International Food Research Journal 30(5): 1074 - 1092 (October 2023)
Journal homepage: *http://www.ifrj.upm.edu.my*

Review

Overview of *Pleurotus* spp., edible fungi with various functional properties

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Article history

Received:
20 June 2022

Received in revised form:
23 November 2022

Accepted:
8 May 2023

Keywords

Pleurotus-molecules,
therapeutic use,
nutritional value,
economic importance,
Pleurotus-genetic modifications

Abstract

Pleurotus fungi, also known as basidiomycetous fungi, have been a part of human culture for thousands of years. They exhibit anticancer, antitumor, antibacterial, and immunomodulatory effects, having biotechnological, medicinal, and aesthetic applications. They are also versatile, highly resistant to illnesses and pests, and do not require special growing conditions. These properties make them readily marketable, and can be found in supermarkets worldwide, generating multimillion-dollar sale revenues. The global edible mushroom market was valued at USD 5.08 billion in 2021, which is expected to grow to USD 6.43 billion in 2028. China produces about 87% of *Pleurotus* spp. globally; other Asian countries generate 12%, and Europe and America account for approximately 1%. *Pleurotus* spp. have distinct functional characteristics, including high protein content with a proper essential amino acid score pattern, dietary fibre profile, high amounts of vitamins (*e.g.*, B and D) and minerals (*e.g.*, Fe, Zn, Cu, and Se), and low fat. Therefore, *Pleurotus* spp. can provide alternative industrial tools. The present review discusses *Pleurotus* spp. as biotechnological tools for acquiring metabolites of interest, studying them, and analysing bioactive substances that can be used in various fields, including medicine and food.

DOI
https://doi.org/10.47836/ifrj.30.5.01

Introduction

Mushrooms are the spore-bearing fruiting bodies of macroscopic fungi. Their applications vary, ranging from obtaining metabolites with potential therapeutical properties (Rathee *et al*., 2012) to the preparation of traditional "Mexican quesadillas" (tortillas with asadero cheese). *Pleurotus* spp., commonly known as oyster mushrooms, are edible mushrooms with gastronomic, nutritional, and medicinal properties (Figure 1). *Pleurotus* spp. are one of the most important commercially farmed edible mushrooms, with a global estimated annual production of 6.46 × 10^6 tons (Sánchez and Royse, 2017). *Pleurotus* spp. have numerous benefits, including in human nutrition, animal feed, medicine, pharmacy, chemical industry, biological control, and soil decontamination (Maftoun *et al*., 2015; Sánchez and Royse, 2017). To date, approximately 70 species of this genus have been reported; however, only a few are commercially viable, such as *P. ostreatus*, *P. florida*, *P. sajor-caju*, and *P. eryngii* (Maftoun *et al*., 2015). Approximately 99% of *Pleurotus* spp. are produced on the Asian continent, particularly in China. The commercial output of *Pleurotus* spp. from South America is predominantly from Brazil, Mexico, Colombia, Argentina, and Guatemala (Sánchez and Royse, 2017).

Pleurotus spp. cultivation is simple and inexpensive because it does not require sophisticated

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equipment or technology (Figure 2), or other resources (Tesfaw *et al*., 2015). *Pleurotus* spp. can grow on a variety of lignocellulosic substrates and other agrowastes such as wheat straw, oat, rice, sawdust, cotton waste, banana leaves, and corn stalks. It has a short cultivation cycle, and grows between 25 and 30°C (Bautista *et al*., 1998; Sánchez, 2004; Sánchez and Royse, 2017).

To date, studies on *Pleurotus* spp. have led to the generation of patents in various fields, including medicines, foods, and cosmetics (WIPO, 2020) (Table 1). Therefore, research that confirms the biological activities of *Pleurotus* spp., and outlines strategies to obtain specific compounds are crucial. In the present review, we examine the importance of *Pleurotus* spp. as a therapeutic agent, their functional qualities and biomolecules involved, and mechanism of action. The information presented herein will also highlight the economic value of *Pleurotus* spp. in the food business. Finally, we discuss our thoughts on future studies on *Pleurotus* spp.

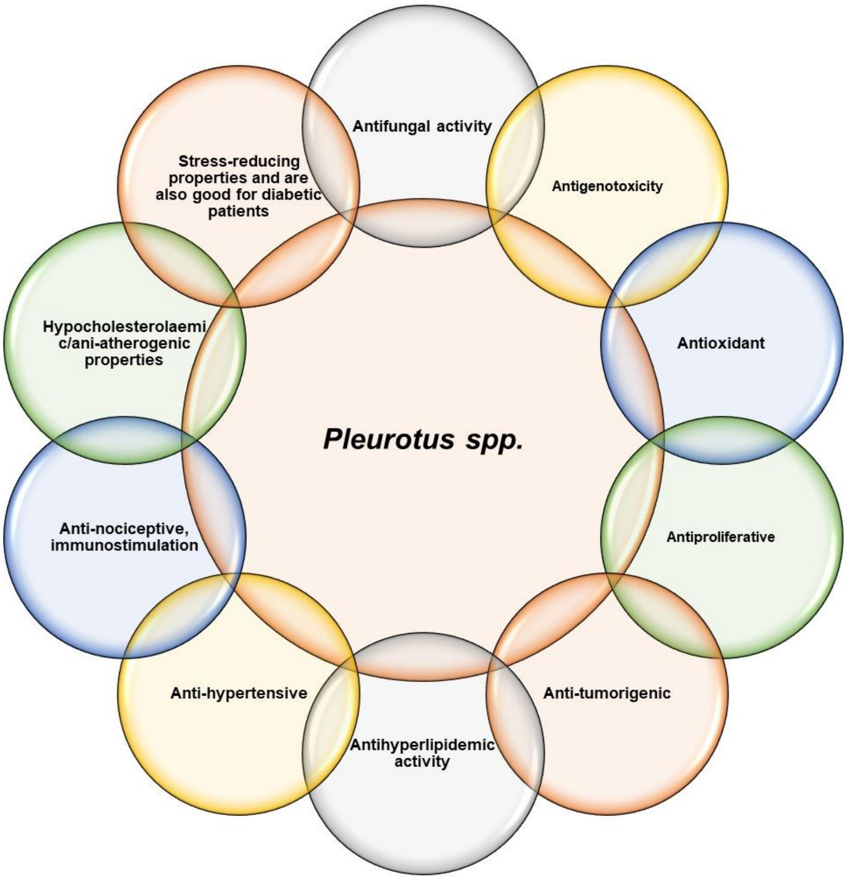

Figure 1. Physiological effects exerted by metabolites produced by *Pleurotus* spp.

(a) (b)

Figure 2. *Pleurotus* spp. production. **(a)** *Pleurotus* spp. mycelium inoculated in sterile straw as substrate and incubated for approximately 21 days. **(b)** Fruiting bodies of *Pleurotus* spp. growing on the substrate.

Table 1. Examples of patents generated with *Pleurotus* spp.*

Publication number	Title	Species	Use
109091422	Cosmetics containing *P. citrinopileatus* extracting solution and preparation method thereof	*P. citrinopileatus*	Cosmetics
1999169193	Production of trehalose from fungus belonging to genus *Pleurotus*	*P. eryngii* (ATCC No.36047), *P. cystidiosus* (ATCC No. 48751), *P. sajor-caju* (ATCC No.32078)	Foods, cosmetics, medicines
109293572	Method for extracting ergothioneine and polysaccharides from *P. citrinopileatus*	*P. citrinopileatus*	Cosmetics
1995258062	Cosmetics	*P. cornucopiae*	Cosmetics
10199500292765-	Methyl-5-0-(alpha-d-xylopyranosyl)-d-erythroascorbic acid	*P. ostreatus*	Therapeutic agents, food additives
WO/2007/132900	Skin moisturizer and therapeutic agent for dermatitis	*P. cornucopiae*	Therapeutic agent-dermatitis
2001064194	Therapeutic agent of hyperlipemia and therapy of hyperlipemia	*P. eryngii*	Therapeutic agent-hyperlipemia
2009029786	Pancreatic lipase inhibitor, its production method and therapeutic method	*P. eryngii*	Therapeutic agent-pancreatic lipase inhibitor

*WIPO (2020).

Nutritional value of Pleurotus

Edible mushrooms are commonly used as functional foods, or as raw materials for functional foods. They are also an excellent food supplement (Kakon *et al.* 2012). In healthcare, they are used to treat diseases such as infections, diabetes, and hypertension owing to their nutritional value (Figure 3). Some of the most important biomolecules present in *Pleurotus* spp. are described in the following sections.

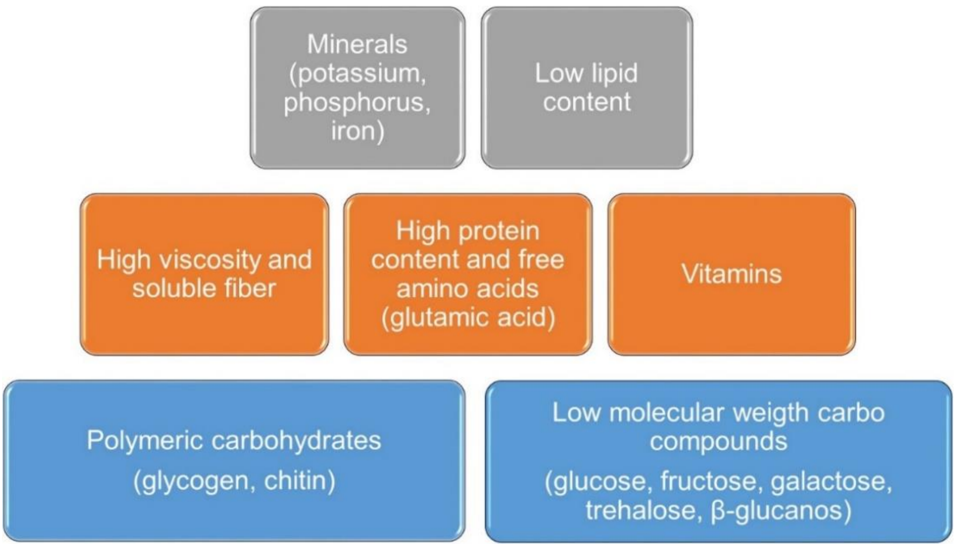

Figure 3. Nutritional components of *Pleurotus* spp.

Proteins, lectins, and amino acids

The protein content of *Pleurotus* spp. is important, and their nutritional value has been recognised for a long time. These fungal proteins have better nutritional value than many plant proteins, with their quality resembling that of animal proteins (Lelley, 1987; da Silva *et al*., 2012). The protein content of *Pleurotus* spp. (9.29 to 37.4 per 100 g) is higher than that in rice (7.1 to 8.3 g per 100 g) (Juliano, 1985), which is an important staple food (FAO, 2020). The protein content of *Pleurotus* spp. is affected by the species and strain, in addition to the maturation stage, fungal body, collection location, and substrate composition where the fungus was cultivated (Bano and Rajarathnam, 1988; Alam *et al*., 2008). *Pleurotus* spp. cultivation is essential because agrowastes without apparent use are transformed into biomass with high-quality protein content (Wang *et al*., 2001; Ancona *et al*., 2005; Gupta *et al*., 2013; Fernandes *et al*., 2015).

Owing to its protein benefits, *Pleurotus* spp. have been used as an alternative to improve the quantity of protein in different foods. For example, *P. sajor-caju* powder (25 - 50%) has been added to chicken and beef burgers. Sensory evaluation showed that consumers accepted hamburgers with different concentrations (25 and 50%) of mushroom powder. In these products, the preference scores for the sensory attributes (aroma, colour, elasticity, juiciness, and flavour) and acceptability were not significantly different from those of the unfortified samples (Wan Rosli *et al*., 2011; Wan Rosli and Solihah, 2012). In addition, Saiful Bahri and Wan Rosli (2016) investigated the effect of replacing coconut milk powder with *P. sajor-caju* (4 and 20%) on the nutritional composition and sensory acceptability of ready-to-eat pasta in Malaysia. The formulations had high and low protein fat contents. In addition, consumers accepted formulations containing more than 40% mushroom powder (Saiful Bahri and Wan Rosli, 2016). Additionally, replacing wheat flour with a low concentration (5%) of *P. ostreatus* powder-fortified bread did not negatively affect sensory acceptability (Ndung'u *et al*., 2015). Ng *et al*. (2017) found that 8% supplementation with *P. sajor-caju* powder in cookies resulted in a more desirable aroma, colour, and taste, as compared to cookies without supplementation.

On the other hand, *Pleurotus* contains lectins which are proteins that do not exhibit enzymatic activity. However, lectins can recognise and bind selectively, specifically, and reversibly to carbohydrates. Lectins are also involved in biological functions such as cell-cell recognition, cell adhesion, and innate immune response against pathogens (Perduca *et al*., 2020). Furthermore, exhibiting antiproliferative activity against human cancer cells is one of the most critical functions of lectins, thus making them crucial compounds in cancer treatment (Perduca *et al*., 2020). Lectins obtained from *P. citrinopileatus* have displayed antitumor and antiviral effects (Li *et al*., 2008). Moreover, a lectin present in *P. ostreatus* (POL) reduced tumour burden in S180 sarcoma and H-22 hepatoma in mice by 88.4 and 75.4%, respectively (Wang *et al*., 2000). Lectins isolated from *P. florida* reduced arsenic-induced cytotoxicity in rat renal cells by inhibiting apoptosis (Rana *et al*., 2015).

Pleurotus spp. are suitable for children, adolescents, and adults (FAO, 2013). *Pleurotus* spp. also contain significant percentage (20 - 40%) of free essential amino acids, which are required for a healthy human diet (Maftoun *et al*., 2015; Grabarczyk *et al*., 2019). Leucine and glutamic acid are the most abundant essential and non-essential amino acids, respectively (Kayode *et al*., 2015; Maftoun *et al*., 2015). Another amino acid of significance within the *Pleurotus* genus is ergothioneine which contains a thiol group. Its biological functions include displaying antioxidant activity (protecting the cells from oxidative/nitrosative stress) and preventing and treating atherosclerosis (Abidin *et al*., 2017; Izham *et al*., 2022).

Carbohydrates

Pleurotus spp. contain carbohydrates, particularly polymeric molecules, such as β-glucan, glycogen, chitin, and various low-molecular-weight carbonaceous compounds (*e.g.*, glucose, fructose, galactose, and trehalose). Carbohydrates, along with other components including mannoproteins, galactomannans, celluloses, and polyglucuronic acids, play a key part in the therapeutic effects of mushrooms owing to immune-stimulating glucans (Batbayar *et al*., 2012; Dalonso *et al*., 2015; Ng *et al*., 2017).

β-glucan is one of the main components of the *Pleurotus* spp. dietary fibre (Table 2). This polysaccharide is a soluble fibre with a β-(1→3) backbone linked to D-glucose with no branches, or varying amounts of β- (1→6) branches. The glucose chains of β-glucans twist and form a single or triple helix stabilised by interchain hydrogen bonds (Brown and Gordon, 2005; Rop *et al*., 2009). The relative molecular weight of β-glucans ranges from tens to thousands of kilodaltons (Rop *et al*., 2009). This polysaccharide can reduce elevated serum cholesterol levels (Cheung, 2013). Adding 8% *Pleurotus* powder to biscuits increased dietary fibre content from 3.37 to 8.62%, and decreased glycaemic index *in vivo*. This effect was attributed to the fungal fibre which interfered with the starch granules by reducing their size and inducing uneven and spherical shapes, thus resulting in lower susceptibility of the starch to digestive enzymes (Ng *et al*., 2017). β-glucans possess other beneficial properties, including anti-inflammatory, antitumor, antimicrobial, and antidiabetic activities (Chong *et al*., 2016). For example, carboxymethylated α-(1→3)-glucan from *P. citrinopileatus* showed cytotoxic activity in cervical cancer cells (Wiater *et al*., 2011; 2015), whereas (1→3)-β-D-glucan and mannogalactan of *P. sajor-caju* had an anti-inflammatory effect (Silveira *et al*., 2014; 2015). Besides, the PAP polysaccharide from *P. abalonus* showed antiproliferative activity against human colorectal cancer cells LoVo (Ren *et al*., 2015).

It is important to note that edible fungi have also been demonstrated to act as prebiotics by stimulating the expansion of the gut microbiota, thereby providing health benefits to the host. Carbohydrates such as chitin, hemicellulose, glucan, mannan, xylan, and galactan are thought to be responsible for this effect (Jayachandran *et al*., 2017).

Polysaccharides derived from *Pleurotus* spp. can play an essential role in improving the properties of fermented milk products. For example, a polysaccharide derived from *P. eryngii* was added to milk before fermentation, and its effect was examined. The fermented dairy had acceptable firmness and rubberiness values when compared with the controls (Li and Shah, 2015). Additionally, some lactic acid bacteria produced polysaccharides during fermentation, which were necessary for the optimal consistency and texture of the fermented milk products (Zisu and Shah, 2003).

Table 2. Type and quantity of polysaccharides in several species of *Pleurotus*.

Species	Polysaccharide	Dry mass in 100 g	Reference
P. citrinopileatus	total glucans	18.260 g	Sari *et al*. (2017)
P. eryngii	β-glucans	15.321 g	
*P. ostreatus**	β-glucans	4.6 g	Nitschke *et al*. (2011)
*P. pulmonarius**	β-glucans	2.5 g	

*Mycelium

Phenolic compounds

Phenolic compounds are molecules with aromatic rings containing one or more hydroxyl groups. The functions of phenolic compounds include stabilising lipid oxidation and antimicrobial activity (Torres-Martínez *et al*., 2022). Examples of phenolic compound classes include simple phenolic compounds, phenolic acids, flavonoids, flavones, and phenylpropanoids (Cateni *et al*., 2022).

Phenolic compounds have been reported in *P. ostreatus*, *P. djamor*, *P. florida*, *P. citrinopileatus*, and *P. gigantues*, in amounts of approximately 700 mg/100 g dry mass (Izham *et al*., 2022). Flavonoids, mainly catechin, quercetin, and chrysin, are the most abundant phenolic compounds in *Pleurotus* spp. (Mohamed and Fargahaly, 2014). Furthermore, several phenolic acids—such as benzoic acid derivatives (protocatechuic, gallic, vanillic, and syringic acids) and cinnamic acid derivatives (caffeic and ferulic acids)—have been reported in *P. djamor* (Izham *et al*., 2022).

Phenolic compounds and secondary metabolites obtained from *P. florida* extracts have antioxidant and antimicrobial activities (Prabu and Kumuthakalavalli, 2016). Flavonoids from *P. djamor* possess similar properties but act as metal chelators, reducing agents, free radical scavengers, and deactivators of singlet oxygen (Sudha *et al.*, 2016).

Vitamins and minerals

Vitamins and minerals exhibit various health benefits in humans. *Pleurotus* spp. are rich in vitamins and minerals but low in fat and calories, thus making it an ideal food for people with diabetes (Kumar *et al.*, 2021).

Vitamins have been reported to exhibit antioxidant activity (Zehiroglu and Ozturk Sarikaya, 2019). *Pleurotus* spp. are particularly rich in thiamine (vitamin B_1), riboflavin (vitamin B_2), niacin (vitamin B_3), pantothenic acid (vitamin B_5), ascorbic acid (vitamin C), and biotin (vitamin H) (Grabarczyk *et al.*, 2019; Torres-Martínez *et al.*, 2022). Additionally, *Pleurotus* spp. contain tocopherol (vitamin E) and ergosterol. Moreover, *Pleurotus* spp. contain folic acid (vitamin B_9), which decreases the risk of anaemia, diabetes, and high blood pressure (Galappaththi *et al.*, 2021).

Pleurotus spp. contain elements such as potassium, phosphorus, calcium, magnesium, sodium, copper, zinc, iron, manganese, cadmium, lead, and selenium (Khatun *et al*., 2012; Lavelli *et al*., 2018; Torres-Martínez *et al.*, 2022). Minerals are essential nutrients involved in different metabolic processes and nerve impulse transmission (Gogavekar *et al*., 2014). The metal elements found in *Pleurotus* spp. are found in low concentrations; therefore, their consumption would not pose a health risk (Egra *et al.*, 2019).

Lipids

Low levels of lipids are present in edible fungi. In *Pleurotus* spp., it has been reported to range from 0.5 to 20% of fat in dry weight (Grabarczyk *et al*., 2019; González *et al*., 2021). These variations depend on the species and the substrate on which they are growing (González-Tijera *et al*., 2014; Torres-Martínez *et al*., 2022). Lipids are mono- and polyunsaturated fatty acids (Sande *et al*., 2019). Linoleic and oleic acids are essential lipids; they are saturated, and the most abundant fatty acids in *P. ostreatus* and *P. levis* (González-Tijera *et al*., 2014). Linoleic acid (omega-6) is anticarcinogenic, and helps to reduce the risk of cardiovascular diseases and the expression of pro-inflammatory compounds. Besides, it has an essential effect as an inhibitor of the cycle of oxidative stress (COX) (Schneider *et al*., 2011; Ha *et al*., 2020). The linoleic and oleic acids also exhibit antioxidant activity (Gnanwa *et al*., 2021). Another example of a highly abundant saturated fat found in *P. ostreatus* and *P. levis* is palmitic acid which exhibits selective cytotoxicity against human leukemic cells, and induces apoptosis in the MOLT-4 human cell line. It also stimulates glucose incorporation into the adipocytes (Ragasa *et al*., 2015).

On the other hand, the presence of ergosterol has been found in *P. florida, P. djamor*, and *P. eryngii* (Ragasa, 2018). Ergosterol is a precursor of vitamin D_2 produced *via* exposure to UV light, and exhibits antioxidant activity and prevents cardiovascular diseases (Selvamani *et al*., 2018; González *et al*., 2021; Koutrotsios *et al*., 2022). *P. florida* also contains ergosterol peroxide and cerevisterol (Marquez-Fernandez *et al*., 2014; Ragasa *et al*., 2015) which have an inhibitory effect on the NO production, and in the peroxyl radical-scavenging activity (Ha *et al*., 2020).

Molecules and extracts involved in anticancer, hypolipidemic, and anti-obesity activity

Pleurotus spp. are rich in biomolecules which play an essential role in human health. These biomolecules possess a variety of therapeutic properties and have different medicinal qualities, including anticancer, hypolipidemic, and anti-obesity.

Anticancer activity

In recent years, *Pleurotus* spp. have gained importance because of its ability to combat cancer. It has been observed that crude extracts and chemical fractions from *Pleurotus* fruiting bodies or mycelium contain compounds that exhibit anticancer effect toward several types of tumour cells, but this activity depends on the species. Extracts from *P. pulmonarius*, *P. florida*, and *P. djamor* have demonstrated efficacy against several cancer types or cell lines, including human hepatoma HepG2 cells, bladder carcinoma, and ovarian cancer, respectively (Selvi *et al*., 2011; Xu *et al*., 2012; Ragasa, 2018).

Polysaccharides, proteins, lectins, vitamins, and selenium from *Pleurotus* spp. have play an important role in the anticancer activity. For instance, according to Cao *et al*. (2015), the polysaccharide POMP2 isolated from *P. ostreatus* mycelium suppressed the proliferation of the BGC-823 human gastric cancer cell line in a concentration-dependent manner, and lowered their ability for invasion. Additionally, an *in vivo* test showed that POMP2 could stop the development of tumours in mice. In this case, the sarcoma 180 sizes were reduced by around 75% by the so-called fraction II polysaccharides from *P. ostreatus* mycelium with doses of 10 and 30 mg/kg (Wisbeck *et al*. 2017). Besides, the extracellular polysaccharides obtained from *P. djamor* showed a tumour inhibition rate of 94% on the sarcoma 180 animal model at a dose of 30 mg/kg (Borges *et al.*, 2014).

Similarly, various techniques are used to extract molecules, which may impact the effectiveness of the recovered compounds as anticancer agents. Polysaccharides from *P. ostreatus* fruiting bodies showed cytotoxic activities toward Ehrlich ascites carcinoma cell line, suppressing more than 90% of the abnormal cells with a dose of 1000 g/mL (Uddin *et al*., 2019). Although selenium was considered dangerous to humans in the 1930s, its introduction to *Pleurotus* cultures boosted protein content and antioxidant activity, which is connected to anticancer activities (Khandrika *et al*., 2009; Kaur *et al*., 2018).

It has been noted that consumption of *P. ostreatus* supplemented with selenium and zinc during the cultivation process decreases the number of tumour nodules in mice lungs. Besides, an increment in the glutathione peroxidase and superoxide dismutase activities was observed (Yan and Chang, 2012). The ethanolic extract from the mycelium, which lacking selenium in the culture medium, had a poor cytotoxic effect on LS174 and He-La cells (Milovanovic *et al*., 2014).

On the other hand, selenium polysaccharide SPMP-2a from *P. geesteranus* decreased the amount of swollen and vacuolar mitochondria in the H_2O_2-treated cells as compared to the controls. Besides, this polysaccharide reduced the amount of reactive oxygen species, and improved the catalase and superoxide dismutase activities (Sun *et al*., 2017). The activation of apoptotic mechanisms, which are produced by the generation of reactive species (Wang *et al*., 2014; Yang *et al*., 2018) or due to the up-down regulation of numerous proteins are thought to be the causes of *Pleurotus* anticancer activities. For instance, in a concentration-dependent manner human colorectal adenocarcinoma cell SW480 viability was decreased by *P. ostreatus* protein extract. The production of reactive oxygen species, glutathione depletion, and a loss in mitochondrial transmembrane potential are the apoptotic mechanisms that result in the proteins present in the *P. ostreatus* extract on SW480 cells (Wu *et al*., 2011); however, the type of proteins present in this extract is unknown.

Interestingly, human breast (MCF-7) and colon cancer (HT-29) cell proliferation is inhibited by using *P. ostreatus* methanolic extracts. The effect might have been due to an up-regulation of p53 and p21 that arrested the G0/G1 cell cycle (Jedinak and Silva, 2008). Likewise, the water-soluble proteoglycan from *P. ostreatus* arrested the Sarcoma-180-bearing mice model cells in the pre-G0/G1 phase (Sarangi *et al*., 2006). Besides, it has been detected that extracts from *P. highking* induce apoptosis in breast cancer cells by altering the balance of proapoptotic and antiapoptotic genes (Haque and Islam, 2019). Also, the viability of HT-29 human colon cancer cells was reduced by 60.1 and 59.3%, respectively, using methanolic extracts from the fruiting bodies of *P. ostreatus* and *P. salmoneostramineus* (Kim *et al*., 2009).

Based on previous findings, *Pleurotus* spp. exhibited anticancer characteristics. However, there may be variations in the anticancer activities and efficacies, depending on the species and the variety of the extracted compounds.

Hypolipidemic activity

It has been reported that the use of 5% of *P. ostreatus* fruiting bodies in the diet of hypercholesterolemic rats decreased the plasma triglyceride, cholesterol, and total lipid and phospholipid levels (Alam *et al*., 2011). Likewise, a hypolipidemic effect was observed by using the aqueous extract or pellets of *P. eryngii* in the diet of laboratory animals (Mizutani *et al*., 2010; Choi *et al*., 2017). It was found that polysaccharides from *P. eryngii* mycelium extracted by alkaline or acid methods had hypolipidemic activity (Ren *et al*., 2017; Xu *et al*., 2017). Also, exopolysaccharides from *P. geesteranus* were responsible for decreasing in cholesterol and triacylglycerol concentrations (Doubin *et al*., 2013). Huang *et al*. (2014) suggested that β-glucans and fibre contained in the exopolysaccharides of *P. tuber-regium* might be responsible for the hypolipidemic activity. However, the mechanism for this action is unknown. The same authors pointed out that polysaccharides may act as agonists of a transcriptional factor (PPAR-α) that regulates genes involved in lipid metabolism.

Chrysin, a flavonoid with antioxidant activity from *Pleurotus* has a hypolipidemic effect in rats. This phenomenon can be due to the reactivation of a mechanism involving lipolytic enzymes (Anandhi *et al*., 2013). Interestingly, extracts from *P. citrinopileatus* containing nicotinic acid and ergosterol reduced triglycerides and cholesterol in rats (Schneider *et al*., 2011; Zeb *et al*., 2013).

Anti-obesity activity

Obesity has become one of the most critical health problems worldwide, requiring an urgent need for efficient control. In this regard, *Pleurotus* spp. are rich in bioactive molecules that can contribute to reaching this goal. For example, in one study, the anti-obesity and lipid-lowering effect of *P. citrinopileatus* water extract (PWE) was evaluated using a series of biochemical assays in randomised C57BL/6J mice with high-fat diet-induced obesity (DIO). Results showed that PWE significantly reduced the mice's weight gain, fat accumulation, and food intake. PWE also decreased serum triglycerides, cholesterol, and low-density lipoprotein, and improved glucose tolerance in high-fat-fed mice (Sheng *et al.*, 2019). The role of *P. ostreatus* in reducing obesity, maintaining glucose homeostasis, and modulating the gut microbiota has been demonstrated in mice (Hu *et al*., 2022). Also, it has been detected that polysaccharides from *P. eryngii* had a positive effect in reducing obesity in mice. Data showed that *P. eryngii* polysaccharides had anti-obesity and LDL cholesterol-lowering effects in obese mice, probably through an increment in the excretion of bile acids and lipids, and its impact in altering the microbiota (Nakahara *et al*., 2020).

Other biological activities of Pleurotus spp.

Extracts from various *Pleurotus* spp. have been found to have a variety of actions, including anti-inflammatory, anticancer, and proinflammatory properties. The extract components induce the immune response, signal transduction, and phagocytic activities. For example, Table 3 shows a list of crude extracts, their active molecules, and physiological effects (Paulík *et al*., 1996; Nozaki *et al*., 2008; Jedinak *et al*., 2011; Xu *et al*., 2014; Hu *et al*., 2018; Ma *et al*., 2020; Llauradó *et al*., 2021).

Mutants and overexpression of genes

Different molecular methods have enabled the transformation of *Pleurotus*. The generation of recombinant strains has enhanced our knowledge about the function of other genes, and the possibility of increasing the nutritional properties, fruit body quality, pathogen resistance, and biotic-abiotic stresses, thus increasing productivity, enhancing shelf life, and producing sporeless/low-sporing strains. These improvements have been accomplished using selection techniques, hybridisation, mutation breeding, molecular breeding, genetic transformation, and genome editing techniques (Ravishankar *et al.*, 2006; Barh *et al.*, 2019).

Different protocols have been developed to transform *Pleurotus* spp., such as polyethylene glycol/$CaCl_2$, electroporation, particle bombardment, and *Agrobacterium*-mediated transformation (Honda *et al*., 2000; Sunagawa and Magae, 2002; Sharma and Kuhad, 2010; Barh *et al*., 2019). Recently, CRISPR/Cas9 has been used for efficient genome editing in *P. ostreatus.* This powerful tool can contribute to the molecular breeding of non-genetically modified strains that can contribute to the acceptance in different countries (Boontawon *et al.*, 2021).

For instance, knockout and overexpression of a carbon catabolite repressor (*cre1*) in *P. ostreatus* PC9 generated mutants that showed an increase or decrease in the cellulolytic activity. However, overexpression of *cre1* did not produce a higher glucose yield relative to the wild type (Yoav *et al.*, 2018).

In contrast, the overexpression of the enzyme manganese peroxidase *pomnp6* and versatile peroxidase *povp3* in *P. ostreatus* led to higher lignin degradation in cotton stalks. These data suggested that *pomnp6* and *povp3* might help develop sustainable energy (Wang *et al*., 2019). Likewise, the protein kinase A catalytic subunit (*PKAc*) is essential for inducing the wood degradation system in *P. ostreatus*. Overexpression of *PKAc* in *P. ostreatus* resulted in faster degradation of beechwood lignin (Toyokawa *et al*., 2016). *Pleurotus* spp. use the ligninolytic system to transform agrowastes into products that can be used for their growth, thus producing valuable food products (Cohen *et al.*, 2002). Another gene overexpressed in *P. ostreatus* is the methionine sulfoxide reductase A which is encoded for the *PoMsrA* enzyme that reverses the oxidation of methionine sulfoxide (oxidised methionine). The overexpression of *PoMsrA* generated tolerance at high temperatures, osmotic pressure, and oxidative stress, thus suggesting its role in cellular protection against oxidative stress (Yin *et al*., 2015). The production of β-glucans in *P. ostreatus* was improved by replacing the promoter of the β-1,3-glucan synthase gene (*GLS*) with the promoter of the glyceraldehyde-3-phosphate dehydrogenase gene from *Aspergillus nidulans*. This transformation led to the overexpression of *GLS*, and consequently, the overproduction of β-glucans (Chai *et al*., 2013).

The role that *Pofst3* plays during the development of *P. ostreatus* was assessed through overexpression and antisense silencing *via Agrobacterium*-mediated transformation. The *Pofst3*-

Table 3. Example of crude extracts, active molecules obtained from *Pleurotus*, and their physiological effect.

Biological activity	Species	Type of extract	Possible molecule responsible	Involved molecule and its effect	Reference
Anti-inflammatory activity	*P. ostreatus*	Water extract	ND	Transcription activity ↓ AP-1, ↓ NF-κB Production ↓ TNF-α, ↓ IL-6, ↓ IL-12, ↓ PGE2, ↓ NO, ↓ IFN-γ, ↓ IL-2	Jedinak *et al*. (2011)
Immune response	*P. eryngii*	Saponified extract	Acidic glycosphingolipid	Secretion ↑ IFN-γ, ↑ IL-4	Nozaki *et al*. (2008)
		Protein purified from fresh fruiting bodies	PEP 1b	Production ↑ NO, ↑ IL-1β, ↑ IL-6, ↑ TNF-α	Hu *et al*. (2018)
Antitumor activity	*P. ferulae*, wild and cultivated	Ethanol/subfractions with different solvents	Methyl linoleate, hexadecanoic acid methyl ester, and other compounds	↑ apoptosis partially mediated by reactive oxygen species	Wang *et al*. (2014); Yang *et al*. (2018)
Proinflammatory activity	*P. ostreatus*	Aqueous	ND	↑ NO, ↑ iNOS expression, ↑ TNF-α, ↑ IL-6	Llauradó *et al*. (2021)
Signal transduction	*P. eryngii*	Protein isolate	PEP 1b	MAPK pathway: ↑ expression Mif, ↑expression Rap1b, ↑ Gpnmb, ↑ Sod1, ↑ C5ar1, ↑ Prdx2 Nitric oxide biosynthetic process: ↑ Cox2, ↑Hsp90aa1 ↑ Pyk2, ↑ Itgb2 NF-κB signalling pathway: ↑ expression Sqstm1, ↑ Cox2, ↑ Itgb2	Ma *et al*. (2020)
Hemagglutination	*P. ferulae*	Aqueous and 75% saturated $(NH_4)_2SO_4$	Lectin	ND	Xu *et al*. (2014)
Phagocytic activity	*P. ostreatus*	Purification of the soluble form	Glucan	ND	Paulík *et al*. (1996)

ND: Not determined.

overexpressing strains showed fewer primordia and larger fruiting bodies; however, no statistically significant differences were observed between these strains and the wild-type strain. Nevertheless, the strains with silenced *Pofst3* developed more primordia, and showed smaller fruiting bodies. Therefore, it was observed that *Pofst3* was involved in inhibiting primordial cluster formation and regulating the development of fruiting bodies in *P. ostreatus*. The efficient production of this edible mushroom may benefit from improvements in its development, thereby increasing its possible biotechnological applications (Qi *et al.*, 2019). Furthermore, laccase production by *P. eryngii* var. *ferulae* was improved *via* overexpression of *sspoxa3a/b*, which resulted in small fungal pellets and thin mycelial walls, thus facilitating laccase secretion, and increasing extracellular laccase activity. The increase in laccase quantity may interest the food and chemical industries because laccase has been used for its catalytic properties (Zhang *et al.*, 2021).

Mutations could improve certain properties in *Pleurotus* spp. (Barh *et al.*, 2019). For example, Djajanegara and Harsoyo (2008) generated a mutant PO-4 derived from *P. florida* using gamma radiation which showed a higher antioxidant content relative to the control. Also, sporeless or low-sporing mutants of *P. sajor-caju* was generated after 75 min of UV exposure (Ravishankar *et al.*, 2006). Chemical mutagenesis is another tool used for generating genetic diversity. For instance, NQ2A-12, a new variety of *P. eryngii* with improved medicinal qualities, has been developed; in NQ2A-12, the expression of Pin1 was increased. Pin1 is a peptidyl-prolyl *cis-trans* isomerase that represses Alzheimer's disease (Jeong *et al*., 2017). Random mutagenesis is another technique used to generate *Pleurotus* spp. mutants. For example, a wild strain of *P. ostreatus* was exposed to UV radiation (1.2 × 10^2 J/m^2/S) for incubation periods from 0 to 45 min, and 0.2% of ethidium bromide treatment for exposure periods from 0 to 10 min to enhance the production of manganese peroxidase (MnP). The double-mutated stable strain had an increased MnP activity (368.18 U/L) as compared to the wild strain (86.8 U/L). The aim of this study was to optimise MnP production, as this enzyme is helpful for the biodegradation of textile azo dyes (Arunkumar and Sheik Abdulla, 2014).

Economic value and production

Mushrooms of economic value can be classified differently, mainly as edibles, cosmetics, pharmaceuticals, and wilds (Royse *et al.*, 2017; Grand View Research, 2023). Worldwide, approximately 100 million tons of agrowastes are produced annually, which can cause environmental contamination if they are burned in the open air. Global warming is a problem worldwide, and participating countries in COP26 must contribute to limiting this increment to 1.5°C during the following 20 years (UKCOP, 2021). Fortunately, agrowastes (*e.g.*, corn stalks and leaves) can be used to cultivate edible mushrooms, and using that agricultural biomass in fungal production can contribute to lowering greenhouse gas emissions (Bumanlag *et al.*, 2018). China cultivates the most edible mushrooms worldwide (Niazi and Ghafoor, 2021). The primary cultivated edible fungi and the most consumable in the world are *Lentinula edodes* (shitake), *Pleurotus* spp. (oyster mushrooms), *Auricularia heimuer* (black wood ear), *Agaricus bisporus* (button mushroom), and *Flammulina filiformis* (enokitake) (Li and Xu, 2022; Fortune Business Insights, 2023).

Pleurotus spp. play a significant role in the global mushroom business, accounting for 19 to 25% of the total output (Royse *et al*., 2017; Raman *et al*., 2021). China generates approximately 87% of all *Pleurotus* spp., with the remaining 12% originating from other Asian countries (Japan, South Korea, Taiwan, Thailand, Vietnam, and India). Only 1% is grown in Europe and North-South America (Royse *et al*., 2017). Some of the most cultivated *Pleurotus* spp. are *P. ostreatus*, *P. sajor-caju*, *P. eous*, *P. florida*, and *P. sajor-caju* (Raman *et al*., 2021). Cultivation of other species such as *P. djamor* utilising agrowastes must also be considered (Bumanlag *et al*., 2018). On the other hand, the global edible mushroom market (cosmetics, pharmaceuticals, and foods) was valued at approximately USD 50 billion in 2021, respectively, and it is expected to grow annually by 9.7% from 2022 to 2030 (Grand View Research, 2023). In this regard, in 2021, the global *P. ostreatus* market size was evaluated at USD 5.08 billion, with an annual growth of 3.4%, and expected to reach USD 6.43 billion in 2028 (Business Research Insights, 2022).

In South America, the mushroom cultivation market is concentrated in the production of button mushroom, shitake mushroom, oyster mushroom, and others (nametake, maitake, enokitake, mane mushroom, straw mushroom, shimeji) (Market Data Forecast, 2022), with a global market of USD 4250 million in 2021, and estimated annual growth of 4.8%. Mexico, Brazil, Argentina, Chile, and Colombia are the largest producers of edible mushrooms, and Mexico is the leading producer (EMR, 2023), with around 60% of South-American production (Cano-Estrada and Romero-Bautista, 2016).

These data show the economic significance of *Pleurotus* spp. and other edible mushrooms. In this regard, the yield will probably rise in the following years, not only because these fungi are tasty, but also because of their functional features, thus making them desirable to those looking for natural, minimally processed, and wholesome foods.

Conclusion

As a consequence of different factors such as functional properties, nutritional compositions (carbohydrates, proteins, vitamins, and fibres), and green technology facilities, the consumption of mushrooms, specifically *Pleurotus* spp., has increased. China is a leading mushroom grower, and the production in North and South America is still low as compared to China. Therefore, given the global relevance of *Pleurotus*, farmers and producers should strategically focus on commercial mushroom cultivation, which would be an essential source of income. Furthermore, because fungal manufacturing uses lignocellulosic waste, this activity aids in reducing agrowastes, which are often burned in the field, thus causing air pollution.

While numerous *Pleurotus* patents have been recorded, it is possible to produce new ones, mainly if they are focused on discovering novel metabolites for use in various industries, such as therapeutics, foods, and cosmetics. Even though *P. ostreatus* is the most well-studied *Pleurotus* species; it is vital to concentrate efforts on lesser-studied species, which may contain metabolites with unique functions. Also, several extraction methods have been documented; it is critical to continue researching novel methods to improve the presence of specific activity. Likewise, because there is limited research in this field, it is necessary to expand the development of mutant and transformant lines that overexpress genes of biotechnological interest that may be employed in diverse domains.

It will also be essential to cultivate edible *Pleurotus* spp. of different colours to satisfy different tastes, and promote their consumption through well-targeted marketing, highlighting their fantastic properties. Besides, different recipes that allow their consumption in different ways, and the development of new products that use flour obtained from these mushrooms (*e.g.*, snacks for children) which contain high protein content should be undertaken. Furthermore, it will be important to create culture methods for wild-type species that allow for rapid commercialisation, and measures to extend their shelf life for commercial purposes should also be investigated most likely by technical or physical process improvements.

Acknowledgement

The authors would like to acknowledge the Instituto Politécnico Nacional for the research facilities provided in the completion of the present work.

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