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UTILIZATION OF LIGNOCELLULOSIC WASTE FROM THE AGRO-FOOD INDUSTRY BY EDIBLE BASIDIOMYCETES *PLEUROTUS* SPP.

Pavlo Zubyk, Inna Klechak, Larysa Dzyhun, Larysa Titova, Vita Linovytska*

Address(es):
Department of Industrial Biotechnology and Biopharmacy, National Technical University of Ukraine, “Igor Sikorsky Kyiv Polytechnic Institute”, Kyiv-03056, Ukraine.

*Corresponding author: pv.zubyk@i.ua

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ABSTRACT

This literature review analyzes and synthesizes scientific studies published over the past six years on the use of various agro-industrial wastes for cultivating mushrooms of the genus *Pleurotus* (*P. ostreatus*, *P. eryngii*, *P. pulmonarius*, *P. australis,* and *P. citrinopileatus*). The review identifies the most productive combinations of substrates for growing different mushroom species. Particular attention is given to the chemical composition of substrates such as wheat and rice straw, corn stalks, pulp, husks, and oilcake used as nutrient media for mushrooms. *Pleurotus ostreatus* demonstrates high biological efficiency and yield, particularly when cultivated on wheat and rice straw, corn stalks, and by-products of the flour milling industry. *Pleurotus eryngii* achieves optimal growth on rice straw and sweet sorghum pulp, benefiting from their balanced cellulose and hemicellulose content. *Pleurotus pulmonarius* efficiently utilizes lignocellulosic materials such as corn husks and oilcake, exhibiting notable adaptability to various substrates. *Pleurotus australis* and *Pleurotus citrinopileatus* also show promising growth on different agro-industrial residues, though further studies are needed to optimize their cultivation parameters. Analysis of the chemical composition of the substrates showed that cellulose and hemicellulose content significantly affect fungi growth, while a high lignin content can complicate the decomposition process but is not an obstacle for species that can process it efficiently. A combination of different substrates can increase yields. Cultivating *Pleurotus* on lignocellulosic waste from the agro-food industry significantly changes the chemical composition of the waste, positively impacting the environment. The spent substrate contains a significant amount of lignocellulosic enzymes, which can be useful for further waste processing. Thus, using agro-industrial waste for mushroom cultivation is a promising area that contributes to sustainable resource use and agricultural development.

Keywords: *Pleurotus*, agro-industrial waste, cultivation, chemical composition, mushroom yield, biological efficiency, combined substrates, lignocellulosic enzymes

INTRODUCTION

Mushrooms are a significant focus of modern biotechnology due to their rich nutritional and therapeutic properties. These mushrooms are a valuable source of protein, vitamins, trace elements, carbohydrates (including polysaccharides such as glucans, mannans, and glucosamines), phenols, alkaloids, terpenoids, lectins, and other biologically active compounds. Their therapeutic and prophylactic properties include antiviral, hypotensive, antioxidant, immunomodulatory, and antitumour effects **(Atila, 2019; Zikriyani *et al.*, 2018)**. Key genera of edible mushrooms cultivated for fruiting body production include *Agaricus*, *Lentinula*, *Pleurotus*, *Volvariella*, *Hericium*, *Auricularia*, *Grifola*, *Ganoderma*, *Flammulina*, *Tremella*, *Pholiota*, *Lepista*, *Coprinus* **(Kozarski *et al.*, 2015)** and *Hypsizygus* **(Öztürk *et al.*, 2021)**. Mushroom cultivation is a global industry, spanning over 100 countries. Since 2000, the production of mushrooms has been increasing at an average annual rate of 8.1% (Fig. 1) **(*Food and Agriculture Organization of the United Nations*, n.d.).**

Figure 1 Growth rates of global production of mushrooms and truffles (by FAOSTAT) **(*Food and Agriculture Organization of the United Nations*, n.d.)**

Among edible macromycetes, mushrooms of the genus *Pleurotus* exhibit the largest cultivation volumes, with *P. ostreatus* being particularly prominent (Fig. 2) **(Kosre *et al.*, 2021)**. The market for oyster mushrooms is projected to reach USD 84.33 billion by 2030 **(*Oyster Mushroom Market: Global Industry Analysis and Forecast (2024 -2030) Trends, Statistics, Dynamics, Segmentation by Type, Form, Distribution Channel, Forms and Region*, n.d.)**. *Pleurotus* species have gained widespread popularity due to their ease of cultivation and exceptional nutritional benefits. The primary species cultivated on an industrial scale include *P. ostreatus*, *P. eryngii*, *P. pulmonarius*, and *P. citrinopileatus* **(Rusu *et al.*, 2022).**

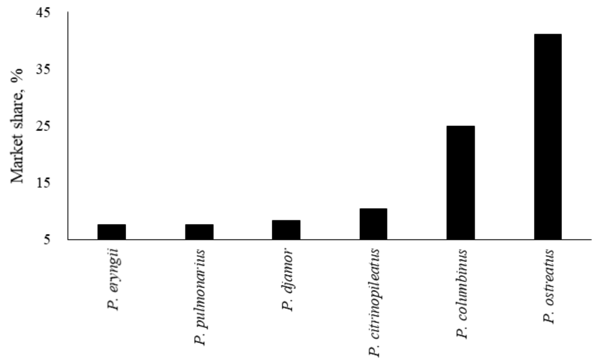

Figure 2 Segmentation of the oyster mushroom market as of 2023 **(*Oyster Mushroom Market: Global Industry Analysis and Forecast (2024 -2030) Trends, Statistics, Dynamics, Segmentation by Type, Form, Distribution Channel, Forms and Region*, n.d.)**

Representatives of the genus *Pleurotus* are basidiomycetes known for their white rot activity on wood, demonstrating high efficiency and selectivity in decomposing lignin, hemicellulose, and cellulose due to their elevated oxidase and hydrolase activities **(Andlar *et al.*, 2018)**. They are among the most effective lignocellulose degraders among edible macrofungi, making lignocellulosic biomass an ideal substrate for their cultivation **(Abdeshahian *et al.*, 2021; Pilafidis *et al.*, 2022; Rusu *et al.*, 2022)**.

Substrates for cultivating *Pleurotus* species primarily consist of various lignocellulosic materials. Lignocellulosic biomass, a promising natural resource, includes waste from forestry, agriculture, food production, pulp and paper industries, among others. This type of waste is ubiquitous, with nearly 2 × 10^{11} tonnes produced annually **(Francois *et al.*, 2020)**, yet only about 5.5 × 10^7 tonnes are effectively utilized in the circular bioeconomy **(Baig, 2022; Dahmen *et al.*, 2019; Rambo *et al.*, 2015; Usman *et al.*, 2023)**. In developed countries, individuals produce approximately 200 kg of food waste per year, including husks, seeds, and pomace (**Osorio *et al.*, 2021**). Nearly 95% of this waste ends up in landfills, generating substantial methane emissions, equivalent to over 1.1 × 10^8 tonnes CO_2-equivalent per year **(Tsegaye *et al.*, 2021)**. Consequently, cultivating edible basidiomycetes on agro-food waste addresses two critical issues: food supply and lignocellulosic waste management **(Abdeshahian *et al.*, 2021; Pilafidis *et al.*, 2022; Rusu *et al.*, 2022).**

Therefore, researching the cultivation of macrofungi from the genus *Pleurotus* on lignocellulosic waste from agriculture and the food industry is highly relevant. Given these considerations, the aim of this article is to review and analyze contemporary literature (2019-2024) to identify and evaluate methods for utilizing lignocellulosic waste in the solid-state cultivation of *Pleurotus* species. Specific objectives include: characterizing lignocellulosic waste, its primary sources, and biochemical composition; assessing the efficiency of *Pleurotus* cultivation on various lignocellulosic waste substrates, whether single-component or mixed; analyzing bioconversion efficiency and enzyme content during cultivation; and summarizing findings to draw relevant conclusions.

REVIEW METHODOLOGY

The review covers studies published between 2019 and 2024 on the solid-phase cultivation of *Pleurotus* species (*P. ostreatus*, *P. eryngii*, *P. pulmonarius*, *P. australis*, *P. citrinopileatus*) using agro-industrial lignocellulosic waste as a substrate. A systematic search was conducted in Scopus, Web of Science, and Google Scholar using the following search terms: "Pleurotus", "Lignocellulosic substrates", "Growth", "Spent brewing grains", "Rice bran", "Pomace", "Pulp", "Bagasse", "Corn cobs", "Husk", "Straw", "Stalk", "Nut shell", "Peel", "Mixed substrate", "Hydrolytic enzyme", "Solid-state fermentation", "Cultivation", "Biological efficiency", "Bioconversion". References of selected studies were also reviewed for additional relevant papers.

The review includes studies from any year for the introduction and first section.

Identified studies were categorized into four themes: fungal strains and cultivation, lignocellulosic waste substrates, biological efficiency, and enzymatic activity.Research on different *Pleurotus* species and their growth on various lignocellulosic substrates, including spent brewing grains, rice bran, pomace, pulp, bagasse, corn cobs, husk, straw, stalk, nut shell, and peel, was grouped. Studies on mixed substrates were also reviewed for their effects on fungal growth and enzymatic production. Data on hydrolytic enzyme production (cellulases, xylanases, laccases) and biological efficiency (fungal biomass yield, substrate degradation) were categorized.

Only peer-reviewed publications in English were included, excluding conference proceedings and technical reports, ensuring the inclusion of high-quality data.

CHARACTERISTICS OF LIGNOCELLULOSIC WASTE FROM THE AGRI-FOOD INDUSTRY

Origin and use

Agriculture and the processing industry generate a significant amount of waste, with by-products accounting for up to 40-50% of total losses **(Coman *et al.*, 2020)**. Lignocellulosic waste from the agro-industrial complex includes substandard grain, husks, bran, pulp, pomace, and more **(Tišma *et al.*, 2021)**. Summarized data on the main types of waste from different sectors of the food processing industry are presented in Fig. 3.

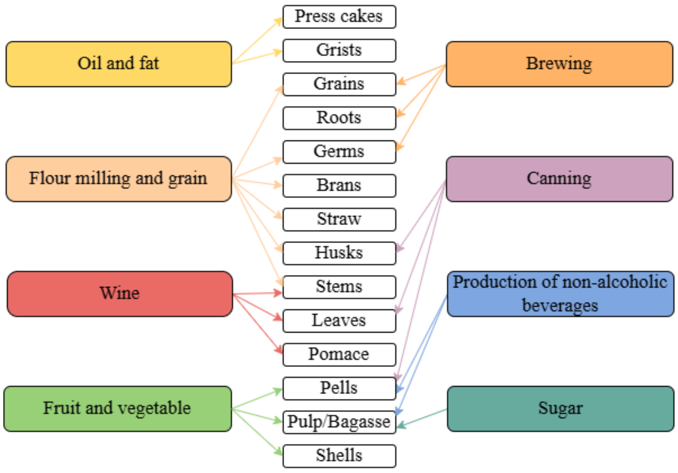

Figure 3 Origin of some lignocellulosic waste from the agri-food industry

Agricultural waste also includes plant residues left on fields after harvesting, such as straw and tops. These residues can be used as animal feed, a significant portion serves as fertilizer, is used to produce biogas, or is disposed of by incineration **(Obi *et al.*, 2016)**. The majority of lignocellulosic biomass in this sector is composed of wheat, corn, barley, and rice, while other sources are relatively insignificant **(Saini *et al.*, 2015)**. Common residues from agricultural production include straw, stems, tops, and husks of cereals (wheat, corn, barley, rice) (**Šelo *et al.*, 2021**). Coffee production generates a significant amount of solid lignocellulosic waste, including peels, pulp, and husks. The top ten coffee-producing countries alone generate more than 10^7 tonnes of waste. Processing 1 tonne of green coffee yields only 35% of the main product, with the remainder being waste, while producing the same amount of instant coffee results in 2 tonnes of wet residues **(Echeverria *et al.*, 2017**).

The confectionery industry also generates substantial volumes of lignocellulosic waste during cocoa production, including cocoa pod husks and cocoa bean shells. Specifically, industrial waste from chocolate production amounts to more than 3.6 × 10^7 tonnes, which is 5.5 times the amount of raw materials used **(Mendoza-Meneses *et al.*, 2021)**. Beer production is another significant source of lignocellulosic by-products, such as brewing grains, spent hops, and germs or roots **(Karlović *et al.*, 2020)**. Lignocellulosic biomass from sugar production includes plant residues from fields, sugar cane and sugar beet pulp, and press sludge or filtration sludge **(Harish *et al.*, 2020)**. Wine production generates various lignocellulosic wastes, such as grape leaves, vines, and pomace. Typical methods of utilizing grapevines include composting, incineration, animal feed, or chemical production **(Maicas *et al.*, 2020).** Grape or apple pomace can also be used as animal feed or for chemical production **(Niculescu *et al.*, 2023).**

The significant amount of lignocellulosic waste from the agro-industrial complex necessitates various methods of utilization or processing. One of the most advanced areas is biotechnology, which includes various methods of biodegradation and bioconversion to produce products for various purposes (Fig. 4). The biotechnological utilization of lignocellulosic waste includes the cultivation of basidiomycetes of various genera, particularly the genus *Pleurotus*, to obtain valuable food materials in the form of edible fruiting bodies.

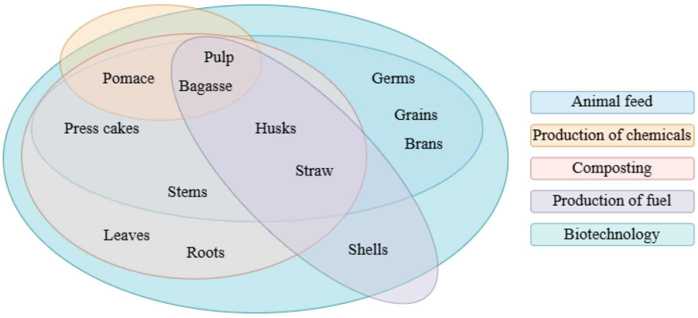

Figure 4 Typical uses of some lignocellulosic waste from the food industry

Chemical content

To select the most efficient methods for bioconversion or biodegradation of lignocellulosic waste, detailed information on its chemical composition is required. This is especially important for its use as a substrate in the cultivation of macromycetes. Lignocellulosic biomass typically consists of 38-50% cellulose, 23-32% hemicellulose, and 10-25% lignin **(Gutiérrez-Macías *et al.*, 2015)**.

Cellulose is a homopolysaccharide whose monomers are glucose residues connected by β-1,4 glycosidic bonds **(Maji, 2019)**. Hemicelluloses are heteropolysaccharides containing two or more different monosaccharide residues. The primary monosaccharide in hardwood and grasses is xylose, while in softwood, seeds, and other sources, it is arabinose, galactose, or mannose **(W. Zhang *et al.*, 2021**). Lignin, the third component of lignocellulosic biomass, is a biopolymer consisting of monolignols (p-hydroxycinnamic alcohols) **(Tobimatsu *et al.*, 2019)**. It is tightly bound to polysaccharides, which complicates the process of their hydrolysis **(Gutiérrez-Macías *et al.*, 2015)**.

Straw and stalks

Straw and stalks are dry by-products left over after growing cereals and after removing grain and chaff in flour mills **(T. S. Khan *et al.*, 2012)**. Given the steady increase in the cultivation of agricultural crops, the amount of straw is also growing. It is reported that the annual volume of straw accumulation exceeds 7×10^9 tonnes, with the bulk (about 90%) consisting of rice, corn, and wheat waste **(Sun *et al.*, 2018)**.Straw contains more than 50% carbohydrates, 21% lignin, and phenolic compounds, primarily represented by ferulic acid. The chemical composition of straw depends on the type of plant, as well as the place and conditions of growth **(Collins *et al.*, 2014)**.

Grape vines, stalks, bunches, and leaf residues separated before vinification account for up to 7% of the grape raw material, with the chemical composition of vines and leaves of red and white grape varieties being almost identical **(Fernandes *et al.*, 2013; Maicas *et al.*, 2020)**. Grapevines contain 20-45% dry matter, which includes cellulose, lignin, hemicellulose, as well as extractive compounds, especially phenols. The total amount of phenolic compounds, including flavan-3-ols and hydroxycinnamic acids, can be up to 5.8% of the dry weight **(Maicas *et al.*, 2020)**.

Husk

Husks are the shells of grain seeds formed at various stages of grain processing. As grains and oilseeds are the main raw materials for the food and feed industry, large quantities of sunflower, rice, and wheat husks are generated. Rice husks, in particular, are often dumped in landfills, causing transportation issues, or openly burned, negatively impacting the environment, thus necessitating new approaches for their utilisation **(Moayedi *et al.*, 2019)**.

The prospects for processing husks of various origins depend on the substances they contain, which vary based on the type of plant from which they are derived. Millet and rice husks contain significant amounts of p-coumaric acid (8.6-9.6 mg/kg and 8.0-8.4 mg/kg, respectively), while the concentration of ferulic acid is half that of wheat bran (1.2-1.4 mg/kg and 1.4-1.6 mg/kg, respectively) **(CAO *et al.*, 2015)**. Additionally, rice husks are reported to contain up to 15% silica **(Azat *et al.*, 2019)**.

Coffee husks, which include the outer skin and pulp of the berry, constitute 50% of the weight of green beans. They are a valuable source of biologically active compounds (caffeine, polyphenols), other organic compounds, and minerals **(Periyasamy *et al.*, 2022)**.

Another type of lignocellulosic waste is the husk of cocoa pods, which makes up 70-80% of the fruit's dry weight **(Periyasamy *et al.*, 2022)**.

Cocoa pod husks are rich in phenolic compounds such as terpenoids, flavonoids, and phenolic acids **(Vásquez *et al.*, 2019)**. Their monosaccharide composition includes arabinose, galactose, fructose, mannose, fucose, glucose, uronic acid, rhamnose, and others **(Barrios-Rodrıguez *et al.*, 2022)**. Cocoa bean husks also contain pectin, constituting about 9% of their composition **(Vásquez *et al.*, 2019)**.

Bran

The processing of grain for the milling industry produces grain bran. Although bran is used in the food industry and in animal feed, its significant potential for valorisation through biodegradation remains largely untapped, including its use as a substrate for the cultivation of macromycetes **(Nemes *et al.*, 2022)**.

Bran is the aleurone layer remaining after sieving the endosperm and the seed coat **(Skendi *et al.*, 2020)**. The majority of this waste consists of by-products from wheat, oats, rice, corn, sorghum, and other grains **(Tufail *et al.*, 2022)**. Bran contains up to 75% dietary fibre, along with inorganic compounds and extractive components such as phenols, peptides, pectin, and lipids **(Nemes *et al.*, 2022)**. It is also rich in phenolic acids, particularly ferulic and p-coumaric acids. For example, corn bran contains esterified derivatives of these acids (11.9-14.3 mg/kg of ferulic xylose and 1.1-1.5 mg/kg of p-coumaric acid), while wheat bran contains much smaller amounts of these compounds (2.1-2.5 mg/kg of ferulic acid and 57-103 µg/kg of p-coumaric acid) **(CAO *et al.*, 2015)**. Additionally, bran is rich in starch, with its content sometimes reaching up to 67% of dry weight **(Roye *et al.*, 2020)**.

Shell

Shells are formed during the processing of nuts. Current production volumes of nuts are approximately $2 \cdot 10^7$ tonnes **(Valdés García *et al.*, 2021)**. The primary use of these shells is in the confectionery industry **(Eliseeva *et al.*, 2017)**. Most shells are used for energy generation, i.e., they are burned, and their potential for creating value-added products remains largely untapped **(Gozaydin *et al.*, 2017)**.

The plants that produce the largest amount of shells during processing are hazelnuts, walnuts, almonds, and peanuts **(Salem *et al.*, 2022)**. Nut shells contain a higher amount of lignin than wood (27.2-52.3% compared to 20-40%), while their cellulose content is lower (22.4-50.7% compared to 7-65%) **(Corbett *et al.*, 2015)**. The highest lignin content is found in walnut shells, whereas pistachio shells have the highest cellulose content. Cocoa bean shells are characterised by low or no hemicellulose, and their pectin concentration reaches 6% **(Vásquez *et al.*, 2019)**. The qualitative composition of phenolic compounds in nut shells is quite diverse, including catechin, theophylline, caffeine, theobromine, tannins, epicatechin, and others **(Rojo-Poveda *et al.*, 2020)**.

Pomace, peels and pulp

Pulp, cake, bagasse and pomace are peels, seeds, and unused pulp generated during the processing of fruits, cereals, and vegetables across various industries. A significant portion of this waste is generated from the most widely grown fruits, cereals, and vegetables, such as citrus fruits, melons, apples, grapes, potatoes, tomatoes, onions, sorghum, sugarcane, and cabbage **(Bayram *et al.*, 2021)**. For instance, approximately 80% of apple processing waste is discarded, with the remainder used as animal feed **(Deveci *et al.*, 2018)**. Beet pulp, the primary waste after sugar production, represents the residues left after juice extraction from cane or beet, leading to substantial waste volumes **(Bhat *et al.*, 2016; Gupta *et al.*, 2011, Ivanova *et al.*, 2019)**.

Generally, this waste is most often used in agriculture as fertilizer and less frequently as animal feed. However, it holds significant potential for producing biologically active compounds, making it one of the most promising solutions to waste management problems **(Arshad *et al.*, 2021)**. Peels, pomace, and seeds of fruits and vegetables are promising sources of dietary fiber, with content ranging from 50% to 70%. Additionally, these plant parts accumulate large amounts of flavonoids, phenolic acids, and tannins. Notably, fruit peels contain more phenols than seeds or pulp **(Bayram *et al.*, 2021)**. Citrus pulp consists of 78% moisture, 18% water-organic compounds (proteins, phenols, fats, carbohydrates, etc.), and 4% inorganic substances. Compared to other wastes, citrus pulp contains a small amount of lignin (up to 4.9% of dry weight(d.w.)) and is a promising source of free sugars (21.1% d.w.), mainly represented by arabinose (8.95% d.w.), glucose (5.79% d.w.), and fructose (3.48%d.w.) **(Cypriano *et al.*, 2018)**. The primary phenolic compounds in citrus fruits are p-coumaric acid (24.68% of the total phenolic content) and ferulic acid (23.78%). Other reported compounds include caffeic acid, chlorogenic acid, gallic acid, syringic acid, and vanillic acid **(B. Singh *et al.*, 2020)**.

The lignocellulosic composition of pomace varies significantly depending on the fruit or vegetable type. For example, apple pomace contains 21.2-47.5% cellulose, 14.8-29.1% hemicellulose, and 18.5-25.4% lignin. Hemicellulose composition is dominated by xylose, glucose, and arabinose, with acetic acid, furfural, and its derivatives being less represented **(Leonel *et al.*, 2020)**.

Apple pomace (pulp and peel) is also a source of phenolic compounds, including gallic, chlorogenic, protocatechuic, caffeic, p-coumaric, gallic acids, catechins, and flavanols. **(Arnold *et al.*, 2023)**. According to Gowman A. *et al.*, the composition of washed and unwashed apple pomace differs. Washed pomace has higher cellulose, hemicellulose, and lignin content than unwashed pomace: 29.2% and 18.9% lignin, 14.3% and 11.6% cellulose, and 11.4% and 10.0% hemicellulose, respectively **(A. Gowman *et al.*, 2019)**.

Wine production generates $2,4 \cdot 10^7$ tonnes of grape pomace **(Niculescu *et al.*, 2023)**, which consists of skins, seeds, and pulp **(Kokkinomagoulos *et al.*, 2023)**. The basis of dry grape pomace is dietary fiber. The monosaccharide composition of polysaccharides includes arabinose, mannose, xylose, galactose, and galacturonic acid, with galacturonic acid being the most prevalent. Grape pomace also contains significant amounts of unextracted polyphenols. In general, phenolic compounds in grape pomace include flavanols, hydroxybenzoic and hydroxycinnamic acids, and stilbenes **(Bordiga *et al.*, 2019)**.

Citrus waste, apple pomace, and sugar beet pulp are characterized by high pectin content (ranging from 12% to 35%) **(Ridley *et al.*, 2001)**. However, pitahaya waste contains the highest amount of water-soluble pectins (up to 47%). Tangerine and orange peels contain 16% and 23% pectin compounds, respectively, of the total polysaccharides **(Shrestha *et al.*, 2021)**.

Sugar beet pulp contains small amounts of lignin, cellulose, and hemicellulose, with pectins making up almost 30% by dry weight **(Almowallad *et al.*, 2022)**. Another component is lignin (up to 4%). The composition of beetroot pulp also includes ferulic acid esters (0.8%) and acetic acid (up to 4%). The polysaccharide composition is represented by glucose, arabinose, uronic acid, galactose, rhamnose, xylose, and mannose, with glucose, arabinose, and uronic acid being the primary components of cellulose and hemicellulose **(Joanna *et al.*, 2018**). Reports indicate that cellulose content can reach 44% **(Sidi-Yacoub *et al.*, 2019)**. A similar amount of cellulose (40-50%) is present in sugar cane pulp, although its lignin content is almost five times higher. Sugar cane press mud contains significant amounts of free sugars (5-15%), with 2% fibers accounting for 1% sugars **(Meghana *et al.*, 2020)**. Additionally, sugar cane press mud contains crude waxes (up to 14%) and a significant amount of ash (up to 10%) **(Gupta *et al.*, 2011)**.

Other

Brewers' grains consist of a mixture of crushed barley seeds and husks **(Geršl *et al.*, 2015; Kurnik *et al.*, 2018)**. Although primarily used as animal feed, these grains can also serve as an inexpensive lignocellulosic raw material for various industries **(Lech *et al.*, 2022)**. The majority of spent grain is composed of barley hulls, but it may also include residues from other cereals such as wheat, rice, and corn. The chemical composition and content of these grains are influenced by factors such as barley variety, harvest time, malt production conditions, and the presence of additional compounds during brewing. The lignocellulosic composition is predominantly made up of cellulose and hemicellulose, with the majority of monosaccharides being xylose, glucose, and arabinose. The principal monolignans include ferulic, syringic, vanillic, p-coumaric, caffeic, and p-hydroxybenzoic acids **(Mussatto, 2009; Olivares-Galván *et al.*, 2022)**.

Another type of waste generated in the brewing industry is hop waste, which consists of the mass and sediment obtained during the separation of wort before fermentation. Although some researchers argue against the necessity of separating hops, the brewing process typically produces up to 300 grams of spent hops per 1 dm³ of finished beer. These spent hops are primarily used as fertilizer or compost, as their distinct taste renders them unsuitable for animal feed **(Karlović *et al.*, 2020)**. Germs and roots accumulated during beer production are separated from malted barley after the malt kiln stage due to their negative impact on the organoleptic characteristics of the finished product. These by-products constitute 3 to 5% of the total weight of barley and are often sold as feed **(Karlović *et al.*, 2020; Neylon *et al.*, 2020)**. Lignocellulosic waste from the brewing industry is rich in extractive compounds. Spent hops, in particular, have a high content of fibers, phenols, and proteins. The fiber's monosaccharide composition includes rhamnose, glucose, xylose, mannose, galactose, and arabinose **(Mussatto, 2009)**. The predominant phenolic compounds are catechins, kaempferol, quercetin, and proanthocyanidins **(Olivares-Galván *et al.*, 2022)**. It is also noted that only 15% of phenolics remain in the finished product **(Karlović *et al.*, 2020)**. Barley roots are a rich source of polyphenols and dietary fiber, with phenolic compounds typically represented by ferulic, p-coumaric, and vanillic acids **(Neylon *et al.*, 2020; Olivares-Galván *et al.*, 2022)**.

Press sludge, or filtration sludge, is a waste product from the sugar industry resulting from juice filtration. Processing one tonne of sugar cane yields 30 kg of sludge and 300 kg of pulp **(Bhat *et al.*, 2016; Gupta *et al.*, 2011)**, while the same quantity of cane sugar produces approximately 10 tonnes of lignocellulosic waste; this figure is about 20 times lower for beet sugar **(Dale, 2003)**. The accumulation of filtration sludge negatively impacts the environment, leading to issues related to its storage and disposal. Consequently, this sludge is often repurposed for chemical production and biogas. Harvesting sugar-containing plants also generates substantial plant residues, which, if left on the field or burned, adversely affect groundwater **(Meghana *et al.*, 2020)**.

Grape leaves, accumulated during harvest, are generally considered of low value. They are frequently used in alternative medicine or as compost **(Niculescu *et al.*, 2023)**. Besides fibers, grape leaves are rich in carotenoids, tannins, and anthocyanins **(Fernandes *et al.*, 2013)**.

Oilcake, or oilseed meal, is a by-product of oil production commonly used as fertilizer, compost, or animal feed. Given the large volumes of global oil production, the amount of lignocellulosic biomass generated is significant, necessitating the exploration of new valorization methods **(Švarc-Gajić *et al.*, 2020)**. Oilseeds are abundant in fiber, fats, carbohydrates, and extractable substances such as phenols, flavonoids, lignans, and tocopherols **(Usman *et al.*, 2023)**. Oilcake typically contains 20 to 60% dietary fiber (with lignin being the majority component), up to 50% proteins, and minerals (less than 1 g per 100 g of biomass) **(Švarc-Gajić *et al.*, 2020)**. In some cases, cellulose predominates, with proteins constituting only 2% of the dry weight of the waste. The hemicellulosic composition includes xylose, glucose, mannose, fucose, arabinose, rhamnose, galactose, and galacturonic acid **(Dornau *et al.*, 2020)**.

Substandard cereal grains are a rich source of proteins and carbohydrates (both starch and non-starch). While starch is the predominant carbohydrate in most cereals, barley has the highest proportion of non-starch carbohydrates among all cereals. Non-starch carbohydrates include pentosans, cellulose, hemicellulose, glucans, and pectins **(Kowieska *et al.*, 2011).**

Thus, the content of the main compounds in waste of different types and origin varies considerably (Table 1).

Table 1 Content of Major Substance Groups in Various Agro-Industrial Wastes

Wastes		Cellulose, %	Hemicellulose, %	Lignin, %	Ash, %	Pectin, %	References
Cake	oil	19.7-20.3	15.8-16.2	33.0-42.0	2.9-6.1	-	**(Abu Tayeh *et al.*, 2020)**
	grape seed	7.8	21.9	47.2	4.2	-	**(González Martínez *et al.*, 2019)**
Spent brewing grains		12-25	20-25	12-28	2-5	-	**(Karlović *et al.*. 2020)**
Spent hops			11,2-26,0		2.2-6.5	-	**(Bravi *et al.*. 2021; Mussatto. 2009)**
Bran	oat	0.7-3.8	6.7-8.9	10.9-11.6	2.7-2.9	-	**(Olt *et al.*, 2020; Roye *et al.*, 2020)**
	rye	1.7-5.7	30.3-3.5	4.2-4.3	4.6	-	
	corn	14.3-15.5	56.0-59.0	1.2-1.3	1.1-1.3	-	**(Afangide *et al.*, 2018; CAO *et al.*, 2015)**
	wheat	7.6-8.2	40.7-43.5	2.4-2.8	5.5-6.5	-	**(CAO *et al.*, 2015; Sibakov *et al.*, 2013)**
	rice	15.2-35.3	20.7-31.3	11.4-11.6	14.9-16.4	-	**(Ghodrat *et al.*, 2015; Sunphorka *et al.*, 2012)**
Bagasse	sweet sorghum	31.7-38.5	17.2-30.9	18.6-21.4	-	-	**(Syadiah *et al.*, 2022)**
	sugar cane	40.9-41.1	29.4-30.8	21.0-21.4	0.4-1.0	-	**(Kunusa *et al.*, 2020)**
Pomace	red beetroot	12.3-16.9	15.1-16.3	4.6-9.2	-	-	**(Chojnacki *et al.*, 2021)**
	grape	10.5-18.2	6.1-8	31.9-51.7	2.72-7.47	3.5-14.2	**(A. C. Gowman *et al.*, 2019; Shrestha *et al.*, 2021)**
	carrot	10.4-14.4	19.3-21.7	3.2-7.0	5.4-5.6	-	**(Chojnacki *et al.*, 2021; K. D. Sharma *et al.*, 2012)**
	tomato	19.9-34.3	25.1-28.2	28.8-32.3	2.9-4.1	-	**(Pirozzi *et al.*, 2022)**
	apple	9.5-7.5	3.1-29.9	5.7-29.2	1.0-4.1	-	**(Chojnacki *et al.*, 2021; A. C. Gowman *et al.*, 2019)**
Pulp	coffee	16.0-25.9	2.3-20	9-22	15-82	13	**(Dissasa, 2022; Phuong *et al.*, 2019)**
	orange	11.8-13.0	7.4-7.6	8.4-9.4	-	-	**(Mantovan *et al.*, 2022)**
	sugar beet	20	17.5	4.4	-	-	**(Almowallad *et al.*, 2022)**
Corn cobs		33,7-41,2	31.9-36.0	6.1-15.9	-	-	**(González Martínez *et al.*. 2019; Passoth *et al.*. 2019)**
Husk	oatmeal	15.5-26.0	23.9-35.2	12.2-27.7	5.1-6.4	-	**(Schmitz *et al.*, 2020)**
	coffee	43	7	9	-	-	**(Periyasamy *et al.*, 2022)**
	cocoa pods	24.2-35.0	8.7-11.0	14.6-26.4	6.7-10.0	-	**(Vásquez *et al.*, 2019)**
	millet	38.0-39.7	15.9-17.7	14.3-15.8	6.5	-	**(CAO *et al.*, 2015; Kuhe *et al.*, 2021)**
	rice	33.1-46.8	21.8-34.0	16.7-23.6	-	-	**(CAO *et al.*, 2015; Prajapati *et al.*, 2022)**
	sunflower	47.2	24	23.2	-	-	**(Cosereanu *et al.*, 2014)**
Straw	oatmeal	31-35	20.0-26.0	10.0-15.0	-	-	**(Passoth *et al.*, 2019)**
	corn	35.19-37.25	29.25-29.83	7.81-10.77	3.03-5.65	-	**(Chu *et al.*, 2021)**

	millet	36.3-37.1	17.2-17.5	19.3-19.6	4.5	-	**(H.-L. Zhang *et al.*, 2019)**
	wheat	32.0-39.3	23-30.2	12.0-21.7	8.1-10.6	-	**(Passoth *et al.*, 2019; Xu *et al.*, 2017)**
	rice	22.0-34.7	12.0-44.1	12.3-20.1	14.7	-	
	sorghum	32.0-35.0	24.0-27.0	15.0-21.0	-	-	**(Passoth *et al.*, 2019)**
	barley	36.0-43.0	24.0-33.0	6.3-9.0	10.2-10.5	-	**(Passoth *et al.*, 2019; Serna-Díaz *et al.*, 2020)**
Stem	banana	44.6	36	19.4	-	-	**(Kusmiyati *et al.*, 2018)**
	corn	31.2-39.6	16.8-35.0	7.0-21.7	-	-	**(Passoth *et al.*, 2019; Zhou *et al.*, 2023)**
	soya	34.5	24.8	19.8	-	-	**(Singh nee' Nigam *et al.*, 2009)**
	sunflower	42.1	29.7	13.4	8.6-9.2	-	
	onion	44.6-46.4	25.2-25.8	24.5-27.9	2.4-3.2	-	**(Reddy *et al.*, 2018)**
	garlic	48.0-51.6	16.6-18.4	27.9-29.3	2.4-2.6	-	
Shell	peanuts	44.8	5.6	36.1	-	-	**(Pączkowski *et al.*, 2021)**
	walnut	36.3-36.4	27.5-28.2	44.1-44.3	-	-	**(Li *et al.*, 2018)**
	cocoa	15.1	-	32.4	6.0-11.4	-	**(Vásquez *et al.*, 2019)**
	coconut	33.9-34.3	20.9-23.8	27.5-28.6	-	-	**(Li *et al.*, 2018)**
	almonds	38.1-38.9	28.6-29.1	29.5-29.7	-	-	
	pistachios	42.9-43.3	25.8-25.7	15.9-16.7	-	-	
Peels	orange	12.0-37.1	5.9-19.9	1.8-8.9	1.4-1.6	23	**(Mantovan *et al.*, 2022; Pilco *et al.*, 2022; Shrestha *et al.*, 2021; Ververis *et al.*, 2007)**
	banana	7.6-9.6	6.4-9.4	6-12	0.0017	8.9-21.7	**(Alzate Acevedo *et al.*, 2021; Shrestha *et al.*, 2021)**
	grapefruit	42	23	19	-	-	**(Pulidori *et al.*, 2023)**
	lemon	12.2-23.1	5.1-22.4	1.5-8.9	1.7-2.1	-	**(Pilco *et al.*, 2022; Ververis *et al.*, 2007)**
	tangerine	20.2-22.5	6.0-17.2	8.6-9.1	-	3-4	**(Pilco *et al.*, 2022; Shrestha *et al.*, 2021)**
	cassava	39.8-43.6	10.4-24.8	7.7-23.3	-	-	**(Hartulistiyoso *et al.*, 2022)**
	pomelo	43	24	19	-	-	**(Pulidori *et al.*, 2023)**
	onions	40.0-42.2	15.6-16.8	37.6-40.2	3.8	-	**(Reddy *et al.*, 2018)**
	garlic	39.6-43.8	19.2-22.4	32.2-37.0	3.1-3.7	-	

Thus, the analysis of lignocellulosic waste from agriculture and the food industry reveals a complex and diverse chemical composition. Such waste serves as a valuable source of mono- and polysaccharides, proteins, minerals, phenolic compounds, and other biologically active substances. This rich chemical profile positions lignocellulosic waste as a promising substrate for the cultivation of basidiomycetes.

YIELD AND BIOLOGICAL EFFICIENCY OF MACROMYCETES DURING CULTIVATION ON AGRO-FOOD RESIDUES

The use of lignocellulosic waste for the solid-phase cultivation of macrofungi to produce fruiting bodies is a well-established practice worldwide. Common substrates for growing macrofungi include corn stalks, rice and wheat straw, sunflower husks, coconut shells, cocoa bean shells, coffee grounds, wood and grape processing waste **(Yildiz *et al.*, 2002; Zubyk *et al.*, 2023)**. The key indicator of substrate quality in terms of conversion to fruiting bodies is biological efficiency (BE). BE is defined as the ratio of the mass of harvested fresh fruiting bodies to the mass of the dry substrate on which they were grown. Literature suggests that a substrate is considered economically viable if its BE exceeds 50%, leading to extensive research in this area **(Kumla *et al.*, 2020)**. For highly productive macrofungi, particularly those from the genus *Pleurotus*, BE values often surpass 100%, which is indicative of multiple harvests **(Kumla *et al.*, 2020; Östbring *et al.*, 2023)**.

Cultivation of basidiomycetes of the genus *Pleurotus* on monocomponent substrates

Straw and stem-based substrates

One of the most well-known substrates for cultivating *Pleurotus* mushrooms is dried stems and leaves of agricultural and wild plants, including straw. However, research has indicated variability in the preferred type of lignocellulosic waste among different *Pleurotus* species. For instance, cultivation of *P. ostreatus* on wheat and oat straw yielded a higher number of fruiting bodies compared to pomace, bran, corn cobs, and coffee residue **(Melanouri *et al.*, 2022)**. Additionally, dried pea stalks were found to be particularly effective for cultivating *P. ostreatus*, showing the highest biological efficiency (BE) among substrates such as sorghum stalks, cottonseed husks, corn cobs, and sawdust **(Keneni, 2023)**. Conversely, Dedousi *et al.* reported higher BE values for *P. ostreatus* and *P. eryngii* when grown on wheat straw compared to other substrates. No statistically significant differences were observed between *P. ostreatus* and *P. eryngii* when barley-oat straw was used, although higher yields were obtained with a mixture of barley and oat straw compared to wheat straw and rice pomace **(Dedousi *et al.*, 2023)**. Saha *et al.* found no statistical difference in yields of *P. ostreatus* and *P. djamor* on these substrates **(Saha *et al.*, 2023)**.

Generally, barley straw without additives is associated with a low BE rate for *P. ostreatus*, as demonstrated by Mata *et al.* **(Mata *et al.*, 2019)**. It was found that BE for *P. ostreatus* was significantly lower on millet straw without additives **(Olana *et al.*, 2020)**. Fufa *et al.* also observed that millet straw, especially when combined with various additives, yielded the highest BE and overall fruiting body yield for *P. ostreatus* **(Fufa *et al.*, 2021)**.

Rice straw is another significant type of crop waste generated globally. Its potential as a substrate for *Pleurotus* species has been explored by various researchers, revealing significant variability in effectiveness. Rao *et al.* recorded the highest yield of *P. pulmonarius* fruiting bodies on rice straw compared to wheat straw **(Rao *et al.*, 2023)**. Conversely, *P. cornucopiae* achieved the highest yields on wheat straw, outperforming rice straw, corn stalks, and sawdust **(Kumar *et al.*, 2021)**. Another study found that *P. ostreatus* produced the maximum fruiting body yield on rice straw **(Bhatt *et al.*, 2024; Prajapati *et al.*, 2022)**. In contrast, *P. djamor* showed low efficiency on wheat straw but yielded the highest fruiting bodies on quinoa stalks **(İnci *et al.*, 2024)**. Deora *et al.* reported that *P. eryngii* had the highest bioconversion efficiency on rice straw and the lowest on sorghum straw, with rice straw resulting in the highest fruiting body yields **(Deora *et al.*, 2021).**

Research on the use of corn stalks and cobs as substrates for various *Pleurotus* species suggests they are generally less effective compared to other substrates **(Melanouri *et al.*, 2022)**. For example, using corn stalks for *P. eryngii* cultivation resulted in low bioconversion efficiency, despite a long cultivation period (42-48 days), whereas wheat straw produced yields three times higher **(Kaur *et al.*, 2019)**. Alqaisi *et al.* noted that corn cobs could be used as an independent substrate for *P. eryngii*, but the addition of rice and corn husks negatively impacted BE and reduced fruiting body yield **(Alqaisi *et al.*, 2020)**.

Husk-based Substrates

Coffee husks have been used for cultivating four *Pleurotus* species, with the highest yields and biological efficiency (BE) observed for *P. ostreatus*. In contrast, *P. eryngii* demonstrated the lowest yields and BE **(Dissasa, 2022)**. Additionally, *P. ostreatus* showed high substrate conversion efficiency when cultivated on millet husks **(Sanjel *et al.*, 2021)**.

Bran-based Substrates

The use of bran as a substrate for solid-phase cultivation of fungi has been relatively underexplored. Typically, bran is employed as an additive to substrates made from other lignocellulosic waste types **(Dedousi *et al.*. 2023)**.

Shell-based Substrates

When using peanut shells as the sole substrate for cultivating *P. ostreatus*, a BE value of 20.28-22.18% was achieved after three harvests **(Zied *et al.*, 2019)**.
Baobab fruit shells were evaluated as a substrate for cultivating *P. ostreatus*. The study reported that the yields were the lowest among the substrates tested. No significant difference was observed in the yields for the first wave of fruiting bodies, but baobab shells yielded the lowest values in the third wave of collection **(Tavarwisa *et al.*, 2021)**.
For *P. cornucopiae* grown on hazelnut shells, the biological efficiency (BE) did not exceed 15% **(Puliga *et al.*, 2022)**, while for *P. ostreatus*, the BE was more than double **(Akcay *et al.*, 2023)**.

Substrates Based on Pomace, Pulp, and Cake

Pomace as a substrate generally results in low bioconversion rates for macrofungi. **Papadaki *et al.* (2019)** assessed the efficiency of grape pomace for cultivating *P. pulmonarius* and *P. ostreatus*. They observed significant differences in the number of fruiting waves: *P. ostreatus* produced one wave, whereas *P. pulmonarius* produced three waves. Despite this, the yield of *P. ostreatus* was only half that of *P. pulmonarius*. BE values were 16.2% for *P. ostreatus* and 31.4% for *P. pulmonarius*. The biomass productivity of *P. ostreatus* on this substrate was 20% higher than that of *P. eryngii* **(Melanouri *et al.*, 2022)**. Buglione *et al.* investigated pear pomace for cultivating *P. ostreatus* on Petri dishes, noting a reduction in dry mass from 16.04 g to 10.96 g, indicating bioconversion efficiency **(Buglione *et al.*, 2022)**.
Sugarcane bagasse has been used to cultivate various *Pleurotus* strains. Although *P. ostreatus* and *P. pulmonarius* showed no statistical differences in biomass yield, the average fresh fruiting body weight for *P. ostreatus* was 13% higher **(Obiaigwe *et al.*, 2023)**. For *P. cornucopiae*, this substrate showed intermediate results, outperforming sawdust and corn stalks **(Kumar *et al.*, 2021)**. Agave pulp yielded a BE of 58.33% and productivity of 0.97 for *P. djamor*, with these figures being higher when urea was added to the substrate as an additional nitrogen source **(Velázquez-De Lucio *et al.*, 2022)**.
Cassava and sugarcane peels were found to be ineffective substrates for *P. ostreatus*, with BE values of 0% and 3.28%, respectively. The dry weight of *P. ostreatus* on sugarcane peels did not exceed 6.67 g **(Okere, Ibeanu, *et al.*, 2021)**. Otieno *et al.* studied various fruit peels (mango, pineapple, orange, banana, and melon) for the cultivation of *P. ostreatus*, *P. eryngii*. The highest yields for *P. eryngii* were obtained on all peels except melon and banana. For *P. ostreatus*, banana peels were the most effective substrate, while orange and melon peels yielded the lowest results. BE values for *P. ostreatus* generally correlated with fruiting body yield **(Otieno *et al.*, 2022)**.

Substrates Based on Brewer's Grains

The study by **Lozano Rocha *et al.*, (2023)** demonstrated the high efficacy of using spent brewer's grains as a substrate for cultivating *P. ostreatus*. The average biological efficiency (BE) was 27.25%, with a productivity of 272.8 g/kg of substrate.
Data on solid-phase cultivation of Pleurotus mushrooms on agro-food waste are summarized in Table 2.

Table 2 Efficiency Indicators of Monocomponent Agro-Industrial Waste Substrates for Cultivating Macrofungi of the Genus *Pleurotus*

Substrate		**Species**	**Yield, g/kg of substrate**	**BE, %**	**References**
Spent brewing grains		*PO*	272.8	27.25	**(Lozano Rocha *et al.*. 2023)**
Rice bran		*PO*	109.0-134.9	26.2-37.0	**(Dedousi *et al.*. 2023)**
		PE	96.9-116.4	25.6-29.7	
Pomace	pear	*PO*	-	30	**(Buglione *et al.*, 2022)**
	grape	*PO*	-	16.2	**(Papadaki *et al.*, 2019)**
		PO	272.2	-	**(Melanouri *et al.*, 2022)**
		PE	227.1	-	
		PP	-	31.4	**(Papadaki *et al.*, 2019)**
Pulp	**coffee**	*PO*	174.4	43.6	**(Akcay *et al.*, 2023)**
	sugar beet	***PO***	222-268	63.4-76.6	**(Östbring *et al.*, 2023)**
Bagasse	sugarcane	*PO*	447.7	44.8	**(Mapayi *et al.*, 2021)**
Corn cobs		***PO***	1170-1390	106-140	**(Keneni. 2023)**
		PE	293	105.8	**(Alqaisi *et al.*. 2020)**
		PP	336.1	106	**(Wachira *et al.*. 2022)**
Husk	**coffee**	***PO***	1583.4-1828.6	14.6-195.1	**(Keneni, 2023)**
		PE	332.4-333.5	27.3-28.1	**(Dissasa, 2022)**
		PC	490.7-491.9	40.4-41.4	
		PS	668.0-669.4	55.1-56.3	
	millet	***PO***	780.6	135.8	**(Sanjel *et al.*, 2021)**
	rice	***PO***	-	119.0	**(Prajapati *et al.*, 2022)**
Straw/stalk	**pea**	***PO***	3193.8-3262.2	274.1-371.9	**(Keneni, 2023)**
		PP	284.1	80.9	**(Wachira *et al.*, 2022)**
	corn	***PO***	-	93.8	**(Zárate-Salazar *et al.*, 2020)**
		PE	750	-	**(Kaur *et al.*, 2019)**
		PE	-	20.6-29.2	**(Deora *et al.*, 2021)**
		PP	223	71	**(Wachira *et al.*, 2022)**
	millet	***PO***	-	138.3	**(Olana *et al.*, 2020)**
	wheat	*PO*	172.5-820	43.1	**(Akcay *et al.*, 2023)**
		PE	767.4	76.7	**(Deora *et al.*, 2021)**
		PP	297.5-857.6	29.74-85.7	**(Rao *et al.*, 2023)**
	rice	***PO***	835	83.5	**(G. Singh *et al.*, 2021)**
		PE	884	88.4	**(Deora *et al.*, 2021)**
		PP	350.6-1082.4	35.1-108.2	**(Rao *et al.*, 2023)**
		PP	-	130	**(Wachira *et al.*, 2022)**
		P	811.5	81.2-121.7	**(Mapayi *et al.*, 2021)**

	soybeans	***PO***	207	62.2	**(Nirmalkar *et al.*, 2024)**
	sorghum	***PO***	-	68.3-89.3	**(Keneni, 2023)**
		PE	474.8	47.5	**(Deora *et al.*, 2021)**
Shell	peanuts	*PO*	131.7	39.5	**(Baig, 2022)**
		PP	373.2	18.2	**(N. A. Khan *et al.*, 2022)**
	baobab	*PO*	482	48.2	**(Tavarwisa *et al.*, 2021)**
	hazelnut	*PO*	157.5	39.4	**(Akcay *et al.*, 2023)**
Peel	**orange**	***PO***	51.8	68.6	**(Otieno *et al.*, 2022)**
		PE	82.8	86.8	
	pineapple	***PO***	71.2	90.6	
		PE	87	93.4	
	banana	***PO***	73.8	83.6	
		PE	69.2	76	
	melons	***PO***	54.7	78	
		PE	71.2	75.6	
	mango	***PO***	67.9	72.8	
		PE	84	89.9	

Notes:
PO - P. ostreatus; PE - P. eryngii; PP - P. pulmonarius; PC - P. citrinopileatus; BE
- *biological effectiveness;*

*species with high BE and substrates that provided profitable cultivation are highlighted in **bold***

Combined Substrates for Cultivating Basidiomycetes of the Genus Pleurotus

Lignocellulosic agricultural waste can be utilized as mono-substrates or combined with other materials to enhance fruiting body yields **(Muswati *et al.*, 2021)**. Research indicates that combined substrates often result in improved outcomes compared to single substrates **(N. A. Khan *et al.*, 2022)**.

Zhou *et al.* (2023) investigated the yield and biological efficiency (BE) of *P. eryngii* grown on various substrate combinations, including different proportions of sawdust, corn stalks, sugarcane pulp, and fixed amounts of cottonseed hulls, wheat bran, corn powder, and soybean flour. The highest yields and BE were observed in substrates with 21% pulp and 10.5% stems and sawdust, 21% sawdust and 10.5% pulp and stems, 21% corn stalks and pulp, and 42% stems. These results were not significantly different from the control group, which had 21% sawdust and pulp. Substrates lacking sugarcane pulp showed the lowest BE and fruiting body weight, indicating less efficiency for cultivating *P. eryngii*.

Other scientists studied *P. eryngii* cultivation on substrates composed of various combinations of rice, wheat, and mustard straw, cotton waste, and water chestnut peel. Among these, the highest yields were achieved with cotton and wheat straw waste (1:1) and cotton and mustard straw waste (1:1) **(Khatana *et al.*, 2024)**.

Cultivation of *P. ostreatus* on rice straw combined with horseradish, African basil, and bitter leaf (*Vernonia amygdalina*) at concentrations of 2%, 4%, and 6% showed no statistically significant differences in fruiting body size or weight **(Mapayi *et al.*, 2021)**. A similar trend was observed when corn husks were added to sawdust at concentrations of 25%, 50%, and 75%, with no significant differences in yield or BE **(Rakib *et al.*, 2020)**. However, *P. ostreatus* yields decreased when cultivated on a combined substrate of wheat and rice straw compared to the individual use of these substrates **(Soni *et al.*, 2020)**. The combination of wheat straw with cotton waste and baobab fruit shells demonstrated high biological efficiency and fruiting body yields for *P. ostreatus*. Conversely, other combinations, such as 50% baobab fruit shells and 50% wheat straw, exhibited a 20% reduction in BE and yields. The highest values were obtained with a substrate comprising equal parts of cotton waste, baobab fruit shells, and wheat straw **(Muswati *et al.*, 2021)**.

G. Singh *et al.* (2021) explored the use of rice straw combined with various defatted oilcakes, including soybean, mustard, neem, and peanut oilcakes, for cultivating *P. ostreatus*. Their study assessed both the yield and nutritional properties of the fruiting bodies. They found that the combination of rice and wheat straw was particularly effective for growing *P. ostreatus*. Additionally, incorporating wheat straw into sawdust substrates resulted in a significant yield increase of 65% **(Elattar *et al.*, 2019)**.

Combined substrates, such as corn cobs with millet straw and millet straw with bamboo waste, demonstrated higher yields and biological efficiency for *P. ostreatus* compared to single-component substrates like corn cobs or millet straw. Conversely, a substrate comprising corn cobs and bamboo waste yielded the lowest rates, suggesting that this combination is less effective **(Fufa *et al.*, 2021)**.

A study reported low yields of *P. ostreatus* fruiting bodies when using a substrate of corn stalks, medium veins of banana leaves, and sugarcane pulp. Among combined substrates, the highest yield was achieved with corn stalks and banana leaf veins, although it did not exceed 150 g/kg **(Iwuagwu *et al.*, 2020)**.

Incorporating cereal and legume husks into other substrates or mixing different types of husks can significantly enhance the yield and efficiency of oyster mushroom cultivation. For instance, a study on *P. ostreatus* cultivation on millet husks with various additives found that adding rice bran resulted in the highest total yield and biological efficiency compared to other additives such as molasses, wheat bran, and mustard seed cake **(Sanjel *et al.*, 2021)**.

Another study investigated the use of combinations of cassava, coffee, and coconut waste as substrates for *P. ostreatus*. The highest fruiting body weight was achieved with a substrate containing 80% cassava waste, 10% coconut flakes, and 10% coffee waste. The lowest results were observed with a mixture of 50% cassava waste, 40% coconut flakes, and 10% coffee waste **(Elsisura *et al.*, 2022)**.

P. ostreatus was cultivated on sawdust substrates supplemented with Brazil nut residues; however, the biological efficiency (BE) values were low, not exceeding 20% **(Aguiar *et al.*, 2021)**.

Other studies have demonstrated that high productivity of *P. ostreatus* can be achieved using substrates based on coniferous sawdust combined with rice bran or sweet potato sludge. The highest yield was recorded on bamboo straw combined with rice bran **(Yamauchi *et al.*, 2019)**. Conversely, a different study found that a combination of sawdust and rice husk produced the highest fruiting body weight and BE, indicating its effectiveness for supporting the growth of *P. ostreatus* **(Akter *et al.*, 2022)**.

Increasing the proportion of coffee grounds in a substrate of wheat straw led to reduced productivity and BE for *P. ostreatus*. Among combined substrates, a mixture of coffee grounds and wheat straw (1:1) showed the highest performance **(Makas *et al.*, 2024)**.

Similarly, combining wheat straw with cottonseed cake and rice pomace reduced the yield of *P. ostreatus* by 11% compared to pure cottonseed cake **(N. A. Khan *et al.*, 2019)**. Another study observed a decreased BE for *P. ostreatus* with the addition of sugar cane straw to rubber tree sawdust, despite a 23.5% increase in yield **(Zakil *et al.*, 2019)**.

P. pulmonarius was cultivated on peanut shells with various additives, including other agro-industrial waste (wheat straw, cotton waste) and pulp and paper waste. The yield of *P. pulmonarius* nearly doubled when using a combined substrate of peanut shells and cotton waste in a 1:1 ratio **(N. A. Khan *et al.*, 2022)**.

Wachira *et al.* reported that for *P. pulmonarius* and *P. ostreatus*, the highest BE was observed with a substrate comprising corn cobs and stalks (1:1). The maximum yield was achieved with a combination of corn stalks and pea straw (1:1) **(Wachira *et al.*, 2022)**. **Chai *et al.* (2021)** found no statistically significant difference in BE indicators for *P. pulmonarius* and *P. ostreatus*. An increase in the content of used coffee pulp in mixed substrates led to a decrease in the yield of *P. ostreatus* compared to control wood-based substrates. However, *P. pulmonarius* showed higher yields with mixed wood-based substrates containing 10% (by weight) coffee pulp compared to other studied combinations.

The combination of hazelnut shells with wheat straw as a substrate for *P. cornucopiae* did not result in significant improvements in yield or BE. The yield of fruiting bodies of *P. cornucopiae* cultivated on hazelnut shells was twice as high compared to both the standard substrate (wheat straw and beech chips in a 1:1 ratio) and a mixture of hazelnut shells and wheat straw (1:1) **(Puliga *et al.*, 2022)**.

P. ostreatus was also grown on a substrate comprising rope peels and sawdust (1:1) with the addition of wheat bran. The study identified the optimal carbon to nitrogen (C/N) ratios for both BE and bioconversion efficiency. The highest BE value was recorded for a substrate with a C/N ratio of 17:0, while the maximum bioconversion efficiency was observed at a C/N ratio of 17:3 **(Okere, Onyekachi, *et al.*, 2021)**.

In another study, *P. ostreatus* and *P. australis* were cultivated on substrates of pomegranate peels, wheat bran, and wheat straw, with varying proportions of peels and bran (from 0 to 88%), along with gypsum. *P. ostreatus* consistently achieved higher BE and yield across all substrate combinations compared to *P. australis* **(Nadir, 2019)**.

Different concentrations of wheat bran were tested to determine the optimal level for sugarcane pulp in the cultivation of *P. pulmonarius* and *P. ostreatus*. *P.*

pulmonarius reached the highest yield and BE with a 10% bran addition, while *P. ostreatus* demonstrated the best overall yield and BE with a 15% bran addition **(Obiaigwe *et al.*, 2023)**.

The use of pineapple leaves also proved effective for cultivating both *P. pulmonarius* and *P. ostreatus*. Adding 60% dry and wet pineapple leaf waste to sawdust resulted in the maximum fruiting body yield and BE **(Munir *et al.*, 2024)**.

Banana leaves combined with sugarcane bagasse at ratios of 1:4 and 4:1 had statistically similar effects on the biological efficiency and growth rate of *P. ostreatus* and *P. djamor*. However, *P. djamor* achieved the highest BE when cultivated on a substrate with a higher proportion of pulp **(Valenzuela-Cobos *et al.*, 2023)**.

Thus, various literary sources indicate that a range of combined substrates can be employed for cultivating macro-mycetes of the genus *Pleurotus* (see Table 3). Notably, there is substantial variability in yield and biological efficiency (BE) based on the specific fungal species and the composition and ratio of components in the substrates.

Table 3 Indicators of Yield and Biological Efficiency of Combined Substrates with Agro-Industrial Waste for the Cultivation of Macro-Mycetes of the Genus *Pleurotus*

Substrate composition	Species	Yield, g/kg of substrate	BE, %	References
Sawdust : sugar cane pulp (50% : 50%)	***PE***	242.2-307.8	69.6-87.6	**(Zhou *et al.*, 2023)**
Sawdust : sugarcane bagasse : corn stalks (25% : 50% : 25%)		230.2-316.0	66.0-90.0	
Sawdust : sugarcane bagasse : corn stalks (50% : 25% : 25%)		242.8-308.2	69.7-87.7	
Sugarcane bagasse : corn stalks (50% : 50%)		221-320.8	63.2-91.2	
Sawdust : corn stalks (50% : 50%)		199.8-279.0	51.4-85.4	
Wheat straw : cotton waste (50% : 50%)	***PE***	211.5-217.3	59.8-61.3	**(Khatana *et al.*, 2024)**
Wheat straw : rice straw (50% : 50%)		128.8-133.7	35.9-57.0	
Wheat straw : mustard straw (50% : 50%)		207.7-209.6	58.3-59.5	
Wheat straw : water chestnut shell (50% : 50%)		176.0-82.7	50.3-51.5	
Cotton waste : rice straw (50% : 50%)		156.7-162.5	44.7-45.7	
Cotton waste : mustard straw (50% : 50%)		217.3-223.1	61.3-62.6	
Cotton waste : water chestnut shells (50% : 50%)		184.6-191.3	52.8-54.3	
Rice straw : mustard straw (50% : 50%)		136.5-140.4	38.2-39.2	
Rice straw : water chestnut shell (50% : 50%)		117.3-120.2	32.7-35.9	
Mustard straw : water chestnut shell (50% : 50%)		169.2-173.1	47.5-49.5	
Sawdust : corn husks (75% : 25%)	***PO***	45.79	83.87	**(Rakib *et al.*, 2020)**
Sawdust : corn husks (50% : 50%)		51.92	84.23	
Sawdust : corn husks (25% : 75%)		51.06	84.1	
Rice straw : soybean cake (97,5% : 2,5%)	***PO***	885	88.5	**(G. Singh *et al.*, 2021)**
Rice straw : soybean cake (95% : 5%)		1014.6	101.5	
Rice straw : soybean cake (90% : 10%)		110.1	11.0	
Rice straw : mustard oil cake (97,5% : 2,5%)		554.3	55.4	
Rice straw : mustard oil cake (95% : 5%)		473.3	47.3	
Rice straw : neem cake (97,5% : 2,5%)		681	68.1	
Rice straw : neem cake (95% : 5%)		519.7	52.0	
Wheat straw : rice straw (50% : 50%)	***PO***	7600*	126.7	**(Elattar *et al.*, 2019)**
Wheat straw : sawdust (50% : 50%)		5550*	92.5	
Wheat straw : water hyacinth (50% : 50%)		49908	83.2	
Wheat straw : rice straw (50% : 50%)	*PO*	806.248	-	**(Soni *et al.*, 2020)**
Cotton waste : wheat straw : baobab fruit shells (33%:33%:33%)	***PO***	1289	85.9	**(Muswati *et al.*, 2021)**
Baobab fruit shell : cotton waste (50%:50%)		729	48.6	
Baobab fruit shell : wheat straw (50%:50%)		638	42.5	
Cotton waste : wheat straw (50%:50%)		994	66.3	
Millet straw : corn cobs (50%:50%)	*PO*	233.3-234.2	48.0-50.2	**(Fufa *et al.*, 2021)**
Corn cobs : bamboo waste (50%:50%)		100.6-102.4	20.4-21.2	
Millet straw : bamboo waste (50%:50%)		201.1-212.1	41.5-43.1	
Banana leaf vein : corn straw (50%:50%)	*PO*	118.0-159.9	-	**(Iwuagwu *et al.*, 2020)**
Banana leaf vein : sugar cane pulp (50%:50%)		44.8-86.6	-	
Corn straw : sugarcane bagasse (50%:50%)		85.5-127.3	-	
Corn straw : banana leaf vein : sugar cane pulp (40%:30%:30%)		26.2-69.2	-	
Millet husk : rice bran *	***PO***	317.2	137.9	**(Sanjel *et al.*, 2021)**
Millet husk : molasses *		305.3	132.7	
Millet husk : wheat bran *		288.8	125.5	
Millet husk : mustard cake *		208.7	90.8	
Sawdust : rice bran : molasses (78%:20%:1%)	*PO*	152.2	-	**(Elsisura *et al.*, 2022)**
Cassava husk : rice bran : molasses (78%:20%:1%)		202	-	
Cassava husk : coconut residues : coffee pulp : rice bran : molasses (62%:8%:8%:20%:1%)		234.3	-	
Cassava husk : coconut residues : coffee pulp : rice bran : molasses (55%:16%:8%:20%:1%)		168.7	-	
Cassava husk : coconut residues : coffee pulp : rice bran : molasses (39%:31%:8%:20%:1%)		132.9	-	
Acai palm seeds : brazil nut shells (80%:18%)	*PO*	59.3-109.0	18.6-31.4	**(Aguiar *et al.*, 2021)**
Pine sawdust : brazil nut shells (80%:18%)		44.1-60.0	14.0-19.7	
Pine needle sawdust : rice bran : fossil shells (46%:50%:4%)	*PO*	139.2-161.8	-	**(Yamauchi *et al.*, 2019)**
Bamboo sawdust : rice bran : fossil shells (46%:50%:4%)		156.7-169.7	-	

Pine needles : sweet potato sludge : fossil shells (46%:50%:4%)		140.2-164.8	-	
Bamboo sawdust : sweet potato sludge : fossil shells (46%:50%:4%)		150.5-163.5	-	
Coffee pulp : wheat straw (80%:20%)	***PO***	38.0-39.6	60.2-62.6	**(Makas *et al.*, 2024)**
Coffee pulp : wheat straw (70%:30%)		34.3-34.9	67.4-69.4	
Coffee pulp : wheat straw (60%:40%)		30.8-32.0	78.5-79.1	
Coffee pulp : wheat straw (50%:50%)		26.1-27.1	106.1-107.3	
Peanut shells : wheat straw (50%:50%)	*PP*	486.7	23.7	**(N. A. Khan *et al.*, 2022)**
Peanut shells : paper waste (50%:50%)		440.4	22.59	
Peanut shells : cotton waste (50%:50%)		675.4	33.38	
Peanut shells : wheat straw : paper waste : cotton waste (25%:25%:25%:25%)		558.3	27.22	
Corn stalks : pea straw (50%:50%)	***PP***	403.7	112.8	**(Wachira *et al.*, 2022)**
Corn stalks : corn cobs (50%:50%)		374.2	118.4	
Corn stalks : rice straw (50%:50%)		273.4	84.4	
Pea straw : corn cobs (50%:50%)		303.1	90.8	
Pea straw : rice straw (50%:50%)		260.2	76.1	
Pea straw : leaves *Melia volkensii* (50%:50%)		136.2	37.1	
Corn cobs : rice straw (50%:50%)		295.7	91.0	
Sawdust : rice bran (89%:10%)	*PP*	110.1-128.9	14.7-17.2	**(Chai *et al.*, 2021)**
	PO	127.8-143.0	17.0-19.1	
Sawdust : coffee pulp : rice bran (79%:10%:10%)	*PP*	156.9-178.1	17.4-19.8	
	PO	112.3-135.9	12.5-15.1	
Sawdust : coffee pulp : rice bran (69%:20%:10%)	*PP*	93.9-138.1	8.9-13.2	
	PO	83.0-103.6	7.9-9.9	
Wheat straw : beech sawdust (50%:50%)	*PC*	1.8-12.1	18.6-26.6	**(Puliga *et al.*, 2022)**
Wheat straw : hazelnut shells (50%:50%)		7.4-11.2	1.6-8.8	
Pomegranate peel : wheat bran (88%:10%)	***PO***	141.3-228.3	43.1-72.6	**(Nadir, 2019)**
	PA	9.0-28.3	2.5-9.3	
Pomegranate peel : wheat straw : wheat bran (76%:12%:10%)	***PO***	268.5-309.8	83.4-96.6	
	PA	9.8-65.2	6.4-20.1	
Pomegranate peel : wheat straw : wheat bran (66%:22%:10%)	*PO*	44.6-152.2	14.2-47.1	
	PA	13.0-128.3	7.8-40.2	
Pomegranate peel : wheat straw : wheat bran (44%:44%:10%)	***PO***	140.2-218.5	43.6-70.1	
	PA	103.3-304.3	32.4-95.6	
Pomegranate peel : wheat straw : wheat bran (22%:66%:10%)	***PO***	225.0-291.3	70.6-92.7	
	PA	97.-182.6	30.4-57.4	
Pomegranate peel : wheat straw : wheat bran (12%:76%:10%)	***PO***	268.5-375.0	83.4-117.2	
	PA	103.3-193.5	31.4-60.3	
Wheat straw : wheat bran (82%:10%)	***PO***	291.3-337.0	89.7-106.4	
	PA	101.1-187.0	29.9-58.5	
Sawdust : rice husk (75%:25%)	***PO***	285.2	56.5	**(Akter *et al.*, 2022)**
Cotton seed cake : rice bran (50%:50%)	*PO*	607.6	-	**(N. A. Khan *et al.*, 2019)**
Cotton seed cake : wheat straw (50%:50%)		666.8	-	
Cotton seed cake : wheat straw : rice bran (25%:50%:25%)		725.2	-	
Empty oil palm fruits : sawdust (25%:75%)	***PO***	250.8	62.7	**(Zakil *et al.*, 2019)**
Empty oil palm fruits : sawdust (50%:50%)		214.7	53.7	
Palm press fibre : sawdust (25%:75%)		238.9	59.7	
Palm press fibre : sawdust (50%:50%)		194.0	48.5	
Sugarcane bagasse : sawdust (25%:75%)		250.2	62.6	
Sugarcane bagasse : sawdust (50%:50%)		250.8	62.7	
Empty oil palm fruits : palm press fibre : sawdust (25%:25%:50%)		241.6	60.4	
Palm press fibre : sugarcane pulp : sawdust (25%:25%:50%)		318.9	79.7	
Sugar cane bagasse : green banana leaves (80%:20%)	***PO***	-	70.1-98.6	**(Valenzuela-Cobos *et al.*, 2023)**
Sugar cane bagasse : green banana leaves (20%:80%)		-	58,24-100,7	
Grape pomace : wheat straw (80%:20%)	*PO*	66,0-216,0	3,09	**(Doroški *et al.*, 2021)**
Grape pomace : wheat straw (50%:50%)		294,0-464,0	8,92	
Grape pomace : wheat straw (20%:80%)		505,7-736,3	15,64	

Notes:
** - the source does not specify the ratio of substrate components;*
PO - P. ostreatus; PE - P. eryngii; PP - P. pulmonarius; PC - P. citrinopileatus; PA - P. australis;
*species with high BE and substrates that provided profitable cultivation are highlighted in **bold***

BIOCONVERSION OF LIGNOCELLULOSIC WASTE IN THE CULTIVATION PROCESS

In the cultivation of macrofungi, particularly those of the genus *Pleurotus*, on agro-industrial waste, the primary components utilized by the fungi for nutrition are cellulose, hemicellulose, and lignin. The enzymatic activity during this process results in changes to the content of these components within the substrates. Several studies have addressed this aspect.

For instance, the research conducted by **Akcay *et al.* (2023)** demonstrated that the decomposition of holocellulose and α-cellulose was more pronounced than that of lignin across various substrates utilized for cultivating *P. ostreatus*. Specifically, substrates such as hazelnut waste, wheat straw, used coffee grounds, and rice husks exhibited differing degrees of change in their chemical components based on their initial composition and cultivation conditions. Notably, the amount of lignin in the substrate tended to increase, as it was less effectively degraded compared to holocellulose and α-cellulose. Among these, coffee residues showed the highest rate of extractive compound utilization.

Furthermore, *P. ostreatus* cultivation led to nearly complete biodegradation of hemicellulose in substrates containing coffee grounds. In contrast, substrates composed of wheat straw, coffee grounds, and olive prunings, in ratios of 1:1:1 and 4:1:1, exhibited less than 80% hemicellulose degradation. The greatest loss of lignin was observed in substrates containing wheat straw **(Abou Fayssal *et al.*, 2021)**.

In the cultivation of *P. ostreatus* on substrates including nut shells, wheat straw, and corn cobs, selective decomposition of hemicellulose was observed, with minimal changes in the proportions of other components **(Koutrotsios, Mountzouris, *et al.*, 2014)**. Cellulose degradation was also less pronounced. Among the studied lignocellulosic wastes, the highest biodegradation rates were noted for substrates containing grape pomace with cotton waste, oil production waste, and oilseed meal. Changes in lignin content were relatively minimal, although wheat straw exhibited considerable lignin loss, whereas pomace and cotton saw increases in lignin content **(Koutrotsios & Zervakis, 2014)**.

Hutabarat *et al.* (2022) reported that the cultivation of *P. djamor* on substrates made from oil palm leaves, corn straw, and their 1:1 combination led to a significant reduction in fiber content due to the breakdown of structural carbohydrates. Additionally, there was an 81-86% reduction in extractive compounds in these substrates.

Certain strains of *P. ostreatus* demonstrated high utilization efficiency, achieving 44.0-46.0% for straw stalks and 36.4-38.1% for rice straw **(Zárate-Salazar *et al.*, 2020)**.

The study on pear pomace revealed statistically similar losses in lignin and cellulose (19.9-35.7% and 26.9-32.8%, respectively). However, non-structural carbohydrates (such as mono- and disaccharides and starch) were consumed more efficiently due to their greater availability, resulting in relatively low cellulose biodegradation (up to 20.7%) compared to other components **(Buglione *et al.*, 2022)**.

P. cornucopiae cultivated on wheat straw demonstrated complete destruction of hemicellulose xylan and efficiently utilized aromatic lignin compounds and cellulose monomers **(Puliga *et al.*, 2022)**. The loss of organic matter varied, with values ranging from 74.0-79.4% for wheat straw. The addition of coffee grounds and olive tree trimmings reduced this figure to no more than 64.4% **(Fayssal *et al.*, 2023)**.

When cultivated on substrates containing peanut shells, *P. ostreatus* showed a low level of organic matter loss (17%). This loss rate increased by 2-7% when corn stalks were added in amounts ranging from 10% to 90%. The highest organic matter loss (24.1%) was observed for a substrate consisting of equal parts peanut shells and corn stalks. Cultivation on combined substrates also resulted in higher lignin utilization (up to 32.8%) compared to 13.2% on the mono-substrate of peanut shells. **Anike *et al.* (2016)** also reported that substrates with a high content of lignin exhibited slower lignin degradation. Hemicellulose was the first component to decompose, while the shell substrate remained largely intact, with cellulose being the main component that decomposed.

Peels used as substrates for cultivation were characterized by low bioconversion rates. For a combination of cassava and sugarcane peels, the bioconversion rate of *P. ostreatus* did not exceed 0.27%, while pure sugarcane peels yielded a rate of 0.68% **(Okere, Ibeanu, *et al.*, 2021)**.

In addition to studies on the biodegradation of main plant waste components (cellulose, hemicellulose, and lignin), there are reports on changes in the concentrations of other organic compounds in substrates. *P. ostreatus* and *P. pulmonarius* effectively degraded phenolic compounds from grape pomace, with a decrease in total phenols by 72% and 75%, respectively **(Papadaki *et al.*, 2019)**.

In all studied substrates, which included wheat straw and coffee grounds with added alfalfa aqueous extract, significant reductions in phenols and caffeine were recorded after cultivation of *P. ostreatus*. The highest degradation of these compounds occurred in substrates with a high content of coffee pulp **(Makas *et al.*, 2024)**.

The biodegradation of lignocellulosic waste can also be assessed by determining the total amount of organic matter remaining in the substrate. The efficiency of the utilization process is inversely proportional to the percentage of organic matter remaining. For instance, when *P. ostreatus* is cultivated on wheat straw, the remaining organic matter ranges from 74.0% to 79.4%. In contrast, with the addition of coffee grounds and olive tree trimmings, this value does not exceed 64.4% **(Fayssal *et al.*, 2023)**.

These findings highlight the potential of using basidiomycetes of the genus *Pleurotus* for the bioconversion of lignocellulosic waste from the agro-food industry. Furthermore, the cultivation of mycelial biomass and fruiting bodies can lead to the production of biologically active substances, including enzymes that could be utilized in enzyme preparations for other industries and agriculture.

PRODUCTION OF ENZYMES DURING THE CULTIVATION OF MACROMYCETES ON AGRO-FOOD RESIDUES

During the colonization of substrates by mycelium and the formation and growth of fruiting bodies, macromycetes synthesize various hydrolytic and oxidative enzymes that decompose polysaccharides, polyphenols, and other components of lignocellulosic waste. The bioconversion of waste by basidiomycetes of the *Pleurotus* genus is facilitated by enzymatic activities including laccase, peroxidases, monooxygenases, cellulases, and pectinases **(Ganash *et al.*, 2021)**. Consequently, solid-phase cultivation and the subsequent use of substrates post-fruiting body production are of significant interest due to the potential for obtaining commercially valuable enzymes **(Steudler *et al.*, 2019)**.

Studies investigating corn residues (stalks, cobs) and corn silage as substrates for *P. ostreatus* cultivation revealed insights into lignocellulolytic enzyme production, including cellulases, laccase, and manganese-dependent peroxidase. Among these substrates, corn silage exhibited the highest activity levels of all studied enzymes. This is primarily attributed to the higher availability of free sugars, which enhances colonization efficiency. In contrast, no statistically significant differences in enzymatic activity were observed between stalks and cobs **(Ganash *et al.*, 2021)**.

The study conducted by **Melanouri *et al.* (2022)** reported that the colonized substrates remaining after the harvest of fruiting bodies of *P. ostreatus* and *P. eryngii* displayed high laccase activity. The most favorable substrates for enzyme accumulation were corn cobs and a mixture of barley and oat straw. Additionally, straw and rice husks also contributed to high levels of exoglucanase activity. High laccase activity was also noted when *P. ostreatus* and *P. pulmonarius* were cultivated on grape pomace, although exoglucanase activity was comparatively lower **(Papadaki *et al.*, 2019)**.

To optimize laccase synthesis by *P. pulmonarius*, different combinations of orange pulp and wheat bran were evaluated. The enzyme activity ranged from 213 to 25,447 units/dm³, with the highest activity observed for the substrate comprising 3.5 g of orange pulp, 1 g of wheat bran, 2 g of starch, and 0.2 g of yeast extract **(Contato *et al.*, 2020)**.

A comprehensive study of enzyme activities in substrates after cultivating *P. citrinopileatus* and *P. eryngii* on grapevine assessed several enzymes: laccase, manganese-dependent peroxidase, lignin peroxidase, avicellase, carboxymethyl cellulase, and xylanase. *P. citrinopileatus* demonstrated higher enzyme activities overall, whereas *P. eryngii* did not produce lignin peroxidase **(Costa-Silva *et al.*, 2022)**.

Using sugarcane and wheat bran as substrates for *P. ostreatus* cultivation proved promising for producing a range of enzymes, including cellulases, avicellulases, β-glucosidase, β-xylosidase, xylanase, laccase, manganese-dependent peroxidase, and lignin peroxidase **(de Oliveira Rodrigues *et al.*, 2020)**. **S. Sharma *et al.* (2020)** found that *P. ostreatus* had the highest productivity of manganese-dependent and lignin-dependent peroxidases on rice bran, while cellulase and laccase activities were highest on rice and wheat straw, respectively.

The production of lignocellulolytic enzymes was also assessed using substrates composed of walnut shells and pine needles combined with barley straw. Walnut shells enhanced cellulase and xylanase activities, while pine needles and straw substrates yielded higher laccase activity **(Ibarra-Islas *et al.*, 2023)**.

The data on enzyme production from the solid-phase cultivation of *Pleurotus* fungi on agro-food waste are summarized in Table 4.

Table 4 Indicators of Enzyme Activity in Substrates After Cultivation of *Pleurotus* sp.

Substrate composition	**Species**	**Enzyme**	**Enzyme activity, units/g$_{substrate}$ (*units/ml$_{extract}$)**	**References**
Rice bran	PO	Laccase	515.0-1043.1	**(Melanouri *et al.*, 2022)**
			420.9-492.3	**(S. Sharma *et al.*, 2020)**
		Endoglucanase	0.059-0.125	**(Melanouri *et al.*, 2022)**
		Xylanase	51.5-61.1	**(S. Sharma *et al.*, 2020)**
		CMCase	72.3-86.7	
		Phase	27.8-32.4	
		Lignin peroxidase	58.9-70.9	
		Manganese peroxidase	149.8-158.8	
	PE	Laccase	1460.1-2202.1	**(Melanouri *et al.*, 2022)**
		Endoglucanase	0.022-0.084	

Grape pomace	PO	Laccase	1059.2-1538.0	**(Melanouri *et al.*, 2022)**
			4046.7-28015.6	**(Papadaki *et al.*, 2019)**
		Endoglucanase	0.034-0.048	**(Melanouri *et al.*, 2022)**
			0.043-0.075	**(Papadaki *et al.*, 2019)**
	PE	Lactase	742.62-1090.45	**(Melanouri *et al.*, 2022)**
		Endoglucanase	0.034-0.051	
	PP	Laccase	9852.2-15418.7	**(Papadaki *et al.*, 2019)**
		Endoglucanase	0.024-0.048	
Coffee pulp	PO	Laccase	779.02-1279.5	**(Melanouri *et al.*, 2022)**
		Endoglucanase	0.054-0.059	
	PE	Laccase	474.5-1625.7	
		Endoglucanase	0.006-0.036	
Corn cobs	PO	Laccase	936.7-1810.13	
			2.8-4.1*	**(Ganash *et al.*, 2021)**
			0.3	**(An *et al.*, 2021)**
		Endoglucanase	0.049-0.182	**(Melanouri *et al.*, 2022)**
		Manganese-dependent peroxidase	0.4-2.9*	**(Ganash *et al.*, 2021)**
		FPase	19.0-55.2*	
		CMCase	36.9-212.6*	
	PE	Laccase	828.3-2170.3	**(Melanouri *et al.*, 2022)**
		Endoglucanase	0.012-0.054	
Wheat straw	PO	Laccase	708.7-1112.6	
			497.6-575.6	**(S. Sharma *et al.*, 2020)**
		Endoglucanase	0.091-0.138	**(Melanouri *et al.*, 2022)**
		Xylanase	11.0-16.8	**(S. Sharma *et al.*, 2020)**
		CMCase	133.1-163.9	
		FPase	17.2-22.5	
		Lignin peroxidase	63.5-70.1	
		Manganese peroxidase	186.1-226.7	
	PE	Laccase	1163.5-1684.2	**(Melanouri *et al.*, 2022)**
		Endoglucanase	0.058-0.153	
Barley and oat straw	PO	Laccase	1562.4-2086.1	**(Melanouri *et al.*, 2022)**
		Endoglucanase	0.074-0.168	
	PE	Laccase	1009.4-2075.5	
		Endoglucanase	0.11-0.194	
Olive meal	PO	Laccase	1063.7-1392.6	
		Endoglucanase	0.024-0.038	
	PE	Laccase	465.0-1477.4	
		Endoglucanase	0.012-0.101	
Rice straw	PO	Laccase	245.5-277.7	**(S. Sharma *et al.*, 2020)**
		Xylanase	35.6-43.2	
		CMCase	32.5-47.3	
		FPase	16.0-22.2	
		Lignin peroxidase	77.4-86.8	
		Manganese peroxidase	131.2-152.2	
Sorghum straw	PO	Laccase	178.1-195.1	
		Xylanase	43.7-51.5	
		CMCase	126.0-148.4	
		FPase	26.9-34.5	
		Lignin peroxidase	89.0-104.4	
		Manganese peroxidase	152.2-164.6	
Corn straw	PO	Laccase	2.1-4.8*	**(Ganash *et al.*, 2021)**
			335.2-364.8	**(S. Sharma *et al.*, 2020)**
		Manganese-dependent peroxidase	1.1-2.7*	**(Ganash *et al.*, 2021)**
			134.0-152.2	**(S. Sharma *et al.*, 2020)**
		FPase	16.4-55.2*	**(Ganash *et al.*, 2021)**
			13.3-18.3	**(S. Sharma *et al.*, 2020)**
		CMCase	69.9-227.2*	**(Ganash *et al.*, 2021)**
			100.3-118.5	**(S. Sharma *et al.*, 2020)**
		Xylanase	23.8-35.2	
		Lignin peroxidase	212.5-230.3	
Corn silage	PO	Laccase	6.3-11.7*	**(Ganash *et al.*, 2021)**
		Manganese-dependent peroxidase	2.5-6.7*	
		FPase	82.8-181.0*	
		CMPase	93.2-374.8*	
Sugarcane bagasse : wheat bran (1:1)	PO	FPase	5.7-7.7	**(de Oliveira Rodrigues *et al.*, 2020)**
		CMCase	18.9-21.0	

		Avicellase	38.7-40.0	
		β-glucosidase	1.6-1.7	
		β-xylosidase	0	
		Xylanase	4.5-12.9	
		Laccase	2.1	
		Manganese peroxidase	2.3	
		Lignin peroxidase	0.5	
Grapevine	PE	Laccase	1.9	**(Costa-Silva *et al.*, 2022)**
		Manganese-dependent peroxidase	2.2	
		Lignin peroxidase	0	
		Avicelase	0.4	
		CMCase	0.5	
		Xylanase	1.1	
		Feruloylesterase	0.9	
	PC	Laccase	2.8	
		Manganese-dependent peroxidase	1.9	
		Lignin peroxidase	1.1	
		Avicelase	0.4	
		CMCase	0.9	
		Xylanase	2.4	
		Feruloylesterase	1.2	

Notes:
PO - P. ostreatus, PE - P. eryngii, PP - P. pulmonarius, PC - P. citrinopileatus; FPase - filter paper cellulase activity-, CMCCase - carboxymethyl cellulase activity

DISCUSSION

Cultivating mushrooms on agricultural waste is increasingly recognized for its efficiency and environmental benefits. Recent research has focused on optimizing different *Pleurotus* fungi and substrates to enhance productivity and develop new biotechnologies.

The results of the literature search and their analysis showed that among all the studied representatives of the genus *Pleurotus*, *P. ostreatus* predominantly exhibits the highest yield and biological efficiency on various substrates, which is especially relevant for Ukraine, including on waste from the flour and cereal industry, such as straw and stalks **(Keneni, 2023; Mapayi *et al.*, 2021; Olana *et al.*, 2020; G. Singh *et al.*, 2021; Zárate-Salazar *et al.*, 2020)**. This species also performs well on corn cobs and coffee husks **(Dissasa, 2022; KENENI, 2023; Wachira *et al.*, 2022)**. Meanwhile, *P. eryngii* and *P. pulmonarius* also show high performance on substrates like rice straw and sweet sorghum cake **(Rao *et al.*, 2023)**.

Analyzing the impact of the chemical composition of substrates on the growth of fungi of the genus *Pleurotus*, several important trends can be identified.

Substrates with high cellulose and hemicellulose content and low lignin content, such as straw, stalks, pulp, and corn cobs, generally exhibit the highest biological efficiency among lignocellulosic waste. This is likely because both cellulose and hemicellulose serve as favorable carbon sources for fungi of the genus *Pleurotus*. For example, *P. ostreatus* and *P. eryngii* demonstrate significantly better results on substrates with high levels of these components **(Almowallad *et al.*, 2022; González Martínez *et al.*, 2019; Keneni, 2023; Nirmalkar *et al.*, 2024; Östbring *et al.*, 2023; Passoth *et al.*, 2019; Rao *et al.*, 2023; G. Singh *et al.*, 2021; Syadiah *et al.*, 2022; Wachira *et al.*, 2022; Zárate-Salazar *et al.*, 2020)**. Conversely, high lignin content can impede fungal growth due to its complex structure **(Akcay *et al.*, 2023; Baig, 2022; N. A. Khan *et al.*, 2022; Pączkowski *et al.*, 2021; Tavarwisa *et al.*, 2021)**.

Substrates that are combinations of different types of lignocellulosic waste usually show better results than single-component ones. Thus, according to many authors, various combinations of sawdust, corn stalks, sugar cane pulp, wheat bran, and other agricultural residues in different proportions can be used as effective substrates for the cultivation of *Pleurotus* species **(Akter *et al.*, 2022; Elattar *et al.*, 2019; Khatana *et al.*, 2024; Munir *et al.*, 2024; Mussatto, 2009; Okere, Onyekachi, *et al.*, 2021; Rakib *et al.*, 2020; Sanjel *et al.*, 2021; G. Singh *et al.*, 2021; Soni *et al.*, 2020; Wachira *et al.*, 2022; Zakil *et al.*, 2019)**. In general, the majority of the analysed literature relates to studies of multicomponent substrates for *P. ostreatus* cultivation **(Aguiar *et al.*, 2021; Akter *et al.*, 2022; Elattar *et al.*, 2019; Elsisura *et al.*, 2022; Fufa *et al.*, 2021; Iwuagwu *et al.*, 2020; N. A. Khan *et al.*, 2019; Munir *et al.*, 2024; Muswati *et al.*, 2021; Okere, Onyekachi, *et al.*, 2021; Sanjel *et al.*, 2021; G. Singh *et al.*, 2021; Yamauchi *et al.*, 2019; Makas *et al.*, 2024)**. Sawdust combined with corn stalks and sugarcane pulp has proven effective for *P. eryngii* **(Khatana *et al.*, 2024; Zhou *et al.*, 2023)**; while various combinations of rice straw, soybean cake, millet husk, coffee pulp, and sugarcane pulp are suitable for *P. ostreatus* **(Akter *et al.*, 2022; Elattar *et al.*, 2019; Munir *et al.*, 2024; Sanjel *et al.*, 2021; G. Singh *et al.*, 2021; Zakil *et al.*, 2019)**; sawdust with corn husks for *P. ostreatus* **(Rakib *et al.*, 2020)**; cotton husks, corn stalks and other waste for *P. pulmonarius* **(Wachira *et al.*, 2022)**.

These findings underscore the importance of investigating and determining the optimal proportions of lignocellulosic agricultural waste based on the chemical composition of the substrates and the type of mushrooms used **(Akter *et al.*, 2022; Doroški *et al.*, 2021; Elattar *et al.*, 2019; Khatana *et al.*, 2024; Okere, Onyekachi, *et al.*, 2021; Rakib *et al.*, 2020; G. Singh *et al.*, 2021; Soni *et al.*, 2020; Wachira *et al.*, 2022; Zhou *et al.*, 2023)**.

The bioconversion of lignocellulosic waste by *Pleurotus* fungi involves significant changes in substrate composition. For instance, *P. ostreatus* impacts the organic matter content of nut shells and wheat straw, selectively decomposing hemicellulose and lignin **(Akcay *et al.*, 2023)**. The high bioavailability of hemicellulose in wheat straw enhances its decomposition efficiency **(Akter *et al.*, 2022; Koutrotsios, Mountzouris, *et al.*, 2014; Koutrotsios & Zervakis, 2014; Puliga *et al.*, 2022)**. Additionally, certain strains of *P. ostreatus* and *P. pulmonarius* effectively degrade phenolic compounds in agro-food waste, such as grape pomace and coffee pulp **(Akter *et al.*, 2022; Papadaki *et al.*, 2019)**. However, peels and shells are more challenging to bioconvert, showing lower rates of conversion **(Anike *et al.*, 2016; Okere, Ibeanu, *et al.*, 2021)**.

Another notable application of cultivating *Pleurotus* fungi is the production of biologically active compounds, particularly enzymes. The potential for enzyme production during the cultivation of macromycetes on agro-food residues is substantial **(Steudler *et al.*, 2019)**. Studies by a number of authors have shown that species of macromycetes in the genus *Pleurotus* have different enzymatic profiles that can vary depending on the composition of the substrate. This indicates the potential for researching enzymes of different classes synthesized by fungi in the genus *Pleurotus* during the bioutilization of plant waste of various compositions. Most often, the following substrates are considered as sources of enzymes: straw, bran, and cobs after the cultivation of *P. ostreatus* and *P. eryngii* **(Ganash *et al.*, 2021; Ibarra-Islas *et al.*, 2023; Melanouri *et al.*, 2022; Papadaki *et al.*, 2019; Ravindran *et al.*, 2018)**. Taking into account the presence of cellulose, hemicellulose and lignin in lignocellulosic waste, the main enzymes studied are cellulases, xylanases, peroxidases, laccases **(Contato *et al.*, 2020; Costa-Silva *et al.*, 2022; de Oliveira Rodrigues *et al.*, 2020; Ganash *et al.*, 2021; Ibarra-Islas *et al.*, 2023; Melanouri *et al.*, 2022; Papadaki *et al.*, 2019; Ravindran *et al.*, 2018; S. Sharma *et al.*, 2020)**. Some agro-food wastes, like peels and pomace, contain significant amounts of pectin **(Alzate Acevedo *et al.*, 2021; Dissasa, 2022)**, making them promising for pectinase production. Some authors refer pectolytic enzymes to lignocellulosic enzymes **(Ravindran *et al.*, 2018)**, however, research on pectinases in *Pleurotus* cultivation is limited and warrants further investigation.

CONCLUSIONS

This article presents a comprehensive review of the solid-phase cultivation of various *Pleurotus* species and the chemical composition of lignocellulosic waste from the agro-food industry. It evaluates current knowledge on the enzymatic activity in substrates transformed by *Pleurotus* fungi and assesses the potential for enzyme production.

The analysis indicates that substrate selection is crucial for optimizing the growth, development, and yield of *Pleurotus* fungi. High lignin content can impede the decomposition process but does not necessarily prevent growth in species capable of efficiently processing lignin. Effective substrates identified include wheat and rice straw, corn stalks, pulp, husks, and cake. Specifically, *P. ostreatus* demonstrated high yields and biological efficiency, particularly with flour milling industry waste. Other species, such as *P. eryngii* also showed promising results when cultivated on rice straw and sweet sorghum pulp, respectively. Overall, *P. ostreatus*, *P. eryngii* emerged as the most productive fungal species.

Utilizing agro-industrial lignocellulosic waste for mushroom cultivation not only offers an effective method for waste management but also facilitates the production of *Pleurotus* fruiting bodies. To achieve optimal results, it is essential to carefully select the substrate composition and the concentration of additional components based on the fungal species and cultivation conditions.

Future research should expand the range of fungal species and lignocellulosic agro-industrial substrates, assessing their environmental impact. Investigating other fungal species, such as *P.ostreatus*, *P. pulmonarius*, *P. cornucopiae*, *P. citrinopileatus*, and *P. djamor*, and exploring additional lignocellulosic wastes, including shells, peels, pomace, and bran, is necessary. The impact of factors like substrate concentration and their interactions with the growing environment should also be considered.

The qualitative composition and enzymatic activity of substrates after the cultivation of fruiting bodies require further investigation. This research area holds promise for developing new biotechnologies for enzyme production. In particular, studying pectinase activity in substrates could enhance agro-industrial waste processing efficiency, optimize cultivation processes, and identify new biotechnological applications.

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