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REVIEW

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The role of microorganisms and microbial enzymes in commercial fermented mushroom production: a comprehensive review of their action mechanisms, quality attributes and health benefits

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Abstract

Recently, fermented mushrooms are widely consumed worldwide owing to their nutritional, sensory, and health-promoting properties. The edible mushrooms are used as food and food flavoring due to their complex pleasant taste and aroma. Four well-known and most commonly included edible mushroom species are *Ganoderma lucidum*, *Morchella esculenta*, *Lentinula edodes* and *Hericium erinaceus*. Several studies have demonstrated that bioactive compounds from mushrooms exert remarkable biological activities, however, they have low oral bioavailability, restricting their therapeutic application. Fermentation is a method of preserving and transforming raw mushrooms into high-quality, value-added products by utilizing the technology of microorganisms and enzymes. This study provides a multifaceted review on mushroom fermentation from several perspectives including: 1) Different types of fermentation employed in commercial mushroom preparation including lactic acid and enzyme fermentation. 2) Production conditions, fermented mushroom in the market, and associated biochemical changes in fermented mushroom products. 3) Fermentation effect on bioavailability, sensory, and nutritional value of fermented mushrooms. 4) Safety concerns and health prospects of available fermented mushroom products and their health benefits were also introduced herein.

Keywords Fermentation, Fermented mushroom, Lactic acid fermentation, Sensory attributes, Health value

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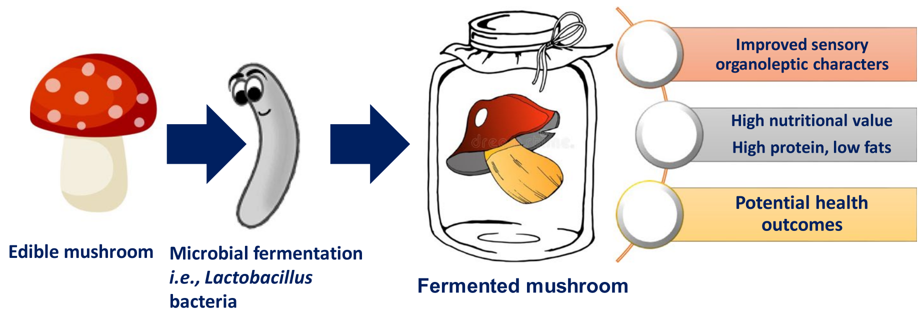
Graphical Abstract



Introduction

Fermented foods are widely consumed worldwide not only due to the low cost but also provide myriad health benefits well beyond the original food materials (Marco et al., 2017). Food fermentation is a well-adopted method suited for food preservation and processing. Bacterial lactic acid fermentation is the most common fermentation pathway that yields several food products, especially mushrooms, with high durability and flavor without chemical or thermal preservation (Marco et al., 2017). Furthermore, nutrient bioavailability can be improved due to preliminary digestion by bacterial enzymes during the fermentation process. Concurrently, the fermentation process counteracts the anti-nutritive or even toxic effects that can arise during mushroom processing. Several raw materials are exposed to lactic acid fermentation, which provides food products with high nutritional value. Lactic fermentation process is commonly used worldwide to preserve different food products, especially dairy products. The use of selected lactic acid bacterial strains guarantees a repeatable course of the process and leads to a product with high sensory quality (Jabłońska-Ryś, Skrzypczak, Sławińska, Radzki, & Gustaw, 2019a). Additionally, the fermentation process improves health outcomes such as anti-oxidative properties because of the presence of viable cells of lactic acid bacteria (Jabłońska-Ryś, Skrzypczak, Sławińska, Radzki, & Gustaw, 2019b) and presenting an added-value aside from preservation and improving sensory attributes. The lactic acid bacteria (LAB) group and *Bifidobacteriaceae* are the main probiotic source that contribute to the prevention of several diseases (Castellone et al., 2021). Owing to such myriad benefits, fermented food is now known as a high-quality dietary supplement besides daily consumed food. Hence, fermentation not only can preserve food, extend shelf life, and improve sensory attributes but enhance health outcomes. Such positive health benefits are largely attributed to active peptides produced by bacteria during fermentation using enzymes such as proteinase and peptidase, as well as certain non-nutrients (Şanlier, Gökcen, Sezgin, & nutrition, 2019). Such enzymes are widely produced naturally by certain living organisms namely animals, plants, and microbes including transferases, oxidoreductases, lyases, hydrolases, ligases, isomerases, and translocases (Jeske et al., 2019). Indeed, plant and animal sources are limited to fit industrial enzyme demands, microbial enzyme synthesis is more efficient, cost-effective, scalable, and genetically manipulable (Nunes & Kumar, 2018). As a result of their higher capacity to synthesize a large variety of extracellular enzymes required for the bioconversion of a wide range of substrates and complexes, *Lactobacillus spp.*, *Streptococcus spp.* and *Aspergillus spp.* are widely involved in fermentation process (Berbee et al., 2017).

Among the most important functional foods, edible mushrooms are widely consumed worldwide in many culinary recipes due to their nutritional value as meat protein substitutes. Recently, Submerged cultivation is effective in growing a wide variety of edible mushroom strains with higher yield of biomass and bioactive substances, including enzymes, lipids, carbohydrates, and proteins (Perveen et al., 2023). The most cultivated edible mushrooms in the world are *Lentinula edodes* (shiitake), *Flammulina velutipes* (enoki), *Agaricus bisporus* (button mushroom), *Pleurotus* species (oyster mushroom), and *Auricularia* species (wood ear mushroom). Such edible mushrooms produce a wide range of metabolites of great interest to human health and pharmaceutical industries (Bains et al., 2021; Yolande et al., 2023). Genus *Pleurotus* produces secondary metabolites such as lovastatin with hypocholesterolemic effects, which have been isolated from both the mycelia and fruiting bodies of oyster mushrooms and improved by the addition of methionine

(Yolande et al., 2023). To grow vegetative mycelium and reach the reproductive stage (fructification), it should be supplemented with nutrients as mushrooms are known as heterotrophic organisms (Das et al., 2021). Being with short shelf-life and prone to spoilage, fermentation processes are well adopted to preserve mushrooms from microbial spoilage, increase shelf-life, and enhance their nutritional, sensory, and culinary values (Nurerk, Junden, & Research, 2022). This review aims to present a multifaceted overview on the role of microorganisms and associated enzymes on sensory attributes and preservation of fermented mushrooms. The production conditions and the major biochemical changes in fermented mushroom products are also mentioned herein to introduce the best factors influencing fermented product quality. Moreover, health benefits and safety concerns are summarized highlighting needs for future perspectives of fermented mushroom research for better capitalization in the food supply chain.

Mushroom processing prior to fermentation

Prior to fermentation, edible mushrooms are subjected to processing through three important steps including washing, blanching, and cutting, Fig. 1. However, each step has its significance to affect mushroom sensory and chemical attributes.

Washing

Washing removes dirt and compost remains from mushroom cultivation. However, washing with water alone induces osmosis and ruptures the delicate cell membrane in the pilei of the mushroom which causes mushroom browning due to peroxidases enzyme release during the washing process. To overcome the browning effect, addition of salts and other chemicals such as hydrogen peroxide, sodium isoascorbate, disodium metabisulphite, and sodium EDTA are suggested with minimal loss of soluble polyphenols with increasing mushroom nutritional value and health benefits (Bernaś et al., 2006). However, mushroom shelf-life is still limited with just washing as the peroxidase enzyme is still active and affects mushroom's nutritional value. Moreover, mushrooms are susceptible to infection from fungus and bacteria warranting for a sterilization step termed blanching.

Blanching and cutting

Blanching is a process in which mushrooms are placed in boiling water then cooled or freeze for a certain period. Blanching is done to inactivate enzymes that can lead to losses of mushroom nutritional value such as gluconase and polyphenol oxidase enzymes that are responsible for browning and reduction of sugar, protein levels in mushrooms (Jabłońska-Ryś et al., 2019a, 2019b, 2019c, 2019d). Blanching in water or brine proved to reduce mushroom weight by 30–40% and contributes to significant loss of several nutrients owing to reduction of glucose and total protein content. An improvement to this method is made by microwaving or even baking in a hot oven to reduce the hardening texture that occurs during blanching. Mushroom hardening can be related to the air pockets inside the mushroom released during the blanching process and replaced by the tissue (Jabłońska-Ryś et al., 2019a, 2019b, 2019c, 2019d). Although this process is often associated with a reduction in nutritional value, it can be remedied by using other chemicals such as citric acid, ascorbic acid, and potassium or sodium metabisulfite (Lespinard et al., 2009). The concentration of lovastatin, a cholesterol-lowering drug produced in the fruiting bodies of *Pleurotus ostreatus* grown on corn cobs significantly reduced by the blanching process (Mobou,

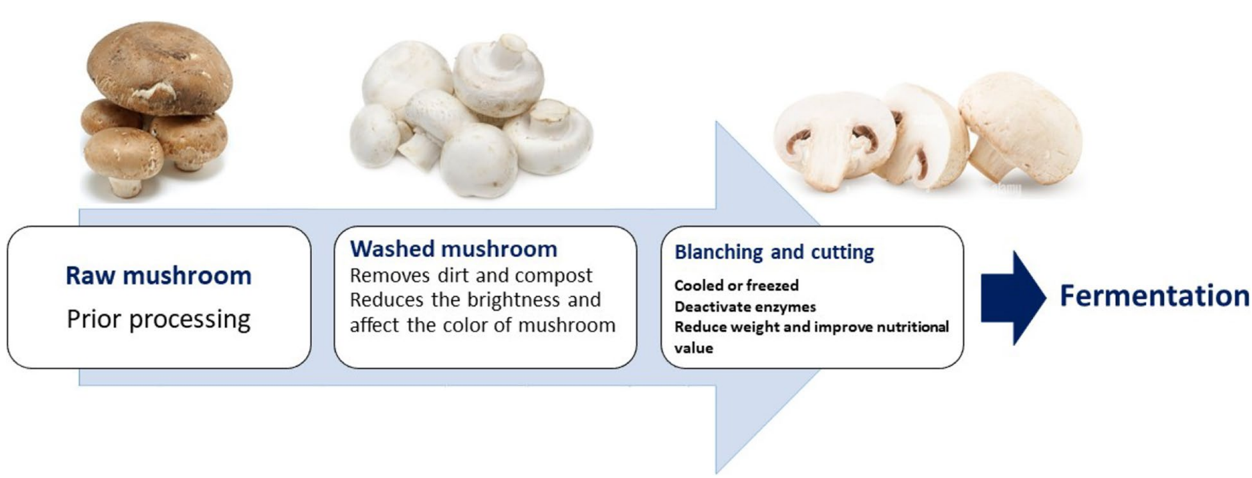


Fig. 1 Mushroom processing steps prior to lactic acid or enzymatic fermentation

Yadang, Begoude, Nkoue, & Kamdem, 2022). Further cutting processing including removal of unwanted stems and separation of mushroom caps which are pickled as a whole or fragmented into slices prior to fermentation (Jabłońska-Ryś et al., 2016). Trials of preprocessing are summarized with benefits and shortcomings in Table 1.

Fermentation as a method for improving functional properties

Fermented mushroom have several positive health outcomes, including antioxidant, anticancer, and anti-inflammatory, enhanced gastrointestinal health, and a decreased risk of metabolic disorders (Sivamaruthi et al., 2018), Fig. 2. Most fermented products have been shown to encompass at least 10^6 microbial cells per gram, with quantities changing based on the region, age, and time of analysis and consumption of the product (Rezac, Kok, Heermann, & Hutkins, 2018). Among microbial taxa, probiotic strains play a pivotal role in normalization of the gut microbiota, defense against pathogen colonization, generation of short-chain fatty acids, or metabolism of bile acid salts (Skowron et al., 2022). Such effects of probiotics is beneficial in the treatment of several ailments viz., obesity, lactose intolerance, diabetes, osteoporosis, and cardiovascular disorders, as well as intestinal diseases (Baky, Elshahed, Wessjohann, & Farag, 2022).

As oxidative damage is responsible for the incidence of several health concerns, production of antioxidant molecules through fermentation may lower the risk of developing such ailments. Fermentation by role can enhance the antioxidant capacity of fermented products as a result of the production of several beneficial phytochemicals, antioxidant polysaccharides, phenolic compounds, vitamins, protein derivatives, and antioxidant peptides by microbial hydrolysis (Zhao et al., 2021). Moreover, bioactive peptides have been shown to exert immunostimulant, anti-microbial, anti-hypertensive, and angiotensin-I-converting enzyme (ACE) inhibitory activities. These protein-derived peptides have anticancer qualities by halting various phases of cancer, and LAB appears to possess anticancer properties as well (Rai, Jeyaram, & beverages, 2015). By altering the intestinal environment, which lowers the population or metabolic activity of bacteria that can produce carcinogenic compounds, removing carcinogens, and synthesizing the product of metabolism like butyrate, which increases the ability to undergo apoptosis, among other methods (Saxami et al., 2017).

Disruption of the gut microbiota may harm the immune system and leads to inflammation (Shahbazi et al., 2020). Through a variety of mechanisms, including the inhibition of pathogen colonization, the induction of antimicrobial peptides production and mucus secretion, the increase of IgA production, the downregulation of the Th17 and pro-inflammatory cytokines like IL-17F and IL-23, and the up-regulation of Tregs, probiotic consumption in the form of fermented foods can improve gut barrier integrity, gut immunity, and maintain gut homeostasis (Shahbazi et al., 2020). Recent studies reported that polyphenolics in fermented mushroom can promote the growth and metabolism of the microbiota, as well as their ability to reduce inflammatory cytokine production and suppress inflammatory reactions (Shahbazi et al., 2021). Fermented mushroom can also be effective delivery systems for probiotic strains to safely enter the gut since some microbial strains in food are able to survive digestion (Heinen et al., 2020).

Potential industrial applications of fermented mushrooms

Mushroom fermentation can vary in the context of several parameters including bacterial type, temperature, and solution type. The first principle in mushroom fermentation lies in exploiting carbohydrates, the most abundant component in most mushroom including glycogen, chitin, and glucans, trehalose and xylans, as raw material to digest them using lactic acid fermentation (Jabłońska-Ryś et al., 2019a, 2019b, 2019c, 2019d). The enzyme produced by lactic acid is α-galactosidase which degrade carbohydrates into galactose and sucrose, and sucrose can further be broken down into glucose and fructose. Additionally, proteins are the second abundant nutrient in mushroom which upon fermentation are denatured owing to enzymatic break down of proteins, and nucleic acids producing biogenic amines, which can survive after blanching (Jabłońska-Ryś et al., 2019a, 2019b, 2019c, 2019d). Consequently, the second principle for fermenting mushrooms is to destabilize these enzymes via salting, or lactic acid producing bacteria and afterward the time of their storage can vary from 4 weeks up to 6 months (Jabłońska-Ryś et al., 2019a, 2019b, 2019c, 2019d). Examples of lactic acid and brine fermentations with their advantages and any limitations were listed in Table 1.

Not only does the fermentation process rely on bacterial count, and brine, but rather on other herbs and spices that can be added during the fermentation process. Of these ingredients that are commonly used are black pepper, basel leaves, chopped onions (Jabłońska-Ryś et al., 2016). Of these spice combinations each has its own taste and flavor that is added as well as beneficial to the fermented product (Jabłońska-Ryś et al., 2019a, 2019b, 2019c, 2019d). These spices can be unique according to consumers preferences suggestive for the need to test several spice combinations to determine best combinations that are favorable for consumption (Zheng et al., 2018).

Functional food with a combination of prebiotics and probiotics is required to maintain a healthy body and

Table 1 List of parameters and processing conditions of mushrooms prior to fermentation and outcomes

Process	*Pleurotos ostreatus*	*Agaricus bisporus*	*Termitomyces robustus*	*Benefits*	*Disadvantages*
Blanching	Boiling water 2–4 min 96–98 °C 4 min	Boiling for 5 min Boiling for 2 min and microwave	Boiling Water	Reduces weight loss of mushroom during fermentation	-Does not eliminate polyphenol peroxidase enzyme unless boiled for 15 min or microwaved -Microwaving reduce antioxidants in mushrooms
Fermentation process	2% salt, 1% sucrose	2–3% salt Brine with sucrose ranging from 0.1–2% 2% salt and 1%sucroes	Soaked in 10% salt solution	Soaking mushrooms retains dry weight prior to blanching by 10% (Choi & Sapers, 1994)	-Brine makes mushroom tough and reduce its flavor quality
Temperature and time	18–22 °C, 7–18 days 9 log cfu/g (Jabłońska-Ryś et al., 2019a, 2019b, 2019c, 2019d; Liu et al., 2016b)	17–21 °C, 7–8 days 9 log cfu/ g (Skapska et al., 2008)	30 °C, days (Bello & Akinyele, 2007)	Destabilizes protease ribonuclease and reduce the production of biogenic amines	Higher temp deactivates glucanase and polyphenol oxidase enzymes

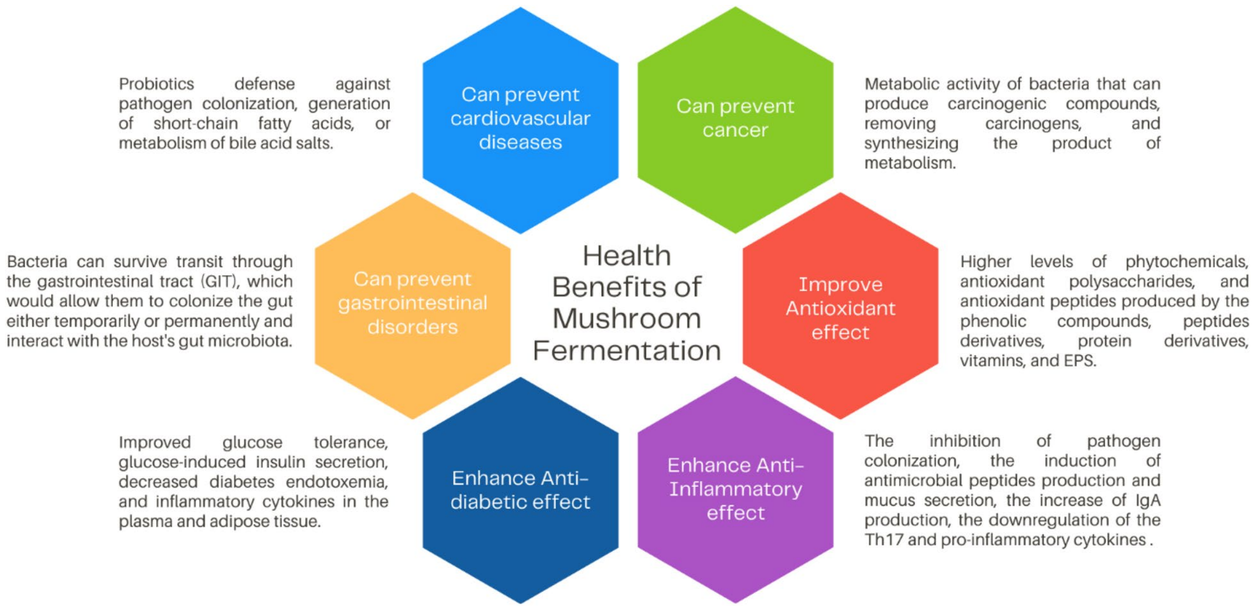


Fig. 2 Health benefits of fermented mushroom products and improved food quality

gut bacterial homeostasis (Tupamahu & Budiarso, 2017). White oyster mushroom powder was employed as a prebiotic agent in yoghurt fermentation products to provide a combination of prebiotics and probiotics. The white oyster mushroom or *Pleurotus ostreatus* is further used as an additive in yoghurt fermentation alongside LABs such as *Lactobacillus bulgaricus* and *Streptococcus thermophilus*. The fermented yoghurt with oyster mushroom powder resulted in a more sour flavor with the addition of LAB as expectedly (Tupamahu & Budiarso, 2017).

Research by Giang et al. (2022) demonstrated the growth and production of amylase and protease enzymes by *Aspergillus oryzae* that hydrolyze complex components from oyster mushrooms koji or *Pleurotus spp.* (Giang, Van Khai, Thuy, & Biotechnology, 2022). *A. oryzae* (Koji) was used as a starter during the initial stage in the fermentation of soy sauce production process (Kim et al. 2017). Moreover, amylase and protease were used to convert starch and proteins into sugars and amino acids producing a sweet sauce. To obtain the maximum enzyme activity for oyster mushrooms koji, Giang et al. suggested that best conditions were at 0.03% mould, pH 6.0, and incubation at 30 °C for 30 h (Giang et al., 2022).

The food waste and spent mushroom substance (SMS) co-fermentation to produce lactic acid was studied by Wei et al. (2020) replacing commercial cellulase with *A. niger* cellulase. SMS is a common lignocellulose left over waste after mushroom harvest (Wei et al., 2020). According to Hřebečková et al. (2020), SMS is rich in polysaccharide, minerals, protein, and active compounds besides cellulose and hemicellulose which is suitable to be used as a substrate for biological fermentation (Hřebečková, Wiesnerová, & Hanč, 2020). However, when SMS is utilized as a biological feedstock, cellulase must be added to the fermentation process to catalyze cellulose and hemicellulose of SMS into fermentable sugars (Ma et al., 2021). At 24 h post addition of *A. niger* cellulase to the co-fermentation system, the highest lactic acid concentration and yield was at 48.72 g/L and 0.91 g LA/g TS, respectively, which were 22.9 and 21.3% higher than the control group with commercial cellulase (Ma et al., 2021). The essential microbial enzymes and its sources yielded from mushroom fermentation, and it is role in industrial production is summarized in Table 2 & Fig. 3.

Fermentation as a tool for improving metabolism and digestion of mushrooms

The mushroom fermentation process can occur in the form of fruiting bodies and/or mycelium through two methods; solid state fermentation (SSF) or submerged fermentation (SMF) (Lübeck & Lübeck, 2022). SSF process involves the growth of microorganisms, metabolism, and end products recovery on moist, solid substrates without free-flowing water. Meanwhile, SMF process includes the cultivation of microorganisms, metabolic process, and recovery of end products carried in liquid substrates that consist of nutrients under controlled conditions. This process contributes to higher yields concurrent with improved productivity (Bakratsas et al., 2023). Consequently, SMF is commonly applied in several industries as this process has better control measures under both sterile and non-sterile conditions. A

Table 2 Essential mushroom microbial enzymes involved in the production of other fermentation products

Mushroom Type/ Species	Enzymes	Microbial Source	Enzymatic Action/ Process	Reference
Schizophyllum commune	Lactate dehydrogenase	*Lactobacillus Streptococcus*	Fermentation to produce a cheese-like food that contains 0.58% P-D-glucan, to exert chemopreventive effects against cancer	(Okamura-Matsui et al., 2001)
Pleurotus ostreatus	α-Galactosidase	*Lactobacillus acidophilus*	Enzyme degrade carbohydrates into galactose and sucrose, and sucrose can further be broken down into glucose and fructose	(Tupamahu & Budiarso, 2017)
Pleurotus spp.	Amylase protease	*Aspergillus oryzae*	Enzyme break down starch and proteins into sugars and amino acids to produce sweet sauce	(Giang et al., 2022)
Spent mushroom substance	Cellulase	*Aspergillus niger*	Enzyme cellulase added to the fermentation process to catalyze the cellulose and hemicellulose of SMS into fermentable sugars	(Ma et al., 2021)

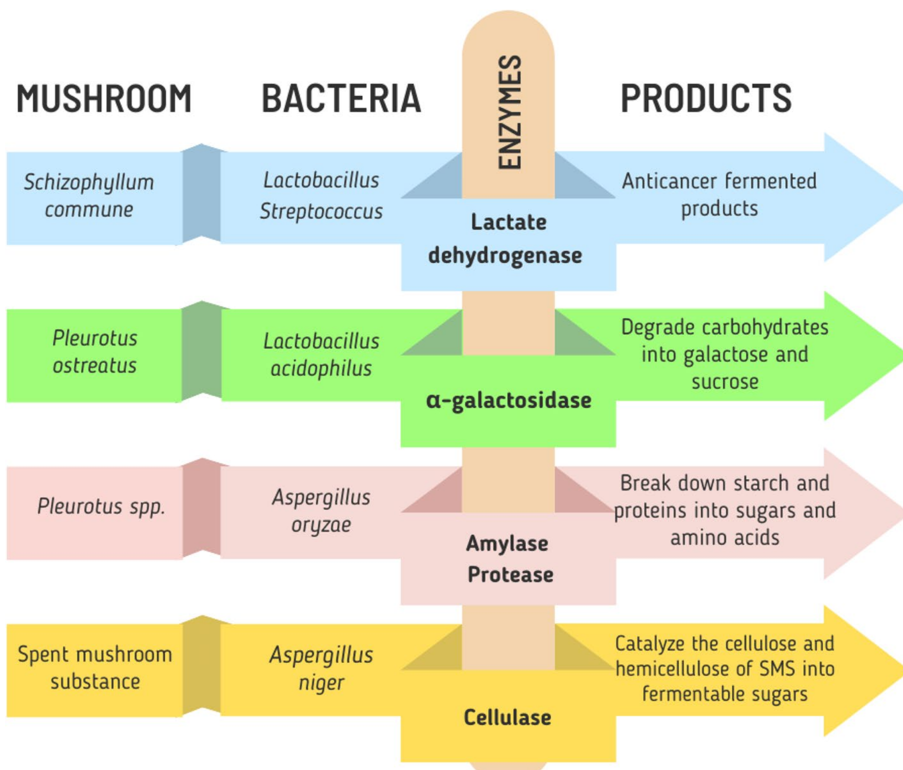


Fig. 3 Industrial application of mushroom microbial enzymes used in mushroom production and action mechanisms

comparison between SMF and SSF revealed that the production results of certain fungal strains perform better in SMF, while some fungal strains perform better in SSF (Lübeck & Lübeck, 2022). Therefore, the choice of fermentation process should be considered during the production of fermented mushrooms, including the selection of the methods that should be appropriate based on the targeted fungal strain.

Various parameters such as pH value, oxygen level, temperature, mass transfer, and distribution of nutrients can be modified and controlled continuously during the fermentation process. Dynamic alterations in pH and levels of free sugars, organic acids, and lactic acid bacteria in mushrooms during fermentation may influence the quality, stability, and safety of the fermented mushroom products (Jabłońska-Ryś et al., 2022). The pH value usually decreases during the fermentation process because of the generation of organic acids, mainly lactic acid released by LAB into the medium during lactic fermentation process. For example, pH value in fully fermented mushrooms was lower (3.55 ± 0.03) in *L. plantarum* EK3-fermented variant compared to mushrooms fermented using *L. plantarum* 299v (3.68 ± 0.03) (Jabłońska-Ryś et al., 2022). In other fermented mushroom species, pH value has been reported within the range of 3.3 to 4.6, depending on other factors such as fermentation temperature, the number of available carbohydrates, or additives utilized during fermentation process (Jabłońska-Ryś, Skrzypczak, Sławińska, Radzki, Gustaw, et al., 2019a). The lower pH value ensures stability of fermented mushrooms with simultaneous maintenance of anaerobic conditions (Jabłońska-Ryś et al., 2022).

On account of their richness in proteins, mushrooms became an alternative protein source instead of the animal-derived protein (Sexton et al., 2019). However, several parameters should be considered during the production of fermented mushrooms such as the ability of the human gastrointestinal tract to hydrolyze proteins and the rate of free amino acids absorption into the bloodstream. Mushroom fermentation typically increases protein digestibility which is dependent on the protein material solubility, presence of anti-nutrients including phytic acid and protease inhibitors (Afify, El-Sawah, Ali, El-Rahman, & Biotechnology, 2012). During digestion, phytic acid acts as a powerful chelating agent that interferes with the absorption of important minerals such as iron, calcium, zinc, and magnesium in the gastrointestinal tract (A. J. Clark, B. K. Soni, B. Sharkey, T. Acree, E. Lavin, H. M. Bailey, H. H. Stein, A. Han, M. Elie, & M. J. L. Nadal, 2022). Meanwhile, phytases, enzymes responsible for hydrolyzing phytic acid into inositol and phosphate are distributed widely among fungi including shiitake mushroom (Jatuwong et al., 2020). Shiitake mushroom secreted proteases might break down protein substrate first before reaching the digestive system and improve protein digestibility. The increased solubility of the fermented protein, especially at a low pH value may be attributed to the increased digestibility in fermented mushroom compared to raw type. Furthermore, phytate level decreases during fungal fermentation process concurrent with increased protein digestibility. The degradation of anti-nutrient papain inhibitor protein during sterilization process could partially contribute to the reduced enzyme inhibition in fermented protein blend (A. J. Clark, B. K. Soni, B. Sharkey, T. Acree, E. Lavin, H. M. Bailey, H. H. Stein, A. Han, M. Elie, & M. Nadal, 2022).

Effect of mushroom fermentation on sensory attributes, organoleptic characteristics, and nutritional value

Sensory and organoleptic attributes are important parameters which affect consumer demand for plant-derived proteins. One of the main obstacles in producing mushrooms lies in how to enhance their organoleptic characteristics. The fermentation process contributes to a reduction in off-note compounds in fermented blends eventually enhancing its organoleptic features (A. J. Clark, B. K. Soni, B. Sharkey, T. Acree, E. Lavin, H. M. Bailey, H. H. Stein, A. Han, M. Elie, & M. Nadal, 2022). For example, a fermented mushroom known as *Nham Hed* is one of the famous appetizers in Thailand. *Nham Hed* is produced by a mixture of minced mushroom, glutinous rice, sugar, garlic, and salt, and then, wrapped in a bundle to allow the fermentation process until the taste becomes sour (Tangsombatvichit et al., 2021). LAB plays a role in enhancing the sensory characters of fermented mushrooms by producing organic acids from carbohydrates (Jabłońska-Ryś et al., 2022). *Staphylococcus aureus* further attributes to flavor formation and is known as the source of lipolytic and proteolytic enzymes (Nurerk et al., 2022). The addition of pigmented rice to fermented mushrooms is an alternative approach to improve taste and palatability of fermented mushroom and adding to its nutritional value (Nakaew & Sungthong 2018). Lactic acid fermentation of *Agaricus bisporus* (white and brown) revealed characteristic changes including lower pH, lightness, redness, and yellowness than non-fermented ones, higher acceptability, and higher emotions induced for consumers (Bartkiene et al., 2023).

A sensory evaluation test between fermented mushroom mixed with three different types of glutinous rice such as black glutinous rice, Riceberry, and Rai Dok Kha rice demonstrated that black glutinous fermented mushroom was the most favored with regards to all sensory characteristics with the score ranging from 7.47 to 8.30 towing for its likable smell and texture (Nurerk et al., 2022). Meanwhile, the score for fermented mushroom mixed with Riceberry rice and Rai Dok Kha rice were much lower, within the range of 6.30 to 7.0, and 6.17 to 6.7, respectively. The abundance of amylopectin in black glutinous rice contributed for the slower decomposition rate of the fermentation process, producing a better smell and texture, thus, becoming the most favorite ingredient when mixed with fermented mushroom (Nurerk et al., 2022). The duration of storage may also affect the physical and chemical properties of fermented mushroom such as color change, decreased pH value, and reduced anthocyanin content (Nurerk et al., 2022).

Owing to pretreatment stages i.e., washing and blanching, fermentation significantly reduces the brightness and affects the color of mushroom fruiting bodies. Mushroom lactic fermentation stabilizes brightness, significantly reduce redness parameter, and increases the yellowness parameter (Jabłońska-Ryś et al., 2016). Moreover, blanched mushrooms are subjected to 9–26% loss of their brightness during fermentation. Such changes in mushroom brightness can be perceived by the consumers as loss of quality and hence affect consumer demand (Erbay et al., 2011). Moreover, adding certain spices to fermented mushrooms can affect the color, taste and odor of mushroom product (Jabłońska-Ryś et al., 2016). Additionally, adding aqueous onion extract enhance lightening of the color by deactivating enzymatic browning of *Agaricus bisporus* fruiting bodies and add to its nutritional value (Bernaś & Jaworska, 2015). Color analysis of fermented oyster mushrooms within 18 days fermentation revealed a systematic decrease in brightness by shifting to the dark color by the reason of enzymatic and nonenzymatic browning (Liu et al., 2016a). Moreover, the sensory characteristics of fermented mushroom such as appearance, taste, texture, and general acceptance were evaluated and *Pleurotus* spp., *P. cornucopiae* obtained the highest sensory characteristics (Jabłońska-Ryś, Skrzypczak, et al., 2019a). In comparison to the first fermentation day, the crude protein (CP) concentration and total calories on the last fermentation days were significantly higher ($P<0.05$) (Chu et al., 2012). Compared to the fermentation of mushroom by LAB, attempts using yeast (*Sacchromyces cerevisiae*) showed likewise improvement in palatability. Shinekhuu et al. (2009) suggestive that yeast fermentation can improve the palatability of mushroom by-products for pigs (Shinekhuu et al., 2009). Furthermore, when compared to the first day in fermentation, CP concentration and total calorie value were higher towards the end of the experiment and in agreement with (Chu et al., 2012).

Available fermented mushroom products and their health benefits

Shiitake mushroom

Shiitake mushroom is known for its high fiber content, vitamin B complex, and minerals. Pure shiitake exhibit antibacterial, antifungal, anticancer effects along with improving immunity (Gaitán-Hernández, López-Peña, Esqueda, & Gutiérrez, 2019). Fermentation of Shiitake mycelium further improves its functionality, digestibility, and nutritional value; protein solubility is increased by fermentation along with decrease of anti-nutrient molecules such phytates and protease inhibitors (A. Clark et al., 2022). Fermented Yamabushitake (*Hericium erinaceus*) is one of the most popular mushrooms that is widely consumed for both nutritional value and medicinal purposes (Chutimanukul et al., 2023). *Lactobacillus plantarum* was used for fermentation of shiitake mushrooms (*Lentinus edodes*) providing the strongest umami flavor (Chen et al., 2021).

Chaga mushroom

The effect of fermented Chaga fungus on lipid profile and liver marker enzymes was studied in diabetic rats, (Fig. 4) via comparing effects of fermented Chaga diet to that of nondiabetic age-matched control group. Serum triglycerides were found higher in the control group, lots of fat depositions were found in the livers of the control group, while no change was detected following the fermented Chaga diet. Fermented Chaga mushroom appears to exert effective role in non-insulin-dependent diabetes mellitus caused by obesity (Cha et al., 2006).

Reishi mushroom

The immunomodulatory and antitumor effects have been associated with Reishi fermented mushroom (Rubel et al., 2018) (Fig. 4). Mice immunity following administration of Reishi diet showed changes as manifested by increase in $CD3^+$, $CD4^+$, and $CD8^+$ cells, whereas $CD19^+$ and $CD16^+$/ $CD32^+$ showed decrease, alongside TNF-α and IFN-γ levels with marked decrease in lower tumor weight compared with control group (Rubel et al., 2018).

A. brasiliensis mushroom

Fermented mushrooms of *A. brasiliensis* (FMAE) and wild-growing *A. brasiliensis* (WMAE) exerted a potential hepatoprotective effect. Reduction in CCl_4-induced toxicity was observed following fermented mushroom diet administration. ALT and AST activities have been suppressed concurrent with an increase in antioxidant enzyme activities (Zhang, Han, Zhao, & Yu, 2012).

Trametes versicolor (Tv, Turkey tail)

The immune-modulating features of mycelium differ from that of the fermented substrate. Immunomodulation effect of the initial substrate (IS), fermented substrate (FS), and *Trametes versicolor* mycelium (TvM) were tested on human peripheral blood mononuclear cell cultures. Results revealed that CD69 was strongly induced by both solid and aqueous fractions of TvM, minor activation was observed in case of FS, while IS had no effect. The fermented substrate-induced increase in the immune-activating proinflammatory cytokines. The mycelium itself along with fermented substrate accounted mostly for the immune-activating bioactivity of a mycelial-based medicinal mushroom preparation (Benson et al., 2019).

Fermented Cordyceps sinensis (CS) enriched in selenium

The effect of CS on uterine cervical cancer in mice was investigated using methylcholanthrene (MCA)-induced tumor model. Application of fermented *Cordyceps*

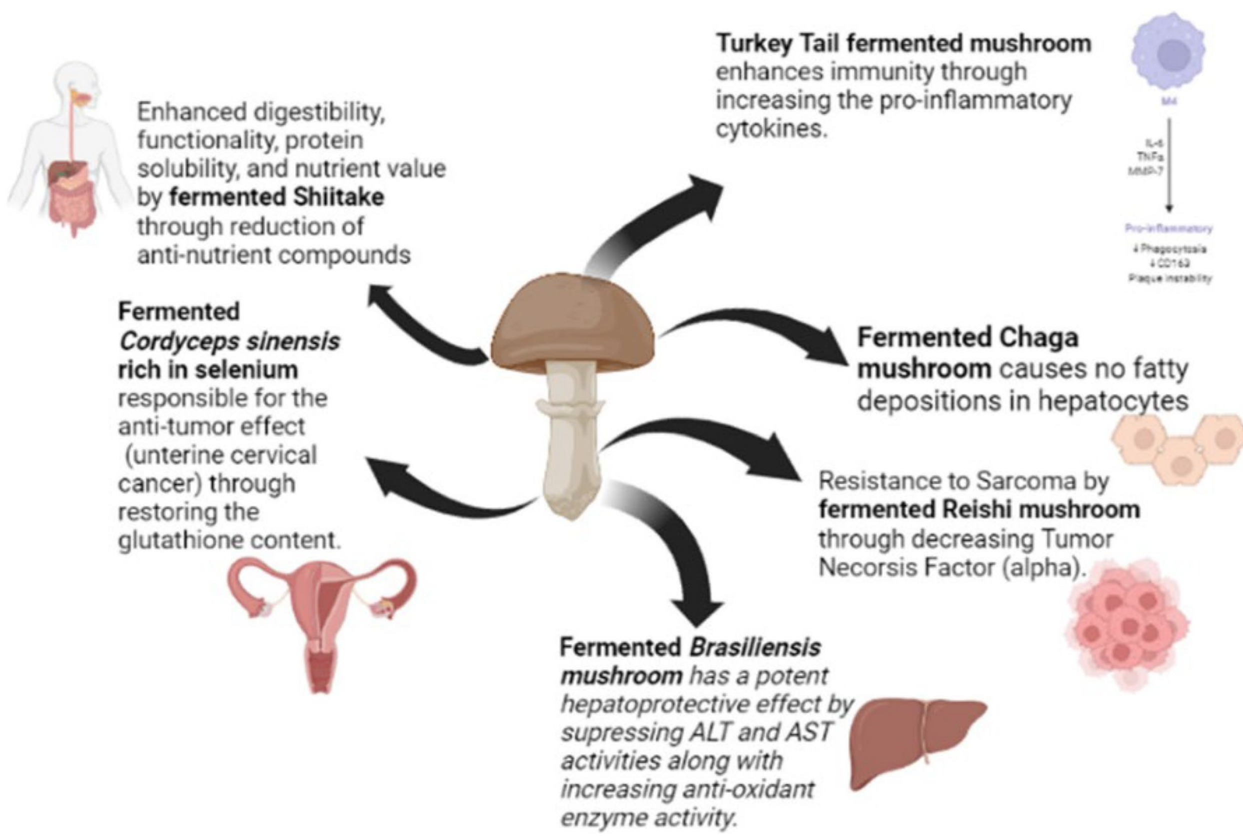


Fig. 4 Different types of mushrooms with their health benefits in terms of anti-inflammatory, anti-cancer, and hepatoprotective functions

sinensis (CS) enriched in selenium (Se-CS) resulted in remarkable restoration of glutathione content, lipid peroxidation, glutathione reductase activity, catalase activity, $Na+/K+$-ATPase activity, and glutathione S transferase activity, as well as immunity enhancement. Uterine cervical cancer has been treated by fermented Se-CS (Ji, Liu, Liu, & Wang, 2014).

Fermented Coprinus comatus
The hypoglycemic action of fermented *Coprinus comatus* rich in vanadium (CCRV) mushrooms was investigated, Fig. 5. Vanadium was absorbed by the fermented mushroom *Coprinus comatus*, which can absorb trace elements, at lower dosages (0.18 mg/kg/d). The blood glucose and HbA1c of alloxan-induced hyperglycemic mice showed a decrease, and the sugar tolerance of normal mice was improved after mice were administered CCRV. In hyperglycemic rats, lesser doses of vanadium coupled with fermented *C. comatus* caused significant reductions in blood glucose and HbA1c levels (Han, Yuan, Wang, Li, & Biology, 2006). More importantly, fermented *C. comatus* has the ability to acquire trace metals such as chromium (Han et al., 2006). Moreover, fermented *Coprinus comatus* showed anti-inflammatory, antioxidant, peripheral antinociceptive and antihyperalgesic activity in various models of inflammatory pain (Ren et al., 2012).

Lentinus squarrosulus (Mont.) mycelium
L. squarrosulus mycelium exhibits a potential antioxidant effect through various mechanisms posing it as a promising product for improving feed nutrition. Fermentation is generally regarded as an effective method to enhance antioxidative features in final food products (Abdullah et al., 2016). Furthermore, utilizing *L. plantarum* 299v probiotic strain improved the antioxidant activity of fermented mushrooms to a level comparable of that in fresh mushrooms (Jabłońska-Ryś, Skrzypczak, et al., 2019b).

Conclusions and future directions
Recently, fermented food has emerged as a novel era in preserving and enhancing sensory attributes of food products. Edible mushrooms are preserved by fermentation due to their short shelf life in addition to the presence of endogenous enzymes that help break down

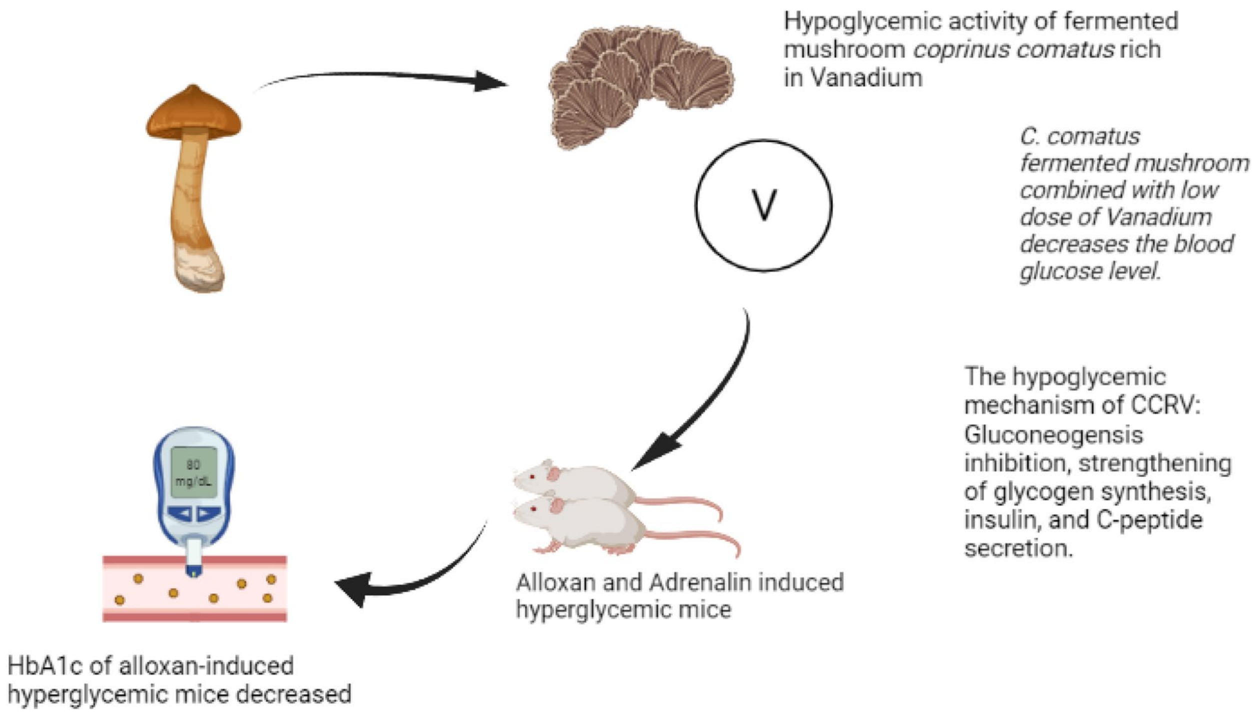


Fig. 5 The antidiabetic activity of fermented mushroom *Coprinus comatus* and action mechanisms

carbohydrates and proteins. Preprocessing mushrooms prior to fermentation is important to prevent these enzymatic reactions, especially polyphenol peroxidase. To our knowledge, there has not been any industrial scale of fermenting mushrooms, warranting the need to focus on optimization for preprocessing and fermentation at low cost to meet industrial needs. However, several recent studies discussed ways to improve such preservation techniques from certain technological aspects, and studies on the nutritional and health value of fermented fungi are still limited.

Several future studies analyzing the impact of fermentation on mushrooms bioactive compounds are recommended. Moreover, ensuring the microbiological safety of the fermented product and investigation of biogenic amines levels should be studied. Indigenous starter cultures acquisition which targeted to mushroom fermentation to ensure fermentation control and produce a standardized product is recommended. Further studies on screening the health-promoting effects and nutritional value of fermented mushroom as a replacement of animal protein in the context of safety measures are advised in the future alongside the identification of the exact active agents underlying these effects post fermentations for the potential to be formulated in drug regimens.

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M. F.: Conceptualization, Supervision, Writing-review and editing; N. K.: Writing original draft H. S. H.: Writing original draft; M. S.: Writing original draft; J.Z.: Writing-review and editing; A. M.: Writing original draft M. H. B.: Writing original draft, Writing-review and editing. The author(s) read and approved the final manuscript.

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All data related to this review are included in this published article.

Declarations

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Competing interests
The authors declare that they have no competing interests.

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