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ENZYME AND METABOLITE PROFILING IN FUNGAL IDENTIFICATION: CURRENT ADVANCES, APPLICATIONS, AND FUTURE PERSPECTIVES. A REVIEW

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The identification of microorganisms, specifically fungal species, is a fundamental process to understand the taxonomy, diversity, ecology, pathogenicity, and applications. The traditional identification techniques hold limitations of accuracy based on morphological and phenotypical characters only. However, biochemical approaches, such as enzymes and metabolite profiling, have profound contributions before molecular and phylogenetic analysis. The enzyme studies relate the species diversity with intracellular and extracellular enzymes involved in various functions such as pathogenicity, nutrients, metabolism, habitat, etc. Similarly, metabolites, including both primary and secondary, provide insights into closely related taxa with emphasis on ecological and genetic adaptations. Such detailed characters require advanced techniques, including high-performance liquid chromatography (HPLC), gas chromatography-mass spectrometry (GC-MS), liquid chromatography-mass spectrometry (LC-MS), and nuclear magnetic resonance (NMR) spectroscopy for metabolites. This review aims to provide the principles, techniques, applications, and advanced research areas related to enzymes and metabolites profiling. The integration of enzymatic and metabolomic markers is expected to play an increasingly important role in fungal systematics, diagnostics, and biodiversity assessment.

Keywords: Biochemical, Enzymes, Fungi, Identification, Metabolites

Introduction

Microorganisms, especially fungi, play major roles in ecosystem functioning, including nutrient cycling, decomposition, growth, productivity, and development[1]. The fungal mycelium network, along with the enzymatic profile, promotes complex phenomena of decomposition such as cellulose and lignin[2,1]. The fungal enzymes hold vast potential in converting plant organic waste into bioproducts with minimal to negative harmful impact on the environment[3]. Such bio-products produced by microorganisms, such as fungal species, are cost-effective, harmless to the environment, living beings, and ecosystem functioning.

In the past years, fungal species have played diverse roles in various sectors such as industries (*Aspergillus oryzae*)[4], biotechnology (*Saccharomyces cerevisiae*)[5], agriculture (*Aspegillus niger*)[6], and pharmaceuticals (*Penicillium chrysogenum*)[7]. The fungal community addresses a huge demand in growing sectors with high consumption and a promising role in the coming years. The wide range of enzymes and metabolites highlights their importance and potential in industries such as biofuel, nutraceuticals, medicine, bioremediation, biofertilizers, and many others[8,9,10].

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The enzymes obtained from the fungal community have marked a significant role in industries with diverse processes of production and manufacturing. Food paper, textiles, therapeutics, feeds, nutraceuticals, etc, have primarily obtained sources from fungal species with high utilisation of various enzymes such as protease, phytase, L-asparaginase, cellulases, xylanase, amylase, pectinase, etc.[11]. The natural products of fungi, such as metabolites, have gained significant insights in applications such as biotechnology, medicine, and other industrial sectors. Alkaloids, terpenoids, polyketides, and other secondary metabolites have contributed widely to biological activities in industrial and other useful systems[12,13].

The present review highlights the biochemical identification based on enzymes and metabolites of fungal species in the review. The current advances, along with the applications of the various enzymes and secondary metabolites of fungal species, have been discussed in the present review.

The biochemical characterisation of species based on their metabolic or physiological traits represents a valuable approach to identify microbial, especially fungal species. This study involves several factors, including varied environmental conditions, enzyme production, metabolites, etc. The analysis of fungal metabolites, including the mycotoxins, pigments, and other specific metabolites, has contributed significantly to mycological systematics and taxonomy. Over the past few decades, molecular techniques have enhanced the identification accuracy related to biochemical assays such as gas chromatography–mass spectrometry (GC–MS) and liquid chromatography–mass spectrometry (LC–MS) to new advancements. The traditional systematics with microscopy and cultural methods to new biochemical, molecular, and phylogenetic advancements in fungal identification could lead to novel research with improvement in biodiversity, biotechnology, industrial and agricultural applications worldwide[14].

Biochemical identification of fungal species

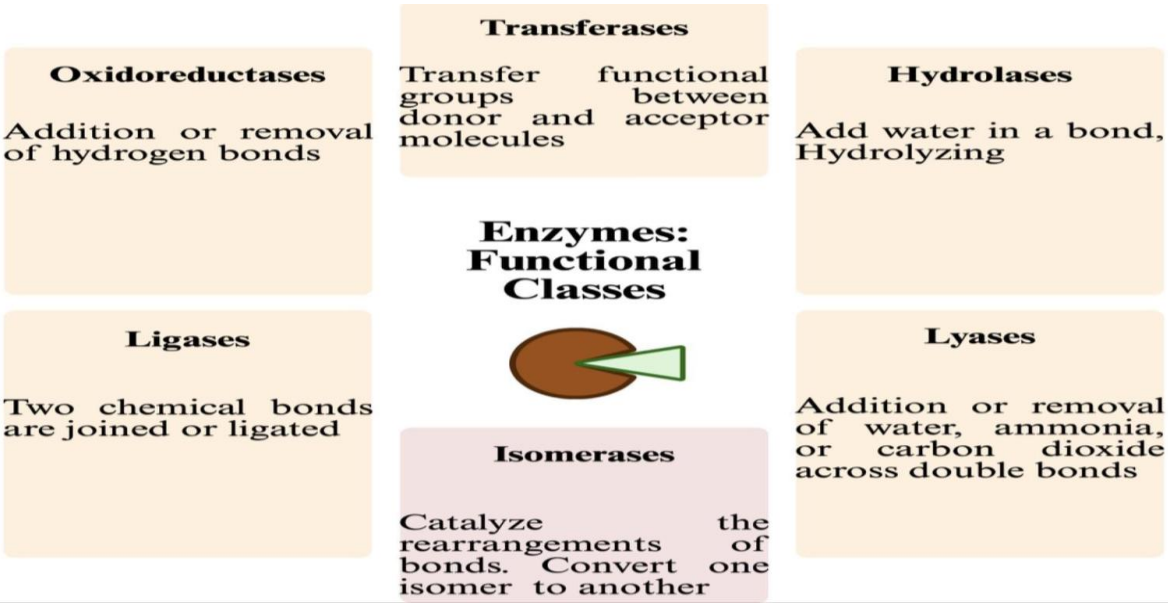

Figure 1. The functional classes of enzymes. The six classes have been classified and described according to the International Union of Biochemists

Enzymes profiling

Enzymes or biocatalysts are found in living organisms that speed up biochemical reactions in the processes. The term enzyme was first implicated in 1877 at the University of Heidelberg, Germany, by Wilhelm Friedrich Kühne[15,16]. They are known to play an important role in accelerating biological reactions and lowering the energy of activation without causing major modifications in the organisms. The functional enzymes include six categories with diverse roles and strategies (**Figure 1**).

The microbial enzymes, including the fungal and bacterial, are known to produce faster, cost-effective, and stable enzymes compared to those of plants and animals[17,18,16]. Among microorganisms, fungal species have been marked as a potential source of enzymes with high utilisation in industries, pharmaceuticals, and biotechnology. Such filamentous enzymes are known to survive under extreme environmental conditions, rapid multiplication and purification in nature. In addition, contribute to several applications such as baking, fermentation, food, animal feeds, forest-based products, fuel, and several others[19]. The past years of research suggest more than 60% of the use of fungal enzymes from the total enzymes used across the globe in different industrial sectors[20,21,22]. Among fungal species, *Trichoderma*, *Aspergillus*, *Rhizopus*, and *Penicillium* are the most common and potential enzyme producers used in various industrial sectors worldwide[16,23] (Table 1). In addition, mushrooms have also been studied for enzyme production used in applications such as antioxidant activities, biofuel, antimicrobial activities, etc.[24,16].

Enzymes: extraction, purification, and processing

Enzyme extraction: The different strategies of enzyme extraction can be broadly categorised into methods:

1. Homogenization, 2. Centrifugation 3. Precipitation[67,68,69] (**Figure 2**).

1. Homogenisation: The fresh cultures or microbial samples are crushed with a suitable extraction medium using a homogeniser or mortar and pestle. This extraction medium or a buffer varies from type of enzyme to be isolated and is adjusted based on the pH and molarity to ensure solubility and enzyme extraction. Several other solvents, such as EDTA (Ethylene diamine tetraacetic acid) or Triton-X (detergent) helps remove unwanted substances like heavy metals and solubilise the membranes. Additionally, thiols like mercaptoethanol are recommended to be added to the buffer to prevent the formation of disulfide bonds, causing disruption in the enzymes. The enzyme extraction is preferably conducted at low temperatures ranging from 0 to 3 °C. The APV-Manton-Gaulin homogeniser is preferably used for the process.

2. Centrifugation**:** The extracted enzymes in the homogenisation stage are centrifuged to separate from the unwanted debris of cell organelles, leading to the first form of purification. In addition, the enzymes are characterised and moved based on molecular mass and shape, which provides primary identification of the enzymes. The cold temperatures are maintained in the centrifugation stage as well. The speed and duration of centrifugation depend on the location and size of the enzymes to be extracted.

3. Precipitation**:** The enzymes are considered highly charged molecules requiring neutralising chemicals for the precipitation process. The enzymes are regarded as charged molecules that need to be

Table 1. Fungal enzymes profiling. The different fungal species have been reviewed for producing enzymes. The mode of extraction and applications in different sectors have been studied.

S. N.	Enzyme	Fungi	Method of extraction	Application	Ref.
1.	Ligninases	*Chytridiomycetes* sp. *Irpex lacteus*, *Pleurotus dryinus*, *Bjerkandera adusta*, and *Trametes versicolor*	ABTS, Azure B	Biofuel, Biodegradation, synthesis of bioactive compounds, antioxidant activity	16,25-27
2.	Laccases	*Myceliophthora thermophilia, Pycnoporus cinnabarinus, Irpex lacteus and Pleurotus ostreatus, Marasmius* sp., *Coriolopsis gallica, Pycnoporus sanguineus, Coprinopsis cinerea, Mucor circinelloides*	ABTS	Decolorization, Bioremediation, Biodegradation, Pulp, and paper industry, Food industry	28,29,16, 30,31
3.	L-Asparaginases	*Aspergillus oryzae, Aspergillus oryzae* CCT 3940*, and Fusarium culmorum* ASP-87*, Aspergillus terreus*	Plate assay	Antimicrobial, antibiofilm activity, food industry, anticancer treatment	32-35
4.	Chitinases	*Aspergillus niger* LOCK 62*, Trichoderma harzianum, Trichoderma viride* AUMC 13021*, Aspergillus niveus*	4MU-GlcNac, submerged fermentation	Antimicrobial, anticancer activity, pharmaceutical, food, environmental management, paper, and cellulose industry	36-39
5.	Pectinases	*Aspergillus pulverulentus* F23*, Aspergillus flavus* F30*, Aspergillus niger, Candida orthopsilosis, Aspergillus fumigatus*	Well plate, DNS methods, submerged fermentation	Textile, Food industry,	40-42
6.	Amylases	*Aspergillus niger, Aspergillus flavus* 9261	Submerged fermentation, dish screening	Textile, decolorization, antimicrobial activity	41,43,44
7.	Xylanases	*Aspergillus terreus, Aspergillus niger, Trichoderma longibrachiatum*	Response Surface Methodology	Bioethanol, Food industry, pulp, and paper, antimicrobial	45-47,43

8.	Cellulases	*Aspergillus terreus, Trichoderma reesei*, *Aspergillus awamori*	Miller's DNS assay, Rice straw submerged fermentation, Solid State Fermentation (SSF)	Bioethanol and biogas production, pulp, and paper industry, food industry,	48-51,46
9.	Lipases	*Aspergillus oryzae, Aspergillus flavus, Aspergillus niger*	Solid-state fermentation (SSF), submerged fermentation	Antimicrobial activity, biodiesel, ester synthesis, biopolymers, leather, pulp, and paper production, bioremediation.	52-54
10.	Tannases	*Rhizopus oryzae* MUCL 28168*, Fusarium solani, Aspergillus niger, Aspergillus awamori, Penicillium verrucosum, Rhodosporidium diobovatum, Aspergillus glaucus*	Solid-state fermentation (SSF	Detoxification, food industry	55-60
11.	Proteases	*Pleurotus* spp*., Aspergillus oryzae, and Aspergillus flavipes*	Solid-state fermentation (SSF	Antimicrobial activity, bioactive compounds	61,62
12.	Peroxidases	*Geotrichum candidum, Chaetomium globosum* IMA1*, Irpex lacteus, and Pleurotus ostreatus, Bjerkandera adusta, Mucor circinelloides*	Plate assay method, Solid-state fermentation (SSF), submerged fermentation	Abiotic stress tolerance, biodegradation, bioremediation	63-66

ABTS: *2,2'-Azino-bis (3-ethylbonzotiazoline-6-sulfonic acid.*
4MU-GlcNac: *4-methylumbelliferyl N-acetyl-β-D-glucosaminide*
DNS: *3,5-dinitrosalicylic acid*

neutralised for the precipitated form. The chemicals, such as an acid or base (adjust pH to isoelectric points), ammonium sulphate-like salts (cause change in protein conformations), organic solvents like acetone, methanol, ethanol (decrease protein solubility), water-soluble non-ionic polymers such as polyethene glycol, alginate, pectate, cellulose, acrylic acids, etc. For large-scale precipitation and enzyme extraction, polyethyleneimine is commonly used, which primarily removes the solvent sphere of the enzyme proteins.

Enzyme purification: The extracted enzymes are further purified using the following techniques: 1. Ultrafiltration 2.

Electrophoresis 3. Gel filtration 4. Chromatography 5. Dialysis (**Figure 2**).

1. Ultrafiltration**:** A membrane-based process for large-scale enzyme purification. Prominently, two types of ultrafiltration membranes are used, including the isotropic porous membrane and the diffusive membrane system. The former membrane resembles conventional filters more closely, possessing the capacity to allow average-sized particles ranging from 0.05 to 0.5 microns. The latter membrane system possesses a selective membrane with hydrogel layers. The diffusive membrane follows the diffusion technique with the passage of both solvent and solute through the filters. Studies reveal different types of ultrafilters, including thick-channel, tubular, helical tubers, hollow fibre, spiral wrapped, and many others[70].

2. Electrophoresis**:** Electrophoresis is a widely used and accepted molecular technique in which nucleic acids, proteins, enzymes, and isoenzymes are separated by net charges by using externally applied electric fields. In this technique, polyacrylamide gel is commonly used to separate the enzymes[71].

3. Gel filtration**:** This technique is also known as molecular exclusion chromatography or molecular sieve chromatography, based on the separation of enzymes and proteins according to their molecular sizes. The method, similar to adsorption chromatography, uses a glass or steel column packed with a gel that promotes the movement of enzymes according to their molecular sizes from larger to smaller sizes. The gel widely accepted in the process is 'Sephadex', produced by bacterial strains. Additionally, the gel filtration technique holds an advantage in determining the molecular weight of the extracted enzymes and proteins[72,73].

4. Chromatography**:** This is the most common and widely used technique of enzyme purification. The adsorption chromatography includes the usage of a column packed with inert materials such as charcoal, silica, alumina, calcium phosphate, hydroxyapatite, etc., in a single glass or steel tube. The solution, including the precipitated enzyme, is collected in small fractions of 1.0-2.0.1 estimated by measuring the adsorption at 280 nm using a spectrophotometer. The advantage of using the adsorption chromatography is the separation of various enzymes such as RNAase, acidic RNAase, phosphodiesterase, and several others.

   Other chromatography techniques useful in enzyme and protein purification are Ion Exchange and affinity chromatography. The former separates the molecules based on charges, while the latter is based on the purification according to the specificity for a particular substrate present in the solution[72].

5. Dialysis**:** A purification process to remove small molecules from extracted enzymes. The buffer solution for precipitation acts as a base solution in the dialysis procedure. A 'dialysis bag' is taken with the enzyme precipitated with the buffer and sealed. The bag is suspended in autoclaved distilled water or another buffer solution with additional salts or chemicals for the prevention of enzyme activity. The process is time-consuming with a regular change of outer solution. The inner enzyme solution is filtered through a membrane and observed for small molecules[74].

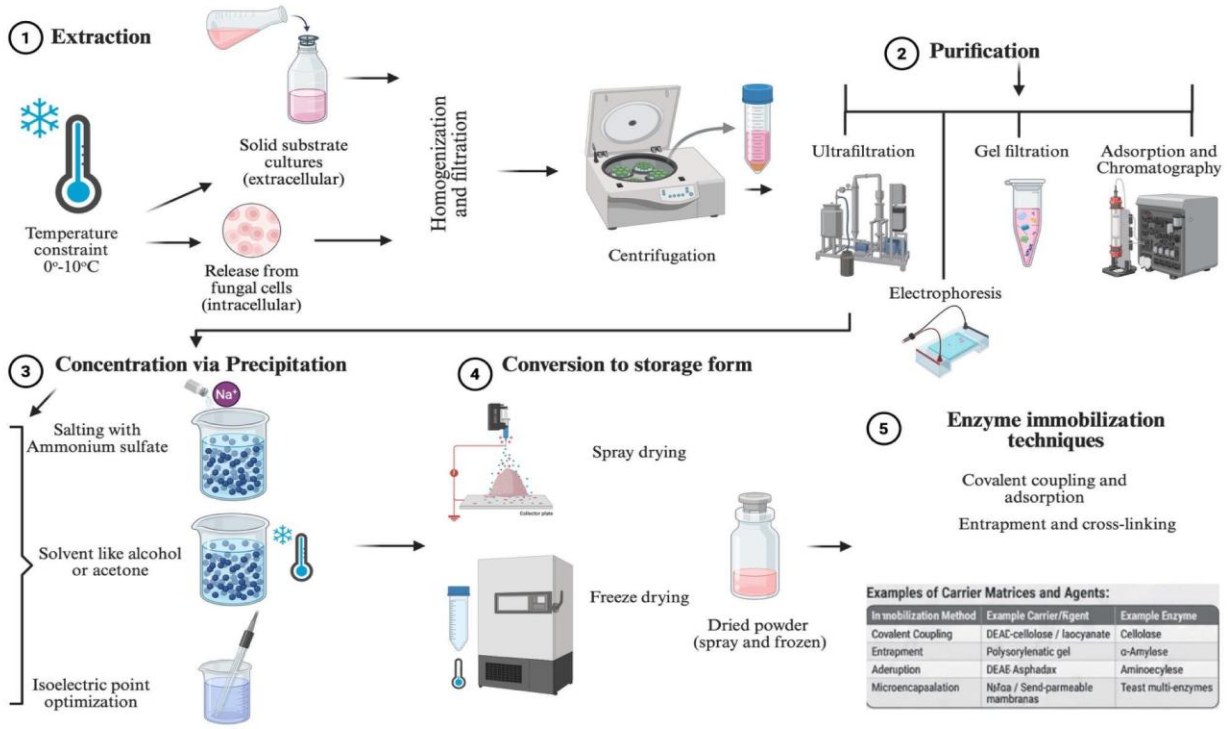

Figure 2. The enzyme assay. The different stages and techniques of extraction, purification, and final processing of enzymes.

Enzymes' final processing and storage: The enzymes at commercial platforms, such as industries and molecular laboratories are transported and utilised in appropriate storage and stabilised forms. These stored enzymes can be in either liquid or solid form, with protection against microbial or environmental contamination and protein denaturation. To maintain the appropriate enzymatic activity, chemical preservatives such as alcohols, sugars, and other chemicals can be considered. In addition, optimal pH, temperature (cold), stabilising ions, substrates or inhibitors can be used while conducting the final processing and preserving the enzymes.

Spray drying and freeze-drying are widely used and accepted techniques for the storage, stabilisation, and preservation of enzymes. The two methods are effective and well-experimented for enzymes, but only under the required favourable conditions[75] (Figure 2).

Metabolites profiling

Fungi are known to produce natural products such as metabolites, which have essential applications in industries, pharmaceuticals, agriculture, and research sectors. The fungal chemo diversity includes compounds with antibiotic, toxic, signalling, and enzyme-related roles [76,77,78]. Fungi produce two main classes of metabolites: primary (essential compounds) and secondary metabolites (bioactive compounds not essential for benzopyrones, and phenols. Their growth novel fungal-derived compounds were discovered, predominantly terpenoids (40%), polyketides (31%), and alkaloids (12%)[79]. Fungal secondary metabolites are

Table 2. Metabolites produced by fungi and their applications.

S.N.	Metabolites	Fungi	Applications	Ref
1.	Citric acid	*Aspergillus niger*	Food flavoring/preservative, prevents oxidation of fats/oils; emulsifier in ice cream	83,84
2.	Itaconic acid	*A. terreus*	Cloth industries; chemical synthesis	85
3.	Acetic acid	*A. oryzae, A. flavus*	Commercial pickling; condiments (mayonnaise, mustard); chemical production	86
4.	Lovastatin	*Aspergillus*	Cholesterol-lowering	87
5.	Lactic acid	*Rhizopus*	Food preservative; pharmaceutical /cosmetic industries	88
6.	Indole acetic acid	*Fusarium, Trichoderma, Aspergillus*	Plant growth and development	89,90,91
7.	Penicillins	*Penicillium, Aspergillus, Cephalosporium*	Treat bacterial infections (strep throat, syphilis, Lyme disease)	92
8.	Fusidic acid	*Fusidium coccineum*	Anti-bacterial; treats osteomyelitis, skin infections	93
9.	Pleuromutilin	*Pleurotus mutilis*	Protein synthesis inhibitor; veterinary use, research on ribosomal targeting	94
10.	Polyketides (Alfatoxin, Citrinin, Ochratoxin, Patulin, Rubratoxin, Sterigmatocystin, Tremorgens)	*Aspergillus, Penicillium, Fusarium*	Mycotoxin research, Food safety monitoring, Food contamination studies	95
11.	Zearalenone	*Fusarium*	Endocrine disruption studies	96
12.	Ergot	*Cleviceps*	Contract the uterus, relieve severe migraine, manage Parkinson's disease	97,98
13.	Fumonisin	*Fusarium*	toxicology research, sphingolipid studies, and biomarker development	99
14.	Trichothecenes	*Fusarium, Trichothecium*	Biomedical research, agricultural pathology, and as biological standards	100
15.	Fumagillin	*A. fumigatus*	Inhibits the synthesis of essential proteins (binds to enzyme type 2 methionine aminopeptidase (MetAP2)	101
16.	Cyclosporine	*Tolypocladium, Trichoderma, Acremonium*	Immunosuppressant	102,103
17.	Cephalosporin	*Acremonium, Cephalosporium*	Pharmaceutical industry, produces cephalexin and cefixime	104
18.	Griseofulvin	*Penicillium griseofulvum*	Antifungal agent	105
19.	Gibberellic acid	*Gibberella fujikuroi*	Plant growth regulator	106,107
20.	Astaxanthin	*Phaffia rhodozyma, Blakeslea trispora*	A potent antioxidant in human dietary supplements, cosmetics, and pharmaceuticals	108

primarily classified into four major biosynthetic categories: polyketides, terpenes, alkaloids, and non-ribosomal peptides (NRPs), with hybrid classes such as meroterpenoids and polyketide-NRPs[80] (**Figure 3**).

Polyketides are the most abundant fungal secondary metabolites and include structurally diverse compounds such as aflatoxins, chromones, quinones, macrolides, biosynthesis through the iterative

condensation of acetyl-CoA (starter unit) and malonyl-CoA (extender unit) by multi-domain polyketide synthase (PKS) enzymes, which often lack reducing domains found in typical fatty acid synthases, allowing for complex, non-reduced poly-β-keto chain formation[81,82]. Fungal alkaloids are nitrogen-containing secondary metabolites produced by various fungi, particularly within the Ascomycota phylum. The most prominent class is ergot alkaloids, produced predominantly by *Claviceps* species (such as *Claviceps purpurea* on rye) and some Ascomycota, which include clavines, simple amides of lysergic acid, and ergopeptines. Well-known examples include lysergic acid and its derivative lysergic acid diethylamide (LSD), a powerful hallucinogen, as well as gliotoxin, a sulfur-containing alkaloid isolated from fungi. Other bioactive fungal alkaloids are produced by genera such as *Boletus*, *Fusarium*, and *Psilocybe* (which produces psilocybin) (**Table 2**).

Metabolites: extraction and purification

Fungal secondary metabolites are typically extracted using a combination of fungal fermentation, solvent extraction, and chromatographic purification[109]. Firstly, cultivate filamentous fungi in appropriate liquid or solid media for several days to allow metabolite production. Solid media often mimics natural conditions and can enhance metabolite diversity, also known as solid state fermentation, while submerged fermentation grows fungi in liquid media with controlled parameters such as pH, temperature, agitation, and lighting to optimise yield. For extraction, the most common approach involves soaking the fermented biomass (mycelium plus media) in organic solvents; polar metabolites like

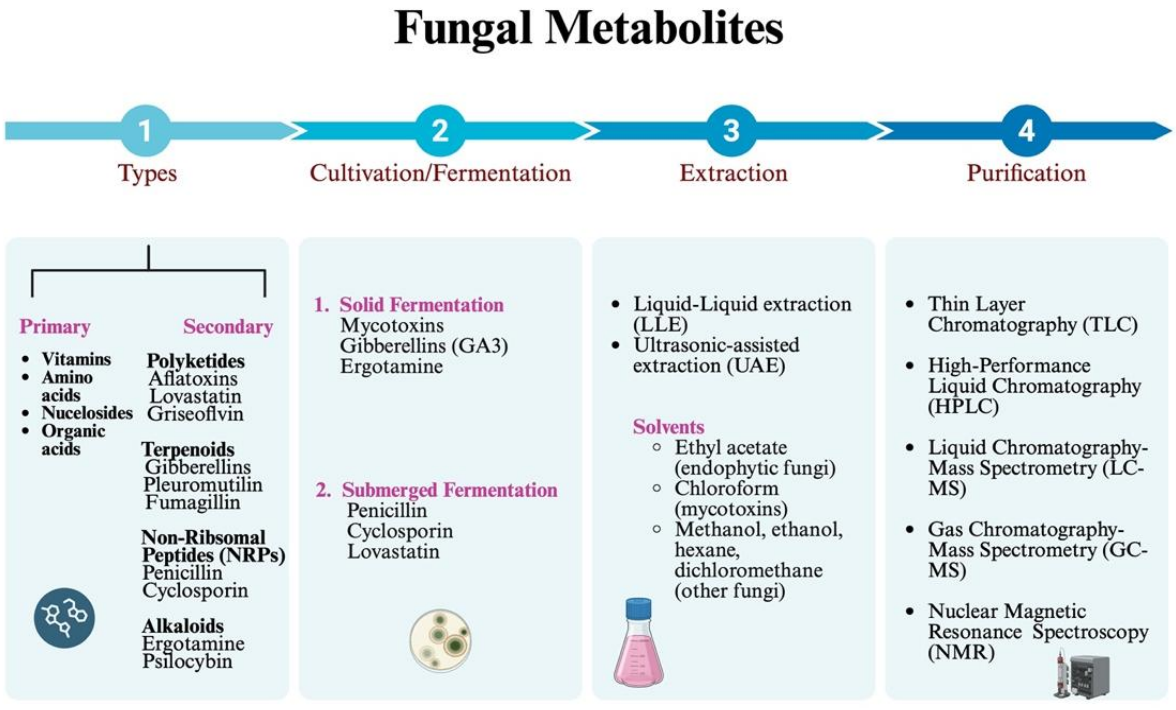

Figure 3. The fungal metabolites. The types, extraction, and purification of fungal metabolites have been studied.

many NRPs and alkaloids are extracted with methanol, ethanol, or methanol-water mixtures (e.g., 1:1 or 4:1 v/v), while less polar compounds such as polyketides and terpenes often require liquid-liquid extraction (LLE) using biphasic systems like Folch (chloroform-methanol 2:1) or Bligh-Dyer (chloroform-methanol-water) and ultrasonic-assisted extraction (UAE) methods[109,110].

Purification of the crude extract relies primarily on chromatographic techniques. Thin-layer chromatography (TLC) is used first for rapid screening and fractionation, where bands are visualised under UV light or by spraying with reagents like aluminium chloride. For higher-resolution purification, column chromatography (normal-phase silica or reverse-phase) separates metabolites into fractions based on polarity differences. The main analytical and purification method is high-performance liquid chromatography (HPLC), particularly reverse-phase HPLC, which isolates individual pure compounds with high precision. HPLC is often coupled with Liquid chromatography-mass spectrometry (LC-MS) for simultaneous identification and quantification of known and unknown metabolites. Additional techniques include gas chromatography (GC) for volatile metabolites and preparative TLC for preliminary fractionation. The final pure metabolite is typically confirmed using spectroscopic methods like Nuclear magnetic resonance spectroscopy (NMR)[111-113] (Figure 3).

Conclusions

Identification methods of fungal species have undergone remarkable progress from morphological to molecular and biochemical approaches. Among them, enzymes and metabolites play a significant role and have gained attention in understanding the species-specific characteristics of the fungal community. The myco-organisms have a variety of enzymes, primary and secondary metabolites that could provide a remarkable contribution to the systematics of closely related fungal species. In addition, valuable insights into evolutionary and ecological roles, pathogenicity, industrial and agricultural importance could also be highlighted.

These biochemical approaches of fungal species are highly influenced by several factors, such as temperature, pH, growth, ecology, and other developmental stages of the species. Therefore, the traditional morphological observations along with the advanced molecular techniques could complement the taxonomy of the mycological community. The integration of multiple methodologies offers a more comprehensive understanding of fungal diversity and will contribute significantly to the discovery of novel fungal resources.

Future perspectives

Future research in fungal taxonomy could utilise advanced molecular and genetic systems of high-throughput, multi-omics platforms integrating metabolomics, proteomics, genomics, and transcriptomics. The applications of high-technology machines with a blend of artificial intelligence in recognition of fungal species could uncover hidden patterns among closely related taxa. These valuable technological advancements, along with traditional approaches, could shape the future research strategies to a higher level in the fungal world. The integration of biochemical profiling with DNA-based identification methods will provide a new way toward a more reliable and comprehensive fungal taxonomy, with broad implications for agriculture, medicine, environmental monitoring, and industrial biotechnology.

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