

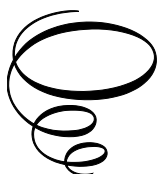
Present Status and Prospects of Plant Associated Fungi

Present Status and Prospects of Plant Associated Fungi

Edited by

Saba Siddiqui, Vineet Meshram,
Roopa Sangvikar Patil and Mahiti Gupta

**Cambridge
Scholars
Publishing**



Present Status and Prospects of Plant Associated Fungi

Edited by Saba Siddiqui, Vineet Meshram, Roopa Sangvikar Patil
and Mahiti Gupta

This book first published 2024

Cambridge Scholars Publishing

Lady Stephenson Library, Newcastle upon Tyne, NE6 2PA, UK

British Library Cataloguing in Publication Data

A catalogue record for this book is available from the British Library

Copyright © 2024 by Saba Siddiqui, Vineet Meshram, Roopa Sangvikar Patil,
Mahiti Gupta and contributors

All rights for this book reserved. No part of this book may be reproduced,
stored in a retrieval system, or transmitted, in any form or by any means,
electronic, mechanical, photocopying, recording or otherwise, without
the prior permission of the copyright owner.

ISBN: 978-1-0364-0808-4

ISBN (Ebook): 978-1-0364-0809-1

TABLE OF CONTENTS

Chapter 1	1
Phylogenetic Diversity of Endophytic <i>Colletotrichum</i> Species and their Biotechnological Potential	
Gunjan Sharma, Marcel Maymon, Stanley Freeman	
Chapter 2	34
Horizontal Gene Transfer: A Significant Phenomenon in the Evolution and the Adaptation of Plant-associated Endophytes	
Ami Naik, Pragy Tiwari, Hanhong Bae, Laurent Dufosse	
Chapter 3	57
Exploring the Rich Diversity of Endophytic Fungi: Insights from Different Ecological Habitats	
Aditi Gupta, Sumit Satpaty, Kamlesh Kumar Shukla	
Chapter 4	77
Diversity of Manglicolous Yeasts Associated with Phylloplane of Mangrove Plants in Central Kerala	
K.A. Nimsi, K. Manjusha	
Chapter 5	95
Diversity of Wild Mushrooms Geasters from Fungal Wealth of Jharkhand	
Vineet Vishal, Geetanjali Singh, Shalini Lal	
Chapter 6	132
Diversity, Ecology and Adaptations of Mycorrhizal Fungi	
Goskula Kiran, Konathachira Sreeja, Ankam Shashank, Ponaganti Shiva Kishore, Veera Suresh, N. Sumlatha	
Chapter 7	156
Wood Rotting Fungi Associated with <i>Taxus baccata</i>	
Avneet Pal Singh, Ellu Ram, Avneet Kaur, Haradesh Kumar	

Chapter 8	180
Diversity of Ectomycorrhizal Mushrooms in Tropical Sal (<i>Shorea robusta</i>) Forest of Central India	
Samay Tirkey, Srishti Verma, RV Shukla, Kamlesh Shukla	
Chapter 9	199
Biochemical Analysis of Healthy and Infected Mulberry Leaves	
Mukti Sharma, Imran Ahmad Salmani, Tarun Yadav, Lukman Ahamad, Harendra Kumar	
Chapter 10	218
Genomic Approaches for <i>Botrytis</i> Grey Mould Resistance Gene-Discovery in Winter Pulse Crops	
Supriya Sachdeva, C. Bharadwaj, Neeraj Kumar, Neha Tiwari, D. R. Saxena, Upasana Rani	
Chapter 11	266
Endophytic Fungi: Present in Different Medicinal Plants and their Ability to Produce Bioactive Compounds of Medicinal Importance	
Debajani Das, Tikendrajit Baro, Papia Das, Sandeep Das	
Chapter 12	285
Antioxidative Potential of Rhizosphere Soil Fungi	
Nethravathy V, Aqsa Alam, Swagatika Priyadarshini L. A., Ankita Kalita	
Chapter 13	309
<i>Amanita muscaria</i> , an Ectomycorrhizal Fungus with Untapped Bioactive Potential	
Shachar Jerushalmi, Joshua Fooks, Stanley Freeman	
Chapter 14	321
Metabolic Engineering Initiatives in Fungi for Enhanced Production of Functional Food	
Pragya Tiwari, Laurent Dufosse	
Chapter 15	337
Fungal Endophytes: A Promising Future in Pharmaceuticals	
Sana Sheikh, Roseanne Mascarenhas, Sareen Sheikh	

Chapter 16	351
Metabolites of Fungi and Applications in the Agricultural	
Laith Khalil Tawfeeq Al-Ani, Ivana Mitrović, Beata Zimowska,	
Mohammad Sharif Sarker, Mitzuko Dautt-Castro, Syeda Fasiha Amjad,	
Ghulam Hussain Jatoi, Surono Surono, Lobna Hajji-Hedfi,	
Dalia Sukmawati	
Chapter 17	398
A Review on Plant Growth Promoting Ability of Fungal Endophytes	
Karthika M., Rasmi A.R.	
Chapter 18	415
Fungal Endophytes: Alleviating Biotic and Abiotic Stressors in Plants	
G. Razia Sulthana Begum, Rishu Sharma	
Chapter 19	454
The Role of Plant Associated Fungi on Secondary Metabolism	
in Corroboration with Stress in Crop Species	
Gulzar A. Rather, Arti Manhas, Noopur Sharma	
Chapter 20	481
Role of Endophytic Fungi in Bioremediation	
Madhavi Tiwari, Aditi Gupta, Ashish Saraf, Kamlesh Kumar Shukla	
Chapter 21	500
Arbuscular Mycorrhizal Fungi Can Promote Stress Tolerance in Plants	
Ravneet Kaur, Harleen Kaur, Swapnil Singh, Neetu Jagota, Ashish	
Sharma	
Chapter 22	531
Arbuscular Mycorrhizal Fungi (AMF): Role in Mitigating Biotic Stress	
in Plants	
Lopamudra Behera, Shraddha Bhaskar Sawant, Saswati Premkumari,	
Ashal Ilyas, Dilip Kumar Chaurasiya, Shailendra Singh	
Chapter 23	564
Cadmium (Cd) Tolerance and Mitigation in Plants: The Role	
of Arbuscular Mycorrhizal Fungi (AMF)	
Dipanjali Ray, Sibor Boro, Uma Rai, Pallavi Sharma, Papia Das,	
Sandeep Das	

Chapter 24	584
Plant Associated Fungi: Application and Promises in Pharmaceutical and Other Industries	
Uma Rai, Dipanjali Ray, Sibor Boro, Pallavi Sharma, Papia Das, Sandeep Das	

CHAPTER 1

PHYLOGENETIC DIVERSITY OF ENDOPHYTIC *COLLETOTRICHUM* SPECIES AND THEIR BIOTECHNOLOGICAL POTENTIAL

GUNJAN SHARMA¹, MARCEL MAYMON²,
STANLEY FREEMAN²

¹Department of Plant Biotechnology, Gujarat Biotechnology University,
Gandhinagar, Gujarat, India.

²Department of Plant Pathology and Weed Research, Agricultural
Research Organization, Volcani Institute, Rishon LeZion, Israel.

Abstract

Colletotrichum is a phylogenetically complex fungal genus exhibiting pathogenic, saprobic, and endophytic lifestyles with their host plants. This genus is reported to be associated with diverse host crops, including ornamentals, fruits, and vegetables worldwide. The growth and physiology of a host plant may benefit from the occurrence of endophytic fungal species. Additionally, fungal endophytes have been reported to protect their hosts from plant pests and pathogens. Colletotrichin, Colletotric acid, and Colletotricone are some commonly reported secondary metabolites from *Colletotrichum* species, with phytotoxic, antimicrobial, and cytotoxic activities, respectively. *Colletotrichum acutatum*, *C. boninense*, and *C. gloeosporioides* are some of the common species complexes reported as pathogens and endophytes. It is important to study and characterize in detail the various secondary metabolites produced by *Colletotrichum* species, to understand more about their survival strategies and sustainability. This chapter discusses the diversity of endophytic *Colletotrichum* species, the secondary metabolites produced, and their potential biotechnological applications.

Keywords: antimicrobial properties, bioactive compounds, diversity, endophytic fungi, secondary metabolites

1. *Colletotrichum* genus: a cluster of complexes

Colletotrichum is a genus of filamentous fungi (family Glomerellaceae, class Sordariomycetes). *Colletotrichum* taxonomy has experienced multiple revisions over the past decade. Currently, there are more than 200 accepted species names in this genus that are designated within 15 species complexes (Hyde et al. 2009, Damm et al. 2012a, b, Cannon et al. 2012, Weir et al. 2012, Crouch 2014, Liu et al. 2014, Bhunjun et al. 2021, Damm et al. 2019, Talhinhos and Baroncelli 2021). *Colletotrichum* is a common plant pathogen causing anthracnose disease in a wide range of plant hosts, including ornamentals, cereals, legumes, and fruits (Dean et al. 2012, Sharma et al. 2013a, 2015, 2017, 2022); and is considered a model genus to study plant-pathogen interactions (Perfect et al. 1999). *Colletotrichum* species are also common foliar endophytes within a wide range of host plants (Manamgoda et al. 2013, De Silva et al. 2017) and a variety of bioactive secondary metabolites have been reported from endophytic *Colletotrichum* species (Kim and Shim 2019).

2. *Colletotrichum*: versatile lifestyles

Colletotrichum species exhibit diverse lifestyles and survival strategies (Agrios 2004). An endophytic fungal species exists as a beneficial symbiont within its host and has no detrimental effects on its growth. Necrotrophic fungi are responsible for causing disease and tissue damage in their host plant. Hemibiotrophic fungi require a living plant host for their existence and eventually switch to a necrotrophic lifestyle causing disease. *Colletotrichum* species commonly exhibit a hemibiotrophic lifestyle (Münch et al. 2008) but can also be present in its host as a necrotroph and an endophyte (Peres et al. 2005, O'Connell et al. 2012, Crouch et al. 2014, De Silva et al. 2017). Some *Colletotrichum* species are host-specific, whereas others have a broad host range (Freeman et al. 1998, De Silva et al. 2017, Talhinhos and Baroncelli 2021), others can cause disease in certain hosts while the same species can remain asymptomatic in weeds and other crops (Freeman et al. 2001).

3. *Colletotrichum*: as an endophyte

Endophytic *Colletotrichum* species have been reported from boninense (Damm et al. 2012b, Huang et al. 2013), caudatum (Tao et al. 2013), dematium (Damm et al. 2009; Jayawardena et al. 2016), dracaenophilum (Noireung et al. 2012), gigasporum (Silva et al. 2018, Ma et al. 2018; Zhou et al. 2019), gloeosporioides (Rojas et al. 2010, Weir et al. 2012, Manamgoda et al. 2013, Diao et al. 2017; Ferreira et al. 2017, Vieira et al. 2017, Ma et al. 2018, De Silva et al. 2019a, Wang et al. 2019, De Silva et al. 2021, Silva et al. 2021), graminicola (Crouch and Beirn 2009, Tao et al. 2013), magnum (Damm et al. 2019), orbiculare (Katoch et al. 2017) and spathianum (Tao et al. 2013) species complexes (Talhinhas and Baroncelli 2021). Besides, two singleton species, *C. bambusicola* and *C. guangxiense* are also reported as endophytic (Wang et al. 2021).

The diversity of *Colletotrichum* endophytes associated with common tropical grass species: *Pennisetum purpureum* (dwarf Napier) and *Cymbopogon citratus* (lemon grass) in Thailand was investigated, and *C. endophytica*, *C. fruticola*, *C. tropicale* and *C. siamense* species with gloeosporioides species complex were reported (Manamgoda et al. 2013). *Colletotrichum aeshchynomene* belonging to gloeosporioides species complex, was reported as an endophytic species associated with *Vellozia gigantea*, an endangered plant species in Brazil (Ferreira et al. 2017). In a study on *Colletotrichum* diversity associated with *Mangifera indica* in Brazil, *C. asianum*, *C. fruticola*, *C. tropicale*, *C. karstii*, *C. cliviae*, *C. endomangiferae*, *C. dianesei* were reported (Vieira et al. 2014). *Colletotrichum* endophytes have also been reported from the model plant *Arabidopsis thaliana* in Spain (Hiruma et al. 2016).

Within the gigasporum species complex, an endophytic species was isolated from *Cattleya jongheana*, a rare orchid species, in Brazil and described as *C. serranegrense* based on multilocus phylogenetic analysis (Da Silva et al. 2018). In China, *C. jishouense* belonging to gigasporum species complex and *C. tongrenenses* belonging to the dracaenophilum species complex were isolated from tissue extracts of the *Nothapodytes pittosporoides* plant, which is widely used in traditional Chinese medicine, suggesting the role of these endophytic fungi in the therapeutic properties of *N. pittosporoides* (Zhou et al. 2019). In another study with three orchid species, *Dendrobium cariniferum*, *D. catenatum*, and *D. harveyanum*; multiple *Colletotrichum* species were identified as endophytes (Ma et al. 2018). Similarly, two endophytic species, *C. yulongense* and *C. rhombiforme* were reported from *Vaccinium dunalianum* var. *urophyllum*, a cultivated blueberry and an

important medicinal plant in China (Wang et al. 2019). Endophytic *Colletotrichum* species belonging to boninense and gloeosporioides species complexes were also reported from aquatic plants in China (Zheng et al. 2022). Furthermore, mutations in *C. magna* resulted in the conversion of a pathogenic strain to a nonpathogenic endophytic mutualist (Freeman and Rodriguez, 1993).

4. Endophytic *Colletotrichum* species: phylogenetic diversity and distribution

To perform phylogenetic analysis and create a neighbour-joining tree (NJ), (Saitou and Nei 1987), more than 600 sequences of the internal transcribed spacer/5.8S rRNA gene (ITS) of the endophytic *Colletotrichum* species were downloaded from NCBI-GenBank (accessed on May 01, 2023), of which 150 sequences were used for phylogenetic analysis (selected based on sequence length and unique names). As previously described (Sharma et al. 2013b), a phylogenetic tree was created using MEGA 11 software (Tamura et al. 2021) with bootstrap analysis (Felsenstein 1985) of 100 replicates (Figure 1), representing the most reported endophytic *Colletotrichum* species. Endophytic species of *Colletotrichum* are widely reported within gloeosporioides and boninense species complexes; however, accurate species designation using multilocus phylogenetic analysis is lacking in most cases. This chapter uses the ITS sequence to create a representative phylogenetic tree, as it is the widely sequenced marker available at NCBI-GenBank (accessed on May 01, 2023).

Based on sequence search, endophytic *Colletotrichum* species are reported from tropical medicinal hosts such as *Ageratina adenophora* (Mexican devil), *Albizia lebbbeck* (Siris tree), *Anemopsis californica* (Yerba mansa), *Artemisia* spp., *Blepharocalyx salicifolius* (Kunth), *Cinnamomum malabatrums* (Country cinnamon), *Citrus limon* (Lemon), *Dacrycarpus dacrydioides* (Kahikatea), *Dendrobium aqueum* (Orchid), *Fraxinus* spp. (Ash tree), *Ginkgo biloba* (Maidenhair tree), *Gynura procumbens* (Longevity spinach), *Huperzia serrata* (Toothed clubmoss), *Lycium* spp. (Goji berry), *Phragmites australis* (Common reed), *Tibouchinha granulosa* (Purple Glory Tree), *Vitex negundo* (Chinese chastetree) etc.; and countries including Argentina, Brazil, Cameroon, China, Denmark, India, Malaysia, New Zealand, Panama, South Korea, Spain and USA; as detailed in Supplementary Table 1.

5. Endophytic *Colletotrichum* species: biotechnological potential

Endophytic microbes possess a unique symbiotic relationship with their host plant species (Ludwig-Müller 2015). Endophytic fungi secrete secondary metabolites and enzymes that benefit plants' growth and development, and in return, plants provide nutrition and shelter to endophytic fungi (Mishra et al. 2021, Poveda et al. 2021, Baron and Rigobelo 2022). Secondary metabolites produced by endophytic fungi can act as effector molecules and facilitate multifaceted plant-microbe interactions (Alam et al. 2021). These intricate plant-microbe interactions lead to the production of bioactive metabolites, which exhibit a variety of properties such as antimicrobial, antioxidant, anticancer, immunosuppressive, and cardioprotective activities (Wen et al. 2022, Omomowo et al. 2023). Endophytes also have a role in biocontrol against various plant pathogens and pests (Latz et al. 2018, De Silva et al. 2019b, Fontana et al. 2021). In this chapter, we focus on the latest reports of endophytic fungi and their metabolites and bioactivities from 2010 onwards. The structures of selected secondary metabolites (Table 1) derived from *Colletotrichum* species, discussed in this chapter are provided in Figure 2.

6. *Colletotrichum*: epigenetic regulation and secondary metabolite biosynthesis

Endophytic *Colletotrichum* species produce secondary metabolites that are organic, natural, and bioactive compounds having significant role in ecological interactions as well as in pharmaceutical industries. The structural and biological properties of secondary metabolites from *Colletotrichum* such as Colletotrichins, Colletotric acid, and Colletotrichones are well documented (García-Pajón and Collado 2003, Kim and Shim 2019, Moraga et al. 2019). However, there are limited reports on the molecular mechanisms of the synthesis and epigenetic regulation of *Colletotrichum* secondary metabolites (Brakhage et al. 2011).

Histone modification via methylation, demethylation, acetylation, and deacetylation has a role in the secondary metabolite production of various fungi (Bok et al. 2009, Connolly et al. 2013, Studt et al. 2016). In *C. higginsianum* that causes anthracnose in brassica species, deletion of the *CclA* subunit of the COMPASS complex mediating methylation of Histone H3 lysine K4 (H3K4) in eukaryotes resulted in the enrichment of the production of three terpenoid family secondary metabolites: colletochlorins

(colletorin A and colletochlorins A, B, and D, colletorin D, colletorin D acid.), higginsianins (higginsianin A, B, and C, 13-epi-higginsianin C), and sclerosporide (Dallery et al. 2019).

Huperzine A (HupA) is a secondary metabolite important as a therapeutic for the treatment of Alzheimer's disease. Hup A is produced by *C. gloeosporioides* isolate Cg01 under the activity of histone methyltransferase (HMT) and histone deacetylase (HDAC) (Kang et al. 2019). Previously, it was reported that ethanol and methanol treatment of *C. gloeosporioides* isolate ES026 mycelia can improve Huperzine production (Zhao et al. 2013). This is another cogent evidence of the importance of epigenetic regulation to produce industrially important fungal secondary metabolites.

Epigenetic regulation mediated by histone modification is also important in the pathogenesis of *Colletotrichum* species. In *C. fructicola*, causing Glomerella leaf spot in apples, deletion of the HDAC gene *Cfhos2* along with transcriptome sequence data suggests its role in secondary metabolism and virulence (Cao et al. 2022). In China, Histone Acetyltransferase (HAT) gene *CfGcn5* of *C. fructicola*, causing anthracnose of *Camellia oleifera*, was revealed to be involved in the regulation of autophagy-related genes and pathogenesis (Zhang et al. 2022).

7. *Colletotrichum*: therapeutics

With a rise in lifestyle-related diseases and increasing awareness of traditional herbal medications and supplements, researchers are focused on discovering novel bioactive metabolites for therapeutics. *Colletotrichum* endophytes have also been explored for their potential to produce bioactive metabolites for therapeutics. Endophytic *C. gigasporum* isolated from *Withania somnifera* produced pentacyclic triterpenoids (PTT) that had inhibitory effects on pancreatic lipase (PL) providing an alternative treatment for obesity (Patil et al. 2021). Kojic acid derived from *C. gloeosporioides* isolated from *Sonneratia apetala* exhibited antimicrobial activity against *Pseudomonas aeruginosa* and *Micrococcus luteus* (Nurunnabi et al. 2018). *Colletotrichum coccodes* isolated from the healthy leaf tissues of *Houttuynia cordata* (chameleon plant) exhibited antimicrobial activity against *Staphylococcus aureus* strain MTCC 737, *Pseudomonas aeruginosa* strain MTCC 424, *Escherichia coli* strain MTCC 443, and *Candida albicans* strain MTCC 227. Further characterization of secondary metabolites revealed that *C. coccodes* isolate HCS3 produced antimicrobial metabolites such as geranylgeraniol, farnesol, hexacosanol, oleic acid, and squalene (Talukdar et al. 2020). In another study, a widely known

phenylethanoid compound, tyrosol was reported from the same fungal isolate that exhibited antimicrobial activity (Talukdar et al. 2021). *Colletotrichum gloeosporioides* isolate LC585212 which was isolated as an endophyte from *Ocimum indicum* produced thirty-five different bioactive compounds that exhibited antitumor and antiproliferative activity by altering the expression of apoptosis-related genes (Rai et al. 2023).

Phosphoinositide 3-kinases (PI3Ks) is an enzyme family involved in cell growth and proliferation. PI3Ks are important targets for anti-cancer therapy. *Colletotrichum gloeosporioides* GT-7 isolated from *Uncaria rhynchophylla* produced nine compounds, of which Cyclo(L-leucyl-L-leucyl) and Brevianamide F compounds exhibited PI3K α -inhibitory activity suggesting their potential use as anticancer compounds (Yang et al. 2019). Five isocoumarins and a novel phthalide compound were isolated from an endophytic *Colletotrichum* sp. that exhibited potent radical scavenging and antioxidant activities (Tianpanich et al. 2011). Endophytic *C. dematium* isolated from *Pteromischum* sp. produced a novel immunosuppressive peptide, Colutellin A, that is active against the pathogenic fungal species *Botrytis cinerea* and *Sclerotinia sclerotiorum* (Ren et al. 2008).

8. *Colletotrichum*: plant growth properties

Endophytic fungi co-exist within plant tissues and support the overall growth and development of their host plant. Lu et al. (2000) reported endophytic *Colletotrichum* sp. isolated from the stem of *Artemisia annua*, that produced three new antimicrobial compounds, along with seven known bioactive metabolites and the plant hormone Indole-3-acetic acid (IAA). These compounds displayed antimicrobial activity against plant pathogenic bacterial species such as *Bacillus subtilis*, *Staphylococcus aureus*, *Sarcina lutea*, and *Pseudomonas* sp.; and plant pathogenic fungi such as *Gaeumannomyces graminis* var. *tritici*, *Rhizoctonia cerealis*, *Helminthosporium sativum*, and *Phytophthora capsici*. *Colletotrichum siamense* isolates JB224.g1 and JB252.g1 had positive effects on the growth of tomato plants, including protection against vascular wilt pathogen *F. oxysporum* (Silva Santos et al. 2022). *Colletotrichum tofieldiae* was isolated as a root endophyte from natural *Arabidopsis thaliana* populations in Spain and exhibited plant growth promotion properties by assisting in the transfer of phosphorus to shoots under phosphorus stress conditions (Hiruma et al. 2016). *Colletotrichum tofieldiae* isolate Ct0861 conferred growth and enhanced silique production in *A. thaliana* under low phosphate conditions (Díaz-González et al. 2020). In another study, the role of the phosphorylated pathway of serine

biosynthesis (PPSB) was linked to the biosynthesis of indolic glucosinolate and plant growth promotion activity of the root endophyte *C. tofieldiae* in *A. thaliana* (Zimmermann et al. 2021).

Plant biomass and the artemisinin content of *Artemisia annua* were increased after treatment with an endophytic isolate of *C. gloeosporioides* (Wang et al. 2001, Hussain et al. 2017). IAA production by endophytic fungi is widely reported (Waqas et al. 2012, Khan et al. 2015, Ikram et al. 2018, Mehmood et al. 2019) which accelerates plant growth. Among endophytic fungi isolated from *Coffea arabica* in Thailand, *C. fruticola* isolate CMU-A109 produced IAA via the indole 3-acetamide pathway and induced elongation of rice, corn, and rye coleoptiles (Numponsak et al. 2018). *Colletotrichum alatae* R10 isolated from the roots of *Dendrobium moniliforme*, produced high levels of IAA and contributed to the development of the protocorms and higher chlorophyll content in *Rhynchostylis retusa* (Shah et al. 2018).

9. *Colletotrichum*: biocontrol agents

Endophytic *Colletotrichum* species are important as biocontrol agents against different plant pathogens, mainly fungi. In China, endophytic *Colletotrichum* sp. D4115 exhibited antifungal activity against common plant pathogens *C. gloeosporioides*, *Scopulariopsis* sp., and *Trichoderma viride* (Li et al. 2005). *Colletotrichum gloeosporioides* isolate Mc-7 isolated from the leaves of *Michelia champaca* exhibited antifungal activity against phytopathogenic fungi *Cladosporium cladosporioides* and *C. sphaerospermum*. Additionally, the same isolate displayed antitumor and acetylcholinesterase inhibition properties by producing different bioactive metabolites (Chapla et al. 2014). An endophytic *C. gloeosporioides* isolated from *Camellia sinensis* in Assam, India, conferred resistance against two common tea pathogens, *Pestalotiopsis theae* and *Colletotrichum camelliae* (Rabha et al. 2014). In another study, *C. crassipes* was isolated as an endophyte from the leaves of *Casearia sylvestris* that displayed antifungal activity and biosynthesis of a novel natural product, 1-phenylethyl-*O*- α -*L*-rhamnopyranoside, along with other known diketopiperazines and benzene derivatives (Chapla et al. 2018). Endophytic *C. siamense* isolated from healthy leaves of *Paullinia cupana* var. *sorbilis* (Guarana plants), elicited the induction of defence-related genes and exhibited antifungal activity against *C. fruticola* species (Casas et al. 2021). Furthermore, a mutation in *C. magna* resulted in conversion from a pathogen to an endophytic mutualist, conferring the

protection of watermelon to the wild type and Fusarium wilt disease (Freeman and Rodriguez, 1993).

10. Conclusions and future directions

Endophytic fungi are beneficial fungi that inhabit host plant tissues and produce bioactive secondary metabolites and growth hormones that are important for plant-microbe interactions. More than hundred secondary metabolites have been reported so far from *Colletotrichum* species (Kim and Shin 2019). The secondary metabolites produced by endophytic *Colletotrichum* species are structurally diverse and have biotechnological applications in various industries, such as agriculture, pharmaceuticals, nutraceuticals, and cosmetics. The biosynthesis of secondary metabolites is regulated via various regulatory genes and epigenetic mechanisms that should be investigated in detail. The molecular understanding of biosynthesis and regulation of fungal secondary metabolites could be further utilised in industries for large-scale production of commercially important metabolites.

Figure 1: Neighbor-joining phylogenetic tree of selected endophytic *Colletotrichum* species based on internal transcribed spacer (ITS) sequence. The NCBI-GenBank accession number of the sequence has been highlighted in dark blue and the isolate numbers are highlighted in red font colour. *Plagiostoma conradii* strain CBS 109761 is the designated outgroup taxon.



Figure 2: Chemical structures of selected secondary metabolites derived from *Colletotrichum* species, discussed in this chapter.

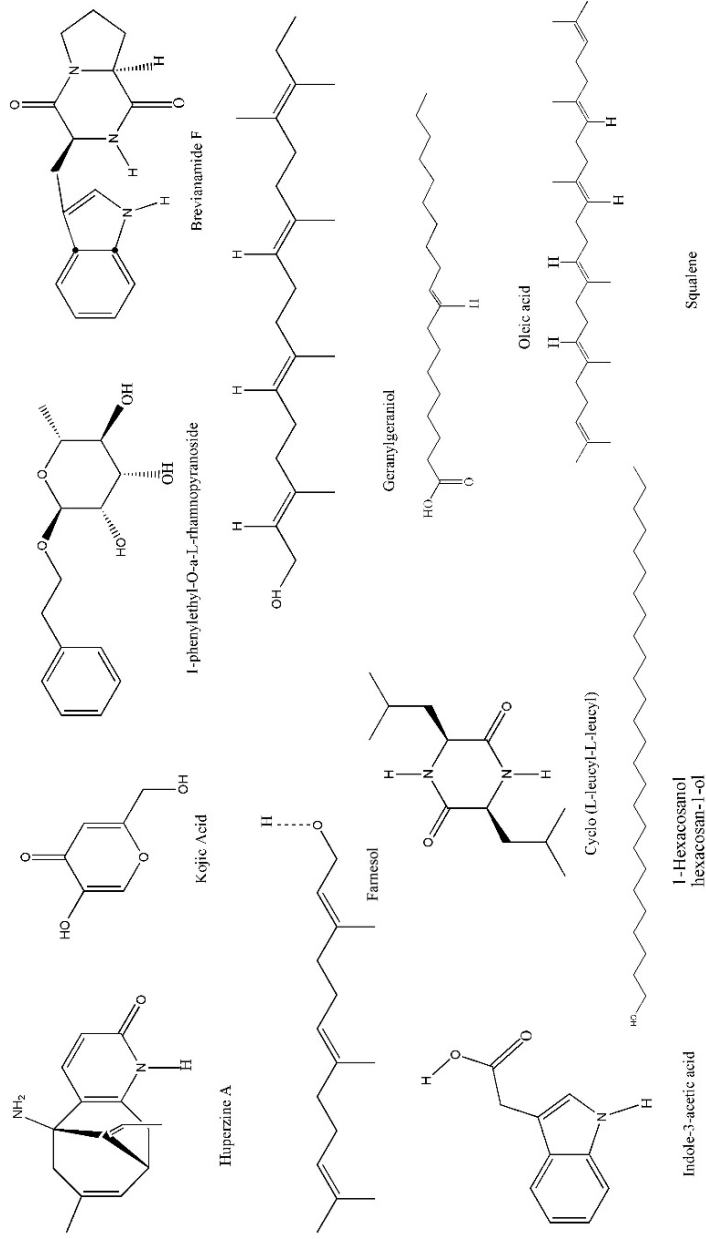


Table 1: List of selected secondary metabolites derived from *Colletotrichum* species, discussed in this chapter.

<i>Colletotrichum</i> sp.	Secondary metabolite	Property	Reference
<i>C. coccodes</i>	Geranylgeraniol	Antimicrobial	Talukdar et al. 2020
<i>C. coccodes</i>	Farnesol	Antimicrobial	Talukdar et al. 2020
<i>C. coccodes</i>	Hexacosanol	Antimicrobial	Talukdar et al. 2020
<i>C. coccodes</i>	Squalene	Antimicrobial	Talukdar et al. 2020
<i>C. coccodes</i>	Oleic acid	Antimicrobial	Talukdar et al. 2020
<i>C. crassipes</i>	1-phenylethyl- <i>O</i> - α - <i>L</i> -rhamnopyranoside	Antifungal	Chapla et al. 2018
<i>C. fruticola</i>	Indole-3-acetic acid	Plant growth promotion	Numponsak et al. 2018
<i>C. gloeosporioides</i>	Huperzine A	Therapeutic	Kang et al. 2019
<i>C. gloeosporioides</i>	Kojic acid	Antimicrobial	Nurunnabi et al. 2018
<i>C. gloeosporioides</i>	Cyclo(<i>L</i> -leucyl- <i>L</i> -leucyl)	Anticancer	Yang et al. 2019
<i>C. gloeosporioides</i>	Brevianamide F	Anticancer	Yang et al. 2019

Supplementary Table 1: List of sequences used in the phylogenetic analysis.

GenBank accession number	Taxon	Isolate	Host	Country
GQ407097	<i>Colletotrichum gloeosporioides</i>	13MA/L	<i>Musa acuminata</i>	Malaysia
GU227826	<i>Colletotrichum dematium</i>	CBS:11552 4	<i>Vitis vinifera</i>	South Africa
HM585395	<i>Colletotrichum liriopes</i>	CORCS1	<i>Pleione bulbocodioides</i>	China
HM585400	<i>Colletotrichum boninense</i>	CORCS2	<i>Pleione bulbocodioides</i>	China
HM585405	<i>Colletotrichum karstii</i>	CORCS4	<i>Pleione bulbocodioides</i>	China
HM585410	<i>Colletotrichum crassipes</i>	CORCS3	<i>Pleione bulbocodioides</i>	China
JF288549	<i>Colletotrichum gloeosporioides</i>	SPs8-1	<i>Sarracenia psittacina</i>	USA
JN588550	<i>Colletotrichum gloeosporioides</i>	NJSC8	<i>Ginkgo biloba</i>	China
JQ005216	<i>Colletotrichum karstii</i>	CBS:12495 6	<i>Zamia obliqua</i>	Panama
JQ005233	<i>Colletotrichum parsoniae</i>	CBS:12852 5	<i>Parsonsia capsularis</i>	New Zealand
JQ005236	<i>Colletotrichum dacrycarpi</i>	CBS:13024 1	<i>Dacrycarpus dacrydioides</i>	New Zealand

	Chapter 1	
JQ814365	E153	<i>Hevea brasiliensis</i> Brazil
JX436791	CK13b7	<i>Citrus limon</i> Cameroon
JX436792	C1b5a	<i>Citrus limon</i> Cameroon
JX436793	C3a1	<i>Citrus limon</i> Cameroon
JX997750	C1361	<i>Cucumis sativus</i> Panama
KC702969	CMM3776	<i>Mangifera indica</i> Brazil
KC702972	CMM3780	<i>Mangifera indica</i> Brazil
KC702974	CMM3782	<i>Mangifera indica</i> Brazil
KC702977	CMM3738	<i>Mangifera indica</i> Brazil
KC702979	CMM3741	<i>Mangifera indica</i> Brazil
KC702980	CMM3742	<i>Mangifera indica</i> Brazil
KC702981	CMM3746	<i>Mangifera indica</i> Brazil
KC702985	CMM3767	<i>Mangifera indica</i> Brazil
KC702986	CMM3768	<i>Mangifera indica</i> Brazil
KC702988	CMM3735	<i>Mangifera indica</i> Brazil
KC702989	CMM3736	<i>Mangifera indica</i> Brazil
KC702990	CMM3797	<i>Mangifera indica</i> Brazil

KC702991	<i>Colletotrichum asianum</i>	CMM3804	<i>Mangifera indica</i>	Brazil
KC702992	<i>Colletotrichum cliviae</i>	CMM3808	<i>Mangifera indica</i>	Brazil
KC702993	<i>Colletotrichum fructicola</i>	CMM3811	<i>Mangifera indica</i>	Brazil
KF907247	<i>Colletotrichum gloeosporioides</i>	UOM J	<i>Vitex negundo</i>	India
KF923853	<i>Colletotrichum gloeosporioides</i>	UOM N	<i>Vitex negundo</i>	India
KJ651254	<i>Colletotrichum fructicola</i>	CNU12203 1	<i>Lycium chinense</i>	South Korea
KJ651255	<i>Colletotrichum brevisporum</i>	CNU12203 2	<i>Lycium chinense</i>	South Korea
KJ651259	<i>Colletotrichum truncatum</i>	CNU12203 6	<i>Lycium chinense</i>	South Korea
KM513575	<i>Colletotrichum boninense</i>	JL7	<i>Huperzia serrata</i>	Korea China
KM513606	<i>Colletotrichum gloeosporioides</i>	JS1	<i>Huperzia serrata</i>	China
KM513609	<i>Colletotrichum acutatum</i>	JS4	<i>Huperzia serrata</i>	China
KM513611	<i>Colletotrichum gloeosporioides</i>	JS6	<i>Huperzia serrata</i>	China
KM513617	<i>Colletotrichum gloeosporioides</i>	JS12	<i>Huperzia serrata</i>	China
KM816755	<i>Colletotrichum coccodes</i>	G112	<i>Anemopsis californica</i>	USA
KM816756	<i>Colletotrichum coccodes</i>	G113	<i>Anemopsis californica</i>	USA

KP689157	<i>Colletotrichum gloeosporioides</i>	FL1	<i>Huperzia serrata</i>	China
KP689204	<i>Colletotrichum gloeosporioides</i>	FS1	<i>Huperzia serrata</i>	China
KP689205	<i>Colletotrichum acutatum</i>	FS2	<i>Huperzia serrata</i>	China
KP689224	<i>Colletotrichum cymbidicola</i>	FS21	<i>Huperzia serrata</i>	China
KP689225	<i>Colletotrichum boninense</i>	FS21	<i>Huperzia serrata</i>	China
KP689226	<i>Colletotrichum gloeosporioides</i>	SL1	<i>Huperzia serrata</i>	China
KP689228	<i>Colletotrichum truncatum</i>	SL3	<i>Huperzia serrata</i>	China
KP689230	<i>Colletotrichum boninense</i>	SL5	<i>Huperzia serrata</i>	China
KP689237	<i>Colletotrichum gloeosporioides</i>	SL12	<i>Huperzia serrata</i>	China
KP689241	<i>Colletotrichum gloeosporioides</i>	SR1	<i>Huperzia serrata</i>	China
KP689255	<i>Colletotrichum gloeosporioides</i>	SS1	<i>Huperzia serrata</i>	China
KP689256	<i>Colletotrichum truncatum</i>	SS2	<i>Huperzia serrata</i>	China
KT795465	<i>Colletotrichum gloeosporioides</i>	CM S 3	<i>Cinnamomum malabattrum</i>	India

KT821351	<i>Colletotrichum karstii</i>	CN1	<i>Blepharocalyx salicifolius</i>	Argentina
KT821352	<i>Colletotrichum boninense</i>	PL1p	<i>Blepharocalyx salicifolius</i>	Argentina
KT821353	<i>Colletotrichum karstii</i>	CN2	<i>Blepharocalyx salicifolius</i>	Argentina
KT821354	<i>Colletotrichum boninense</i>	PL2p	<i>Blepharocalyx salicifolius</i>	Argentina
KT821355	<i>Colletotrichum karstii</i>	CN3	<i>Blepharocalyx salicifolius</i>	Argentina
KT821356	<i>Colletotrichum boninense</i>	PL3p	<i>Blepharocalyx salicifolius</i>	Argentina
KT821357	<i>Colletotrichum karstii</i>	CN4	<i>Blepharocalyx salicifolius</i>	Argentina
KT821358	<i>Colletotrichum boninense</i>	PL4p	<i>Blepharocalyx salicifolius</i>	Argentina
KT821359	<i>Colletotrichum karstii</i>	CN5	<i>Blepharocalyx salicifolius</i>	Argentina
KT821360	<i>Colletotrichum karstii</i>	PL5p	<i>Blepharocalyx salicifolius</i>	Argentina
KT821361	<i>Colletotrichum karstii</i>	CN6	<i>Blepharocalyx salicifolius</i>	Argentina
KT821362	<i>Colletotrichum karstii</i>	PL6p	<i>Blepharocalyx salicifolius</i>	Argentina
KT821363	<i>Colletotrichum karstii</i>	CN7	<i>Blepharocalyx salicifolius</i>	Argentina
KT821364	<i>Colletotrichum boninense</i>	PL7p	<i>Blepharocalyx salicifolius</i>	Argentina
KT821366	<i>Colletotrichum boninense</i>	PL8p	<i>Blepharocalyx salicifolius</i>	Argentina
KT821368	<i>Colletotrichum boninense</i>	PL9p	<i>Blepharocalyx salicifolius</i>	Argentina

KT821369	<i>Colletotrichum karstii</i>	CN10	<i>Blepharocalyx salicifolius</i>	Argentina
KT821370	<i>Colletotrichum boninense</i>	PL10p	<i>Blepharocalyx salicifolius</i>	Argentina
KT821371	<i>Colletotrichum karstii</i>	EP10	<i>Blepharocalyx salicifolius</i>	Argentina
KU356914	<i>Colletotrichum kahawae</i>	DA1	<i>Dendrobium aequum</i>	India
KU356915	<i>Colletotrichum gloeosporioides</i>	DA1	<i>Dendrobium aequum</i>	India
KU356916	<i>Colletotrichum boninense</i>	DA1	<i>Dendrobium aequum</i>	India
KU360628	<i>Colletotrichum truncatum</i>	HCH328	<i>Artemisia brachyloba</i>	Spain
KU360631	<i>Colletotrichum gloeosporioides</i>	HCH334	<i>Artemisia lavandulifolia</i>	Spain
KU555982	<i>Colletotrichum destructivum</i>	DLM125	Coastal plant	South Korea
KU556012	<i>Colletotrichum guajavae</i>	ESO116	Coastal plant	South Korea
KU593526	<i>Colletotrichum alatae</i>	DMW1043	<i>Persea americana</i>	USA
KU727689	<i>Colletotrichum aeshynomenes</i>	UFMGCB9682	<i>Vellozia gigantea</i>	Brazil
KX243296	<i>Colletotrichum acutatum</i>	G242014	Olive	Portugal
KX243297	<i>Colletotrichum acutatum</i>	GAGa2011	Olive	Portugal
KY367488	<i>Colletotrichum acutatum</i>	S1_T32_L3_A	<i>Fraxinus ornus</i>	Switzerland

LC171691	<i>Colletotrichum godetiae</i>	P10	<i>Fraxinus pennsylvanica</i>	Denmark
LC171706	<i>Colletotrichum acutatum</i>	RH10	<i>Fraxinus chinensis</i> subsp. <i>rhynchophylla</i>	Denmark
MF380695	<i>Colletotrichum</i> <i>gigasporum</i>	ALE-90	<i>Albizia lebbeck</i>	India
MF380700	<i>Colletotrichum</i> <i>gloeosporioides</i>	ALE-46	<i>Albizia lebbeck</i>	India
MF380702	<i>Colletotrichum siamense</i>	ALE-67	<i>Albizia lebbeck</i>	India
MF380708	<i>Colletotrichum clivicola</i>	ALE-159	<i>Albizia lebbeck</i>	India
MF380716	<i>Colletotrichum</i> <i>taiwanense</i>	ALE-109	<i>Albizia lebbeck</i>	India
MF380781	<i>Colletotrichum siamense</i>	ALE-179	<i>Albizia lebbeck</i>	India
MF380813	<i>Colletotrichum crassipes</i>	ALE-156	<i>Albizia lebbeck</i>	India
MF380823	<i>Colletotrichum</i> <i>gloeosporioides</i>	ALE-96	<i>Albizia lebbeck</i>	India
MF380869	<i>Colletotrichum siamense</i>	ALE-37	<i>Albizia lebbeck</i>	India
MF380872	<i>Colletotrichum</i> <i>gigasporum</i>	ALE-87	<i>Albizia lebbeck</i>	India
MF380873	<i>Colletotrichum</i> <i>gloeosporioides</i>	ALE-130	<i>Albizia lebbeck</i>	India
MG182676	<i>Colletotrichum clivicola</i>	KCS3a	Soybean	USA
MH102383	<i>Colletotrichum alatae</i>	LCS1	<i>Lycopodium</i>	India

MH370829	<i>Colletotrichum boninense</i>	LA-7	<i>Limonia acidissima</i>	India
MH371126	<i>Colletotrichum alienum</i>	LA-8	<i>Limonia acidissima</i>	India
MK303992	<i>Colletotrichum boninense</i>	Y36	<i>Ageratina adenophora</i>	China
MK304001	<i>Colletotrichum taiwanense</i>	S171	<i>Ageratina adenophora</i>	China
MK304008	<i>Colletotrichum boninense</i>	C56	<i>Ageratina adenophora</i>	China
MK304048	<i>Colletotrichum guajavae</i>	N42	<i>Ageratina adenophora</i>	China
MK304101	<i>Colletotrichum boninense</i>	Y51	<i>Ageratina adenophora</i>	China
MK304115	<i>Colletotrichum clivicola</i>	S34	<i>Ageratina adenophora</i>	China
MK304123	<i>Colletotrichum boninense</i>	N39	<i>Ageratina adenophora</i>	China
MK304227	<i>Colletotrichum boninense</i>	S40	<i>Ageratina adenophora</i>	China
MK304343	<i>Colletotrichum indonesiense</i>	Y53	<i>Ageratina adenophora</i>	China
MK304365	<i>Colletotrichum guajavae</i>	X138	<i>Ageratina adenophora</i>	China
MK304368	<i>Colletotrichum boninense</i>	N41	<i>Ageratina adenophora</i>	China
MK304425	<i>Colletotrichum guajavae</i>	N23	<i>Ageratina adenophora</i>	China
MK446313	<i>Colletotrichum alienum</i>	JS015	<i>Jasminum sambac</i>	India

MN148264	<i>Colletotrichum karstii</i>	Tg13	<i>Tibouchinha granulosa</i>	Brazil
MN148279	<i>Colletotrichum jiangxiense</i>	Tg111	<i>Tibouchinha granulosa</i>	Brazil
MN153755	<i>Colletotrichum brevisporum</i>	BP1569	Bamboo	India
MN202694	<i>Colletotrichum brevisporum</i>	OTU35	Crucifer	China
MN202695	<i>Colletotrichum chlorophyti</i>	OTU35	Crucifer	China
MN202696	<i>Colletotrichum destructivum</i>	OTU37	Crucifer	China
MN202698	<i>Colletotrichum higginsianum</i>	OTU39	Crucifer	China
MN202699	<i>Colletotrichum siamense</i>	OTU40	Crucifer	China
MN202701	<i>Colletotrichum truncatum</i>	OTU42	Crucifer	China
MN611421	<i>Colletotrichum asianum</i>	MT21-5	<i>Mangifera indica</i>	Taiwan
MT012102	<i>Colletotrichum truncatum</i>	SN3	<i>Gynura procumbens</i>	Malaysia
MT012107	<i>Colletotrichum asianum</i>	SN8	<i>Gynura procumbens</i>	Malaysia
MT012108	<i>Colletotrichum brevisporum</i>	SN9	<i>Gynura procumbens</i>	Malaysia
MT012110	<i>Colletotrichum gloeosporioides</i>	SN11	<i>Gynura procumbens</i>	Malaysia

		Chapter 1			
MT068551	<i>Colletotrichum salicis</i>	FREC145	<i>Salix nigra</i>	USA	
MT068552	<i>Colletotrichum fioriniae</i>	Hlb2	<i>Malus domestica</i>	USA	
MT735253	<i>Colletotrichum destructivum</i>	AI_contig_18	<i>Thymus</i> sp.	Saudi Arabia	
MZ509302	<i>Colletotrichum godetiae</i>	AL Col1	<i>Fraxinus</i>	Ireland	
NR 120032	<i>Colletotrichum parsonsiae</i>	CBS	<i>Parsonsia capsularis</i>	New Zealand	
NR 144792	<i>Colletotrichum dacrycarpi</i>	128525 ^T CBS	<i>Dacrycarpus dacrydioides</i>	New Zealand	
OM262257	<i>Colletotrichum magnum</i>	130241		USA	
OM262325	<i>Colletotrichum magnum</i>	clone 074	<i>Phragmites australis</i>	USA	
OP048084	<i>Colletotrichum siamense</i>	clone 163	<i>Phragmites australis</i>	USA	
OQ162348	<i>Colletotrichum gloeosporioides</i>	-	-	India	
OQ518427	<i>Colletotrichum sojae</i>	AAH7-3	<i>Lycium barbarum</i>	Iran	
OQ518428	<i>Colletotrichum sojae</i>	F308.6_R8_	<i>Glycines max</i>	USA	
	<i>Colletotrichum sojae</i>	SD1.9.3UC. 4	<i>Glycines max</i>	USA	
KX929768	<i>Plagiostoma conradii</i>	CBS	<i>Hudsonia tomentosa</i>	USA	
		109761			