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Review

Diversity and biological functions of fungal secondary metabolites: Biocontrol agents for sustainable agriculture. A review

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Abstract

Fungi produce a wide variety of secondary metabolites, including mycotoxins, antibiotics, and bioactive compounds, which have significant implications for human health and agriculture. These metabolites are synthesized through specialized biosynthetic pathways, which are often organized into gene clusters. Terpenoids, polyketides, non-ribosomal peptides, and hybrid compounds are primary categories of secondary metabolites, each with distinct biological roles. For example, terpenoids, such as deoxynivalenol and helvolic acid, polyketides, such as aflatoxins and lovastatin, and non-ribosomal peptides, such as penicillin G, have diverse applications, including as pharmaceuticals and biocontrol agents. Fungal metabolites also play a crucial role in microbial communication and agricultural pest control. Volatile metabolites released by fungi, including Fusarium and Trichoderma species, can inhibit plant pathogens and promote plant growth, thereby offering potential biocontrol strategies. Furthermore, entomopathogenic fungi produce secondary metabolites with insecticidal properties that facilitate their pathogenicity, including enzymes, toxins, and bioactive compounds. These metabolites have emerged as potential alternatives to synthetic insecticides in sustainable agricultural practices. A growing understanding of fungal secondary metabolites and their applications can contribute to advancements in pharmaceuticals, agriculture, and pest management.

Keywords: Diversity, Biological, Fungal, Secondary metabolites, Agriculture.

1. Introduction

The discovery of penicillin, derived from the fungus Penicillium, marked the beginning of significant research on its metabolites. Fungi produce a wide variety of secondary metabolites, although only a small proportion has been fully identified and studied [1]. These metabolites include mycotoxins, which can be harmful to plants, animals, and humans [2], as well as beneficial compounds that contribute to sustainable agricultural practices [3]. Although primary metabolites are essential for an organism's growth and basic functions, secondary metabolites play diverse roles, sparking considerable scientific interest. Some, such as antibiotics, have positive impacts on human health, whereas others, such as mycotoxins, can pose significant risks. By 2014, approximately 22,500 bioactive metabolites had been identified, with fungi accounting for 40% of these compounds. Fungi utilize secondary metabolites as part of their defence mechanisms [4]. These metabolites, which vary greatly in structure and function, are synthesized through specialized biosynthetic pathways that are often organized into gene clusters. Primary categories of secondary metabolites include terpenoids, polyketides, non-ribosomal peptides, and hybrid compounds [1]. Although not directly involved in growth, these metabolites play essential biological roles that aid the survival of the organism [5]. Terpenoids, which are synthesized via the mevalonate and deoxyxylulose phosphate pathways, are volatile compounds with significant biological activities. Examples include carotenoids, sesquiterpenoids such as trichothecenes, and diterpenoids such as gibberellins. Notable terpenoids include deoxynivalenol, a mycotoxin produced by Fusarium, and helvolic acid, an antibiotic derived from Aspergillus spp. [1]. Fungal species, such as Candida albicans, secrete metabolites with antibiofilm properties, such as farnesol [6]. Polyketides are another important group of fungal metabolites that include mycotoxins, such as aflatoxins, produced by Aspergillus flavus and Aspergillus parasiticus [4]. Other harmful polyketide mycotoxins such as zearalenone and fumonisin are produced by Fusarium spp. [7]. Polyketides such as lovastatin, a cholesterol-lowering drug, are produced by Monascus ruber and Aspergillus terreus [8].

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This study aimed to provide an overview of the diverse and important secondary metabolites produced by fungi, with a focus on their biological activities and potential applications in pharmaceuticals, agriculture, and biotechnology. It includes various classes of fungal metabolites.

2. Anti-biofilm and bioactive compounds produced by fungi

Terreic acid, a compound produced by the fungus Aspergillus terreus, inhibits biofilm formation in Escherichia coli. Similarly, myriocin, a polyketide with anti-biofilm properties, was initially isolated from Myriococcum albomyces and later from Mycelia sterilia and Isaria sinclairii (Table 1) [9]. Polyketides, the largest and most diverse group of secondary metabolites, are synthesized through a series of enzymatic reactions starting with acetyl-CoA [1]. Among non-ribosomal peptides, penicillin G, produced by Penicillium fungi, is the most famous antibiotic. Its discovery by Alexander Fleming has prompted significant research on fungal metabolites [4]. Although over 2.5 million fungal species have been identified, only a small fraction has been studied in detail [10]. Additionally, cyclosporine A, an immunosuppressant, is derived from Tolypocladium fungi, whereas ergotamine, an alkaloid, originates from the Claviceps species. Another important category of fungal metabolites is mycotoxins, including enniatin B, which is produced by Fusarium spp. These low molecular weight compounds are synthesized through non-ribosomal pathways, which are distinct from ribosomal protein synthesis. The Norine non-ribosomal peptide database currently contains 544 monomers, of which 1,740 peptides have been synthesized [1]. A hybrid class of non-ribosomal peptides and polyketides includes the antibiotic equisetin, which is produced by Fusarium fungi, along with mycotoxins such as ochratoxin A (Penicillium, Aspergillus), fusarin C (Fusarium), and cyclopiazonic acid (Penicillium, Aspergillus) [1]. In addition to antibiotics and mycotoxins, fungal pigments play vital biological roles, including β-carotene from Blakeslea trispora, astaxanthin from Phaffia rhodozyma, and a variety of pigments from Monascus species, such as ankaflavin, monascin, rubropunctatin, and monascorubrin, as well as oosporein and tennelin from Beauveria bassiana [5].

3. Importance of volatile fungal metabolites in fungal communication and agricultural applications

The volatile metabolites produced by fungi are essential for the communication between symbiotic partners, whether in mutualistic or antagonistic interactions [11]. For instance, non-pathogenic Fusarium species release volatile compounds that serve as biocontrol agents in agriculture. These Fusarium strains have been shown to inhibit the growth of *Fusarium oxysporum* sp. cubense tropical race 4 (FocTR4) [12]. Likewise, various Trichoderma species produce volatile metabolites that help manage plant diseases [13], and certain Trichoderma strains have been shown to suppress FocTR4 growth [14]. The volatile compounds not only facilitate microbial communication but also influence the behavior and physiology of other microbes, such as bacteria and fungi. They can also affect host plants, with *Trichoderma* species, such as isobutyl alcohol, isopentyl alcohol, 2-methyl-propanol, 3-methylbutanal, 3-methyl-acetate, sesquiterpenes, diterpenes, tetraterpenes, and pyranones, all of which enhance plant growth and stress tolerance [15]. In symbiotic (Fig. 1) relationships between fungi and host plants under stress, chemical metabolites from both partners drive the interactions [16]. Endophytic fungi release a variety of volatile compounds that facilitate symbiosis with host plants, act as growth promoters, and provide protection against pathogens [17]. For example, *Sarocladium brachiariae*, an endophytic fungus, releases volatile compounds such

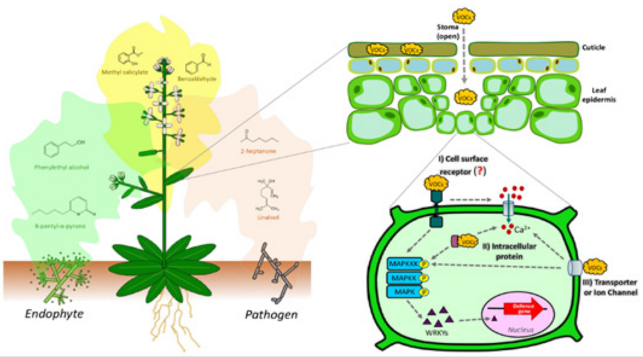

Fig. 1. The importance of volatile fungal metabolites in fungal communication and agricultural applications [22].

Table 1. Fungal producers and their secondary metabolites with diverse biological activities and applications.

Compounds	Producer Organisms	Significance	References
Terreic acid	*Aspergillus terreus*	Inhibits biofilm formation in Escherichia coli.	[9]
Myriocin	Myriococcum albomyces, Mycelia sterilia, Isaria sinclairii	Polyketide with anti-biofilm properties.	[9]
Polyketides	Penicillium spp.	Famous antibiotic; discovery by Alexander Fleming stimulated significant research on fungal metabolites.	[4]
Mycotoxins	Fusarium, Penicillium, Aspergillus	Includes enniatin B (Fusarium spp.), ochratoxin A (Penicillium, Aspergillus), fusarin C (Fusarium), and cyclopiazonic acid (Penicillium, Aspergillus).	[1]
Equisetin	Fusarium spp.	Hybrid non-ribosomal peptide/polyketide antibiotic.	[1]
Fungal pigments	Blakeslea trispora, Phaffia rhodozyma, Monascus spp., Beauveria bassiana	Includes β-carotene, astaxanthin, and pigments such as ankaflavin, monascin, rubropunctatin, monascorubrin, oosporein, and tennelin.	[5]
Non-ribosomal peptides	Various fungi	Synthesized through non-ribosomal pathways. Norine database contains 544 monomers and 1,740 peptides.	[1]

as 2-methoxy-4-vinylphenol, 3,4-dimethoxystyrol, and caryophyllene, which exhibit antifungal activity against *Fusarium oxysporum* sp. cubense [18]. Similarly, the Hypoxylon anthochroum strain Blaci releases metabolites such as phenylethyl alcohol, 2-methyl-1-butanol, phellandrene, elemene, and eucalyptol, which contribute to biological weed control and suppress fungal pathogens [19]. *Curvularia eragrostidis*, another endophytic species, emits volatile metabolites including 1-H-indene 1-methanol acetate, tetroquinone, and naphthalene, which have antimicrobial properties [20]. Dark septate endophytes (DSE), a group of fungi with growing recognition for their role in sustainable agriculture, also produce volatile compounds with significant antimicrobial effects. For instance, DSE fungi, such as *Leptodontidium* sp., release metabolites, such as chamigrene and 1,3-cyclopentadiene, which help combat plant pathogens [21].

4. Secondary metabolites (SMs) produced by fungi

Fungi produce a variety of low-molecular-weight compounds known as secondary metabolites (SMs), which have diverse biological activities and potential applications in fields such as pharmaceuticals, agriculture, and biotechnology [23]. SMs are classified into four main categories: polyketides (PKS), non-ribosomal peptides (NRPs), terpenoids, and compounds derived from shikimic acid. Ascomycetes are particularly abundant in SM-related genes compared with basidiomycetes, archaeo-ascomycetes, and chytridiomycetes, whereas hemi-ascomycetes and zygomycetes generally lack these genes [24]. Fungal species, such as Macrophomina phaseolina, Aspergillus flavus, and Magnaporthe oryzae, are known to possess extensive SM gene families [35]. Polyketides form a large and diverse class of compounds, including polyphenols, macrolides, polyenes, and polyethers, synthesized by polyketide synthases (PKS), which are multidomain enzymes similar to fatty acid synthases [26]. The core structure of PKS enzymes comprises domains such as acyl carrier protein (ACP), acyltransferase (AT), and ketoacyl-CoA synthase (KS) as well as additional domains such as ketoreductase, dehydratase, enoyl reductase, methyltransferase, and thioesterase [23]. PKS enzymes share a common biosynthetic pathway involving the condensation of acyl-CoA starter units with malonyl-CoA elongation units, and their structures are formed by poly β-keto chains created through the coupling of acetic acid units via condensation reactions [27]. In fungi, the most common form of PKS is iterative type I, which includes three subtypes: non-reducing PKS (nrPKS), partially reducing PKS (prPKS), and highly reducing PKS (hrPKS). Other variants include iterative type III and hybrid non-ribosomal peptide synthetase (PKS-NPRS) [26]. PKS compounds have various roles such as serving as pigments, virulence factors, signaling molecules, antibiotics, and antiparasitic agents. Some PKS compounds have shown potential as biocontrol agents for agriculture. For instance, polyketide derivatives, such as O-methylated SMA93 and radicinin from the endophytic fungus Fusarium proliferatum ZS07, isolated from the long-horned grasshopper (Tettigonia chinensis), exhibit phytotoxic effects on Amaranthus retroflexus seed radicle growth. Rhodolamprometrin demonstrated antibacterial activity against Bacillus subtilis (ATCC 6633), further emphasizing the biocontrol potential of PKS compounds [28].

4.1. Terpenoids are metabolites derived

Terpenoids are a broad class of metabolites derived from five-carbon precursors, specifically isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP). In fungi, their synthesis occurs via the mevalonate pathway with acetyl-CoA serving as the initial substrate. Terpenoid production involves a variety of enzymes including terpene synthases, terpene cyclases, cytochrome P450 monooxygenases, NAD(P)+-dependent oxidoreductases, and flavin-dependent oxidoreductases. These enzymes help to modify the structure of terpenoids, resulting in the formation of bioactive compounds [29]. Terpenoids consist of isoprene units that can be either linear or cyclic and may be saturated or unsaturated. They are categorized based on the number of isoprene units, and range from hemiterpenoids (C5) to tetraterpenoids (C40). Fungi primarily produce sesquiterpenoids, diterpenoids, and triterpenoids [30]. While volatile terpenes are well documented, fungi also produce other bioactive terpenoids, such as aristolochenes, carotenoids, gibberellins, indole-diterpenes, and trichothecenes [23]. Carotenoids, which are tetraterpenoid pigments, are synthesized by plants, fungi, and certain bacteria. These compounds are valuable in various industries including food, cosmetics, medicine, and agriculture [31]. Fungal carotenoid production is often triggered by stress in the growth medium, with β-carotene being the most prevalent carotenoid [32]. Furthermore, fungi such as arbuscular mycorrhizal fungi (AMF) can enhance carotenoid production in crops such as sorghum and tomatoes and increase the levels of lycopene and β-carotene [33]. Pankin et al. [34] used chemometric methods and spectroscopy to identify carotenoids in Fusarium species in oat grains and demonstrated their potential for rapid, low-cost plant disease detection. Additionally, trichothecenes, mycotoxins derived from sesquiterpenes, pose significant concerns in agriculture. Over 150 trichothecene analogs have been identified, and their production is regulated by the TRI genes [35]. Gibberellins are diterpenoid phytohormones produced by fungi to support plant growth [36]. Endophytes, such as Epichloë, generate gibberellins and auxins that stimulate plant growth and enhance defence mechanisms through alkaloid production [37].

5. Entomopathogenic fungi as biological control agents

As global agricultural systems face growing challenges owing to food demand and climate change, there is an increasing need for sustainable pest control strategies [38]. Although chemical pesticides are commonly used, their long-term effectiveness is uncertain, necessitating the development of alternative pest control methods [39]. Insect growth regulators (IGRs) derived from natural sources, particularly entomopathogenic fungi, are promising alternatives to synthetic insecticides [40]. These fungi, which have been studied for over a century, inhabit diverse ecosystems and are rich sources of bioactive compounds for pest control [41]. The insecticidal properties of entomopathogenic fungi are largely attributed to their secondary metabolites that play a role in host infection and invasion. These metabolites include enzymes, toxins, and bioactive compounds with antifungal, antibacterial, antioxidant, antiviral, and insecticidal activities, which make them ideal pest management candidates [42]. Secondary metabolites from these fungi include peptides, cyclic depsipeptides, amino acid derivatives, polyketides, and terpenoids

[43]. Interestingly, entomopathogenic fungi contain gene clusters responsible for synthesizing these metabolites, although many of these genes are activated only under specific conditions such as stress or interaction with other organisms [44]. Fungi from the order Hypocreales are particularly notable for producing a wide range of secondary metabolites that aid in their pathogenicity and help them compete with other microbes during insect infections [45]. The infection process begins when conidia attach to the insect cuticle, germinate, and form appressoria to penetrate the cuticle using enzymes, such as chitinases, lipases, and proteases. After the insect succumbs to physical damage, malnutrition, and toxicosis, fungi proliferate in the digestive tract, releasing secondary metabolites that target gut bacteria and suppress the growth of competing microorganisms, which aids fungal growth. This process typically takes 6–14 days from infection to death [46]. Well-known entomopathogenic fungi include species from Beauveria (e.g., B. bassiana and B. brongniartii), Metarhizium (e.g., M. anisopliae, M. flavoviride, and M. robertsii), Isaria (e.g., I. fumosorosea and I. tennuipes), Lecanicillium (e.g., L. longisporum and L. lecani), and Hirsutela (e.g., H. danubiensis and H. thompsonii) [46, 47]. These fungi produce species-specific metabolites, including Beauveria bassiana, which is known to produce bioactive compounds such as alkaloids, pigments, cyclopeptides, and volatile compounds, making it a widely used bioinsecticide [48]. The alkaloids produced by B. bassiana include pyridine derivatives such as bassianin, pyridomacrolidin, and tennelin, although their roles in fungus-host interactions are still under investigation [49]. Additionally, B. bassiana produces red pigments such as oosporein, which may contribute to its insecticidal activity by reducing the number of insect hemocytes [49]. Cyclopeptides, such as bassianolides, beauverolides, and beauvericins, are also significant metabolites produced by Beauveria, and their insecticidal properties are being actively investigated [50].

The infection process of *Beauveria bassiana* involves distinct stages, including initial germination, secondary infection, and severe colonization of the host, as illustrated in Figure 2.

6. Conclusion

Fungi are prolific producers of secondary metabolites that play crucial roles in ecological interactions and human applications. These metabolites, including terpenoids, polyketides, non-ribosomal peptides, and hybrid compounds, not only serve as defense mechanisms for fungi, but also exhibit a range of biological activities with applications in pharmaceuticals, agriculture, and biotechnology. Studies of fungal secondary metabolites have uncovered compounds with significant potential as antibiotics, antifungal agents, and biocontrol agents, which can aid in the development of sustainable agricultural practices and alternative pest control strategies. Entomopathogenic fungi, in particular, have demonstrated the potential of fungal metabolites as natural insecticides. These fungi produce a range of bioactive compounds, including enzymes, peptides, and toxins, which help them infect and control insect pests. Species such as Beauveria bassiana, Metarhizium anisopliae, and Isaria fumosorosea are notable for their ability to produce insecticidal compounds, which makes them valuable tools for biological pest management. The discovery of new metabolites and the expansion of our understanding of fungal biosynthesis pathways will likely lead to the development of innovative and environmentally friendly pest control options. In addition to their agricultural significance, fungal metabolites also hold promise for human health, with compounds such as penicillin and cyclosporine providing critical medical benefits. The exploration of fungal biodiversity and identification of new metabolites offer exciting opportunities for drug discovery and development of novel therapeutic agents.

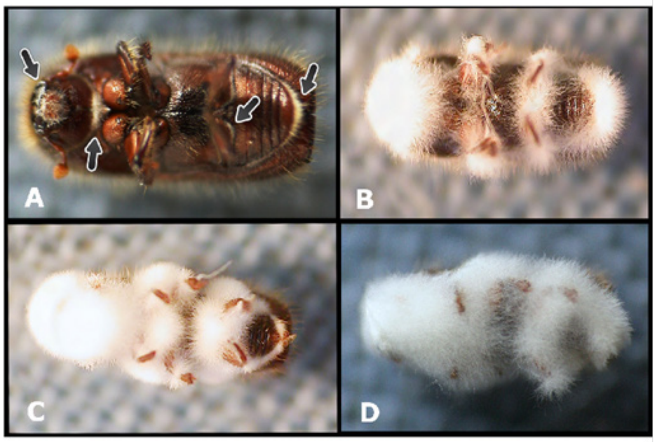

Fig. 2. A – First signs of germination of *Beauveria bassiana*, B– Secondary infection caused by *Beauveria bassiana*, C–D – Severe infection caused by *Beauveria bassiana* [51].

Authors contribution

All authors contributed to the conception and design of this study. The paper was written by **Z.J.,** edited and grammar checked by **N.K,** and **W.Z.** All authors approve the manuscript.

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Informed consent statement

Not applicable.

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