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BIOLOGY

LIGNICOLOUS BASIDIOMYCETES AS VALUABLE BIOTECHNOLOGICAL AGENTS

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Lignicolous basidiomycetes are highly specialized organisms that are capable of degrading lignin, one of the most abundant and resistant organic compounds. Through their enzymes and secondary metabolites, these fungi have a great potential that can be successfully used in various biotechnological processes, ranging from mycoremediation of different pollutants and isolation of bioactive molecules with applications in the pharmacological industry and agriculture, as biocontrol agents of phytopathogens.

Key words: lignicolous basidiomyetes, biotechnology, mycoremediation, biocontrol.

1. INTRODUCTION

Fungi belong to a very diverse group of eukaryotic organisms that populate various habitats and due to an extraordinary plasticity they can colonize different substrates using resources that are inaccessible or hardly accessible to other species, like keratin, collagen, elastin, lignin, cellulose, hemicellulose etc. [Chang & Miles, 2004].

The estimated number of world fungi is considered to be between 1–1.5 million species, many of them still unidentified. According to the 10th edition of Dictionary of Fungi, so far 97.330 species of fungi belonging to 75.337 genera are described [Hawksworth, 2009].

The vegetative body of the fungi is called mycelium and it consists of septate and aseptate filamentous structures – hyphae, which have different arrangements depending on the taxonomical position of the considered species [Tănase & Şesan, 2006]. The filamentous fungi can explore large volumes of substrate and given the wide contact area of the surface of the hyphae, the nutrient uptake is very efficient [Zamfirache & Toma, 2000].

Fungi are heterotrophic organisms with great adaptability and a high capacity of using every available resource. They can be saprotrophic species that decompose organic and inorganic substrates or can be part of symbiotic relations with photosynthetic organisms and also parasitic species on plants and animals [Dix & Webster, 1995].

Because of their morphological and physiological versatility and their great biotechnological potential, these unique organisms captured the interest of the scientific community. The enzymes and secondary metabolites produced by fungi have been isolated and tested with significant results in various biotechnological processes from pharmacological industry and agriculture to habitat bioremediation.

Used properly, fungi represent an important bioresource that can solve many of the environmental problems that the society is facing nowadays, without involving products and techniques which would have additional negative effects.

2. BIOLOGY AND ECOLOGY OF FUNGI

Although fungi use different substrates as sources of organic nutrients, these can only be absorbed as simple, soluble compounds, which can diffuse and penetrate through the cell wall inside the hyphae. Low weight molecular compounds such as monosaccharides, amino acids or various salts can easily get inside the cells [Howard & Gow, 2007] and are used to synthesize all cellular components. To transform the natural substrates into assimilable compounds the fungi are secreting extracellular enzymes which break the organic macromolecules into simpler structures and secrete organic acids to solubilize the inorganic nutrients.

The enzymes have high molecular weight and don't diffuse at large distance around the hyphae [Dix & Webster, 1995] making necessary the exploration of a new area through hyphal elongation.

Fungi need in their nutrition high quantities of nitrogen and phosphorus, having biochemical mechanisms to obtain these nutrients, such as: using the inorganic nitrogen or only one type of amino acid (they produce transaminases); synthesizing phosphatases to mobilize the phosphates from the organic matter; solubilizing the inorganic phosphate *etc*.

Fungi can produce energy *via* several oxidative mechanisms either by the oxidation of the organic compounds in the Embden-Meyerhof cycle or through the tricarboxylic acid cycle [Deacon, 2006] and in the absence of oxygen they can obtain the necessary energy through lactic or alcoholic fermentation.

To complete the entire biological cycle, the saprotrophic fungi need an optimal quantity of nutrients, developing various types of strategies [Dix & Webster, 1995] to occupy different ecological niches.

Depending on the manner in which they colonize and use an available resource, the saprotrophic fungi are: *ruderal species* which have a high rate of

colonizing a substrate, however they can't use complex substances but only low molecular weight compounds easily assimilable; *stress tolerant species* which can develop under conditions that are improper for other species and occupy free ecological niches (extremophile fungi); *competitive species* that can inhibit the growth of antagonistic species through biochemical mechanisms (secretion of inhibitory compounds: bactericidal and bacteriostatic agents, fungicides, nematicides) or by mechanical action (overgrowing the other mycelia). These species possess the ability of efficiently using the substrate, decomposing resistant macromolecular organic compounds like cellulose, lignin and tannins. Many species can partially use all the mentioned strategies, depending on the development stage, type of substrate and environmental factors.

Saprotrophic fungi can colonize almost every habitat (grasslands, forests, swamps and peats, arid areas) that contains degradable organic matter, from aquatic (marine or fresh water) to terrestrial ecosystems, subpolar or equatorial areas [Stamets, 1993]. Some species are ubiquitous and can be found in different biogeographical regions, while others are specific to a certain climate or to habitats with distinctive vegetation.

Among the saprotrophic fungi, the lignicolous species are highly specialized organisms belonging mainly to the Basidiomycota Phylum, one of the few organisms capable to degrade lignin, one of the most abundant and resistant organic compound as well as other main components of the vegetal cell wall such as cellulose and hemicellulose. Lignin is a tridimensional biopolymer with high molecular weight and hydrophobic properties [Tišma *et al*., 2010]. The decomposition of this biopolymer is crucial for the recycling of carbon. Lignin is found along with hemicellulose (together they form an amorphous complex) in the spaces between the cellulose microfibrils, playing an important role as a ligand, giving strength to the cell wall [Schmidt, 2006].

Due to the fact that it is unhydrolysable and insoluble [Jurcoane *et al*., 2006] lignin usually represents an obstacle blocking the enzymes for reaching the cellulose and hemicellulose.

The lignicolous fungi have developed over the time specific mechanisms capable of degrading lignocellulosic substrates – cellulasic polyenzymatic system and lignolytic polyenzymatic system.

These mechanisms involve a series of both morphological and physiological adaptations that enable their developing and survival onto specific substrates and biochemical adaptations consisting in the ability to synthesize enzymatic complexes which attack lignin, making available the celluloses from the lignin matrix.

Jurcoane *et al.* [2006] describes the importance of three types of cellulases that break the β-glycosidic bounds from the cellulose macromolecule: *exo-1,4-β-glucanases* that systematically attack the cellulose macromolecule from the non-reducing end of the polysaccharide chain, releasing glucose or cellobiose

molecules; *endo-1,4-β-gluconases* that randomly operates within the cellulose chain, generating oligosaccharides with different degrees of polymerization; *β-glucosidases*, that hydrolyze oligosaccharides forming glucose. These enzymes act synergistically to hydrolyze native cellulose. The type of hemicelluloses varies from softwood to hardwood and therefore the lignicolous fungi developed specificity according to the wood species [Deacon, 2006].

The brown rot is produced by a small number of lignicolous basidiomycetes, that use in the degradation of cellulose and hemicellulose both enzymes and non-enzymatic metabolites, while the structure of lignin is only easily modified. This type of rot is found especially in coniferous wood; in this case the wood changes its color into brown. The species that cause brown rot are less efficient in colonizing various substrates and show slow growth rates on artificial media [Balaeş & Tănase, 2012 a,b]. The white rot is caused by the lignicolous basidiomycetes species that can enzymatically degrade lignin, as well as cellulose and hemi-cellulose. This type of rot is found mainly in hardwood; in this case the wood turns white. *In vitro* the species responsible for white rot show considerable higher growth rates compared to the species that cause brown rot [Petre & Tănase, 2013 a,b].

The species that cause white rot possess three types of mechanisms involved in the degradation of lignin [Schmidt, 2006]. The first one implies the simultaneous degradation of lignin and cellulose (*Fomes fomentarius*, *Phellinus igniarius*, *Trametes versicolor*), the second one referes to the degradation of lignin and hemicellulose before the metabolization of cellulose (*Heterobasidion annosum*, *Xylobolus sp*.) and the third mechanisms involves the degradation of lignin and hemicellulose while the cellulose is scarcely denaturated (*Bjerkandera adusta*, *Porodaedalea pini*).

The process of wood degradation by lignicolous basidiomycetes requires a series of enzymes belonging to different classes, among which some oxidoreductases are involved in the degradation of lignin [Schmidt, 2006]. These enzymes are produced differently, one, two or more enzymes being simultaneously synthesized depending on the species; lignin, cellulose and hemicellulose are being therefore selectively decomposed [Fang *et al*., 2008].

Some species can synthesize several types of laccases, lignin-peroxidase, manganese-dependent peroxidase [Moharčič *et al*., 2006] or other enzymes involved in the degradation of lignin and other aromatic compounds: manganese-independent peroxidase, aryl alcohol oxidase [Palmieri *et al*., 2005], versatile peroxidase [Karimi *et al*., 2009], H_2O_2-producing glyoxal oxidase [Trupkin *et al*., 2003], cytochrome P_{450} monooxigenase [Asgher *et al*., 2008]. The degradation of lignin is strongly dependent on oxygen, not being able to take place in anaerobic conditions. Another category of peroxidases synthesized by fungi that plays an important role in the decomposition of lignin and several other compounds is represented by the dye-decolorizing peroxidases – DyP (e), atypical enzymes that don't oxidize

manganese [Liers *et al*., 2010], but show impressive ability in the degradation of complex substrates such as lignin and synthetic dyes, especially under stress conditions [Faraco *et al*., 2007].

The diversity of basidiomycetes species is influenced by several factors, including the type of substrate (wood species) and the other organisms that they come in contact with [Dix & Webster, 1995]. Lignicolous basidiomycetes manage to develop efficient mechanisms in order to survive under the harsh conditions within the wood substrate: low nitrogen content (the C:N ratio is frequently 500:1), low phosphorus content, the presence of various chemicals synthesized by the host (tannins, terpenes, flavonoids, stilbenes), low levels of oxygen, high levels of carbon dioxide, low water content [Dix & Webster, 1995; Deacon, 2006; Schmidt, 2006].

Although wood is the main substrate colonized by lignicolous basidiomycetes, many species are also able to grow on soil (*Trametes* sp., *Phanerochaete* sp, *Pleurotus* sp.), decomposing the litter. These species are responsible for the modification of soil permeability and for the ion changes that influence the matter and energy flows between the organisms and the abiotic substrate [Dix & Webster, 1995]. Lignicolous fungi play an active role in the degradation of rocks and minerals – *bioweathering*, due to their capacity of synthesizing organic anions, especially oxalates (*Bjerkandera fumosa*, *Phlebia radiata*, *Trametes versicolor*) forming chelating agents involved in complex oxidation processes [Gadd, 2007; Hoffland *et al*., 2004].

3. LIGNICOLOUS BASIDIOMYCETES IN BIOTECHNOLOGIES

The term *biotechnology* is referring to the usage of organisms and natural compounds in order to put together products and develop industrial processes. It is an interdisciplinary domain that involves knowledge from different sciences like biology (information about the organisms involved), economy (costs), kinetics (chemical and physical influences) and also process management [Lafferty, 1981].

A very important category of organisms involved worldwide in numerous biotechnologies is represented by fungi, fact proven by the introduction of the term *mycotechnology* [Bennett, 1998] in the scientific literature precisely to emphasize the impact that these organisms have in this field.

Lignicolous basidiomycetes through their enzymes and metabolites demonstrate a great potential in many biotechnological applications: mycoremediation of several classes of pollutants, synthesis of bioactive molecules for the pharmacological industry or agriculture, in the biocontrol of phytopathogens.

3.1. MYCOREMEDIATION OF SYNTHETIC DYES

Based on their ability to decompose and mineralize lignin as well as various toxic compounds, lignicolous fungi are considered to be unique organisms. Their enzymatic system makes them potential biodegradation agents for many industrial

and agricultural products, bioremediation of polluted habitats, the interest for researching these fungi growing considerably in the last few decades [Tišma *et al*., 2010].

Bioremediation is a term used to describe the usage of several biological and biochemical methods and processes in order to remove or inactivate pollutants from water, soil and air. *Mycoremediation* or *mycodecontamination* involves using fungal organisms. For this purpose various species that show potential in removing one or more toxic compounds are cultivated. In the bioremediation of pollutants three main mechanisms are involved: *biosorption* (concentration of a certain compound either at the surface of the organisms through adsorption or inside the organisms through absorption), biotransformation (transformation of toxic chemical compounds in less toxic substances) and proper biodegradation to compounds with lower molecular weight or even complete mineralization.

In comparison with the physicochemical methods of removing pollutants, biological methods have no negative side effects towards the environment, they don't affect the natural ecosystems and have low costs [Corso & Almeida, 2009]. Through the hyphae fungi have the capacity to explore large areas of substrate, fact that assures a favorable biosorption / biodegradation of high amounts of toxic compounds. The complex and versatile enzymatic system, the low specificity showed by the enzymes towards the substrate and the high adaptability establish the grounds for a very efficient degradation of organic pollutants.

Research on lignicolous fungi showed that besides the important role played in the decomposition of lignin these organisms are responsible as well for degrading: polycyclic aromatic hydrocarbons and chlorophenols – *Bjerkandera* sp., *Irpex* sp., *Pleurotus* sp., *Trametes* sp. [Gadd, 2007; Valentin *et al*., 2007]; polychlorinated biphenyls – *Bjerkandera adusta*, *Lentinula edodes*, *Phanerochaete crysosporium*, *Pleurotus ostreatus*, *Trametes versicolor* [Singh, 2006]; synthetic dyes – *Bjerkandera adusta*, *Irpex lacteus*, *Pleurotus ostreatus*, *Tramestes hirsuta*, *Trametes versicolor*, [Eichlerová *et al*., 2007; Kariminiae–Hamedaani *et al*., 2007; Singh, 2006]; pesticides – *Hypholoma fasciculare*, *Lentinula edodes*, *Phanerochaete crysosporium*, *Pleurotus ostreatus*, *Stereum hirsutum*, *Trametes versicolor* [Pointing, 2001; Singh, 2006; De Sousa Fragoiero, 2005]; substances used in the pharmacological industry such as ibuprofen and carbamazepine – *Trametes versicolor* [Marco-Urrea *et al*., 2009].

Lignicolous basidomycetes have the ability to accumulate heavy metals [Cozma *et al*., 2010; Gabriel *et al*., 1994; Tănase *et al*., 2008a,b] and radionuclides [Popa *et al*., 2010; Tănase *et al*., 2009] in the mycelium and within the fruiting bodies: lead, cadmium, copper, zinc, aluminum, mercury, uranium, cesium, strontium, therefore having the impressive potential in bioremediation and ecological reconstruction of polluted habitats.

An important category of organic pollutants is represented by the synthetic dyes, organic compounds with complex chemical structure, resistant to bio-

degradation. Lignicolous fungi have the ability to degrade synthetic dyes through the extracellular ligninolytic enzymes [Asgher *et al*., 2008], action based on the structural analogies between lignin and synthetic dyes.

Several studies demonstrate the possibility of using some isolates of lignicolous fungi to degrade different synthetic dyes. Table 1 shows the main researches made in this field.

The most frequent tested lignicolous species are the ones that have a wide distribution [Balaeş *et al*., 2013], demonstrate a high versatility of the enzymatic systems and present broad adaptability towards the substrate which allows them to efficiently degrade lingo-cellulosic substrates. Many tested isolates belong mainly to the orders Polyporales, Hymenochaetales and Agaricales.

In order to apply the strategies for mycoremediation of synthetic dyes numerous studies have been focused on aspects concerning the full knowledge and understanding of the mechanisms involved in this process, especially of the various factors affecting the decomposition rate. Optimizing these factors is essential in order to raise the efficiency of the biodegradation process. The researches revealed the influence of certain factors such as the pH of the media, the optimal value being located in the slightly acidic domain, 4.00 – 5.00 [Pocedič *et al*., 2008; Radha *et al*., 2005], sometimes alkaline, between 7.00 – 9.00 [Papinutti *et al*., 2006]. The optimal temperature can vary between 25°C [Anastasi *et al*., 2010; Baldrian & Šnajdr, 2006] and 30°C [Zhao *et al*., 2006], sometimes 35°C [Kalpana *et al*., 2012].

The nutrients can also have a positive or negative influence in the degradation processes. Adding an extra nitrogen source leads to a decrease in the degradation rate of the dye [Bhatti *et al*., 2008; Rigas & Dritsa, 2006]. The type of the nitrogen source varies depending on the fungal isolate [Chen *et al*., 2008] and also on the tested dye [Balaeş & Tănase, 2013; Khelifi *et al*., 2009].

The composition of the media can influence the kinetics of the degradation process. A special category of chemical compounds refers to the heavy metal salts which have various effects on the degradation. Copper ions are vital for the activity of laccase, while the absence of manganese ions leads to the inhibition of manganese-peroxidase. But the concentration of these ions must not exceed certain values.

The addition of copper ions can have positive effects even at high levels [Lorenzo *et al.*, 2006], these influences being described in the case of various enzymes others than laccase [Baldrian, 2004]. Galhaup & Haltrich [2001] noticed that the addition of copper ions must be done during the phase of exponential growth in order for the effect to rich the maximum level, while Fonseca *et al.* [2010] noticed a delay in the development when they added 0.5 mM of copper sulfate and a high inhibition when the added quantity was of 1 mM. The effect of manganese ions depends on their concentration but also on the enzymes and the buffer solution involved in the experiment. Li *et al.* [2009] recorded high enzymatic activity when they added manganese ions, but other authors noticed that the addition of these ions determines the inhibition of the enzymatic activity [Ertan *et al.*, 2012], sometimes even for the manganese-peroxidase [Yu *et al.*, 2006].

Table 1
Macromycetes genra tested for bioremediation of synthetic dyes

GENERA	REFERENCES
Armillaria	Balaeş *et al.* [2013]; Rigas *et al.* [2003]
Bjerkandera	Anastasi *et al.* [2010]; Balaeş *et al.* [2013]; Gomi *et al.* [2011]
Cerrena	Michniewicz *et al.* [2008]
Chondrostereum	Anastasi *et al.* [2010]
Coriolopsis	Balaeş *et al.* [2013]; Liu *et al.* [2004]; Reyes *et al.* [1999]
Cyathus	Anastasi *et al.* [2010]; Balaeş *et al.* [2013]; Vasdev *et al.* [2005]
Daedalea	Balaeş *et al.* [2013]; Baldrian [2004]; Chander *et al.* [2004]
Datronia	Lyra *et al.* [2009]
Dichomitus	Chander *et al.* [2004]; Eichlerová *et al.* [2006]
Fomes	Balaeş *et al.* [2013]; Papinutti *et al.* [2006]
Fomitopsis	Balaeş *et al.* [2013]; Lyra *et al.* [2009]
Ganoderma	Anastasi *et al.* [2010]; Asgher *et al.* [2006]; Balaeş *et al.* [2013]; Guerra *et al.* [2008]; Lyra *et al.* [2009]; Murugesan *et al.*[2009]; Rigas & Dritsa [2006]
Gloeophyllum	Anastasi *et al.* [2010]
Hexagonia	Lyra *et al.* [2009]
Hypholoma	Anastasi *et al.* [2010]; Balaeş *et al.* [2013]
Irpex	Balaeş *et al.* [2013]; Chander *et al.* [2004]
Ischnoderma	Kokol *et al.* [2007]
Lentinus	Sarnthima *et al.* [2009]
Lenzites	Anastasi *et al.* [2010]; Balaeş *et al.* [2013]
Panus	Anastasi *et al.* [2010]
Phlebia	Anastasi *et al.* [2010]; Chander *et al.* [2004]
Pholiota	Balaeş *et al.* [2013]; Rigas *et al.* [2003]
Pleurotus	Anastasi *et al.* [2010]; Asgher *et al.* [2006]; Balaeş *et al.* [2013]; Baldrian & Šnajdr [2006]; Eichlerová *et al.* [2003]; Lyra *et al.* [2009]; Nilsson *et al.* [2006]; Palmieri *et al.* [2005]; Rigas *et al.* [2003]; Shanmugam *et al.* [2005]
Polyporus	Anastasi *et al.* [2010]; Balaeş *et al.* [2013]; Chander *et al.* [2004]; Kim *et al.* [2012]; Rigas & Dritsa [2006]
Porostereum	Anastasi *et al.* [2010]
Pycnoporus	Lyra *et al.* [2009]
Schizophyllum	Balaeş *et al.* [2013]; Bhatti *et al.* [2008]
Stereum	Balaeş *et al.* [2013]; Moreira *et al.* [2000]
Trametes	Anastasi *et al.* [2010]; Asgher *et al.* [2006]; Balaeş *et al.* [2013]; Baldrian & Šnajdr [2006]; Gavril & Hodson [2007]; Guerra *et al.* [2008]; Kapdan *et al.* [2000]; Levin *et al.* [2010]; Liu *et al.* [2004]; Lyra *et al.* [2009]; Park *et al.* [2007]; Rosales *et al.* [2002]; Sanghi *et al.* [2006]; Yesilada *et al.* [2010]
Tyromyces	Chen *et al.* (2008)

The degradation of complex mixtures of synthetic dyes is possible only by combination of enzymatic reactions with physicochemical processes [Lucas *et al.*, 2007] or through co-cultivation of fungi and bacteria [Novotný *et al.*, 2010].

Another specific strategy for degrading synthetic dyes involves the immobilization of the mycelium on different solid substrates chosen accordingly to their price and characteristics. Some of the materials used in this case are poly-

urethane foam [Casieri *et al.*, 2010; Novotný *et al.*, 2004; Šušla *et al.*, 2007], sodium alginate [Ramsay *et al.*, 2005] or different wood materials [Novotný *et al.*, 2004, 2010].

3.2. OBTAINING THE LIGNINOLYTIC ENZYMES

Lignicolous basidiomycetes are successfully used for obtaining several enzymes, especially ligninolytic enzymes, with various biotechnological applications. A priority in this field is the development of efficient and low cost schemes and methods in order to obtain these enzymes [Kokol *et al.*, 2007; Levin *et al.*, 2005; Michniewicz *et al.*, 2008].

Currently several species of ligninase-producing fungi were tested (Table 2). Some researches characterized the crude enzyme extract [Couto, 2007], described the processes of obtaining purified enzymes and establishing the optimal conditions for their activity [Baldrian, 2004; Nakade *et al.*, 2010].

In order to transform the production process into a profitable one usually cheap substrates are used: agricultural products such as wheat, rice, barley straws, corn cobs; wood products – splinters, sawdust; products from the food industry – mandarin, banana peels, bran, that can be used as carbon source but also as a solid substrate for the mycelium and for inducing the synthesis of ligninases [Neifar *et al.*, 2010; Tang *et al.*, 2011].

Table 2
Macromycetes species used for obtaining ligninolytic enzymes

SPECIES	ENZYMES*	REFERENCES
Cerrena maxima	MnP	Elisashvili *et al.* [2008]
Coriolopsis polyzona	MnP	Elisashvili *et al.* [2008]
Datronia caperata	MnP şi LiP	Abrahao *et al.* [2008]
Fomes fomentarius	Lac	Neifar *et al.* [2010]
Funalia trogii	MnP	Elisashvili *et al.* [2008]
Ganoderma lucidum	Lac	Murugesan *et al.* [2007]
Hexagonia hirta	MnP şi LiP	Abrahao *et al.* [2008]
Lentinus polychrous	Lac, MnP şi MIP	Sarnthima *et al.* [2009]
Pleurotus ostreatus	MnP	Elisashvili *et al.* [2008]
Pleurotus ostreatus	MnP şi MIP	Shrivastava *et al.* [2005]
Pleurotus ostreatus	VP	Tsukihara *et al.* [2006]
Polyporus tenuiculus	MnP şi LiP	Abrahao *et al.* [2008]
Pycnoporus coccineus	MnP	Elisashvili *et al.* [2008]
Pycnoporus sanguineus	MnP şi LiP	Abrahao *et al.* [2008]
Schizophyllum sp.	MnP	Xiaobin *et al.* [2007]
Trametes pubescens	MnP	Elisashvili *et al.* [2008]
Trametes pubescens	Lac	Osma *et al.* [2007]
Trametes versicolor	MnP	Elisashvili *et al.* [2008]
Trametes versicolor	Lac	Lorenzo *et al.* [2006]

* Lac–laccase, MnP–manganese peroxidase, MIP–manganese independent peroxidase, LiP–lignin peroxidase, VP–versatile peroxidase, GLOX–glyoxal oxidase

The stimulation of the enzyme system can be done by adding to the culture media materials with high lignin content or polyphenolic compounds [Hernández-Luna *et al.*, 2008]. In order to stimulate the production of ligninolytic enzymes it is necessary that the media contain low quantities of nitrogen compounds.

The enzymatic extracts are used to obtain crude enzymes through various techniques such as polyacrylamide gel electrophoresis [Palmieri *et al.*, 2005], Coomassie-stained gel electrophoresis [Tinoco, 2007], anion exchange chromatography [Nakade *et al.*, 2007], exclusion chromatography [Trovaslet *et al.*, 2007], concentration and membrane microfiltration followed by acetone precipitation [Bryjak & Rekuč, 2010] or ammonium sulfate precipitation [Neifar *et al.*, 2010], etc.

In order to raise the efficiency of ligninolytic enzymes it is necessary to know the optimal conditions of their activity. These conditions can be established by the oxidation of standard substrates under different temperatures, pH values and chemical composition of the solutions, taking into account the values of the physicochemical parameters under which the maximum activity is achieved. Ligninolytic enzymes are active at relatively low temperatures between 25–30°C [Bhatti *et al.*, 2008; Yousefi & Karinimia, 2010] as well at high temperatures of 60–70°C [Abrahao *et al.*, 2008; Baldrian, 2004], even if during these conditions the life span halves [Murugesan *et al.*, 2007]. The optimal pH values for these enzymes can be both acidic, between 3.5–4.00 [Michniewicz *et al.*, 2008; Murugesan *et al.*, 2007] and alkaline [Yousefi & Karinimia, 2010].

3.3. LIGNICOLOUS BASIDIOMYCETES AS BIOCONTROL AGENTS

Saprophytic fungi possess different life and dispersal strategies that combine various nutrition techniques and mechanisms meant to raise the competitiveness towards other organisms. The versatility of the enzymatic system allows several species to survive under severs conditions such as low nutrient availability. As a result of the high competition for nutrients between the communities of microorganisms, saprotrophic fungi have developed various strategies in order to eliminate the antagonistic species.

Depending on the substrate, environmental factors, incubation time and the presence of other organisms, lignicolous basidiomycetes are able to synthesize secondary metabolites with different properties that have important biotechnological potential in numerous industrial branches: chemical, pharmacy, medicine, food industry, cosmetics and perfumery and agriculture – as biocontrol agents of phytopathogens.

Many lignicolous basidiomycetes that grow on dead wood or litter can synthesize toxic compounds that act against other species of fungi, including the plant pathogens. Moreover, these fungi use mechanisms other than the synthesis of toxic compounds to counteract the development of competitive organisms, such as: contact inhibition (mechanical inhibition involving the hyphae), extracellular enzyme

secretion (hydrolases, peroxidases, oxidoreductases), modifying the properties of the substrate (changes in pH values, formation of hydrogen peroxide, discharging several ions and free radicals) and also a more efficient use of nutrients.

The secondary metabolites synthesized by the lignicolous fungi are not vital for their survival but have important ecological functions, especially in inter- and intra-specific communication and defense against predators and parasites [Morath *et al.*, 2012].

Scientific studies revealed that the secondary metabolites produced by the lignicolous basidiomycetes are successfully used in pharmacy (their properties were and are used for centuries in traditional medicine) for treating different conditions such as dysentery, headaches – *Fomitopsis pinicola*, tuberculosis – *Trametes suaveolens*, bleedings – *Fomes fomentarius*, *Piptoporus betulinus*, rheumatism – *Phellinus igniarius*, cancer – *Bjerkandera fumosa*, *Ganoderma* sp., *Lentinula edodes*, *Lenzites betulina*, *Pleurotus ostreatus*, *Schizophyllum commune*, *Trametes versicolor*, liver problems – *Flammulina velutipes*, *Ganoderma lucidum*, gastric conditions – *Armillaria mellea* [Hobbs, 1995].

Researches concerning the extracts of several species such as *Flammulina velutipes*, *Ganoderna adspersum*, *G. lucidum*, *Meripilus giganteus*, showed that these fungi can be used as natural antioxidants [Karaman *et al.*, 2009].

Many species of lignicolous basidiomycetes (*Daedalea quercina*, *Daedaleopsis confragosa*, *Ganoderma* sp., *Gloeophyllum sepiarium*, *Meripilus giganteus*, *Piptoporus betulinus*, *Polyporus arcularius*, *Stereum hirsutum*) synthesize secondary metabolites with antimicrobial and antiviral properties that can be used in order to inhibit the growth and development of several plant and animal pathogens [Suay *et al.*, 2000].

Some secondary metabolites produced by lignicolous basidiomycetes were tested against numerous insects, mites and nematodes that attack and cause damage to crops. From this perspective fungal species can be divided into: i) saprotrophic species that in case of nutrient depletion adjust their enzymatic system in order to use alternative food resources and have the capacity to infect and consume invertebrates; ii) specialized species that have characteristic features to capture and consume terrestrial invertebrates and can also grow as saprophytes in their absence; iii) parasitic species that infect several invertebrates to complete their biological cycle and sporulate even if they can develop their vegetative mycelium in the absence of the host.

Studies in this field proved the impressive potential of *Hohenbuehelia* sp. to attack and consume insects [Kumar & Kaviyarasan, 2012]. Other species such as *Pleurotus ostreatus* are very efficient in consuming insect larvae [Dix & Webster, 1995].

Although there are few studies in this domain, the lignicolous basidiomycetes can be efficiently used to control the populations of nematodes. *Pleurotus* sp. was intensively studied from this point of view: *Pleurotus cystidiosus* presents

toxocysts, blastoconidia-like structures surrounded by a toxin droplet that paralyzes nematodes. The surface of the droplet is covered by a very thin and elastic envelope which bursts and releases the toxin [Truong *et al.*, 2007]; *Pleurotus ferulae* produces compounds with nematocidal activity such as cheimonophyllone [Li *et al.*, 2007]; *Pleurotus ostreatus* captures 30–50% of nematodes that are touching the fungal hyphae (in 30 seconds the victim is paralyzed) – the nematotoxic compound is trans-2-decendioic acid [Truong *et al.*, 2007]. The species from *Nematoctonus* genus: *N. concurrens*, *N. leiosporus*, *N. robustus* (teleomorph *Hohenbuehelia*) present nematocidal activity [Hibett & Thorn, 1994]. Tzean & Liou [1993] identified 17 species of *Hyphoderma* that actively capture and consume nematodes by using adhesive stephanocysts or through ingestion of mycelium by nematodes. This fact was confirmed by Karasiński [2013], who described stephanocysts and echinocytes from species of *Hyphoderma sensu lato* involved in nutrition and capturing insects (*Peniophorella sensu stricto*). Acanthocytes and stephanocysts from *Coprinus comatus* [Luo *et al.*, 2004] and *Stropharia rugosoannulata* [Luo *et al.*, 2006] play an important role in capturing and paralyzing nematodes and insects. The acanthocytes function as attractants for nematodes and for cuticle penetration (these hyphae present structures – acanthae – with the appearance of sharp swords). *Coprinus xathothrix* produce a nematocide compound named xanthothone [Liu *et al.*, 2008], while the culture filtrate of some basidiomycetes presented nematotoxic effect: *Amauroderma*, *Daedalea*, *Filoboletus*, *Fistulina*, *Lentinula*, *Omphalotus*, *Oudemansiella*, *Pleurotus*, *Ramaria* [Dong & Zhang, 2006].

A special class of secondary metabolites with considerable potential in biotechnologies is represented by the volatile organic compounds, chemical compounds that have a low molecular weight, are insoluble in water, have a low boiling point, are volatiles and present a characteristic smell [Wang *et al.*, 1996]. Volatile organic compounds are aromatic and aliphatic hydrocarbons, alcohols, ketones, aldehydes, halogenated compounds [Lindfors & Laurila, 2000; Nichol & Wong, 2011].

In the last few years the interest for these bioproducts grew impressively and besides their important role in the natural ecosystems (communication and defense) their great biotechnological potential in various industries (food industry, cosmetics, perfumery, pharmacy and agriculture) was described.

In nature the volatile organic compounds synthesized by fungi are not produced in a pure form but as complex mixtures of simple hydrocarbons, aldehydes, ketones, alcohols, phenols, esters and several derivatives, including benzene and cyclohexane derivatives [Ortiz-Castro *et al.*, 2009], that raise the specificity of the chemical message [Rolf & Wolf-Rainer, 2012].

These compounds have antibiotic, antifungal, antiviral, cytotoxic, hallucinogenic and plant growth regulating properties [Anke, 1989].

The quantity and quality of the volatile organic compounds synthesized by lignicolous basidiomycetes depends on several abiotic factors such as the chemical composition and pH of the substrate [Chen *et al.*, 1984; Ewen *et al.*, 2004; Wheatley, 2002], temperature [Tronsmo & Dennis, 1978], water content, but also on some biotic ones, such as development stage [Fäldt *et al.*, 1999; Wu *et al.*, 2005] and the presence of other organisms [Griffith *et al.*, 1994; Hynes *et al.*, 2007].

Among the bioactive volatile organic compounds with great potential in biotechnological processes are the terpenes, compounds that have both antimicrobial (antibacterial and antifungal) properties and special aromas [Abraham 2001; Insam & Seequald, 2010]. The terpenes are synthesized especially in the late growth phase and during characteristic conditions: stress, UV radiations, infections and attack from different organisms [Aldered *et al.*, 1999; Rolf & Wolf-Rainer, 2012].

Among the terpenes, sesquiterpenes are lipophilic molecules that target the cellular membranes; their toxicity is determined by the loss of osmotic control [Inoue *et al.*, 2004] and by facilitating the transfer *via* cell membrane of antibiotic compounds inside the cell [Deyrup *et al.*, 2007; De Silva *et al.*, 2006].

Sesquiterpenes have relatively high vaporization pressure which allows the message to be very specific and sent at long distances, this fact explaining the important role played by these molecules in intra- and inter-specific communication [De Bruyne & Baker, 2008].

Fungi use complex mixtures of sesquiterpenes that ensure the protection against various predators, parasites and competitors, preventing at the same time the development of specific resistance among the parasites [Andersen *et al.*, 2010].

The impact of terpenes towards the human health was also considered. Thanks to their high bioactivity, these compounds have a great potential in the pharmaceutical industry, like antifungal, antibacterial and antiviral products [Lindequist *et al.*, 2005]. Organic compounds such as 2-methyl-3-methylbutyl ester and propanoic acid can inhibit the growth and development of some pathogenic organisms – *Mycobacterium tuberculosis* and *Escherichia coli* [Morath *et al.*, 2012].

Many of these volatile organic compounds have different aromas and for this reason they can be used in the cosmetic industry or perfumery: 6-pentyl-α-pyrone presents a coconut flavor, benzyl aldehyde has an almond flavor, isobutyric acid and 2-heptanone a cheese odor and 1-butanol-3-methyl-acetate presents a banana flavor [Morath *et al.*, 2012].

The volatile organic compounds are responsible for the smell and taste of fungi, making these organisms an important food resource (the fruiting bodies of edible basidiomycetes, truffles).

In agriculture the volatile organic compounds are studied especially for their antifungal and antibacterial properties being, from this point of view, efficient biocontrol agents of phytopathogenic species.

The term *biocontrol* refers to the action of reduction pathogen populations using different organisms or their products with no negative impact on the environment or human health limiting the usage of chemical pesticides [Whipps & Lumsden, 2001].

Using the volatile organic compounds produced by fungi as biocontrol agents / biopesticides is a preferable alternative in organic agriculture, the risks of chemical pesticides being limited or completely removed. The scientific literature underlines the antimicrobial properties of some volatile organic compounds synthetized by fungi such as: 6-pentyl-α-pyrone, isobutyric acid, oudemansin A, dezoxyhypnophilin, hypnophilin, hirsutic acid, beauvericin, cinnabarin, ganomycin A and B [Morath *et al.*, 2012; Silva 2007].

Researches in this field have proven that strobilurins and oudemansins are able to inhibit the growth and development of some phytopathogenic fungi, altering the respiratory process in mitochondria [Lorenzen & Anke, 1998]. These compounds have no negative effects on mammals therefore they are the perfect choice in the development of biofungicides [Clough, 1993].

Several studies have shown the great potential of lignicolous basidiomycetes in bio-prospecting. The fungal diversity along with the numerous substrates on which these organisms can develop on, offers countless possibilities of synthesizing volatiles organic compounds with unique properties that can be successfully used in biotechnologies.

Using the volatile organic compounds produced by lignicolous basidiomycetes as main ingredients of biopesticides represents a challenge in understanding and establishing their selective potential [Butt *et al.*, 2001].

Suay and co-workers [2000] tested 317 fungal isolates belonging to 204 species of basidiomycetes and have proven that more than 45% of the isolates (over 109 species) have antibacterial and antifungal properties. Taxonomically, many of these species are found in orders such as Agaricales, Boletales, Ganodermatales, Hymenochaetales, Polyporales and Stearales, many of them being lignicolous macromycetes [Suay *et al.*, 2000].

Concerning the antifungal potential of the volatile organic compounds synthesized by lignicolous basidiomycetes (Table 3), the studies in this field are relatively few in comparison with the ones dedicated to the volatiles produced by micromycetes and streptomycetes.

Antifungal secondary metabolites from basidiomycetes are used directly in the production of fungicides or as precursor molecules, on the basis of which compounds with inhibitory action can be synthesized [Park *et al.*, 2003].

In the biological control of plant pathogens with fungi, there are two main mechanisms based on the mode of action of these organisms.

The first strategy involves the obtaining of propagules (several categories of spores: arthrospores, chlamydospores, basidiospores) or hyphal fragments and their *in situ* dispersal – strategy that can be applied when the fungal species:

i) act directly on the pathogen through mechanisms such as parasitism, mechanical action, enzymatic hydrolysis of the cuticle or cellular walls; ii) indirectly by modifying the substrate so the pathogen can't grow in the new conditions. The second strategy involves obtaining biologically active compounds with inhibitory activity – biopesticides [Evans *et al.*, 2001].

Table 3
Volatile organic compounds synthesized by lignicolous basidiomycetes and their bioactivity

VOLATILE ORGANIC COMPOUNDS	SPECIES	BIOACTIVITY	REFERENCES
(4-methoxyphenyl)-1,2-propanediol	*Bjerkandera adusta*	antifungal (weak)	Zjawiony (2004)
9-methoxystrobilurin A	*Crepidotus* sp., *Mycena* sp., *Oudemansiella* sp.	antifungal	Silva (2007)
hirsutic acid	*Stereum* sp.	antibiotic	Comer *et al.* (1967); Silva (2007)
merulinic acid A, B şi C	*Merulius tremellosus*, *Phlebia radiata*	antimicrobial	Giannetti *et al.* (1978); Zjawiony (2004)
anisaldehyde	*Pleurotus pulmonarius*	antifungal (weak)	Zjawiony (2004)
beauvericin	*Laetiporus sulphureus*	antifungal	Zjawiony (2004)
biformin	*Polyporus sp.*	antimicrobial	Zjawiony (2004)
halogenated compounds	*Bjerkandera adusta*	antimicrobial	Spinnler *et al.* (1994)
volatile organic compounds	*Schizophyllum commune, Tramates versicolor*	antifungal against *Botrytis cinerea*	Schalchli *et al.* (2011)
volatile organic compounds	*Fomes fomentarius, Ganoderma applanatum, Pleurotus ostreatus, Trametes versicolor*	antifungal against *Penicillium expansum*	Florianowicz (2000)
volatile organic compounds	*Trametes hirsuta*	antifungal against *Aspergillus* sp., *Penicillium* sp., *Mucor* sp.	Sivaprakasam *et al.* (2011)
desoxyhypnophilin	*Lentinus crinitus*	antifungal against *Aspergillus*, *Penicillium*, *Mucor*	Zjawiony (2004)
enokipodin A, B, C, D	*Flammulina velutipes*	antibacterial	Ishikawa *et al.* (2001)
fommanosan	*Fomes* sp.	antimicrobial	Kepler *et al.* (1967)
hypnophilin	*Lentinus crinitus*	antifungal against *Aspergillus* sp., *Penicillium* sp., *Mucor* sp.	Zjawiony (2004)
merulidial	*Merulius tremellosus*	antifungal and antimicrobial	Quack *et al.* (1978)
oospolactone	*Gloeophyllum sepiarium*	antifungal against *Alternaria* sp.	Zjawiony (2004)
oudemansin A	*Oudemansiella* sp., *Xerula* sp.	antifungal	Florianowicz (1999); Silva (2007)
pleuromutilin	*Pleurotus* sp.	antifungal	Florianowicz (1999)
saponins	*Flammulina velutipes*, *Ganoderma applanatum, G. lucidum, Meripilus giganteus*	antimicrobial	Karaman *et al.* (2009)
sesquiterpenes	*Heterobasidion occidentale*	antifungal	Hansson *et al.* (2012)
strobilurin A, C şi F	*Crepidotus* sp., *Mycena sp.*, *Oudemansiella* sp., *Xerula* sp.	antifungal	Florianowicz (1999); Silva (2007)
strobilurin E	*Crepidotus* sp.	antifungal	Florianowicz (1999)
tiamulin	*Psathyrella* sp.	antifungal	Florianowicz (1999)
triterpenes	*Ganoderma* sp.	antifungal	Karaman *et al.* (2012); Zjawiony (2004)

Some of the advantages of using fungi and their metabolites in the biocontrol of pathogens are [Butt & Copping, 2000]: i) fungi as well as their metabolites are natural resources which can be, if managed accordingly, inexhaustible; ii) using these resources transforms the agriculture into a more sustainable process; iii) using fungi and their products reduces the negative impact of chemical pesticides on the environment and human health; iv) the quality of the organic products is considerably superior from the nutritional point of view and healthier compared with the quality of the products obtained from a chemical agriculture; v) the quality of the products and the prices of the vegetal commodities (organic products) obtained from an ecological agriculture are higher, the profit being implicitly higher.

Given the intensive agriculture which uses synthetic pesticides with negative effects towards the environment and human health, it is necessary to develop new, eco-friendly products that will protect the crops and provide us with proper quality products.

4. CONCLUSIONS

Lignicolous basidiomycetes are unique organisms that have managed to adapt morphologically and physiologically to the degradation of lignin, one of the most resistant biopolymers found in the vegetal cell wall.

This ability of lignicolous basidiomycetes to degrade lignin using enzymes which they synthesize attracted the interest of the scientific community through their impressive potential in various biotechnological processes.

The fact that these fungi can grow on synthetic media and can produce bioactive molecules *in vitro* classifies them as extremely important bioresources, theoretically inexhaustible, which can be successfully used in bioremediation of habitats affected by different types of pollutants, limiting the use of physicochemical methods with high costs and additional negative effects.

The use of volatile organic compounds synthesized by lignicolous basidiomycetes in the biocontrol of phytopathogens is a viable alternative to synthetic chemical pesticides whose known adverse effects are reflected on both environmental quality and human health.

Research in this area is far from complete, but the results obtained until now encourage the development of bioprocesses and bioproducts based on enzymes and metabolites synthesized by lignicolous basidiomycetes, that can be broadly applied, *in situ,* in order to replace conventional techniques used in different industrial branches.

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