Symbiotic Fungal Endophyte Diversity and Performance

Because water is such a crucial factor in a plant's survival and growth, its drought tolerance can have far-reaching effects on production, variety, and dispersion (Knapp and Smith 2001; Lauenroth and Sala 1992). That this is the case has been demonstrated (Archaux and Wolters 2006; Craine et al. 2013; Knapp et al. 2002; Tilman and El Haddi 1992). Many climate models forecast broad increases in drought frequency and intensity in the future, therefore plants' capacity to tolerate drought will likely grow more essential (Meehl et al. 2007; Schoof et al. 2010; Seager et al. 2007; Solomon et al. 2007). Understanding the processes underpinning drought resistance is crucial for optimising plant growth in water-limited conditions. There is mounting evidence that microbial symbionts can play a role in mediating plant responses to drought and other stresses (e.g., Augé 2001; Márquez et al. 2007; Xu et al. 2008), despite the fact that most studies of plant drought resistance have focused on the plant's physiology and genetics in its abiotic environment.

Common plant symbionts, fungal endophytes, can have a significant impact on how well plants tolerate drought. Osmotic adjustment and other drought tolerance mechanisms may be affected by these factors (Malinowski and Belesky 2000; Morsy et al. 2010; Rodriguez et al. 2009, 2010; Waller et al. 2005). Host plants that were colonised by endophytes during drought showed increased biomass production, decreased evaporation, and increased resistance to water stress (Elmi and West 1995; Kane 2011; Kannadan and Rudgers 2008; Rodriguez et al. 2008). However, not all endophytes are beneficial to their host plants. Actually, the presence of certain endophytes can cause a decline in biomass and an increase in transpiration rates in host plants (Arnold and Engelbrecht 2007; Cheplick 2004; Kleczewski et al. 2012). Complex variables may explain why endophyte function varies between fungal species, genotypes, and habitats (Cheplick 2004; Morse et al. 2007; Rodriguez and Redman 2008).

How and what fungal endophytes perform in communities are likely influenced by a variety of factors, including location, ecology, and evolution (Leibold et al. 2004). Although most assume that bacteria may spread globally, there is mounting evidence that their transmission is confined to regional scales at most (Kivlin et al. 2011; Martiny et al. 2011; Peay et al. 2010; Waldrop and Firestone 2006). Spatial structure and species turnover may result from limited dispersion. For instance, Márquez et al. (2008) discovered that as they travelled further from the coast of Spain, the endophyte community in two different grasses became less similar. Species will naturally separate into several populations in places with varying habitats if there is sufficient dispersal (Leibold et al. 2004). By analysing community data from 158 research, Cottenie (2005) showed that 44% of communities were structured by species sorting, 29% by a combination of species sorting and dispersion effects, and 8% by spatial factors that likely indicate neutral processes or patch dynamics. The review did not consider symbiotic or terrestrial microbial populations. The nonclavicipitaceous endophytes of above-ground plant tissues discussed here are often a result of horizontal transmission from their natural habitats (e.g., soil, other plants, Rodriguez et al. 2009). Horizontal spread of endophytes is less likely to result in symbiotic relationships than vertical transmission via seeds (Higgins et al. 2011; Rodriguez et al. 2009). What's more plausible is that endophytes are influenced by a combination of environmental variables and the way space evolves through time. For instance, Arnold and Lutzoni (2007) discovered that, for 28 host species spanning the northern tundra to the tropical jungle, latitude was the strongest predictor of endophyte diversity. Likely causes include restricted range and a lack of suitable habitat.

The key to developing a prediction paradigm for endophyte function in symbiosis is understanding how endophyte dispersion corresponds to their functional capacities. Since endophyte function is linked to some particularly hostile environments, environmental filtration and local adaptation may both play a role in shaping species' ranges in such settings. Several plant species, for instance, gained salt and heat tolerance through endophytes that had been separated from salty and geothermal habitats (Redman et al. 2002; Rodriguez et al. 2008). Both past drought patterns and current drought levels are likely to operate as environmental filters when we

think about drought stress (Evans and Wallenstein 2012). Current endophyte communities may have emerged in reaction to previous moisture circumstances, but it is unknown how long-term drought stress influences the available species pool. If dispersal is the major controller of endophyte distributions, however, these organisms will be dispersed in a fashion that is unrelated to their function, as established by the spatial arrangement of sites. It may be possible to better anticipate the involvement of endophytes in plants under different environmental conditions if we understand the relative impact of environmental variables (species sorting) and spatial processes (neutral or mass effects) in endophyte community distributions. By learning more about endophytes' function in drought resistance, we could be better able to foresee how plants will react to drought in the future.

3.5 Effect of Climate Change on Fodder and Forage Availability and Livestock

The farming industry as a whole is heavily invested in animal domestication. It is not uncommon for there to be lone or several small farmers in each country of the region, each with between one and five ruminants. To put it another way, climate change has an immediate effect on the production of feed and livestock. The effects of climate change in the 1990s were disastrous across the world. Global surface temperatures increased by 0.6 °C over the twentieth century, and more rises are expected during the twentieth century. At now, the ability of ruminants to transform low-quality forages into nutritious human food is threatened by the global warming phenomenon. The cattle business is a major source of greenhouse gas emissions, including methane (CH_4), nitrous oxide (N_2O), and carbon dioxide (CO_2). The International Panel on Climate Change (IPCC) estimates that ruminants in India, Pakistan, and Bangladesh release as much carbon dioxide as 950 metric tonnes worth of methane every year. More study is required because of the large gap between IPCC estimates and actual situations. There are more than 125 million buffalo in the surrounding area. It's possible that ruminants fed a diet high in roughage, although economically feasible, will emit more of the greenhouse gas methane than ruminants on diets more typical of the rest of the globe (Godde et al. 2021).

The amount of food production and the health of the global environment are both linked to the intensity with which agriculture is practised. Half of all farmable land is already in use, either for extensive livestock ranching or large-scale crop production. The sustainability of food production, aquatic ecosystems, and societal services will be severely tested by the predicted doubling of global food demand over the next 50 years. Most of the world's population lives on grasslands, which account for 40% of the planet's surface and are particularly vulnerable because of this. The ability of the world's grasslands to sustain human, plant, and animal life has diminished as a result of overgrazing. Grasslands are changing due to human activities such as agriculture, urbanisation, and industry. The warming effect of atmospheric

gas buildup over the coming century makes it evident that the world's resource allocation and consumption must alter. Most scientists agree that climate change is happening due to human actions like burning fossil fuels, clearing forests, and using chemical fertilisers, and that poorer nations will be hit harder by the effects of this shift.

Greenhouse gases, like CO_2, methane, and nitrous oxide, that humans release into the atmosphere are a major cause of global warming. The higher prevalence of floods, droughts, cyclones, and heavy rains in recent times is evidence that the accumulation of gases is affecting the climate change globally. Ruminant animals are the most effective users of natural grassland and serve a variety of purposes in global agricultural systems. They provide as a source of food and revenue for both rural and urban dwellers, facilitate movement by providing transport and traction, and generate value-added commodities that can have a multiplicative influence on the economy and the demand for a wide range of services. Reports on the effects of global warming on agriculture indicate that the nations of the tropics and subtropics will be particularly hard hit. The development and maturity of plants, as well as the quality of their forage, can be affected by variations in environmental conditions from year to year, season to season, and location. Because of this, estimating the nutrient content of forages and the variety in how they will be used by ruminants is more difficult than it needs to be. Changes in chemical composition and senescence caused by environmental factors such temperature, moisture, sunlight, soil composition, and pathogens can reduce fodder quality and therefore, intake and digestion. Production and feeding of quality forages, which are impacted by climate and soil, are the main constraints on sustainable livestock production in the South Asian area. Despite the importance of studying the impact of environmental changes on fodder productivity and quality in the Asian area, relatively few research has been done on the topic. The elements that affect plant growth and quality are discussed in this work.

Reasons for the climate change are related to the environment. Cause of global warming. Methane (CH_4), carbon dioxide (CO_2), halocarbons, ozone, nitrous oxide (N_2O), water vapour and aerosols are the most significant greenhouse gases. Human activity is the primary contributor to the steady increase of carbon dioxide in the atmosphere (Fig. 8).

Carbon dioxide levels are rising at a rate of roughly 0.3% each year, according to measurements taken throughout the world. They are expected to reach 600 parts per million by the end of the twenty-first century, from their current level of 370 parts per million (Houghton et al. 1990). Humans contribute at a rate of 1.9% year (Marland 1990; Watson et al. 1992), with most of the increase coming from wealthy countries. The United States and the United Kingdom are responsible for an estimated 18.9 and 8.9 tones, respectively, while India contributes a far more modest 1 tone. Carbon dioxide emissions at a worldwide level increased by 1.6 gigatons per year due to deforestation (Watson et al. 1990, 1992). In 1990, it was projected that Bangladesh produced 13.5–15.5 and 61.2 thousand Gg of carbon dioxide annually from the burning of fossil fuels and biomass, respectively (Ahmed et al. 1996; DOE 1997).

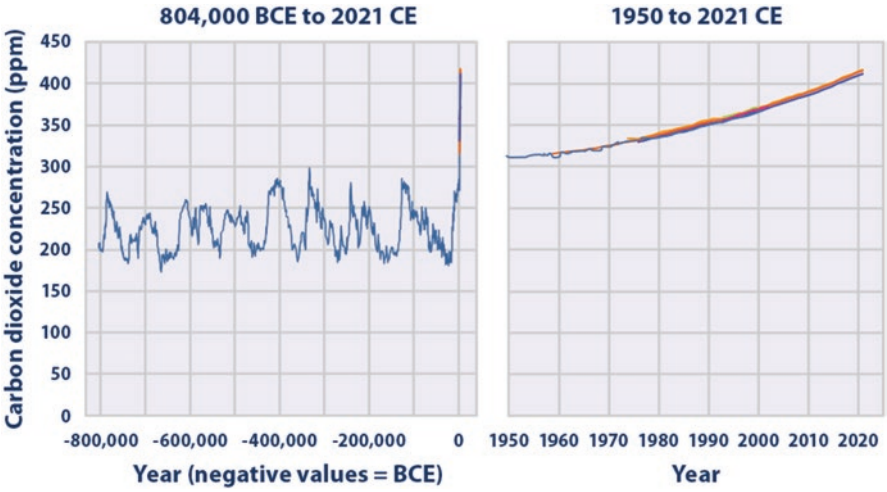

Fig. 8 Global atmospheric concentrations of carbon dioxide over time. (Source: US EPA 2022)

The death of all above-ground vegetation and the resulting shortage of forage can have a devastating effect on animal output. Due to slower stem development and a resultant leafier sward, digestibility is unaffected by or even improved by moderate moisture stress (Wilson 1983). This is crucial information for plants that need a constantly moist environment to thrive. Forage growth and productivity are more severely impacted by water stress than forage quality. Increases in nitrogen (N) content (Wilson and Ng 1975), minerals (Abdel Rahman et al. 1971), and soluble carbohydrates (SC) in forage have all been linked to water stress(Ford and Wilson 1981). Alfalfa output drops by 49% when water stress delays plant development, leading to a higher leaf-to-stem ratio (18%) and higher digestibility (8%). It also caused a 10% boost in CP in the stem and a 14% drop in the leaves (Halim et al. 1989). Forage grasses and legumes exhibited analogous tendencies. Where soil phosphorus levels are low, animal output may be constrained because phosphorus concentrations are often low in water-stressed feed (Abdel Rahman et al. 1971). Elevated levels of alkalinity, hydrocyanic acid, or tannins in forages might diminish their appeal (Hoveland and Monson 1980). Grass that has been sitting in the rain for too long or that grows in low-lying regions may have a high call wall content but low CP (Pate and Snyder 1979). Lower cell wall digestibility from increased lignifications is a common result of high growing temperatures, which has important implications for food quality (Ford et al. 1979). High temperatures have a more noticeable impact on grass quality than legume quality. Plants cultivated at low temperatures are more digestible than those produced at high temperatures, despite the fact that both had the same age at harvest (Fig. 3). A decrease in the N content and digestibility of grasses and tropical legumes may accompany the effect of drought on production and composition of forage legumes and grasses in tropical climates (Wilson and Mannetje 1978).

3.5.1 Nutritional Factors

Fodder, horticultural, vegetable, forest, livestock, and fishery production are all impacted by climate change, as is the capacity to supply the world's ever-increasing food demand. Rapid climate change hinders ecosystems' and species' ability to adapt, speeding up biodiversity loss. Human security is threatened by climate change and the corresponding loss of biodiversity because of the potential for drastic shifts in the food chain on which we rely, the potential for water sources to change, recede, or disappear, and the potential for medicines and other resources to be affected. It may become more challenging for humans to get some resources if plant and flora populations decline or disappear. Climate change in the region has had a significant impact on a wide range of physical and biological systems, and there are signs to suggest it has also had an impact on social and economic structures. As a result of the summer monsoon circulation, India's climate and weather are dominated by the world's most significant seasonal mode of precipitation. Precipitation variability beyond this seasonal mode is primarily inter-annual and intra-seasonal, resulting in extremes in seasonal anomalies that cause widespread droughts and floods and short-period precipitation extremes that take the form of torrential downpours or protracted breaks on the synoptic scale. In addition, India's climate has cold waves throughout the north during the winter and hot waves in the bulk of the nation during the pre-monsoon season. As a significant natural catastrophe connected to climatic extremes, tropical cyclones are responsible for severe destruction and loss of life when they strike coastal areas with heavy rain, strong winds, and storm surges. Human activities are affected by these extremes, thus more attention is needed from all levels of society to combat this threat.

3.5.2 Effect of Climate on Fodder

As a crop or plant, fodder has a high level of variety and the ability to withstand moderate effects of climate change. However, in any particular area, the predominating source of feed is the vegetation and animals that evolved there organically. However, there is a wide range in the development and production capacity of excellent green fodder due to the fact that different cultivable cereals fodder, roughes, legumes, trees, and perennial grasses have distinct climatic requirements. Green forage varied in composition and quality as the climate did. In addition, the same affected the health of animals and the quality of animal products.

3.5.3 Effect of Climate on Livestock

Loss of grazing land, a shortage of forage because of slowing growth and lower green fodder yield (GFY), and lower milk, egg, and meat production are the most notable consequences of climate change for the livestock industry. There will be a drop in income and an increase in rural residents' need for food stamps and

unemployment as a result of all these factors. Weather and extreme events have direct effects on animal health, growth, and reproduction; (a) the availability and cost of livestock feed grains; (b) the production and quality of pastures and forage crops used in livestock production; (c) the distribution of livestock diseases and pests; and (d) the direct effects of weather on livestock. However, it is unclear how global climate change may affect animal productivity because most research has been conducted in industrialised nations and very little in Africa, Asia, and South America. Threats to the animal husbandry industry include habitat loss, altered environmental conditions, disease outbreaks, reproductive obstacles, and decreased productivity.

References

Abdel Rahman AA, Shalaby AF, El Monayeri MO (1971) Effect of moisture stress on metabolic products and ions accumulation. Plant Soil 34:65–90. https://doi.org/10.1007/BF01372762

Abu-Elsaoud AM, Abdel-Azeem AM (2020) Light, electromagnetic spectrum, and photostimulation of microorganisms with special reference to chaetomium. In: Abdel-Azeem AM (ed) Recent developments on genus chaetomium, fungal biology. Springer, Cham, pp 377–393. https://doi.org/10.1007/978-3-030-31612-9_14

Achatz B, von Rüden S, Andrade D, Neumann E, Pons-Kühnemann J, Kogel K-H, Franken P, Waller F (2010) Root colonization by Piriformospora indica enhances grain yield in barley under diverse nutrient regimes by accelerating plant development. Plant Soil 333:59–70. https://doi.org/10.1007/s11104-010-0319-0

Afkhami ME, Strauss SY (2016) Native fungal endophytes suppress an exotic dominant and increase plant diversity over small and large spatial scales. Ecology 97:1159–1169. https://doi.org/10.1890/15-1166.1

Aguilar-Trigueros CA, Rillig MC (2016) Effect of different root endophytic fungi on plant community structure in experimental microcosms. Ecol Evol 6:8149–8158. https://doi.org/10.1002/ece3.2416

Ahmed AU, Islam K, Reazuddin M (1996) An inventory of greenhouse gas emissions in Bangladesh: initial results. R Swed Acad Sci Ambio 25:300–303

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag Adapt For For Manag Chang Clim 259:660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Archaux F, Wolters V (2006) Impact of summer drought on forest biodiversity: what do we know? Ann For Sci 63:645–652. https://doi.org/10.1051/forest:2006041

Arnold AE, Engelbrecht BMJ (2007) Fungal endophytes nearly double minimum leaf conductance in seedlings of a neotropical tree species. J Trop Ecol 23:369–372

Arnold AE, Lutzoni F (2007) Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? Ecology 88:541–549. https://doi.org/10.1890/05-1459

Aschehoug ET, Metlen KL, Callaway RM, Newcombe G (2012) Fungal endophytes directly increase the competitive effects of an invasive forb. Ecology 93:3–8. https://doi.org/10.1890/11-1347.1

Aschehoug ET, Callaway RM, Newcombe G, Tharayil N, Chen S (2014) Fungal endophyte increases the allelopathic effects of an invasive forb. Oecologia 175:285–291. https://doi.org/10.1007/s00442-014-2891-0

Atkin OK, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. Trends in Plant Science 8:343–351. https://doi.org/10.1016/S1360-1385(03)00136-5

Atkin OK, Bloomfield KJ, Reich PB, Tjoelker MG, Asner GP, Bonal D, Bönisch G, Bradford MG, Cernusak LA, Cosio EG, Creek D, Crous KY, Domingues TF, Dukes JS, Egerton JJG, Evans JR, Farquhar GD, Fyllas NM, Gauthier PPG, Gloor E, Gimeno TE, Griffin KL, Guerrieri R, Heskel MA, Huntingford C, Ishida FY, Kattge J, Lambers H, Liddell MJ, Lloyd J, Lusk CH, Martin RE, Maksimov AP, Maximov TC, Malhi Y, Medlyn BE, Meir P, Mercado LM, Mirotchnick N, Ng D, Niinemets Ü, O'Sullivan OS, Phillips OL, Poorter L, Poot P, Prentice IC, Salinas N, Rowland LM, Ryan MG, Sitch S, Slot M, Smith NG, Turnbull MH, VanderWel MC, Valladares F, Veneklaas EJ, Weerasinghe LK, Wirth C, Wright IJ, Wythers KR, Xiang J, Xiang S, Zaragoza-Castells J (2015) Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. New Phytol 206:614–636. https://doi.org/10.1111/nph.13253

Augé RM (2001) Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. Mycorrhiza 11:3–42. https://doi.org/10.1007/s005720100097

Bais AF, McKenzie RL, Bernhard G, Aucamp PJ, Ilyas M, Madronich S, Tourpali K (2015) Ozone depletion and climate change: impacts on UV radiation. Photochem Photobiol Sci 14:19–52. https://doi.org/10.1039/C4PP90032D

Barazani O, Benderoth M, Groten K, Kuhlemeier C, Baldwin IT (2005) Piriformospora indica and Sebacina vermifera increase growth performance at the expense of herbivore resistance in Nicotiana attenuata. Oecologia 146:234–243. https://doi.org/10.1007/s00442-005-0193-2

Beardall J, Sobrino C, Stojkovic S (2009) Interactions between the impacts of ultraviolet radiation, elevated CO2, and nutrient limitation on marine primary producers. Photochem Photobiol Sci 8:1257–1265. https://doi.org/10.1039/b9pp00034h

Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296:1692–1694. https://doi.org/10.1126/science.1071329

Beaugrand G, Brander KM, Alistair Lindley J, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–664. https://doi.org/10.1038/nature02164

Behie SW, Bidochka MJ (2014) Nutrient transfer in plant-fungal symbioses. Trends Plant Sci 19:734–740. https://doi.org/10.1016/j.tplants.2014.06.007

Bever JD, Platt TG, Morton ER (2012) Microbial population and community dynamics on plant roots and their feedbacks on plant communities. Annu Rev Microbiol 66:265–283. https://doi.org/10.1146/annurev-micro-092611-150107

Björn LO (ed) (2015) Photobiology. Springer, New York

Boelen P, Obernostere I, Vink AA, Buma AGJ (1999) Attenuation of biologically effective UV radiation in tropical Atlantic waters measured with a biochemical DNA dosimeter. Photochem Photobiol 69:34–40. https://doi.org/10.1111/j.1751-1097.1999.tb05303.x

Boyd PW, Strzepek R, Fu F, Hutchins DA (2010) Environmental control of open-ocean phytoplankton groups: now and in the future. Limnol Oceanogr 55:1353–1376. https://doi.org/10.4319/lo.2010.55.3.1353

Braga GUL, Rangel DEN, Fernandes ÉKK, Flint SD, Roberts DW (2015) Molecular and physiological effects of environmental UV radiation on fungal conidia. Curr Genet 61:405–425. https://doi.org/10.1007/s00294-015-0483-0

Britt AB (1996) DNA damage and repair in plants. Annu Rev Plant Physiol Plant Mol Biol 47:75–100. https://doi.org/10.1146/annurev.arplant.47.1.75

Buma A, Zemmelink H, Sjollema K, Gieskes W (1996) UVB radiation modifies protein and photosynthetic pigment content, volume and ultrastructure of marine diatoms. Mar Ecol Prog Ser 142:47–54. https://doi.org/10.3354/meps142047

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427:731–733. https://doi.org/10.1038/nature02322

Callaway RM, Bedmar EJ, Reinhart KO, Silvan CG, Klironomos J (2011) Effects of soil biota from different ranges on Robinia invasion: acquiring mutualists and escaping pathogens. Ecology 92:1027–1035. https://doi.org/10.1890/10-0089.1

Casadevall A (2019) Global catastrophic threats from the fungal kingdom: fungal catastrophic threats. Curr Top Microbiol Immunol 424:21–32. https://doi.org/10.1007/82_2019_161

Casadevall A (2020) Climate change brings the specter of new infectious diseases. J Clin Investig 130:553–555. https://doi.org/10.1172/JCI135003

Cheplick GP (2004) Recovery from drought stress in Lolium perenne (Poaceae): are fungal endophytes detrimental? Am J Bot 91:1960–1968. https://doi.org/10.3732/ajb.91.12.1960

Ciais P, Chris S, Govindasamy B, Bopp L, Brovkin V, Canadell J, Chhabra A, Defries R, Galloway J, Heimann M (2014) Carbon and other biogeochemical cycles. In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Climate change 2013: the physical science basis. Contribution of Working Group I to the fifth assessment report of the Intergovernmental Panel on Climate Change, pp 465–570

Clay K, Holah J (1999) Fungal endophyte symbiosis and plant diversity in successional fields. Science 285:1742–1745. https://doi.org/10.1126/science.285.5434.1742

Clay K, Shearin ZRC, Bourke KA, Bickford WA, Kowalski KP (2016) Diversity of fungal endophytes in non-native Phragmites australis in the Great Lakes. Biol Invasions 18:2703–2716. https://doi.org/10.1007/s10530-016-1137-y

Cloern JE, Schraga TS, Lopez CB, Knowles N, Grover Labiosa R, Dugdale R (2005) Climate anomalies generate an exceptional dinoflagellate bloom in San Francisco Bay. Geophys Res Lett 32:n/a-n/a. https://doi.org/10.1029/2005GL023321

Cosme M, Lu J, Erb M, Stout MJ, Franken P, Wurst S (2016) A fungal endophyte helps plants to tolerate root herbivory through changes in gibberellin and jasmonate signaling. New Phytol 211:1065–1076. https://doi.org/10.1111/nph.13957

Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. Ecol Lett 8:1175–1182. https://doi.org/10.1111/j.1461-0248.2005.00820.x

Craine JM, Ocheltree TW, Nippert JB, Towne EG, Skibbe AM, Kembel SW, Fargione JE (2013) Global diversity of drought tolerance and grassland climate-change resilience. Nat Clim Chang 3:63–67. https://doi.org/10.1038/nclimate1634

Crous KY (2019) Plant responses to climate warming: physiological adjustments and implications for plant functioning in a future, warmer world. Am J Bot 106:1049–1051. https://doi.org/10.1002/ajb2.1329

Crous KY, Quentin AG, Lin Y-S, Medlyn BE, Williams DG, Barton CVM, Ellsworth DS (2013) Photosynthesis of temperate Eucalyptus globulus trees outside their native range has limited adjustment to elevated CO2 and climate warming. Glob Chang Biol 19:3790–3807. https://doi.org/10.1111/gcb.12314

Crous KY, Drake JE, Aspinwall MJ, Sharwood RE, Tjoelker MG, Ghannoum O (2018) Photosynthetic capacity and leaf nitrogen decline along a controlled climate gradient in provenances of two widely distributed Eucalyptus species. Glob Chang Biol 24:4626–4644. https://doi.org/10.1111/gcb.14330

Damian DL, Matthews YJ, Phan TA, Halliday GM (2011) An action spectrum for ultraviolet radiation-induced immunosuppression in humans. Br J Dermatol 164:657–659. https://doi.org/10.1111/j.1365-2133.2010.10161.x

Dawson W, Schrama M (2016) Identifying the role of soil microbes in plant invasions. J Ecol 104:1211–1218. https://doi.org/10.1111/1365-2745.12619

de Crecy E, Jaronski S, Lyons B, Lyons TJ, Keyhani NO (2009) Directed evolution of a filamentous fungus for thermotolerance. BMC Biotechnol 9:74. https://doi.org/10.1186/1472-6750-9-74

DOE (1997) Global climate change – Bangladesh episode. Department of Environment

Doughty CE, Goulden ML (2008) Are tropical forests near a high temperature threshold? J Geophys Res 113:n/a–n/a. https://doi.org/10.1029/2007JG000632

Dusenge ME, Duarte AG, Way DA (2019) Plant carbon metabolism and climate change: elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration. New Phytol 221:32–49. https://doi.org/10.1111/nph.15283

Elmi AA, West CP (1995) Endophyte infection effects on stomatal conductance, osmotic adjustment and drought recovery of tall fescue. New Phytol 131:61–67. https://doi.org/10.1111/j.1469-8137.1995.tb03055.x

El-Sayed A, Kamel M (2020) Climatic changes and their role in emergence and re-emergence of diseases. Environ Sci Pollut Res Int 27:22336–22352. https://doi.org/10.1007/s11356-020-08896-w

Evans SE, Wallenstein MD (2012) Soil microbial community response to drying and rewetting stress: does historical precipitation regime matter? Biogeochemistry 109:101–116

Farber DA (2021) The intersection of international disaster law and climate change law. YIDO 2:87–115. https://doi.org/10.1163/26662531_00201_005

Feeley KJ, Joseph Wright S, Nur Supardi MN, Kassim AR, Davies SJ (2007) Decelerating growth in tropical forest trees. Ecol Lett 10:461–469. https://doi.org/10.1111/j.1461-0248.2007.01033.x

Fisher MC, Henk DA, Briggs CJ, Brownstein JS, Madoff LC, McCraw SL, Gurr SJ (2012) Emerging fungal threats to animal, plant and ecosystem health. Nature 484:186–194. https://doi.org/10.1038/nature10947

Ford C, Wilson J (1981) Changes in levels of solutes during osmotic adjustment to water stress in leaves of four tropical pasture species. Funct Plant Biol 8:77. https://doi.org/10.1071/PP9810077

Ford C, Morrison I, Wilson J (1979) Temperature effects on lignin, hemicellulose and cellulose in tropical and temperate grasses. Aust J Agric Res 30:621. https://doi.org/10.1071/AR9790621

Fourtouni A, Manetas Y, Christias C (1998) Effects of UV-B radiation on growth, pigmentation, and spore production in the phytopathogenic fungus *Alternaria solani*. Can J Bot 76:2093–2099. https://doi.org/10.1139/b98-170

Fu F, Tatters A, Hutchins D (2012) Global change and the future of harmful algal blooms in the ocean. Mar Ecol Prog Ser 470:207–233. https://doi.org/10.3354/meps10047

Garcia-Solache MA, Casadevall A (2010) Global warming will bring new fungal diseases for mammals. mBio 1:e00061–e00010. https://doi.org/10.1128/mBio.00061-10

Garnica S, Riess K, Schön ME, Oberwinkler F, Setaro SD (2016) Divergence times and phylogenetic patterns of sebacinales, a highly diverse and widespread fungal lineage. PLoS One 11:e0149531. https://doi.org/10.1371/journal.pone.0149531

Gill SS, Gill R, Trivedi DK, Anjum NA, Sharma KK, Ansari MW, Ansari AA, Johri AK, Prasad R, Pereira E, Varma A, Tuteja N (2016) Piriformospora indica: potential and significance in plant stress tolerance. Front Microbiol 7:332

Godde CM, Mason-D'Croz D, Mayberry DE, Thornton PK, Herrero M (2021) Impacts of climate change on the livestock food supply chain; a review of the evidence. Glob Food Sec 28:100488. https://doi.org/10.1016/j.gfs.2020.100488

Görner H (1994) New trends in photobiology: photochemistry of DNA and related biomolecules: quantum yields and consequences of photoionization. J Photochem Photobiol B Biol 26:117–139. https://doi.org/10.1016/1011-1344(94)07068-7

Gunderson CA, O'Hara KH, Campion CM, Walker AV, Edwards NT (2009) Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate: photosynthetic acclimation to warmer climates. Glob Chang Biol 16:2272–2286. https://doi.org/10.1111/j.1365-2486.2009.02090.x

Halim RA, Buxton DR, Hattendorf MJ, Carlson RE (1989) Water-stress effects on alfalfa forage quality after adjustment for maturity differences. Agron J 81:189–194. https://doi.org/10.2134/agronj1989.00021962008100020010x

Harsch MA, HilleRisLambers J (2016) Climate warming and seasonal precipitation change interact to limit species distribution shifts across Western North America. PLoS One 11:e0159184. https://doi.org/10.1371/journal.pone.0159184

He Y-Y, Häder D-P (2002) UV-B-induced formation of reactive oxygen species and oxidative damage of the cyanobacterium Anabaena sp.: protective effects of ascorbic acid and N-acetyl-l-cysteine. J Photochem Photobiol B Biol 66:115–124. https://doi.org/10.1016/S1011-1344(02)00231-2

Higgins KL, Coley PD, Kursar TA, Arnold AE (2011) Culturing and direct PCR suggest prevalent host generalism among diverse fungal endophytes of tropical forest grasses. Mycologia 103:247–260. https://doi.org/10.3852/09-158

Hogue VE, Wilkerson FP, Dugdale RC (2005) Ultraviolet-B radiation effects on natural phytoplankton assemblages of Central San Francisco Bay. Estuaries 28:190–203. https://doi.org/10.1007/BF02732854

Houghton JT, Jenkins GJ, Ephraums JJ (eds) (1990) Climate change: the IPCC scientific assessment. Cambridge University Press, Cambridge/New York

Hoveland CS, Monson WG (1980) Genetic and environmental effects on forage quality. In: Crop quality, storage, and utilization. Wiley, pp 139–168. https://doi.org/10.2135/1980.cropquality.c6

Huang S-J, Lin C-P, Mau J-L, Li Y-S, Tsai S-Y (2015) Effect of UV-B irradiation on physiologically active substance content and antioxidant properties of the medicinal caterpillar fungus Cordyceps militaris (Ascomycetes). Int J Med Mushrooms 17:241–253. https://doi.org/10.1615/intjmedmushrooms.v17.i3.40

Inderjit, van der Putten WH (2010) Impacts of soil microbial communities on exotic plant invasions. Trends Ecol Evol 25:512–519. https://doi.org/10.1016/j.tree.2010.06.006

Jones RL (ed) (2013) The molecular life of plants. Chichester/Hoboken, Wiley-Blackwell

Jones RL, Ougham H, Thomas H, Waaland S (eds) (2013) The molecular life of plants. Wiley-Blackwell, Chichester/Hoboken

Kane KH (2011) Effects of endophyte infection on drought stress tolerance of Lolium perenne accessions from the Mediterranean region. Environ Exp Bot 71:337–344. https://doi.org/10.1016/j.envexpbot.2011.01.002

Kannadan S, Rudgers JA (2008) Endophyte symbiosis benefits a rare grass under low water availability. Funct Ecol 22:706–713. https://doi.org/10.1111/j.1365-2435.2008.01395.x

Kivlin SN, Hawkes CV, Treseder KK (2011) Global diversity and distribution of arbuscular mycorrhizal fungi. Soil Biol Biochem 43:2294–2303. https://doi.org/10.1016/j.soilbio.2011.07.012

Kivlin SN, Emery SM, Rudgers JA (2013) Fungal symbionts alter plant responses to global change. Am J Bot 100:1445–1457. https://doi.org/10.3732/ajb.1200558

Kleczewski NM, Bauer JT, Bever JD, Clay K, Reynolds HL (2012) A survey of endophytic fungi of switchgrass (Panicum virgatum) in the Midwest, and their putative roles in plant growth. Fungal Ecol 5:521–529. https://doi.org/10.1016/j.funeco.2011.12.006

Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417:67–70. https://doi.org/10.1038/417067a

Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. Science 291:481–484. https://doi.org/10.1126/science.291.5503.481

Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298:2202–2205. https://doi.org/10.1126/science.1076347

Lauenroth WK, Sala OE (1992) Long-term forage production of North American shortgrass Steppe. Ecol Appl 2:397–403. https://doi.org/10.2307/1941874

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology: the metacommunity concept. Ecol Lett 7:601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Madronich S, McKenzie RL, Björn LO, Caldwell MM (1998) Changes in biologically active ultraviolet radiation reaching the Earth's surface. J Photochem Photobiol B Biol 46:5–19. https://doi.org/10.1016/S1011-1344(98)00182-1

Malinowski DP, Belesky DP (2000) Adaptations of endophyte-infected cool-season grasses to environmental stresses: mechanisms of drought and mineral stress tolerance. Crop Sci 40:923–940. https://doi.org/10.2135/cropsci2000.404923x

Mangla S, Callaway RM (2008) Exotic invasive plant accumulates native soil pathogens which inhibit native plants. J Ecol 96:58–67. https://doi.org/10.1111/j.1365-2745.2007.01312.x

Marcoval MA, Villafañe VE, Helbling EW (2007) Interactive effects of ultraviolet radiation and nutrient addition on growth and photosynthesis performance of four species of marine phytoplankton. J Photochem Photobiol B 89:78–87. https://doi.org/10.1016/j.jphotobiol.2007.09.004

Marland G (1990) Global and natural CO 2 emission from fossil fuel burning, cement production and gas, planning. In: Boden TA, Kancirk P, Farvell MP (eds) TRENDS' 1990: a compensation of date on global change. ORNL/CDIAC-36. Carbon Dioxide Information Analysis Centre, Oak Ridge National, Oak Ridge, pp 92–93

Maron JL, Klironomos J, Waller L, Callaway RM (2014) Invasive plants escape from suppressive soil biota at regional scales. J Ecol 102:19–27. https://doi.org/10.1111/1365-2745.12172

Márquez LM, Redman RS, Rodriguez RJ, Roossinck MJ (2007) A virus in a fungus in a plant: three-way symbiosis required for thermal tolerance. Science 315:513–515. https://doi.org/10.1126/science.1136237

Márquez S, Bills G, Zabalgogeazcoa I (2008) Diversity and structure of the fungal endophytic assemblages from two sympatric coastal grasses. Fungal Divers 33:87–100

Martiny JBH, Eisen JA, Penn K, Allison SD, Horner-Devine MC (2011) Drivers of bacterial beta-diversity depend on spatial scale. Proc Natl Acad Sci U S A 108:7850–7854. https://doi.org/10.1073/pnas.1016308108

Mayerhofer MS, Kernaghan G, Harper KA (2013) The effects of fungal root endophytes on plant growth: a meta-analysis. Mycorrhiza 23:119–128. https://doi.org/10.1007/s00572-012-0456-9

McKenzie RL, Aucamp PJ, Bais AF, Björn LO, Ilyas M, Madronich S (2011) Ozone depletion and climate change: impacts on UV radiation. Photochem Photobiol Sci 10:182–198. https://doi.org/10.1039/c0pp90034f

Meehl G, Stocker T, Collins W, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, JM M, Noda A, Raper S, Watterson IG, Weaver A, Zhao Z-C (2007) Global climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Climate change 2007: the physical science basis. Cambridge University Press, New York, pp 747–845

Meinhardt KA, Gehring CA (2012) Disrupting mycorrhizal mutualisms: a potential mechanism by which exotic tamarisk outcompetes native cottonwoods. Ecol Appl 22:532–549. https://doi.org/10.1890/11-1247.1

Mercado LM, Medlyn BE, Huntingford C, Oliver RJ, Clark DB, Sitch S, Zelazowski P, Kattge J, Harper AB, Cox PM (2018) Large sensitivity in land carbon storage due to geographical and temporal variation in the thermal response of photosynthetic capacity. New Phytol 218:1462–1477. https://doi.org/10.1111/nph.15100

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625–627. https://doi.org/10.1038/nature01317

Morse LJ, Faeth SH, Day TA (2007) Neotyphodium interactions with a wild grass are driven mainly by endophyte haplotype. Funct Ecol 21:813–822. https://doi.org/10.1111/j.1365-2435.2007.01285.x

Morsy MR, Oswald J, He J, Tang Y, Roossinck MJ (2010) Teasing apart a three-way symbiosis: transcriptome analyses of Curvularia protuberata in response to viral infection and heat stress. Biochem Biophys Res Commun 401:225–230. https://doi.org/10.1016/j.bbrc.2010.09.034

Nnadi NE, Carter DA (2021) Climate change and the emergence of fungal pathogens. PLoS Pathog 17:e1009503. https://doi.org/10.1371/journal.ppat.1009503

Oberhofer M, Güsewell S, Leuchtmann A (2014) Effects of natural hybrid and non-hybrid Epichloë endophytes on the response of Hordelymus europaeus to drought stress. New Phytol 201:242–253. https://doi.org/10.1111/nph.12496

Omacini M, Chaneton EJ, Ghersa CM, Müller CB (2001) Symbiotic fungal endophytes control insect host-parasite interaction webs. Nature 409:78–81. https://doi.org/10.1038/35051070

Pate FM, Snyder GH (1979) Effect of high water table in organic soil on yield and quality of forage grasses-Lysimeter study. Proc Soil Crop Sci Soc Fla 38:72–75

Peay KG, Garbelotto M, Bruns TD (2010) Evidence of dispersal limitation in soil microorganisms: isolation reduces species richness on mycorrhizal tree islands. Ecology 91:3631–3640. https://doi.org/10.1890/09-2237.1

Redman RS, Sheehan KB, Stout RG, Rodriguez RJ, Henson JM (2002) Thermotolerance generated by plant/fungal symbiosis. Science 298:1581. https://doi.org/10.1126/science.1072191

Reinhart KO, Packer A, Van der Putten WH, Clay K (2003) Plant–soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. Ecol Lett 6:1046–1050. https://doi.org/10.1046/j.1461-0248.2003.00539.x

Rho H, Hsieh M, Kandel SL, Cantillo J, Doty SL, Kim S-H (2018) Do endophytes promote growth of host plants under stress? A meta-analysis on plant stress mitigation by endophytes. Microb Ecol 75:407–418. https://doi.org/10.1007/s00248-017-1054-3

Riess K, Oberwinkler F, Bauer R, Garnica S (2014) Communities of endophytic sebacinales associated with roots of herbaceous plants in agricultural and grassland ecosystems are dominated by Serendipita herbamans sp. nov. PLoS One 9:e94676. https://doi.org/10.1371/journal.pone.0094676

Rodriguez R, Redman R (2008) More than 400 million years of evolution and some plants still can't make it on their own: plant stress tolerance via fungal symbiosis. J Exp Bot 59:1109–1114. https://doi.org/10.1093/jxb/erm342

Rodriguez RJ, Henson J, Van Volkenburgh E, Hoy M, Wright L, Beckwith F, Kim Y-O, Redman RS (2008) Stress tolerance in plants via habitat-adapted symbiosis. ISME J 2:404–416. https://doi.org/10.1038/ismej.2007.106

Rodriguez RJ, White JF Jr, Arnold AE, Redman RS (2009) Fungal endophytes: diversity and functional roles. New Phytol 182:314–330. https://doi.org/10.1111/j.1469-8137.2009.02773.x

Rodriguez RJ, Woodward C, Redman RS (2010) Adaptation and survival of plants in high stress habitats via fungal endophyte conferred stress tolerance. In: Seckbach J, Grube M (eds) Symbioses and stress, cellular origin, life in extreme habitats and astrobiology. Springer, Dordrecht, pp 461–476. https://doi.org/10.1007/978-90-481-9449-0_23

Rudgers JA, Koslow JM, Clay K (2004) Endophytic fungi alter relationships between diversity and ecosystem properties. Ecol Lett 7:42–51. https://doi.org/10.1046/j.1461-0248.2003.00543.x

Rudgers JA, Mattingly WB, Koslow JM (2005) Mutualistic fungus promotes plant invasion into diverse communities. Oecologia 144:463–471. https://doi.org/10.1007/s00442-005-0039-y

Schoof JT, Pryor SC, Surprenant J (2010) Development of daily precipitation projections for the United States based on probabilistic downscaling. J Geophys Res Atmos 115. https://doi.org/10.1029/2009JD013030

Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang H-P, Harnik N, Leetmaa A, Lau N-C, Li C, Velez J, Naik N (2007) Model projections of an imminent transition to a more arid climate in Southwestern North America. Science 316:1181–1184. https://doi.org/10.1126/science.1139601

Shipunov A, Newcombe G, Raghavendra AKH, Anderson CL (2008) Hidden diversity of endophytic fungi in an invasive plant. Am J Bot 95:1096–1108. https://doi.org/10.3732/ajb.0800024

Solomon S, Intergovernmental Panel on Climate Change (eds) (2007) Climate change 2007: the physical science basis: contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge/New York

Stinson KA, Campbell SA, Powell JR, Wolfe BE, Callaway RM, Thelen GC, Hallett SG, Prati D, Klironomos JN (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. PLoS Biol 4:e140. https://doi.org/10.1371/journal.pbio.0040140

Tilman D, El Haddi A (1992) Drought and biodiversity in grasslands. Oecologia 89:257–264. https://doi.org/10.1007/BF00317226

Torres S, González-Ramírez M, Gavilán J, Paz C, Palfner G, Arnold N, Fuentealba J, Becerra J, Pérez C, Cabrera-Pardo JR (2019) Exposure to UV-B radiation leads to increased deposition of cell wall-associated xerocomic acid in cultures of Serpula himantioides. Appl Environ Microbiol 85:e00870–e00819. https://doi.org/10.1128/AEM.00870-19

US EPA, O (2022) Climate change indicators: atmospheric concentrations of greenhouse gases [WWW document]. https://www.epa.gov/climate-indicators/climate-change-indicators-atmospheric-concentrations-greenhouse-gases. Accessed 13 Aug 2022

van de Poll WH, Alderkamp A-C, Janknegt PJ, Roggeveld J, Buma AGJ (2006) Photoacclimation modulates excessive photosynthetically active and ultraviolet radiation effects in a temperate and an Antarctic marine diatom. Limnol Oceanogr 51:1239–1248. https://doi.org/10.4319/lo.2006.51.3.1239

van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA, Suding KN, Van de Voorde TFJ, Wardle DA (2013) Plant–soil feedbacks: the past, the present and future challenges. J Ecol 101:265–276. https://doi.org/10.1111/1365-2745.12054

Villafañe VE, Janknegt PJ, de Graaff M, Visser RJW, van de Poll WH, Buma AGJ, Walter Helbling E (2008) UVR-induced photoinhibition of summer marine phytoplankton communities from Patagonia. Mar Biol 154:1021–1029. https://doi.org/10.1007/s00227-008-0993-0

Vincent WF, Neale PJ (2000) Mechanisms of UV damage to aquatic organisms. In: De Mora S, Demers S, Vernet M (eds) The effects of UV radiation in the marine environment. Cambridge University Press, pp 149–176. https://doi.org/10.1017/CBO9780511535444.007

Waldrop MP, Firestone MK (2006) Response of microbial community composition and function to soil climate change. Microb Ecol 52:716–724. https://doi.org/10.1007/s00248-006-9103-3

Waller F, Achatz B, Baltruschat H, Fodor J, Becker K, Fischer M, Heier T, Hückelhoven R, Neumann C, von Wettstein D, Franken P, Kogel K-H (2005) The endophytic fungus Piriformospora indica reprograms barley to salt-stress tolerance, disease resistance, and higher yield. Proc Natl Acad Sci U S A 102:13386–13391. https://doi.org/10.1073/pnas.0504423102

Watson RT, Rodhe OH, Oeschger H, Siegenthaler U (1990) Greenhouse gases and aerosols. In: Houghton JT, Jenkins GJ, Ephraums JJ (eds) Climate change: the IPCC scientific assessment. Cambridge University Press

Watson RT, Meira Filho LG, Sanhueza E, Janetos A (1992) Greenhouse gases: sources and sinks. In: Houghton JT, Calander BA, Varney SK (eds) Climate change 1992. Supplementary report to the IPCC scientific assessment. Cambridge University Press, Cambridge

Way DA, Oren R (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiol 30:669–688. https://doi.org/10.1093/treephys/tpq015

Way DA, Sage RF (2008) Thermal acclimation of photosynthesis in black spruce [*Picea mariana* (Mill.) B.S.P.]. Plant Cell Environ 31:1250–1262. https://doi.org/10.1111/j.1365-3040.2008.01842.x

Weiß M, Sýkorová Z, Garnica S, Riess K, Martos F, Krause C, Oberwinkler F, Bauer R, Redecker D (2011) Sebacinales everywhere: previously overlooked ubiquitous fungal endophytes. PLoS One 6:e16793. https://doi.org/10.1371/journal.pone.0016793

Williamson CE, Zepp RG, Lucas RM, Madronich S, Austin AT, Ballaré CL, Norval M, Sulzberger B, Bais AF, McKenzie RL, Robinson SA, Häder D-P, Paul ND, Bornman JF (2014) Solar ultraviolet radiation in a changing climate. Nat Clim Chang 4:434–441. https://doi.org/10.1038/nclimate2225

Wilson JR (1983) Effects of water stress on herbage quality, in: proceedings of the XIV international grassland congress. CRC Press

Wilson JR, Mannetje L (1978) Senescence, digestibility and carbohydrate content of buffel grass and green panic leaves in swards. Aust J Agric Res 29:503–516. https://doi.org/10.1071/ar9780503

Wilson JR, Ng TT (1975) Influence of water stress on parameters associated with herbage quality of Panicum maximum var. trichoglume. Aust J Agric Res 26:127–136. https://doi.org/10.1071/ar9750127

Wu X, Lu Y, Zhou S, Chen L, Xu B (2016) Impact of climate change on human infectious diseases: empirical evidence and human adaptation. Environ Int 86:14–23. https://doi.org/10.1016/j.envint.2015.09.007

Xu P, Chen F, Mannas JP, Feldman T, Sumner LW, Roossinck MJ (2008) Virus infection improves drought tolerance. New Phytol 180:911–921. https://doi.org/10.1111/j.1469-8137.2008.02627.x

Zhang H-N, Ma H-L, Zhou C-S, Yan Y, Yin X-L, Yan J-K (2016) Enhanced production and antioxidant activity of endo-polysaccharides from Phellinus igniarius mutants screened by low power He-Ne laser and ultraviolet induction. Bioact Carbohydr Diet Fibre 15:30–36. https://doi.org/10.1016/j.bcdf.2016.11.006