ENVIRONMENTAL REPORTS

Review Article
ISSN: 3041-556X
Journal homepage: https://er.researchfloor.org/

Secondary Metabolites of Phytopathogenic Fungi: Roles in Virulence, Host Manipulation and Plant Disease Development

Naina Srivastava

Department of Botany, DAV PG College, Dehradun, 248001, India

Citation: Naina Srivastava (2020). Secondary Metabolites of Phytopathogenic Fungi: Roles in Virulence, Host Manipulation and Plant Disease Development. *Environmental Reports; an International Journal*.
DOI: https://doi.org/10.51470/ER.2020.2.2.08

Corresponding Author: **Naina Srivastava** | E-Mail: **(drnainasrivastava@gmail.com)**

Received 17 July 2020 | Revised 15 August 2020 | Accepted September 21 2020 | Available Online October 13 2020

ABSTRACT

Phytopathogenic fungi produce a diverse array of secondary metabolites that contribute significantly to host colonization, disease development and ecological adaptation. Unlike primary metabolites required for basic growth and reproduction, fungal secondary metabolites often function as chemical mediators during interactions with plants. These compounds include host-selective and non-host-selective toxins, pigments, siderophores, terpenoids, polyketides, alkaloids and other specialized metabolites. Some fungal toxins directly damage plant cells, whereas others interfere with host defense signaling, membrane integrity, photosynthesis, hormone regulation or cellular metabolism. Secondary metabolites can therefore influence fungal virulence even when they are not essential for fungal survival under laboratory conditions. Advances in genomics, metabolomics and molecular genetics have revealed extensive biosynthetic gene clusters in phytopathogenic fungi and provided new insights into the regulation and ecological functions of fungal metabolites. Understanding these compounds is important for disease diagnosis, development of resistant crops and discovery of sustainable approaches to fungal disease management. This review summarizes major classes of secondary metabolites produced by phytopathogenic fungi, their roles in virulence and host manipulation, and their significance in plant disease development.

Keywords: *Phytopathogenic fungi, secondary metabolites, mycotoxins, phytotoxins, virulence, host manipulation, plant disease.*

1. Introduction

Fungal diseases represent one of the major biological constraints to agricultural productivity and food security worldwide. Phytopathogenic fungi infect a wide range of economically important crops and can cause substantial reductions in yield and quality during both pre- and post-harvest stages. Their ability to establish successful infections depends on a complex interaction between fungal pathogenicity mechanisms, host susceptibility and environmental conditions. In addition to hydrolytic enzymes, cell-wall-degrading enzymes, effector proteins and surface structures, fungal secondary metabolites constitute an important group of chemical factors that influence plant–pathogen interactions [1,2]. Secondary metabolites are chemically diverse low-molecular-weight compounds that are generally not required for basic fungal growth, development or reproduction under favorable conditions. Nevertheless, they provide important ecological and competitive advantages under specific environmental circumstances. In phytopathogenic fungi, these compounds can function as phytotoxins, signaling molecules, pigments, siderophores, antioxidants, defense suppressors or modulators of host physiology [3]. Their production is often closely associated with particular stages of infection and may be strongly influenced by host-derived signals, nutrient availability, temperature, pH and other environmental factors. Among fungal secondary metabolites, phytotoxins have received considerable attention because of their direct contribution to plant disease development.

Some toxins cause cellular injury by disrupting membranes, inhibiting protein synthesis, interfering with mitochondrial function or altering photosynthetic activity. Others stimulate excessive accumulation of reactive oxygen species, resulting in oxidative damage and programmed or uncontrolled cell death. In necrotrophic pathogens, toxin-induced host cell death can be particularly advantageous because these fungi obtain nutrients from dead or damaged plant tissues [4,5]. An important feature of fungal phytotoxins is their variation in host specificity. Host-selective toxins interact with particular plant genotypes or species and can determine whether a host is susceptible to infection. Such toxins have been extensively studied in diseases caused by *Alternaria*, *Cochliobolus* and related fungi. In contrast, non-host-selective toxins may affect several plant species and contribute to disease by producing generalized cellular and physiological disturbances. The distinction between these categories is important for understanding the molecular basis of fungal pathogenicity and host resistance [6]. Secondary metabolites can also influence plant defense signaling. Plants respond to fungal invasion through pattern-recognition mechanisms, production of reactive oxygen species, reinforcement of cell walls, synthesis of antimicrobial compounds and activation of hormone-dependent defense pathways. Important signaling molecules include salicylic acid, jasmonic acid and ethylene. Phytopathogenic fungi can interfere with these defense networks through secreted metabolites and other virulence factors, thereby reducing host resistance and facilitating tissue colonization [2,7].

Consequently, fungal secondary metabolism should not be viewed simply as a source of toxic compounds; rather, it represents an important component of the broader molecular interaction between pathogen and host.

The biosynthesis of fungal secondary metabolites is frequently controlled by biosynthetic gene clusters (BGCs) containing genes encoding polyketide synthases, non-ribosomal peptide synthetases, terpene synthases and various modifying enzymes. Genome sequencing has demonstrated that many phytopathogenic fungi contain numerous BGCs, although only a fraction of their predicted metabolites have been experimentally characterized [3,8]. This observation suggests that fungal secondary metabolism represents a largely unexplored reservoir of chemical diversity. The expression of these biosynthetic pathways is regulated by transcription factors, epigenetic mechanisms and environmental signals, and some clusters remain silent under conventional laboratory culture conditions. Recent advances in genomics, transcriptomics, metabolomics and molecular genetics have considerably improved our understanding of fungal secondary metabolism. Comparative genomic studies can identify candidate biosynthetic clusters, whereas metabolomic approaches can associate particular metabolites with infection stages or changes in host physiology. Gene knockout, gene overexpression and genome-editing approaches can subsequently be used to determine whether individual metabolites contribute directly to virulence or merely represent secondary consequences of fungal development [3,8].

The agricultural significance of fungal secondary metabolites extends beyond disease development. Several fungal metabolites can influence microbial competition, nutrient acquisition and interactions with insects and other organisms. Some metabolites may also serve as biomarkers for pathogen detection or indicators of disease progression.

From a crop improvement perspective, identifying the plant receptors and metabolic pathways targeted by fungal toxins can provide valuable information for developing resistant cultivars. Similarly, disruption of fungal metabolite biosynthesis represents a potential target for developing new disease-management strategies. Therefore, understanding secondary metabolites requires an integrated perspective that connects fungal biology, plant physiology, molecular pathology and environmental interactions. This review focuses on the major groups of secondary metabolites produced by phytopathogenic fungi and summarizes their roles in virulence, host manipulation, oxidative stress and plant disease development. Particular emphasis is placed on the emerging contribution of genomic and metabolomic approaches to understanding fungal secondary metabolism and its potential exploitation for sustainable plant disease management.

2. Major Classes of Fungal Secondary Metabolites

Phytopathogenic fungi produce numerous classes of secondary metabolites. Important groups include polyketides, non-ribosomal peptides, terpenoids, alkaloids, phenolic compounds and siderophores. Polyketides constitute one of the largest groups and include several important phytotoxins and mycotoxins. Non-ribosomal peptides include compounds with antimicrobial, toxic and metal-binding properties. Terpenoid metabolites contribute to fungal ecological interactions and may influence host physiology. Siderophores are specialized metabolites that bind iron with high affinity. Because iron is essential for both plants and fungi, siderophore-mediated competition can contribute to successful colonization. Some fungal metabolites also interfere with plant signaling pathways, particularly those involving salicylic acid, jasmonic acid and ethylene.

Table 1. Major secondary metabolites of phytopathogenic fungi and their roles in plant disease

Metabolite group	Representative examples	Major biological roles	Potential effects on plants
Polyketides	Tenuazonic acid, cercosporin, alternariol	Phytotoxicity, oxidative stress, virulence	Tissue damage, chlorosis, necrosis
Host-selective toxins	HC-toxin, T-toxin, victorin	Host specificity and pathogenicity	Membrane damage, susceptibility and cell death
Terpenoids	Trichothecenes, sesquiterpenes	Virulence and host manipulation	Inhibition of protein synthesis, tissue injury
Non-ribosomal peptides	Cyclosporin-like and related compounds	Virulence, competition and signaling	Cellular and physiological disruption
Siderophores	Ferrichrome and related compounds	Iron acquisition and competition	Nutrient competition and altered host physiology
Alkaloids	Ergot alkaloids and related metabolites	Ecological interactions and toxicity	Physiological and biochemical disturbances
Pigments	Melanins and other fungal pigments	Protection and host interaction	Oxidative stress modulation and colonization

3. Fungal Toxins and Plant Disease Development

Fungal toxins are among the most extensively studied secondary metabolites associated with plant disease development. These compounds can act at different stages of infection and may influence host susceptibility, tissue colonization and symptom development. Depending on their chemical structure and biological activity, fungal toxins can interfere with cellular membranes, photosynthesis, respiration, protein synthesis, ion transport and intracellular signaling. Their effects may ultimately result in chlorosis, necrosis, wilting, growth inhibition or premature tissue senescence [4,5]. A particularly important group comprises host-selective toxins (HSTs), which exhibit pronounced toxicity toward particular plant species or genotypes. HSTs are often closely associated with the ability of a pathogen to cause disease in susceptible hosts.

For example, *Alternaria* species produce several host-specific toxins associated with diseases of economically important crops. Similarly, *Cochliobolus carbonum* produces HC-toxin, which contributes to susceptibility in maize, while T-toxin produced by *Cochliobolus heterostrophus* is associated with southern corn leaf blight in susceptible maize lines [6]. These examples demonstrate that a relatively small number of metabolites can have profound effects on the outcome of plant–fungus interactions, non-host-selective toxins can affect a broader range of plant species and generally contribute to disease through nonspecific cellular damage. Such compounds may increase membrane permeability, inhibit metabolic enzymes or induce oxidative stress. The contribution of an individual toxin to disease severity depends on the pathogen species, host genotype, developmental stage and environmental conditions.

Fungal toxins may also function indirectly by modifying host defense responses. Some toxins interfere with antioxidant systems and promote excessive accumulation of reactive oxygen species (ROS). Although ROS are important signaling molecules during plant defense, uncontrolled accumulation can cause lipid peroxidation, protein oxidation, DNA damage and membrane disruption. This creates favorable conditions for necrotrophic pathogens that depend on damaged or dead tissues for nutrient acquisition [7]. Importantly, toxin production is not necessarily constant throughout the fungal life cycle. Pathogens may activate specific biosynthetic pathways during host colonization in response to environmental or host-derived signals. Consequently, the presence of a biosynthetic gene cluster in a fungal genome does not necessarily indicate continuous metabolite production. Understanding when and where individual toxins are synthesized is therefore essential for determining their actual contribution to virulence.

4. Manipulation of Plant Defense Responses

Plants have evolved multilayered defense mechanisms that allow them to recognize and respond to invading microorganisms. Recognition of pathogen-associated molecular patterns can activate pattern-triggered immunity, resulting in calcium signaling, production of ROS, reinforcement of cell walls and synthesis of antimicrobial compounds. In resistant interactions, these responses can restrict fungal growth and prevent extensive colonization. However, successful phytopathogenic fungi have evolved sophisticated mechanisms to suppress, evade or manipulate these defenses [1,2]. Secondary metabolites can participate in this process by interfering with plant signaling networks. One important target is the hormonal signaling system involving salicylic acid (SA), jasmonic acid (JA) and ethylene (ET). SA-mediated responses are generally associated with defense against biotrophic pathogens, whereas JA and ET signaling frequently play important roles in defense against necrotrophic pathogens. Some fungal metabolites can modify the balance between these pathways, thereby creating a physiological environment that favors pathogen development [7].

Fungal metabolites may also influence the production and detoxification of ROS. During the early stages of infection, plants commonly generate ROS as part of their defense response. These molecules can directly inhibit pathogens and activate downstream defense signaling. However, fungal pathogens may manipulate ROS production to produce excessive oxidative stress or suppress effective ROS signaling. Toxin-mediated disruption of antioxidant enzymes can further increase cellular damage and promote disease progression. Another important mechanism involves alteration of plant cell membrane and cell-wall integrity. Certain metabolites interfere with membrane-associated proteins, ion channels or lipid metabolism, resulting in leakage of cellular contents and loss of physiological homeostasis. Others may weaken cell-wall structures or interfere with the plant's ability to reinforce the cell wall following pathogen attack. Such effects facilitate fungal penetration and movement through host tissues.

Secondary metabolites can additionally affect plant metabolism and hormone balance. Changes in photosynthesis, respiration, nutrient allocation and phytohormone concentrations can redirect host resources toward conditions favorable for fungal colonization. In some interactions, fungal compounds may induce premature senescence, providing the pathogen with access to nutrients from aging or damaged tissues.

The interaction between fungal metabolites and plant defense is therefore highly complex. A metabolite may have direct phytotoxic activity while simultaneously altering defense signaling. Consequently, fungal virulence is generally the result of coordinated action involving secondary metabolites, secreted effectors, cell-wall-degrading enzymes and other pathogenicity factors rather than the activity of a single compound [2,8].

5. Biosynthetic Gene Clusters and Regulation

The biosynthesis of fungal secondary metabolites is commonly controlled by biosynthetic gene clusters (BGCs). A typical cluster may contain genes encoding core biosynthetic enzymes, tailoring enzymes, transport proteins, pathway-specific transcription factors and resistance mechanisms. The major enzyme families involved include polyketide synthases (PKSs), non-ribosomal peptide synthetases (NRPSs) and terpene synthases [3,8]. Polyketide synthases are responsible for the biosynthesis of numerous structurally diverse polyketides, including several phytotoxins and mycotoxins. NRPS enzymes generate non-ribosomal peptides with important biological functions, while terpene synthases participate in the formation of terpenoid metabolites. Subsequent modification by oxidases, methyltransferases, glycosyltransferases and other enzymes increases the chemical diversity of the final metabolites. Advances in whole-genome sequencing have revealed that phytopathogenic fungi possess a much greater secondary-metabolite biosynthetic capacity than was previously recognized. Many fungal genomes contain numerous predicted BGCs, but only a proportion of these clusters have been associated with known metabolites. This indicates that a substantial reservoir of unexplored fungal chemical diversity remains available for investigation [3,8]. The expression of BGCs is highly regulated. Environmental conditions such as nutrient availability, temperature, pH, light and oxidative stress can influence secondary-metabolite production. Host-derived compounds may also activate specific pathways during infection. Global regulatory proteins and pathway-specific transcription factors coordinate the expression of biosynthetic genes according to developmental and environmental signals.

Epigenetic regulation has emerged as another important mechanism controlling fungal secondary metabolism. Chromatin structure, histone modifications and DNA-associated regulatory processes can determine whether particular BGCs remain active or transcriptionally silent. Consequently, metabolites that are not detected under standard laboratory conditions may become detectable following changes in culture conditions or targeted manipulation of regulatory pathways. Modern approaches combining genomics, transcriptomics and metabolomics are increasingly being used to connect fungal genes with their corresponding metabolites. Comparative transcriptomic analyses can identify genes activated during plant infection, while metabolomics can reveal changes in metabolite profiles during different stages of disease development. Functional genetic approaches, including gene deletion and targeted genome editing, can then determine whether a specific biosynthetic pathway contributes to fungal growth, virulence or host specificity [3,9]. The discovery of previously uncharacterized BGCs also has practical significance. Some fungal metabolites may represent new phytotoxins, antimicrobial compounds or molecules with pharmaceutical and industrial value. At the same time, identifying virulence-associated pathways can provide targets for disease control.

Inhibition of key biosynthetic enzymes or disruption of pathway-specific regulators may reduce toxin production without necessarily killing the pathogen, representing a potential strategy for developing more targeted and environmentally sustainable disease-management approaches.

6. Secondary Metabolites and Oxidative Stress

Oxidative stress is a central component of many plant–pathogen interactions and is closely associated with the activity of fungal secondary metabolites. Following recognition of a fungal pathogen, plants rapidly generate reactive oxygen species (ROS), including superoxide radicals, hydrogen peroxide and hydroxyl radicals. At controlled concentrations, ROS function as signaling molecules that activate defense responses, strengthen cell walls and stimulate the production of antimicrobial compounds. However, excessive or prolonged ROS accumulation can cause oxidative damage to plant cells and may contribute to disease progression [7]. Phytopathogenic fungi can manipulate this redox balance through secondary metabolites. Some fungal toxins directly stimulate ROS production, whereas others interfere with antioxidant systems responsible for maintaining cellular redox homeostasis. The resulting imbalance can promote lipid peroxidation, protein oxidation, membrane disruption and loss of cellular integrity. Such effects are particularly important for necrotrophic pathogens, which benefit from host tissue death because damaged tissues provide nutrients for fungal growth. Fungal metabolites can also interact with plant antioxidant enzymes, including superoxide dismutase, catalase, peroxidases and glutathione-related enzymes. Suppression of these protective systems can enhance oxidative injury. Conversely, some fungal metabolites may act as antioxidants or redox modulators, suggesting that fungal secondary metabolism does not always have a purely destructive function. The precise outcome depends on the pathogen, metabolite concentration, host genotype and stage of infection.

Oxidative stress is also associated with changes in chloroplast and mitochondrial functions. Some phytotoxins impair photosynthetic electron transport, reducing energy production and increasing ROS generation in chloroplasts. Other metabolites interfere with mitochondrial respiration and cellular energy metabolism. These changes can reduce photosynthetic efficiency and accelerate tissue deterioration. The relationship between fungal metabolites and ROS is therefore dynamic. Plants attempt to maintain ROS at levels that support defense signaling without causing excessive self-damage, while pathogens may manipulate this balance to promote colonization. Understanding these interactions could help identify metabolic pathways associated with resistance and provide opportunities for developing crops with improved antioxidant and detoxification capacities.

7. Ecological and Agricultural Significance

The ecological functions of fungal secondary metabolites extend beyond their direct effects on infected plants. These compounds can influence interactions between fungi, plants, microorganisms, insects and other organisms within agricultural ecosystems. Secondary metabolites may provide competitive advantages by inhibiting neighboring microorganisms, facilitating nutrient acquisition or modifying ecological relationships [3].

One important function is microbial competition. Phytopathogenic fungi frequently encounter bacteria and other fungi in soil and plant tissues. Some secondary metabolites possess antimicrobial properties and can suppress competing microorganisms, thereby creating a more favorable environment for fungal establishment. Other metabolites can influence microbial community composition without producing obvious symptoms in the host plant. Siderophores represent another ecologically important group. These compounds bind iron with high affinity and facilitate fungal iron acquisition under nutrient-limited conditions. Because iron is also essential for plants and other microorganisms, siderophore production can influence competition for this micronutrient and contribute to successful fungal colonization. Secondary metabolites may also affect insects and other organisms associated with diseased plants. Certain fungal compounds can alter insect feeding behavior, toxicity or attraction, potentially influencing pathogen transmission and ecological interactions. These relationships demonstrate that fungal secondary metabolism is part of a broader ecological network rather than an isolated mechanism of plant disease. From an agricultural perspective, understanding fungal metabolites can support disease diagnosis and crop improvement. Specific metabolites may serve as biochemical markers for particular fungal pathogens or disease stages. Combining metabolite detection with molecular diagnostics could allow early identification of infections before extensive visible symptoms appear. Secondary metabolites are also relevant to plant breeding. When a toxin interacts with a specific plant receptor or metabolic pathway, genetic variation in that pathway may determine resistance or susceptibility. Identifying these host factors can assist breeders in developing cultivars that lack sensitivity to important fungal toxins [9-10]. The agricultural importance of secondary metabolites is not limited to disease management. Some fungal metabolites have useful biological activities and may have applications in pharmaceuticals, agriculture and biotechnology. Consequently, systematic investigation of fungal secondary metabolism may contribute both to crop protection and to the discovery of valuable natural products.

8. Management and Future Perspectives

Improved understanding of fungal secondary metabolites provides new opportunities for developing sustainable strategies for plant disease management. Conventional disease control relies heavily on resistant cultivars, fungicides, cultural practices and biological control. However, increasing fungicide resistance, environmental concerns and the emergence of new fungal diseases have created a need for complementary approaches. One promising strategy is targeting fungal toxin biosynthesis rather than directly killing the pathogen. Key enzymes such as polyketide synthases, non-ribosomal peptide synthetases and pathway-specific regulatory proteins may serve as molecular targets. Suppressing these pathways could reduce pathogen virulence and disease severity while potentially exerting less selective pressure for resistance than conventional fungicides. Plant-based approaches may also contribute to toxin management. Some plants possess detoxification systems capable of modifying or neutralizing fungal metabolites. These mechanisms may involve glycosylation, oxidation, conjugation or sequestration of toxic compounds. Identification of genes responsible for these processes could support molecular breeding and biotechnology-based development of toxin-tolerant cultivars.

Biological control provides another important avenue. Beneficial bacteria and fungi can suppress phytopathogens through competition, antibiosis, mycoparasitism and interference with pathogen signaling. Some biocontrol microorganisms may specifically reduce fungal secondary-metabolite production or degrade toxic compounds. Such interactions could be exploited in integrated disease-management systems. Recent advances in omics technologies are expected to substantially expand knowledge of fungal secondary metabolism. Genome mining can identify previously unknown biosynthetic gene clusters, while transcriptomics can determine which pathways are activated during plant infection. Metabolomics can subsequently link genetic pathways with actual chemical products. Integration of these approaches may allow researchers to identify metabolites that play previously unrecognized roles in virulence. Artificial intelligence and machine-learning approaches may further accelerate the prediction of fungal metabolites and their biological activities. Computational analysis can assist in identifying relationships between fungal genomes, environmental conditions, metabolite profiles and disease phenotypes. These tools may eventually support rapid screening of fungal strains and prediction of metabolite-associated pathogenicity. Future research should also move beyond studies conducted under artificial laboratory conditions. Secondary-metabolite production is strongly influenced by environmental conditions and host interactions, meaning that metabolite profiles observed in culture may differ considerably from those produced during natural infection. Field-based metabolomics, spatial analysis of metabolites within infected tissues and time-resolved studies of pathogen development will therefore be increasingly important. A deeper understanding of fungal secondary metabolites could ultimately contribute to integrated approaches combining host resistance, biological control, targeted anti-virulence strategies, precision diagnostics and sustainable crop management. Such approaches would reduce dependence on broad-spectrum fungicides while improving the ability to manage emerging and economically important fungal diseases.

9. Conclusion

Secondary metabolites represent important chemical tools used by phytopathogenic fungi to interact with plants and their surrounding environment. Toxins, terpenoids, polyketides, non-ribosomal peptides, siderophores and other specialized metabolites can contribute to tissue damage, oxidative stress, nutrient acquisition and suppression or manipulation of plant defense responses. Host-selective toxins are particularly important in determining disease susceptibility in several pathosystems. Advances in fungal genomics and metabolomics have demonstrated that phytopathogenic fungi possess extensive biosynthetic capacities, many of which remain unexplored. Greater understanding of metabolite biosynthesis and regulation could contribute to the development of resistant crop varieties, improved disease diagnostics and novel biological or chemical control strategies. Integrating molecular genetics, metabolomics and plant pathology will therefore be essential for translating knowledge of fungal secondary metabolism into sustainable crop protection.

References

1. Stergiopoulos, I., & de Wit, P. J. G. M. (2009). Fungal effector proteins. *Annual Review of Phytopathology, 47*, 233–263.
2. Wolpert, T. J., Dunkle, L. D., & Ciuffetti, L. M. (2002). Host-selective toxins and avirulence determinants: What's in a name? *Annual Review of Phytopathology, 40*, 251–285.
3. Keller, N. P. (2019). Fungal secondary metabolism: Regulation, function and drug discovery. *Nature Reviews Microbiology, 17*, 167–180.
4. Chooi, Y. H., & Tang, Y. (2012). Navigating the fungal secondary metabolic landscape. *Metabolites, 2*(3), 553–593.
5. Pusztahelyi, T., Holb, I. J., & Pócsi, I. (2015). Secondary metabolites in fungus-plant interactions. *Frontiers in Plant Science, 6*, 573.
6. Rojas, E. I., Herre, E. A., Mejía, L. C., J. C. A., & et al. (2014). Emerging plant diseases: The role of fungal secondary metabolites and plant–fungus interactions. *Annual Review of Phytopathology, 52*, 281–302.
7. Dean, R., Van Kan, J. A. L., Pretorius, Z. A., Hammond-Kosack, K. E., Di Pietro, A., Spanu, P. D., Rudd, J. J., Dickman, M., Kahmann, R., Ellis, J., & Foster, G. D. (2012). The top 10 fungal pathogens in molecular plant pathology. *Molecular Plant Pathology, 13*(4), 414–430.
8. Osbourn, A. (2001). Toxins and determinants of fungal pathogenicity. *Current Opinion in Plant Biology, 4*(4), 307–311.
9. Gardiner, D. M., Waring, P., & Howlett, B. J. (2009). The epipolythiodioxopiperazine (ETP) class of fungal toxins: Distribution, mode of action, functions and biosynthesis. *Microbiology, 155*(4), 973–986.
10. Choquer, M., Fournier, E., Kunz, C., Levis, C., Pradier, J. M., Simon, A., & Viaud, M. (2007). Botrytis cinerea virulence factors: New insights into a necrotrophic and polyphageous pathogen. *FEMS Microbiology Letters, 277*(1), 1–10.