

Review

Pleurotus ostreatus Mushroom: A Promising Feed Supplement in Poultry Farming

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Abstract: *Pleurotus ostreatus* (Jacq. ex Fr.) P. Kumm mushrooms are cultivated on diverse by-products based on substrates that hold promise for mitigating antibiotic usage in the poultry industry and reducing environmental pollution. By incorporating agricultural by-products into mushroom cultivation, the functionality of the mushroom products can be increased, then the final product can be a more effective feed supplement. After mushroom cultivation, spent mushroom substrate (SMS) can be valorized, due to the presence of huge amounts of bioactive compounds like β -glucan, chitin, polyphenols, and flavonoids related to mycelia. As a prebiotic and antimicrobial feed supplement, these mushrooms positively influence gut microbiota, intestinal morphology, and thus overall poultry well-being. This article underscores the potential of solid-state fermentation (SSF) to enhance the bioactivity of oyster mushrooms and their derivatives, offering a cost-effective and efficient strategy for transforming unconventional feeding materials. Moreover, it emphasizes broader implications, including the reduction of antibiotic dependence in poultry farming, highlighting the promising integration of oyster mushrooms and their derivatives for sustainable and environmentally conscious poultry production.

Keywords: solid-state fermentation; spent mushroom substrate; by-products; bioactive compounds; prebiotics; antimicrobial agents; reduction of antibiotic usage; poultry; *Pleurotus ostreatus*



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1. Introduction

Pleurotus ostreatus (Jacq. ex Fr.) P. Kumm., oyster mushroom, is one of the most commonly cultivated mushrooms in Europe, followed by *Agaricus bisporus* (white button mushroom) and *Lentinula edodes* (shiitake) [1]. It belongs to the Pleurotaceae family and the phylum Basidiomycota [2]. *P. ostreatus* is widely used throughout Europe and is known for its significant nutritional [3], and environmental remediation [4], circular economy of agricultural waste [5], utilization of agro-resources [6], and valorization of agricultural and energy applications [7]. This mushroom is rich in antimicrobial and prebiotic compounds for poultry health [2], along with chitin, ergosterol [8], flavonoids, mannans, peptides, polyphenols, and β -(1,3/1,6)-glucan [9]. β -glucan is needed for the microbiota in the gut, which convert these compounds into short-chain fatty acids [10] and enhance nutrient absorption and anti-inflammation effects [11]. Maintaining a healthy equilibrium in the

gut microbiota contributes to enhanced feed efficiency, growth rates, and production performance for preventing diseases and aiding in therapy for poultry producers [12].

A vast array of immunostimulating drugs, derived from both biological and synthetic sources, is available [13]. Nevertheless, significant focus has been directed toward *P. ostreatus*-derived biostimulators due to their high effectiveness and low toxicity [14]. Mushroom-derived antimicrobials and prebiotic agents can provide a natural and sustainable alternative to antibiotics as alternatives compared to commonly used antibiotics (e.g., penicillin, tetracyclines, fluoroquinolones) [12]. Furthermore, bacteria can develop resistance, and the target on which the antibiotics exert their action can be modified [14]. Therefore, there is a need for the valorization of food industrial and agronomical by-products of oyster mushrooms due to their low cost and widespread availability, as well as promising agro-practices in poultry farming [15]. This multifaceted approach involves leveraging agro-wastes for achieving a “zero-waste economy” through the circular economy and effective waste management strategies [16]. Central to this effort is the repurposing of lignocellulosic residues, emphasizing both environmental and economic concerns [17]. Spent mushroom substrate (SMS), enriched with fungal networks and bioactive compounds, acts as a valuable asset that can also be repurposed as a dietary supplement considering the substantial biomass waste generated globally [18]. Additionally, the valorization of agricultural by-products through eco-friendly solid-state fermentation (SSF) emerges as a promising strategy to enhance the bioactivity of oyster mushrooms and their by-products [19]. SSF contributes to an efficient optimization of bioactive compounds, offers potential benefits in nutrition, immunity, and waste management, and adds value for food, feed, and pharmaceutical products [20].

The current study explores the role of using agricultural and food by-products in cultivating *P. ostreatus* mushrooms. The application of the fruiting body and SMS is discussed as a potential prebiotic and antimicrobial drug to reduce antibiotic usage with high efficiency in the poultry industry. This review addresses gaps in the understanding of their benefits, environmental impact, effects on poultry gut microbiota, and mechanisms of action, explores potential technologies like SSF to improve bioactivity, and highlights opportunities for sustainable development.

2. Methodology of the Review

Examining the benefits of integrating oyster mushrooms into animal feed is an interesting future area of research. Nevertheless, there exists a shortage of data, especially the valorization of spent mushroom substrates encompassing recycled substrates and their capacity to improve functionality. This information gap has led to an expanding body of literature exploring the economic and environmental importance of *P. ostreatus* and SMS, along with its potential application in the poultry industry. Several key inquiries emerge from this research. Firstly, what makes agricultural and food industrial by-products promising for mushroom production and how can sustainable development support them? Secondly, what is the main environmental importance of SMS? Furthermore, what influence does the oyster mushroom exert on poultry health? Additionally, how do the gut microbiota contribute to reducing antibiotic usage and preventing diseases? Moreover, how can sustainable development be promoted, especially by enhancing the nutritional properties of mushrooms and agricultural by-products through solid-state fermentation, followed by recycling in the poultry industry? To gather pertinent articles, searches were conducted using diverse keywords on reputable platforms like ScienceDirect, PubMed, and Google Scholar. It is noteworthy that over 85% of the collected articles were from the past five years.

3. Valorization of Oyster By-Products

Agricultural residue, commonly termed agro-waste, denotes the leftover materials remaining following the harvesting of crops [21]. Plants are mainly the source of these waste materials, including coconut coir, corncob, sugar cane bagasse, and rice husk, as

indicated by previous studies [22]. These materials, commonly referred to as lignocellulosic wastes [23], along with agro-food by-products such as fruit peels and seeds, are included [24]. The agricultural and food sectors are generating 190 million tons of by-products each year [25]. The manufacturing process has notable environmental consequences, including biodiversity depletion, elevated water consumption, and a decline in soil fertility [26]. Incorporating certain by-products into animal feeds poses challenges, for example, high moisture content, low feeding value, low protein quality, and the presence of anti-nutritional compounds, allergens, and mycotoxins [15]. Nevertheless, with proper handling and recycling of these by-products, they can contribute to fostering sustainable development [27]. Achieving a substantial reduction in waste generation, as well as effective reuse and recycling of waste, depends on the implementation of circular agricultural production and appropriate waste management models [26,28]. In striving for a “zero-waste economy”, where the repurposing of waste materials is a priority, the essential reutilization of lignocellulosic residues becomes crucial, addressing both environmental and economic considerations [3].

Following the assessment of potential risks and the implementation of appropriate management practices, these can be employed as a source of feed [9]. Additionally, they can serve as a substrate for cultivating mushrooms. Another significant factor is that the mushroom substrate (SMS) can be derived from these materials. Subsequently, SMS is abundant in fungal networks (an interconnected fungal hyphae), which aim to form a mycelial network, and helps interaction with plants [29] with bioactive compounds, which can be utilized as a supplementary feed source [30]. Agricultural biomass utilized as a substrate for mushroom cultivation contains notable proportions of cellulose, hemicellulose, and lignin, as outlined in Table 1. Cellulose, constituting the major portion (30–50%), plays a vital role in plant cells by providing mechanical strength, which is structured through organization of cellulose microfibrils composed of β 1–4-linked glucose chains [31].

Hemicelluloses, a valuable biomaterial, contain various polysaccharides, such as arabinan, arabinogalactan, arabinoxylan, galactose, glucose, glucomannan, glucuronoxylans, mannanose, xylans, and xyloglucans within plant cell walls [32]. It has been formed by monosaccharide units (pentoses, hexoses, acetylated sugars, and uronic acid). The structure of hemicelluloses is formed through the arrangement of cell wall matrix, which consists of β -(1,4)-linked pyranosyl units, leading to cellulose cross-linked hydrogen bonding [32]. Lignin, although the least abundant yet intricate polymer, acts as a binder, filling the gaps between cellulose and hemicelluloses [19]. Several research findings suggest that mushrooms grown on bagasse demonstrate elevated protein levels when contrasted with rice straws, wheat straws, and corn cobs [33]. *P. ostreatus* mushroom is commonly cultivated successfully on these wastes due to its enzymatic capabilities, which allow it to efficiently break down and metabolize these components, leading to robust growth and the production of high-quality mushrooms [34]. Pectin is a complex and diverse component of the mushroom cell walls, which are composed of chains of galacturonic acid (GalA) units, linked together by α (1–4)-glycosidic bonds. It can be successfully metabolized by mushrooms for growth. These chains are often highly branched and can contain side chains of various other sugars, such as rhamnose, galactose, and arabinose [35].

Researchers have utilized various by-products to increase the content of bioactive compounds, thus increasing the biological activity of *P. ostreatus* mushrooms. For instance, Koutrotsios et al. [36] grew *P. ostreatus* on an unconventional substrate composed of grape marc, olive mill by-products, and wheat straw. The inclusion of grape marc and olive mill by-products in the media led to a significant 27% increase in the β -glucan content [34] and prebiotic activity of fruiting bodies. In another study, Koutrotsios et al. [37] valorized olive by-products like olive-mill waste and olive pruning residues as a mushroom substrate, and found that the final product increased the in vitro growth of *Lactobacillus acidophilus*, *L. gasseri*, and *Bifidobacterium longum*. Moreover, the utilization of waste from casings has proven to be efficient in the generation of lignocellulolytic enzymes by *P. ostreatus*. However, *Ganoderma lucidum* has demonstrated even greater effectiveness in this regard. Moreover, an

investigation by Mkhize et al. [38] was conducted to examine the impact of supplementing sugarcane bagasse and sugarcane top with maize flour. The supplementation of maize flour into agricultural waste, ranging from 12% to 18%, was found to enhance the antimicrobial potential of the fruiting body against *Staphylococcus aureus* [38].

Table 1. Substitute compost materials for the substrate of *P. ostreatus* mushroom.

Substrate	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Ref.
Apple pomace	21.78	15.82	13.33	[39]
Banana peel	41.38	9.9	8.9	[40]
Barley straw	33.25	20.36	17.13	[41]
Corn cobs	45.43	29.92	10.93	[42]
Corn husks	45.7	35.8	4.03	[17]
Cornstalk	35.0–39.6	16.8–35.0	7.0–18.4	[43]
Cotton seed hairs	80–95	5–20	0	[44]
Empty fruit bunch	34.9	26.64	31.1	[45]
Japanese red cedar	52.3	7.3	32.6	[46]
Nutshell	35.70	18.70	30.20	[42]
Rice husk	30.43	28.03	36.02	[47]
Sawdust	32.63	37.23	22.16	[48]
Soybean straw	34.4	19.3	21.6	[15]
Sorghum leaf and stalk	31	30	11	[44]
Sugarcane leaf and stalk	40	29	13	[44]
Sugar palm	43.88	7.24	33.24	[49]
Sunflower stalk	34	20.8	29.7	[50]
Wheat bran	31.10	34.30	16.30	[51]
Wheat straw	30	50	15	[52]

Table 2 outlines the nutritional value (protein, carbohydrate, fat, and ash content in g kg^{-1}) of SMS and fruiting bodies of commonly cultivated mushrooms, including *Pleurotus* spp. The comparison between SMS and fruiting bodies of *P. ostreatus* and *P. sajor-caju* mushrooms reveals notable differences. In SMS, *P. ostreatus* exhibits the highest protein content (16.1 g kg^{-1}) compared to *P. sajor-caju* (14.5 g kg^{-1}). *P. sajor-caju* SMS has slightly higher carbohydrate and fat levels. However, in fruiting bodies, *P. ostreatus* surpasses *P. sajor-caju* in protein content (30.40 g kg^{-1} vs. 19.23 g kg^{-1}) and ash content (9.80% vs. 6.32%), while *P. sajor-caju* fruiting bodies show higher carbohydrate and fat levels [53,54]. In summary, the valorization of waste mushroom substrate for agro-applications (e.g., compost, plant growing media and biofertilizer) as alternative energy sources deserves consideration in the future.

Table 2. The chemical characterization of SMS and fruiting body from *P. ostreatus* mushroom.

Substrate	Protein (g kg^{-1})	Carbohydrate (g kg^{-1})	Fat (g kg^{-1})	Ash (g kg^{-1})	Ref.
SMS from <i>Pleurotus ostreatus</i>	$16.1 + 0.32$	$63.57 + 0.02$ $70.67 + 0.06$	$23.78 + 0.04$ $23.22 + 0.03$	$5.29 + 0.011$ $5.14 + 0.002$	[53]
SMS from <i>Pleurotus sajor-caju</i>	$14.5 + 0.32$	$61.45 + 0.03$ $70.27 + 0.02$			[53]
Fruiting body from <i>Pleurotus ostreatus</i>	30.40	57.60	2.20	9.80	[54]
Fruiting body from <i>Pleurotus sajor-caju</i>	19.23	63.40	2.70	6.32	[54]

4. The Environmental Importance of SMS

In mushroom cultivation, the nutrient content and conductivity of the SMS are considered the most important key issues. The rising global consumption of edible mushrooms has led to an escalation in both mushroom stalk and substrate waste [55]. Throughout the process of mushroom cultivation, the substrate undergoes diverse biochemical transformations and metabolic activities, leading to the accrual of valuable bioactive compounds [20].

The nutrient-enriched SMS encompasses essential nutrients such as N, P, and K, along with crucial elements like Mg, Na, Cu, and Fe. It lacks pests, weed seeds, and soluble salts. Moreover, despite having a 45% water content, SMS possesses a compact composition with a comparatively lower bulk density than manure [56]. Furthermore, extractive compounds presented in SMS are derived from fungal biomass (fungal mycelium), encompassing carbohydrates like β -glucans, as well as proteins and sterols [57], chitin–glucan complex, phenolics, and flavonoids [58], which can be extracted with conventional and modern techniques [57] and then used for their antimicrobial and prebiotic benefits in the food, pharmaceutical, and poultry industries [59]. Generally, there are some groups of bioactives that can be found in *P. ostreatus*, including polysaccharides, lovastatin, ergosterols and phytochemicals (Figure 1). These bioactives have distinct benefits for poultry health.

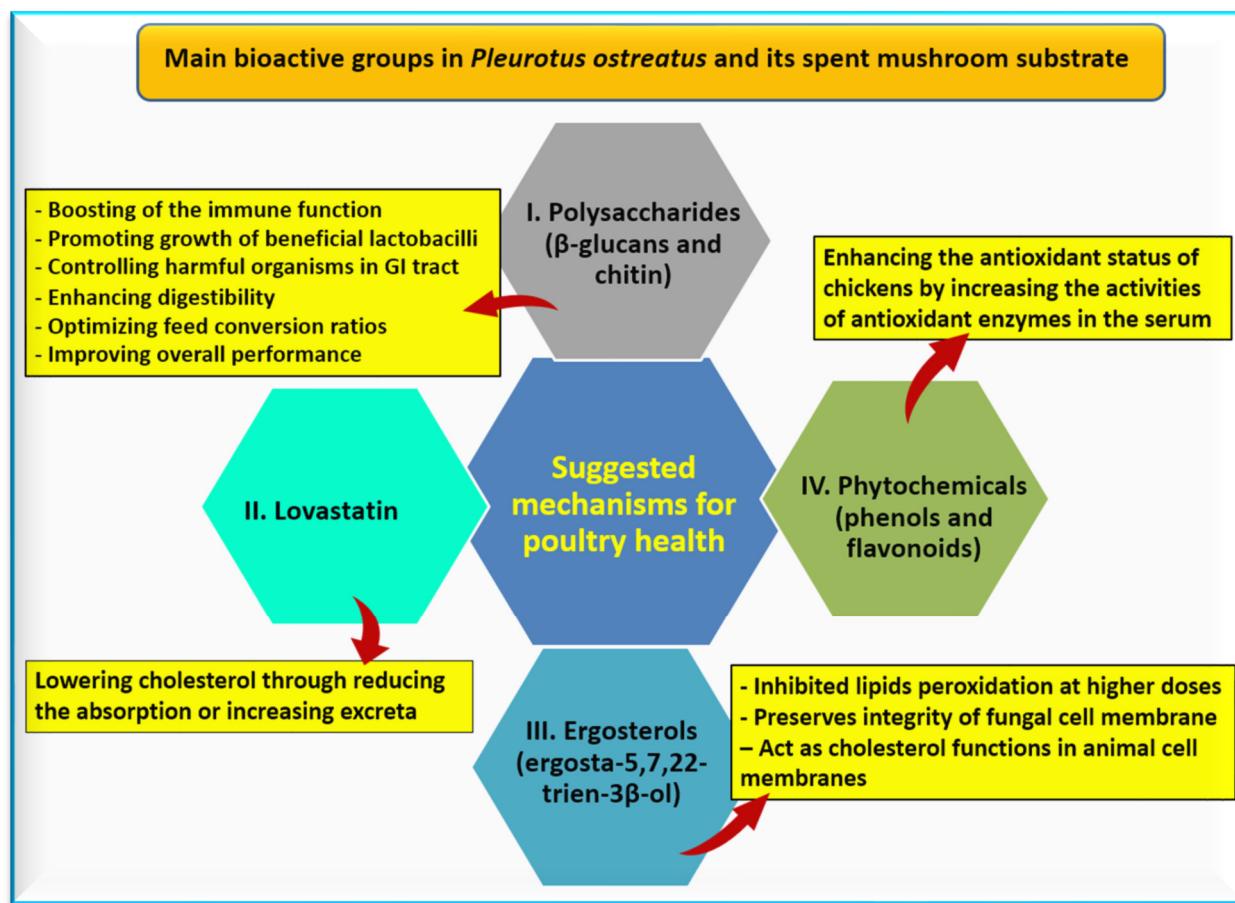


Figure 1. List of the main bioactive compounds that can be found in *P. ostreatus* mushroom, its spent mushroom substrate, and their role in poultry farming and health. Sources: [8].

Global attention has been drawn to the burgeoning field of mushroom cultivation technology, which is expected to yield positive ecological effects that will likely expand in the future [18]. Examples of these impacts include waste reduction, enhanced energy efficiency, improved soil fertility, and mitigation of climate change. Furthermore, numerous applications for SMS have been recommended, including its utilization of the potential of *P. ostreatus* for biosorption of lead (II), nickel (II), iron (III), copper, and absorbing nickel from the effluent (bi-metal solution), representing a significant asset for the removal of pollutants from the environment [35]. Furthermore, recent studies have mentioned its successful application in biogas production [48] and nutrient uptake in mushroom cultivation.

The utilization of recycling food and agro-industrial by-products as a strategy for attaining sustainable farming are presented in Figure 2. Embracing this approach enables farmers to cut costs and protect the environment, contributing substantially to a promising

and sustainable future. However, Gao et al. [35] underscore the importance of future research, emphasizing three key areas regarding SMS: multistage recycling, therapeutic efficiency, and environmental health risks. Hygienic hazards should be noted, such as microbial contamination, as SMS can serve as an ideal nutrient for various microbes due to its high moisture content, high water activity (0.98) and neutral pH [30,35]. Furthermore, radioactive contaminants, degradation of crude oil, and oxo-biodegradable plastic degeneration by mushrooms can also occur [60].

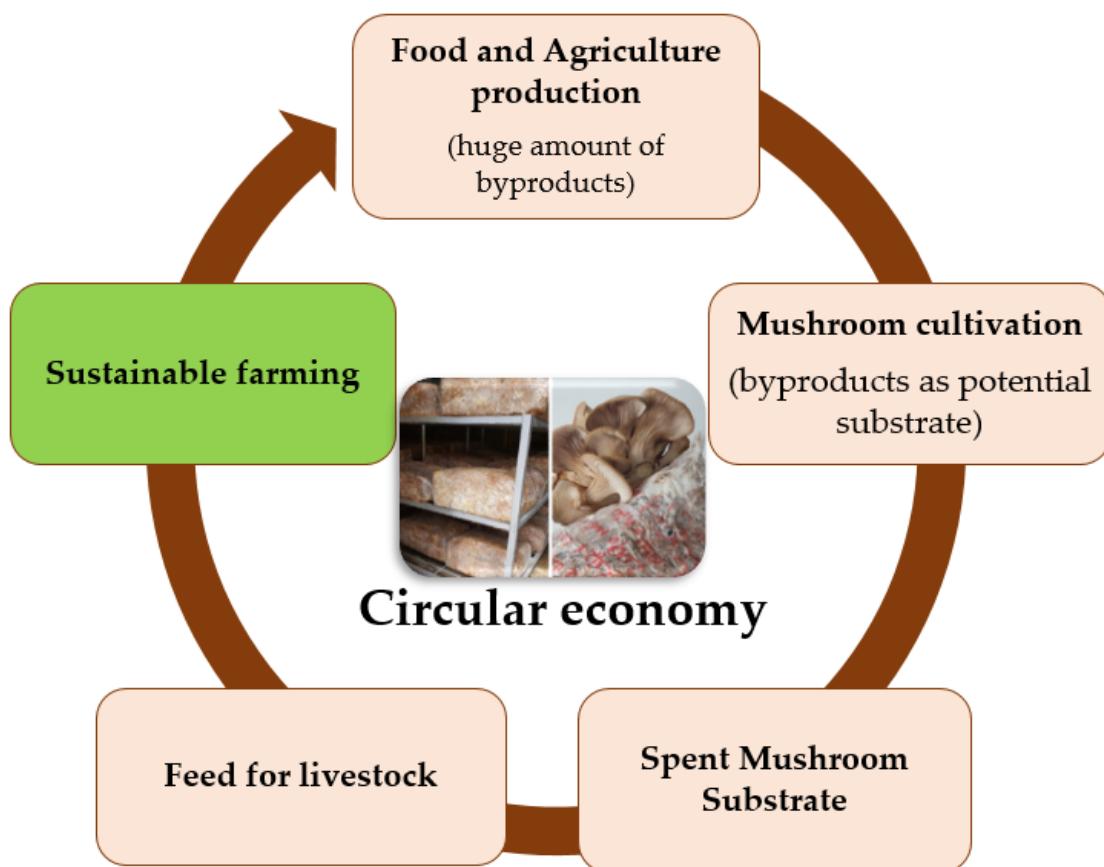


Figure 2. Essential facets of sustainable mushroom farming and the utilization of its by-products. Sources: [15,21,22].

5. Applications of Oyster Mushrooms and Their Derivatives in Poultry Farming

Along with the consumption of edible oyster mushrooms, there are many applications, including the recovery of agro-wastes as mushroom substrate, medical applications, and pharmaceutical properties. Hassan et al. [61] proposed that incorporating dried SMS from oyster mushrooms at a 1% level enhances performance and humoral immune response to disease vaccines and delays lipid oxidative rancidity in poultry meat. This level of inclusion was found to be more effective than higher levels (2%) or groups supplemented with antibiotics, such as enramycin. In general, promoting the integration of the oyster mushroom and its by-products, such as processed SMS, into poultry diets can contribute to the adoption of more sustainable farming practices [62]. Numerous recent research papers have been published examining the effects of the dried oyster mushroom (*P. ostreatus*) from the fraction of fruiting body on various aspects of poultry models, as outlined in Table 3.

These studies underscore the positive outcomes associated with the incorporation of powders derived from the fruiting body, stem residues, and SMS of *P. ostreatus* into poultry diets, particularly for broiler chickens, Japanese quails, grower geese, laying hens. These findings highlight the potential of SMS as a valuable and alternative nutritional element in the poultry industry, which presents a sustainable and economically viable

approach to improving poultry nutrition and productivity. Nevertheless, further research is warranted, considering the limited number of studies on this subject, especially regarding the utilization of SMS and waste mushrooms.

Table 3. The impact of oyster mushroom powder (from the fruiting body) on the well-being of poultry.

Applied Dose of <i>P. ostreatus</i> (%)	Animal Models	Main Results	Ref.
0.5–2	Japanese quail (<i>Coturnix japonica</i>)	Positive impacts on crypt depth and papillae height across various gut segments were observed with the inclusion of 0.5–2%, 2% of <i>P. ostreatus</i> powder.	[63]
1–2	Broiler chicken (ROSS 308)	Positively influence the morphology of their intestines (higher relative length of the ileum).	[64]
1.5	Broiler chicken (ROSS 308)	High live weight and greater profitability.	[65]
1–2	Broiler chicken (ROSS 308)	A notable enhancement in the elevation of villi and the profundity of crypts within the jejunum.	[66]
5, 10 and 15	Grower geese	A 5% inclusion of SMS in the diet positively influences sensory attributes, especially meat flavor and overall acceptability.	[67]
1–2	Broiler chicken (ROSS 308)	1% inclusion of oyster mushroom waste positively influences poultry performance, and immune response to disease vaccines, and reduces meat lipid oxidative rancidity.	[61]
25, 50, 75, and 100% replacement of wheat bran	Broiler chicken (ROSS 308)	The dietary treatment did not exhibit a significant effect ($p > 0.05$) on the breast, thigh drumstick, back, neck, wings, and shoulder.	[68]
0, 5, 10, and 15 mL/L of water and 0, 500, 750, and 1000 ppm	Cockerel chickens	15 mL/L in water and 750 ppm in feed resulted in improved growth performance and blood profile in production.	[69]
0.3, 0.6, 0.9 and 1.2%	Hy-line laying hens	0.6% of mushroom powder led to the maximum egg weight and IOFC (Income Over Feed Cost).	[70]

Present challenges associated with issues like food availability and environmental concerns are prompting the restructuring of food and feed systems to meet sustainable development. Certain agricultural by-products, such as brewer's spent grain, are being considered in this optimization process [71]. Wheat bran [68] and SMS can be a potential source of extracted, purified, and isolated β -glucans and employing the by-products as a substrate that undergoes fermentation or processing by mushroom species capable of β -glucan production [23]. β -glucans derived from *Saccharomyces cerevisiae* stands out as a widely utilized glucan in the poultry industry as a feed additive. Nevertheless, further investigations are essential to assess the variances in biological activity among β -glucans obtained from distinct origins [72] and mushroom species, owing to structural differences [73] and different methods of characterization, extraction, and valorization [74].

There are significant differences in the chemical composition of SMS and the fruiting body of *P. ostreatus* [55]. The main components of SMS are 48.7% cellulose, 34% hemicellulose, and 39.8% lignin. SMS presents several opportunities for the extraction of β -glucans, polypeptides, phenolics, flavonoids, tannins, tocopherols and enzymes through synergistic combinations with other sources. It is worth noting that SMS contains β -glucans sourced from various grains, grain seeds with β 1–4 linkages, and mycelia with β 1–3 and β 1–6 linkages with different structures. Furthermore, the chemical constituents help in creating the physicochemical characteristics, productivity, and biological efficiency of mushroom [18,74]. The fruiting body of *P. ostreatus* typically contains β -glucans, which can range from 8 to 27 g/100 g of the dry weight, while chitin content might be approximately 10–26% [75].

These differences in polysaccharide composition may result in variations in fermentability in the hindgut [76]. More information on β -glucan can be found in the following figure (Figure 3).

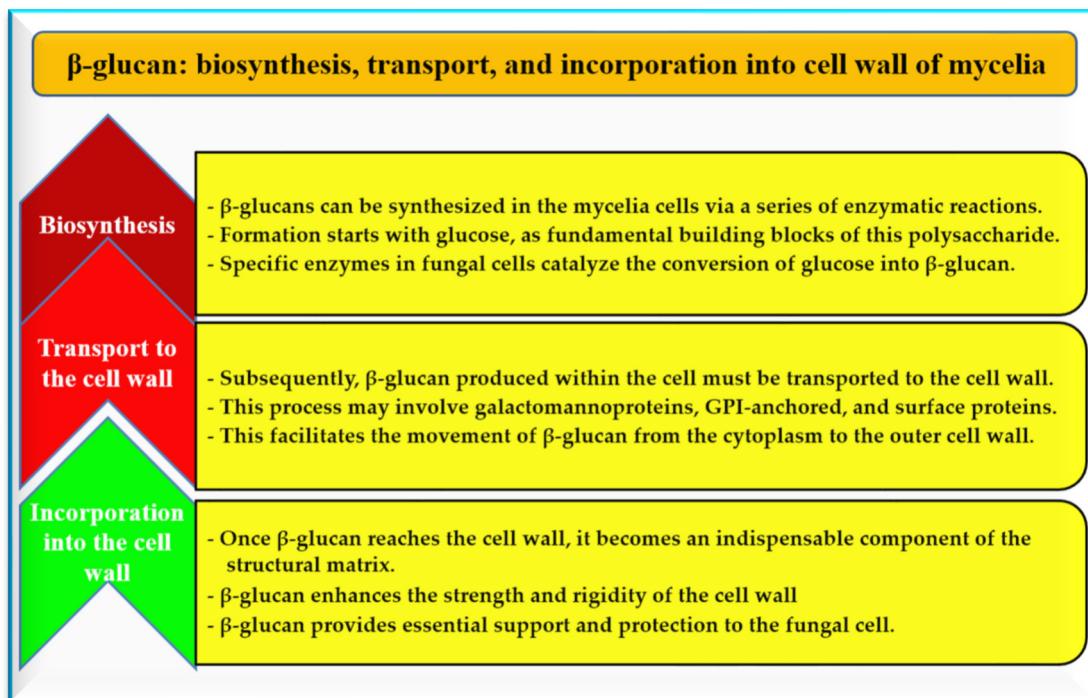


Figure 3. The biosynthesis of β -glucan, its transport to the cell wall, and incorporation into the cell wall of mushroom mycelia. Source: [72].

6. *P. ostreatus* for Feed Supplement in Poultry Industry

6.1. Common Infections in Poultry Industry

Common infections in poultry comprise three main groups (i.e., bacteria, fungi, and virus). According to a report covering 2013 to 2021 in the United States, there was a significant number of diseases linked to pathogenic bacteria, such as *Escherichia coli* [77] and *Staphylococcus aureus* [78], and fungi, such as *Candida albicans* [79], infection in the poultry industry. It is worth noting that the presence of secondary fungal coinfections (*Candida* and *Aspergillus* spp.) in conjunction with cutaneous lesions of avian virus, a common infection at poultry farms, has been identified as an important factor in causing disease, contributing to the debilitation of affected animals and ultimately leading to mortality [80]. Approximately 80% of antibiotics sold in the United States are utilized in animals, including chlortetracycline, oxytetracycline, and virginiamycin [81]. Over the last 70 years, commencing initially in the United States and Western Europe, the widespread adoption of antibiotics in animal farming extended swiftly to emerging regions across Asia, Latin America, and Eastern Europe [82]. Bacterial infections are frequently observed in poultry, as depicted in Figure 4. A notable concern associated with this is the potential presence of antibiotic-resistant pathogenic bacteria in food-producing animals. This poses a substantial risk, as these resistant bacteria may be transmitted to humans through the food supply, presenting a significant threat to global food security [83]. Elevating the demands on the industry to effectively handle these organisms [12] moreover may lead to financial setbacks. On a worldwide scale, over 700,000 fatalities result from bacteria resistant to antibiotics annually. Projections suggest that by 2050, the annual death toll due to antibiotic-resistant bacteria could escalate to 10 million [84].

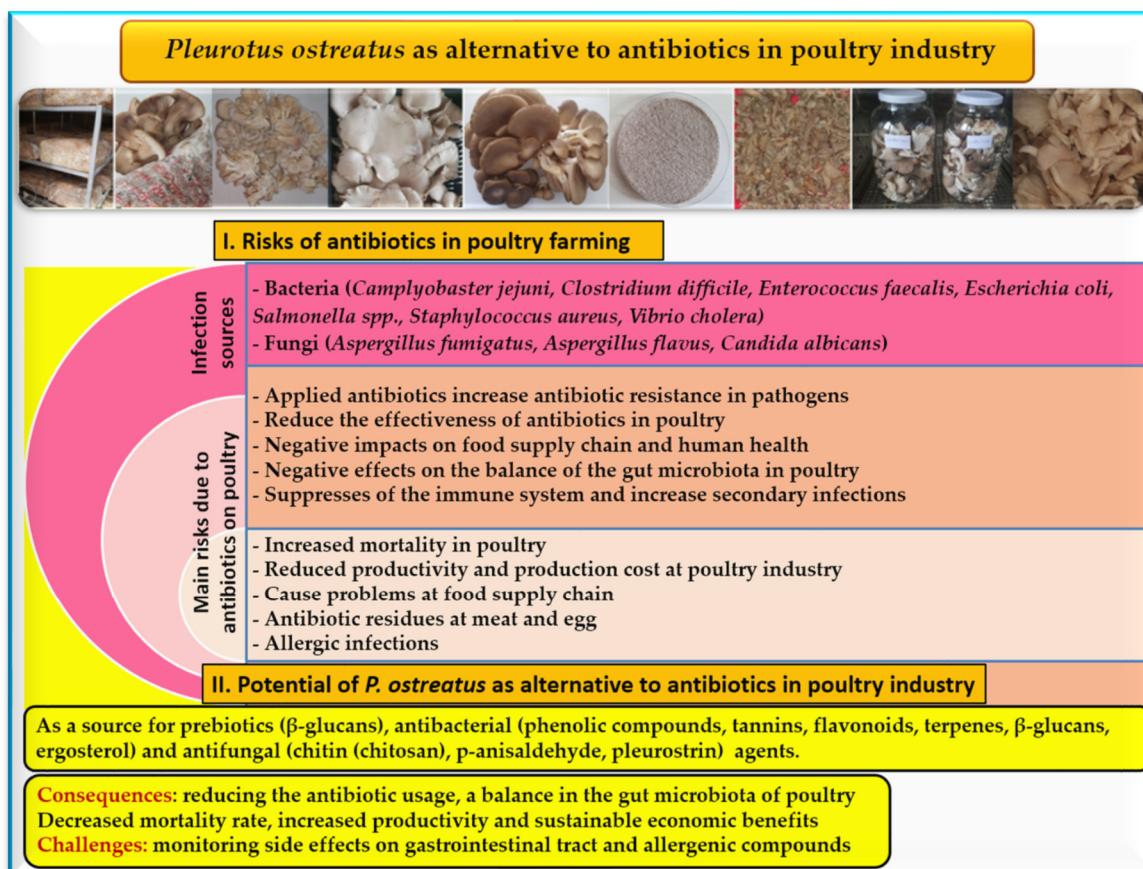


Figure 4. The contribution of *P. ostreatus* in combating pathogen invasion. Source: [9,12,13].

6.2. Alternatives to Antibiotics in the Poultry Industry

Due to many problems with traditional antibiotics, there is an urgent need to find alternatives. These alternatives may include nondigestible fibers (prebiotics), beneficial organisms (probiotics) [85], the combination of probiotics and prebiotics (synbiotics) [86], enzymes [18], organic acids [87], and phytochemicals with antimicrobial properties. Moreover, there is a growing demand for alternative strategies to mitigate antibiotic-related diseases, sustain agriculture, and support the increasing global population [88]. In both advanced and emerging economies, antibiotics are mainly employed to stimulate growth and prevent infections [81], reduce morbidity and mortality, and improve feed efficiency [89]. The administration of antimicrobials to livestock is believed to enhance the general well-being of the animals, resulting in increased yields and a superior-quality end product [81]. However, it is imperative to recognize the significance of reducing the reliance on antibiotics. These drawbacks encompass the emergence of antibiotic-resistant strains, environmental and economic repercussions, concerns regarding public health, and limitations in treatment options [41]. The intestinal microbiome plays a crucial role in protecting against diseases. The influence of the gut microbiome on the host's immune response, encompassing both innate and acquired immunity, is substantial [90]. The gastrointestinal tract (GIT) in poultry contains microbiota (fungi, bacteria, protozoa and viruses in symbiotic relationships) that play a vital role in the birds' overall health and well-being through effects on immune response, nutrient digestion, and absorption. The nature and function of the GIT should be explored and innovative strategies developed to enhance both animal health and productivity [91].

6.3. Oyster Mushrooms for Feed Supplement

To what extent are oyster mushrooms considered a promising feed supplement in poultry farming? As mentioned before, this mushroom is rich in many nutritional and health-promoting effects. Various mushroom by-products contain huge concentrations of β -glucans [92]. To address animal health and nutritional needs, valuable substances such as chitin are utilized [9] for antibiotics [93], and peptides [94] can be also extracted from SMS, offering a range of applications [48]. SMS encompasses bioactive compounds that exhibit gut stimulation effects, including polysaccharides, ergothioneine, and antioxidants [93,95]. Polysaccharides are recognized for their ability to enhance the growth of beneficial bacteria, and it is noteworthy that the primary contributor to anti-inflammatory properties is ergothioneine [96]. Additionally, antioxidants can protect against oxidative stress, a contributing factor to gut inflammation and various gastrointestinal disorders [93,97]. Mushrooms function as a prebiotic [9], impacting the synthesis of short-chain fatty acids (SCFAs). These SCFAs, encompassing acetic acid, propionic acid, butyric acid, valeric acid, isobutyl, and isovaleric acid, originate from the fermentation of nondigestible carbohydrates and proteins in the diet by bacteria present in the gastrointestinal tract of both humans and animals. It is worth noting that SCFAs can be increased by bioactive compounds from mushrooms, such as chitin, β -glucan, inulin, α -glucan, and galactomannans [11]. Oligosaccharides, primarily occurring in the cecum, shed light on the importance of understanding cecum function and its relationship to oligosaccharide utilization [98]. Dietary fiber plays a significant role in shaping various aspects of gut physiology and animal nutrition. Furthermore, several factors contribute to creating a favorable environment for good bacteria, like pH balance, substrate availability, competition and exclusion, and the production of beneficial metabolites like SCFAs. β -glucan has potential negative impacts on intestinal viscosity. High intestinal viscosity can hinder nutrient digestion and absorption while also providing a favorable environment for pathogen growth [99].

Mushrooms are rich sources of antimicrobial agents like phenolic compounds (phenolic acids, flavonoids) [34] and antimicrobial peptides (MBPs) [100], which further contribute to poultry health and the gut microbiota by a reduction in the number of pathogens [101]. There has been limited research conducted on MBPs. A diverse range of antimicrobial peptides has been extracted and purified from edible mushrooms, including *Pleurotus eryngii* and *P. ostreatus*. The potential antimicrobial mechanisms of MBPs may include the regulation and induction of tissue-specific expression patterns or the disruption of bacterial cell membranes, resulting in intracellular protein leakage and bacterial death, thereby achieving antibacterial effects. A suggested mechanism of action for phenolic acids involves a reduction in extracellular pH, exemplified by gallic and chlorogenic acids. Apart from their inherent chemical characteristics, the antibacterial effectiveness relies on the interaction site with target molecules. Phenolic acids exhibit membrane-active properties against bacteria, resulting in the leakage of cellular components, including nucleic acids, proteins, and inorganic ions such as potassium or phosphate [102]. Certain strains from the *Firmicutes* phylum, such as *Agathobacter rectalis* and *Clostridium spiroforme*, exhibit high susceptibility to both free and immobilized phenolic compounds [103].

Chitin can be broken down into smaller molecules by enzymes in the digestive system, allowing for absorption through the intestinal wall. β -glucans may undergo enzymatic digestion, releasing smaller sugar units that can be absorbed by the intestinal lining. It promotes the growth of generally beneficial organisms like *Bacteroidetes*, *Bifidobacterium* and *Lactobacillus*, which help in preserving food safety by serving as a protective barrier against the colonization of foodborne pathogens [104]. Studies have demonstrated the efficacy of mushroom-derived antimicrobial agents in altering the microbial composition in poultry, for example, a reduction in the populations of *Bacteroides* spp., *E. coli*, and *Enterococci*, as well as a decrease in the total counts of aerobic microorganisms in gut microbiota of Japanese quail (*Coturnix japonica*) [63] and broiler chickens (ROSS 308) [66] when subjected to 0.5% and 2% *P. ostreatus* mushroom powder feed supplement [63,66].

7. Why Is SSF a Promising Strategy to Improve the Bioactivity of Oyster and Agricultural By-Products?

Utilizing fermentation technology offers a cost-effective and efficient method to aid agricultural, food, and animal production systems in adhering to established “planetary boundaries”. This entails converting nonconventional feed materials sourced from agricultural by-products and food wastes into animal feed, fostering the sustainable production of animal-derived food products [15]. Solid-state fermentation (SSF) represents a heterogeneous, three-phase environmentally friendly microbial process. It is applicable to preserving and enhancing the functionality of bioactive compounds found in spent mushroom substrate (SMS). Valuable compounds with antimicrobial and prebiotic activity can be significantly increased through SSF. The gastrointestinal tract of poultry harbors a diverse array of microorganisms, playing pivotal roles in poultry health and disease susceptibility, particularly concerning bacterial infections often treated with antibiotics, leading to the formation of antibiotic resistance. Recent studies have shed light on the substantial impacts of SSF on agricultural by-products, *P. ostreatus* mushrooms, and their derivatives, examining various perspectives.

Lu et al. [105] investigated the impact of incorporating corn straw and xylosma sawdust substrates on the production and activity of polysaccharides through solid-state fermentation of *P. ostreatus*. The findings revealed that the addition of lignocellulose, particularly xylosma sawdust, enhanced the synthesis of active polysaccharides derived from cellulose and hemicellulose, demonstrating earlier peaks in hydroxyl radical scavenging activity [105]. While substrates with commercial SMS consistently yield high biomass and biological efficiency for *Pleurotus* species, substrates containing barley and oat straw and coffee residue also support substantial laccase production, which helps phenolic and polyphenolic substances to be oxidized by laccase, forming detoxified and biodegradable compounds [106]. The incorporation of feed (soybean and rapeseed) produced by SSF expands the availability of beneficial probiotic bacteria, such as *Lactobacillus* spp., which has been substantiated to induce the production of immunoglobulin in broilers [107]. Ibrahim et al. [108] found that the incorporation of fermented barley in the feed was found to stimulate lysozyme activity in broiler serum [108], aligning with similar results reported by Zhu et al. [109], who found an increase in serum lysozyme activity with fermented feed supplementation [109]. It is noteworthy that lysozyme, recognized as an antimicrobial enzyme, serves as a crucial factor in disrupting the cell walls of pathogenic bacteria [110]. Furthermore, Zhu et al. [109] reported that the enhancement of broiler diets with fermented feed has the potential to reduce the production of odorous compounds by altering the microbiota in broilers [109].

The utilization of SMS is viable for extracting nutrients from plant biomass through solid-state fermentation [88], with several advantages, as seen in Figure 5. The bioactivity of *P. ostreatus* mushrooms and their by-products is achievable through microorganisms during SSF, taking into account various factors. This enables the production of value-added materials with enhanced functional properties. Nevertheless, the entire process must be optimized, starting from the selection and quality control of the starter material (SMS) to post-fermentation strategies, including extraction, encapsulation, and preservation methods [98].

Fermentation is a potent method capable of enriching foods with bioactive peptides from diverse sources. This augmentation of the immune response offers potential protection against viral infections by modulating immune cells [99]. Moreover, fermentation can result in the generation of bioactive metabolites, encompassing enzymes, organic acids (such as citric acid and lactic acid), antimicrobial agents, gibberellic acids, ergot alkaloids, and antioxidants (like phenolic acids), and the synthesis of immunomodulatory compounds [83,84]. It possesses the capability to remove naturally occurring antinutritional factors (ANFs) in foods, encompassing both heat-stable compounds (such as tannins, saponins, alkaloids) and heat-labile compounds (including protease inhibitors, lectins) [98]. Microorganisms

participating in the fermentation process can decompose intricate organic compounds, including lignocellulose [42].

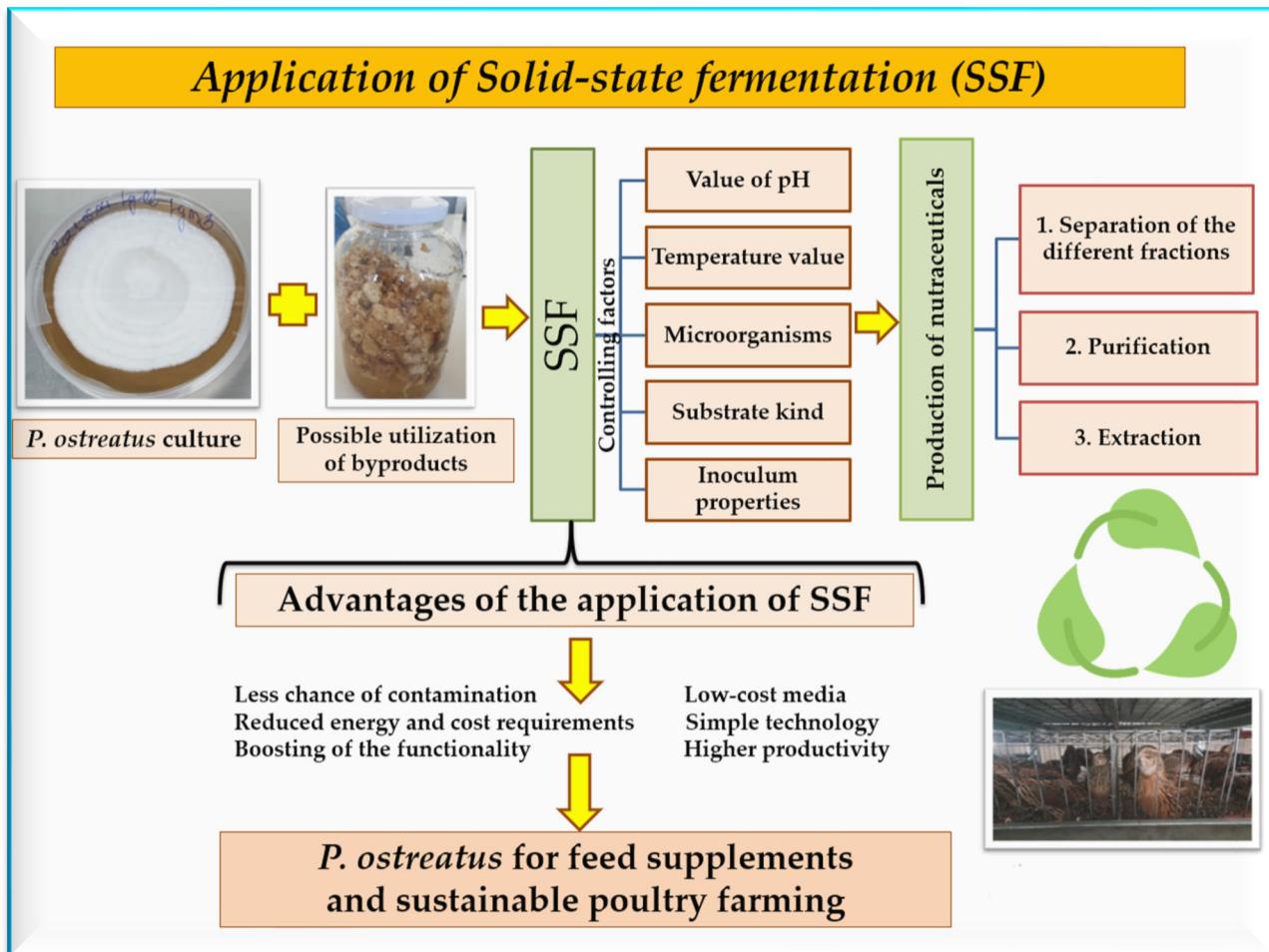


Figure 5. The utilization of mushroom by-products in solid-state fermentation and its benefits for sustainable poultry farming. Sources: [17].

The primary factors influencing the SSF process are illustrated in Figure 6. The selected substrate emulates a conducive environment for microorganisms, functioning either as a nutrient source or being augmented with nutrients. Factors like substrate (chemical composition, humidity, and particle size), inoculum, carbon-to-nitrogen ratio, oxygen concentration, pH [111], temperature, moisture levels, and water activity are important considerations in the SSF process [112]. One crucial factor is the absence of freely flowing water and air. Filamentous fungi (*Rhizopus oryzae*, *Trichoderma asperellum*), yeast (*Saccharomyces cerevisiae*, *Saccharomyces boulardii*), and bacteria (*Lactobacillus acidophilus*, *Lactobacillus plantarum*) are often employed for SSF. Additionally, mycelia from edible mushrooms like *P. ostreatus* are commonly employed to enhance the nutritional and antioxidant properties of by-products.

The primary limitation of this technology lies in the sluggish hydrolysis of lignocelulosic components in certain feedstocks, rendering it impractical as an industrial-scale pretreatment method. To enhance the efficiency and accelerate the process, a viable approach involves combining it with another pretreatment method, such as physical or chemical methods [111]. Many recent studies have been published on the impacts of the solid-state fermentation on oyster mushroom and *Pleurotus* spp. from different points of view. For example, the cell-wall components of crop residues were reduced, and the crude protein content was increased by treatment with *Pleurotus florida*, leading to enhanced

organic matter digestibility, metabolizable energy, net energy, and short-chain fatty acids through solid-state fermentation [113]. Furthermore, barley fermented with *P. ostreatus* containing lovastatin presents a potential alternative as a functional food option. Heidari et al. [113] illustrated that integrating fungal fermentation (through culture of *P. ostreatus*) with mechanical processing of canola meal represents a promising method to enhance its nutritional value and antinutrient levels [113].



Figure 6. Different strategies for enhancing the functionality of bioactive compounds involves various factors through solid-state fermentation (SSF) process. Sources: [3].

8. A Comprehensive Overview

The present review aimed to address the principal applications of oyster mushrooms in the poultry industry, particularly their antimicrobial potential, and elucidate how this species can contribute to sustainable development. This central question serves as the focal point for our research. Overall, mushrooms and their derivatives can serve as a dietary supplement in poultry nutrition. Mushrooms exert a notable influence on the composition of gut microbiota [114], intestinal morphology [61], immune system, and antioxidant capacity [63]. Bioactive compounds derived from mushrooms contribute to the prevention of poultry diseases and improvement in gut health. Poultry's gut microbiota plays a crucial role in their immune response and overall health. Sustaining a balanced gut microbiome is essential for adequate digestion, nutrient absorption, and a robust immune system [63]. The antimicrobial and prebiotic properties of compounds derived from mushrooms contribute to combating bacterial infections in poultry. This in turn diminishes reliance on antibiotics and fosters healthier growth [9].

Incorporating *P. ostreatus* mushrooms and their by-products as a feed supplement represents a promising strategy with numerous advantages [70]. These mushrooms and their by-products are rich in essential amino acids, vitamins, minerals, and bioactive compounds that contribute to various health effects. This makes them a valuable nutritional resource

for poultry [63]. They encompass β -glucans, shown to promote intestinal health, thereby strengthening the immune system and potentially enhancing poultry meat quality. Introducing mushroom derivatives into poultry diets has the potential to enhance overall health and productivity, offering a natural and sustainable alternative to frequently employed antimicrobial medications [53]. The utilization of by-products from food industries and agronomy is crucial for the implementation of sustainable farming practices. Agricultural biomass, which includes cellulose, hemicellulose, and lignin, can function as a nutrient-rich substrate for cultivating *P. ostreatus*. Subsequently, the produced spent mushroom substrate (SMS) also holds significant utility. The comprehensive incorporation of SMS in livestock production can play a role in environmental preservation and economic advancement [101]. Fermentation technology, particularly solid-state fermentation (SSF), is cost-effective and sustainable for agricultural, food, and animal production. Recent studies highlight SSF's impact on diverse substrates, enhancing bioactive compound production, influencing poultry health, and offering potential benefits in nutrition, immunity, and waste management [86].

9. Conclusions and Further Prospects

The incorporation of oyster mushrooms (SMS and fruiting body fraction) into poultry farming offers several benefits, impacting productivity, immune system function, antioxidant capacity, and overall health. *P. ostreatus* mushrooms present a promising feed supplement, given their nutritional composition, bioactive compounds, and positive effects on gut health, potentially reducing the demand for antibiotic usage. Future research should explore the full potential of mushrooms and their by-products in poultry farming, the extraction of several bioactive compounds like β -glucans, chitin, ergosterol, and polyphenols, and employing advanced technological methods to improve their functional properties for food, animal husbandry, and pharmaceutical applications. Integrating these supplements into poultry feed can optimize mushroom compost utilization and reduce antibiotic usage, which can enhance antimicrobial and prebiotic properties. Continuous monitoring, research adaptation, and empirical data utilization are essential for successful implementation, emphasizing the importance of solid-state fermentation in poultry farming.

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