Current Research in Food Science 9 (2024) 100907

Contents lists available at ScienceDirect

Current Research in Food Science

journal homepage: www.sciencedirect.com/journal/current-research-in-food-science

Efficient conversion of tea residue nutrients: Screening and proliferation of edible fungi

Yufei Zhang [a], Yanyin Lu [a], Dandan Pan [a], Yanyan Zhang [b], Chen Zhang [a,*], Zexin Lin [a,b,**]

[a] Ecofood Institute, College of Biological Science and Engineering, Fuzhou University, 350108, Fuzhou, China
[b] Institute of Food Science and Biotechnology, Department of Flavor Chemistry, University of Hohenheim, Fruwirthstraße 12, Stuttgart, 70599, Germany

ARTICLE INFO

Handling Editor: Professor A.G. Marangoni

Keywords:
Edible fungal mycelia
Tea residue
Fermentation
Component transformation

ABSTRACT

Despite lignocellulose hindering the extraction of intracellular components, tea residue can serve as an excellent substrate for fungal fermentation owing to their lignocellulose-degrading abilities. Thus, the fermentation efficiencies of *Lentinus edodes*, *Lentinus sajor-caju (Fr.)*, *Flammulina filiformis*, *Hericium erinaceus*, *Pleurotus pulmonarius*, and *Monascus kaoliang B6* were evaluated using tea residue as a medium. *P. pulmonarius* and *L. sajor-caju (Fr.)* exhibited the fastest growth rates, with colony radii of 33.1 and 28.5 mm, respectively. *M. kaoliang B6* demonstrated substantial degradation abilities for cellulose, hemicellulose, and lignin, with decolorization radii of 12.2, 0.9, and 8.5 mm, respectively. After a 9-days liquid fermentation, *M. kaoliang B6* achieved the highest conversion efficiency at 27.8%, attributed to its high cellulase (191 U•mL^{-1}) and lignin peroxidase (36.9 U•L^{-1}) activities. *P. pulmonarius* and *L. sajor-caju* (Fr.) showed lower conversion rates of 8.6% and 3.8%, despite having high hemicellulase activities (67.1 and 70.9 U•mL^{-1}). Fermentation by *M. kaoliang B6* resulted in a reduction of protein and total sugar content in the tea residue by 174 and 192 mg g^{-1}, by which the mycelium's protein and total sugar content increased by 73 and 188 mg g^{-1}. Co-fermentation of these three strains had little effect on the improvement of conversion efficiency, which might owe to the antagonistic interactions among the strains. Generally, utilizing tea residue for edible fungi fermentation is a sustainable process for bio-waste treatment, enabling efficient nutrient conversion under mild conditions without adding chemicals.

1. Introduction

In recent years, the rapid development of instant tea industry has resulted in significant economic benefits and a substantial increase in the generation of tea residue (Hussain et al., 2018). Tea residue is commonly disposed of through incineration, composting, and used as animal feed. However, these methods often lead to environmental pollution and inefficient resource utilization (Xu et al., 2021). Although containing various nutrients, such as proteins and polysaccharides, the complex network structure composed of cellulose, hemicellulose, and lignin in the cell walls of tea residue hinders the release of these valuable components (Debnath et al., 2021; Lin et al., 2023).

Proteins are commonly extracted using alkaline and enzymatic methods (Lin et al., 2022; Zhang et al., 2016), while polysaccharides are mainly extracted using high temperatures and physical assistance methods, such as ultrasound-assisted extraction (UAE) and microwave-assisted extraction (MAE). Alkaline extraction involves exposing plant materials to a strong alkaline environment, which disrupts pectin components in cell walls and increases protein solubility. However, both alkaline and high-temperature methods may lead to protein degradation or Maillard reaction (Liu et al., 2011; Ye et al., 2024), resulting in the formation of brown substances. Enzymatic methods use enzymes to improve the release of nutrients by the degradation of plant cell wall or protein. However, these methods can be expensive and exhibit low efficiency with leafy biomass (Huang et al., 2021; Lin et al., 2022). In fact, edible fungal can ferment tea residue under mild conditions with low costs and convenient operation, offering a potentially efficient method for its utilization (Cano y Postigo et al., 2021; Xu et al., 2024). Some fungal can produce lignocellulose-degrading enzymes, facilitating tea residue utilization (Cano y Postigo et al., 2021; Wang and Zhao, 2023), while fungal mycelium with high protein content can serve as ingredients in meat

* Corresponding author.
** Corresponding author. Institute of Food Science and Biotechnology, Department of Flavor Chemistry, University of Hohenheim, Fruwirthstraße 12, Stuttgart, 70599, Germany
E-mail addresses: zhangchenfj@sina.com (C. Zhang), zexin.lin@uni-hohenheim.de (Z. Lin).

https://doi.org/10.1016/j.crfs.2024.100907
Received 29 May 2024; Received in revised form 22 October 2024; Accepted 27 October 2024
Available online 29 October 2024

analogues (Zhang et al., 2024). Selecting suitable fungal strains adaptable is crucial for effective fermentation added-value of tea residue.

Edible fungi belonging to genera, such as *Lentinus* (Lechner and Papinutti, 2006), *Flammulina* (Wang et al., 2022), *Hericium* (Xu et al., 2024), *Pleurotus* (Araújo et al., 2021) and *Monascus* (Xu et al., 2024), possess enzymatic systems capable of secreting various enzymes, including cellulases, hemicellulases, and lignin-degrading enzymes. These enzymes have been proven effective in decomposing lignocellulose, making them promising candidates for degrading tea residue cell walls (Arora and Sharma, 2010; Leite et al., 2021; Saini and Sharma, 2021). *Lentinus edodes* and *Flammulina filiformis* can effectively increase the soluble dietary fiber content in the liquid fermentation of rice bran (Arora and Sharma, 2010; Moonmoon et al., 2011). Additionally, *F. filiformis* has demonstrated the capacity to degrade hemicellulose in Eucommia bark by over 50% and cellulose by 83%, which is twice that of *Pleurotus ostreatus* (Bonatti et al., 2004; Dedousi et al., 2024; Lu et al., 2023b; Reddy et al., 2003). *Pleurotus pulmonarius* and *L. sajor-caju (Fr.)* produce cellulases and hemicellulases during their growth, which are influenced by their cultivation time as well as the carbon and nitrogen sources in the medium (Arora and Sharma, 2010; Chai et al., 2021; Gupta et al., 2013; Kayode et al., 2015; Kurt and Buyukalaca, 2010). Both *Hericium erinaceus* and *M. kaoliang B6* have strong lignocellulose-degrading capabilities (Duan et al., 2024; Huang et al., 2020; Wang et al., 2023b). However, although the cell wall degrading effects of these edible fungi have been tested, their efficacy may vary when applied to tea residue.

Thus, this study aimed to identify edible fungi with high degradation efficiency, which were *L. edodes*, *F. filiformis*, *H. erinaceus*, *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6*. Their growth in tea residue medium and discoloration effects on cellulose, hemicellulose, and lignin media in agar plates were assessed. Discrepancies in growth and enzyme production between tea residue and malt extract media were examined, and the biological conversion rate was determined by analyzing the amount of ergosterol using high-performance liquid chromatography (HPLC). Structural changes in the tea residue were examined using optical and scanning electron microscopes. Variations in medium composition pre- and post-fermentation were compared to evaluate growth status and nutrient transformation capacity, aiding in the selection of suitable edible fungi for tea residue fermentation and laying a scientific foundation for the valuable utilization of other leafy biomass.

2. Materials and methods

2.1. Experimental materials

Lentinus edodes, *Flammulina filiformis*, *Hericium erinaceus*, *Pleurotus pulmonarius*, *Lentinus sajor-caju (Fr.)*, and *Monascus kaoliang B6* were purchased from the China General Microbiological Culture Collection Center (CGMCC) and deposited at the Fuzhou University Institute of Food Science and Technology.

Green tea residue was provided by Fujian Damin Food Co., Ltd. (Zhangzhou, China). Green tea residue was obtained by soaking tea leaves in hot water at 85 °C for 45 min, followed by filtration to collect the precipitate, which was then dried at 60 °C for 24 h.

Sodium carboxymethyl cellulose, 1-octen-3-ol, vanillin, and acetophenone were purchased from Shanghai Yuan Ye Biotechnology Co., Ltd. Azure-B was purchased from Sigma (St. Louis, MO, USA), and alkaline lignin was purchased from Shanghai Maclin Biochemical Technology Co., Ltd. 3-Octanone was purchased from Shanghai Aladdin Biochemical Technology Co., Ltd., while xylan was purchased from Xi'an Fohes Biotechnology Co., Ltd. 2-Octanol was purchased from Dr. Ehrensortfer (Augsburg, Germany). All other analytical grade reagents were purchased from Shanghai National Pharmaceutical Group Chemical Reagent Co., Ltd. (Shanghai, China).

2.2. Analysis of strain growth rate and growth status

After the activation of strain, an 8 mm diameter block of mycelium was inoculated onto tea residue medium (with the mycelium side facing down, placed in the center of the medium) and cultured (Monascus kaoliang at 32 °C, and other strains at 24 °C) in a constant temperature incubator (ZWY-2102C; Shanghai Hongji Instrument Equipment Co., Ltd., Shanghai, China). The colony radii were measured every 2 days with a ruler, and photographs were taken and recorded to document the density, length, morphology, and colony color of the mycelium.

2.3. Color change ring experiment

The cellulose-degrading capability of strains was evaluated using the Oxford cup method (Sherwood and De Beer, 1947). A control with 200 μL of physiological saline was applied. From days 0–4, 200 μL of spore suspension was added daily to each well, with strains incubated at 24 °C (for edible fungi) or 32 °C (for Monascus kaoliang). On day 4, the media were stained with 2 mg mL^{-1} Congo red for 15 min, followed by the removal of the dye. Afterward, 1 mol L^{-1} NaCl solution was added to the media for 15 min before being decanted. The resulting change in color of the media was observed, photographed, and measured using ImageJ software (Bethesda, MD, USA) for both colonies and color change rings.

2.4. Enzyme production capacity testing in edible fungi

Spore suspensions were prepared by rinsing the mycelium-covered culture medium with sterile physiological saline (9 g L^{-1}) and filtering through six layers of sterile gauze to obtain a spore suspension. The spore concentration was adjusted to 10^6 spores• mL^{-1} using a hemocytometer.

Cellulase and hemicellulase activities in the fermentation broth were determined following the method of Barr (Barr et al., 2012), while lignin peroxidase activity was assessed according to the procedure reported by Pradeep Kumar (Pradeep Kumar et al., 2023). Glucose and xylose were used as standard substrates for cellulase and hemicellulase assays, respectively. Distilled water was used in place of H_2O_2 solution as a blank control for lignin peroxidase activity.

The cellulase activity (U• mL^{-1}) was calculated using the following formula:

$$\text{Cellulase activity}\left(\text{U}\cdot\text{mL}^{-1}\right) = \text{A} \,/\, \text{t},$$

where A is the content of glucose produced in the reaction (μg), and t is the reaction time (min).

Lignin peroxidase activity $\left(\text{U} \bullet \text{L}^{-1}\right)$ was calculated using the following formula:

$$\text{Lignin peroxidase activity}\left(\text{U}\cdot\text{L}^{-1}\right) = \frac{(\text{A}_1 - \text{A}_0)}{\varepsilon \times \text{t}} \times \frac{\text{V}_1}{\text{V}_2} \times \text{n},$$

where A_1 is the absorbance of the sample, A_0 is the absorbance of the sample blank, and ε is the molar absorption coefficient: $\varepsilon_{310} = 9300$ (mol•L^{-1} min^{-1}). t is the reaction time (min), V_1 is the total volume of the reaction solution (mL), V_2 is the total volume of the fermentation broth (mL), and n is the dilution factor.

2.5. Sample preparation of edible fungi in tea residue liquid medium

Using an 8 mm diameter punched to extract activated mycelium-covered culture medium and it was inoculated into different media (one piece per 20 mL of medium). Then, the media were incubated on a constant temperature shaker (ZWY-2102C; Shanghai Hongji Instrument Equipment Co., Ltd., Shanghai, China) at 150 rpm for 7 d (24 °C for edible fungi, 32 °C for Monascus kaoliang B6) to obtain the seed culture. This seed culture was inoculated into malt extract or tea residue media at a 10% (v• v^{-1}) ratio and incubated under the same conditions. The

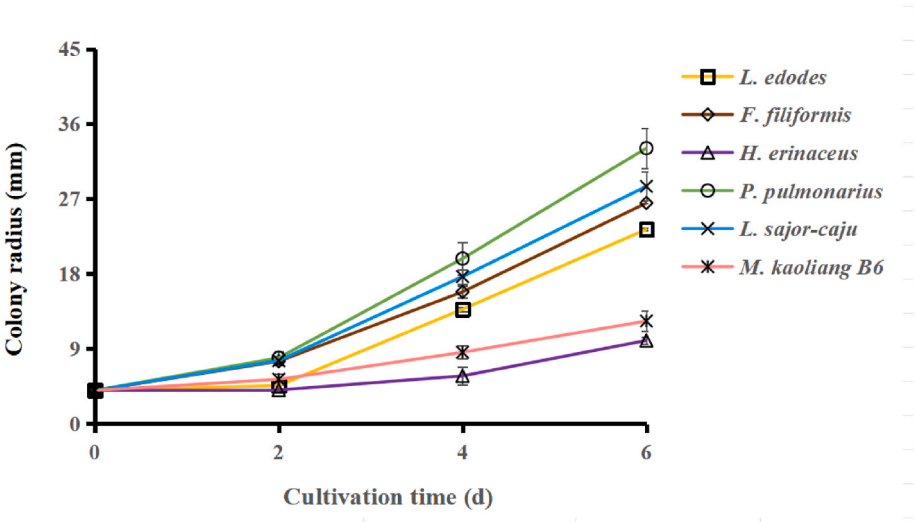

Fig. 1. Colony radius of edible fungi in tea residue medium.

culture liquid was centrifuged (4000 rpm, 10 min) to separate the supernatant and pellet. Then, the supernatant was stored at −20 °C for subsequent analysis. The pellet was washed with distilled water (1:20, v• v^{-1}) and centrifuged to remove the supernatant. This washing process was repeated twice, and afterward, the pellet was freeze-dried and ground into a fungal powder sample for analysis.

2.6. Estimation of mycelium conversion rate and components

The concentrations of tea residue components in the culture medium were calculated by subtracting the total weight of the mycelium from the total sediment weight of the corresponding medium, followed by the calculation of the dry weight of the tea residue. Due to the intertwining of tea residue and mycelium during fermentation, which makes physical separation challenging, it was assumed that the concentrations of components within the mycelium remained constant throughout the fermentation process. The component concentrations in the seed culture mycelium were used for the calculations above.

2.6.1. Determination of biological conversion rate

The fungal powder (0.2 g) was mixed with hexane (6 mL) and vortexed for 5 min on an oscillator (XW-80 A; Shanghai Chitang Electronics Co., Ltd., Shanghai, China), followed by centrifugation at 4000 rpm for 10 min. The supernatant was collected, and this extraction process was repeated twice. Then, combined supernatants were dried using a nitrogen blower, reconstituted in 10 mL of ethanol, and filtered using a 0.45 μm PVDF filter prior to HPLC analysis.

Ergosterol content was quantified using an HPLC system (Thermo Fisher Scientific 3000; Waltham, MA, USA) equipped with a Thermo C18 column (4.6 × 250 mm, pore size: 5 μm). The binary mobile phase consisted of solvent A (methanol/water, 80:20 v• v^{-1}) and solvent B (methanol/dichloromethane, 75:25 v• v^{-1}). The gradient elution program was as follows: 0–5 min, 50–80% B; 5–15 min, 80–100% B; and 15–20.5 min, back to 50% B. The flow rate was set at 1.0 mL min^{-1} with an injection volume of 100 μL. The UV detector was operated at a wavelength of 280 nm (Villares et al., 2014). The equation of the standard curve for ergosterol was y = 0.5849× with an R^2 of 0.99. The ergosterol content in the mycelium of *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6* was found to be 1.1, 1.5, and 1.7 μg mg^{-1}, respectively.

The biological conversion rate was calculated using the following formula:

$$\text{Biological conversion rate (\%)} = \frac{\text{Dry weight of mycelium}}{\text{Amount of tea residue in medium}} \times 100.$$

2.6.2. Dry weight

Samples were dried at 60 °C until a constant weight was reached.

2.6.3. Polyphenols

Polyphenols were determined using the ferrous sulfate-ascorbic acid method (Avelino, 2024) at 540 nm.

2.6.4. Total sugars

The total sugar content of the samples was measured using the anthrone-sulfuric acid method (Leyva et al., 2008). The sample absorbance was measured at 625 nm using a glucose solution (100 μg mL^{-1}) as the standard. Solid samples were fully hydrolyzed before measurement. Then, 20 mg of solid sample were mixed with 6 mL of 65% sulfuric acid, incubated in an 80 °C water bath for 60 min, and centrifuged at 4000 rpm for 10 min. Afterward, the obtained supernatant was used to determine the total sugar content.

2.6.5. Pectin

The pectin content in samples was determined using the carthamin colorimetric method (Bizzani et al., 2020), and the sample absorbance was measured at 530 nm using galacturonic acid (200 μg mL^{-1}) as the standard.

2.6.6. Protein

Protein content in samples was measured using a total organic carbon analyzer (TNM-L ROHS; Shimadzu Corporation, Kyoto, Japan), with a potassium nitrate solution (100 mg L^{-1}) used as the standard and a conversion factor of 6.25.

2.7. Analysis of tea residue cell wall structure

Structural changes in tea residue before and after fermentation were examined using an optical microscope.

2.8. Compatibility test of strains

Following the methodology outlined in Section 2.5, mycelium blocks of *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6* were subjected to antagonistic inoculation at the center of potato dextrose agar solid

Table 1
Growth status of edible fungi in tea residue medium.

Strain	Mycelium density	Mycelium length	Mycelium morphology	Colony color
L. edodes	+++	+++	Carpet-like	White
F. filiformis	+++	++	Velvety	White
H. erinaceus	++	+	Velvety	White, brownish edge
P. pulmonarius	++++	++++	Carpet-like	White
L. sajor-caju	++++	++++	Carpet-like	White
M. kaoliang B6	+	+	Velvety	Orange-yellow interior and white exterior

Note: "+" indicates sparse/short mycelium; "++" indicates sparse/short mycelium; "+++" indicates dense/long mycelium; and "++++" indicates very dense/very long mycelium.

medium, with equidistant spacing between blocks. The plates were incubated at a consistent temperature for 7 d. Subsequent observation focused on the interface of colonies of the three strains, specifically assessing the presence or absence of antagonistic lines (El-Debaiky, 2017).

2.9. Data analysis

Data were statistically analyzed using Microsoft Excel 2016, with samples measured in triplicate and results expressed as "mean ± standard deviation (Means ± SD)." One-way ANOVA and Duncan's multiple range test were used to analyze the significance of differences between groups, with a significance level of $P < 0.05$. Heatmaps were created using the website LianChuan BioCloud Platform (omicstudio.cn).

3. Results and discussion

3.1. Growth analysis of edible fungi on tea residue plates

The colony radii of six fungal strains were measured over time (Fig. 1). Among the strains, *P. pulmonarius* exhibited the fastest growth rate, reaching a colony radius of 33.1 mm after 6 d, followed by *L. sajor-caju (Fr.)*, *F. filiformis*, and *L. edodes*, with colony radii of 28.5, 26.5, and 23.3 mm, respectively. *Monascus kaoliang B6* and *H. erinaceus* exhibited the slowest growth rates, and their colony radii were 12.3 and 10.0 mm, respectively, after 6 d.

Table 1 provides the mycelium density, length, morphology, and color of the six strains after a 6 d growth, and their pictures can be seen in Supplementary Fig. A1. *Pleurotus pulmonarius* and *L. sajor-caju (Fr.)* exhibited longer and denser mycelia, while *L. edodes* and *F. filiformis* displayed relatively sparse and short mycelia. *Hericium erinaceus* and *M. kaoliang B6* had the shortest and sparsest mycelia. Additionally, the surrounding medium of *H. erinaceus* colonies appeared brown, while the center of *M. kaoliang B6* colonies exhibited an orange color, which was attributed to pigment production by these fungi (Chaudhary et al., 2024; Ju et al., 2023). These results showed that *P. pulmonarius* and *L. sajor-caju (Fr.)* stood out for their rapid growth rates and dense, long mycelium, which display a distinct fibrous structure.

3.2. Analysis of decolorization zones of edible fungi on different lignocellulosic plates

Fig. 2 shows the color change observed in carboxymethyl cellulose sodium (CMC-Na), xylan, sky blue, and lignin media assessed for six fungal strains. *Monascus kaoliang B6* demonstrated the most extensive color change zones across all media after 4 d, while *P. pulmonarius* and *L. sajor-caju (Fr.)* exhibited color zones only on CMC-Na and lignin media. *Lentinus edodes*, *F. filiformis*, and *H. erinaceus* showed color change exclusively on the lignin media.

Specifically, the color change zone diameters for *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6* on CMC-Na medium after 4 d were 9.12, 7.76, and 12.23 mm, respectively. In contrast, *L. edodes*, *F. filiformis*, and *H. erinaceus* did not exhibit any colony growth or color change. In xylan medium, only *M. kaoliang B6* produced a faint color with a zone diameter of 0.9 mm. In lignin medium, notable variations in color change were observed among the strains, with *P. pulmonarius* and *L. sajor-caju (Fr.)* having the largest and darkest zones at 8.6 and 6.8 mm, respectively. The other strains, including *L. edodes*, *F. filiformis*, and *H. erinaceus*, had zone diameters of approximately 2.5 mm and produced much fainter color. *Monascus kaoliang B6* in sky blue medium formed larger colonies with distinct color change zones, while the other strains showed no color zones, underscoring its lignin degradation potential.

Pleurotus pulmonarius and *L. sajor-caju (Fr.)* exhibited outstanding enzymatic activities, followed by *F. filiformis*, while *H. erinaceus* and *M. kaoliang B6* were the least effective. The slow growth rate and poor enzymatic activity of *H. erinaceus* might be due to insufficient water content in the solid medium (Lin et al., 2023). The strains that produced cellulase, hemicellulose, ligninase may degrade the lignocellulose structure that traps nutrients, thereby promoting the release and utilization of nutrients in the tea residue.

Due to the slow growth rate and poor enzymatic activity of *H. erinaceus*, *L. edodes*, *F. filiformis*, *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6* were chosen for further investigation into the influence of medium lignocellulose on enzyme production.

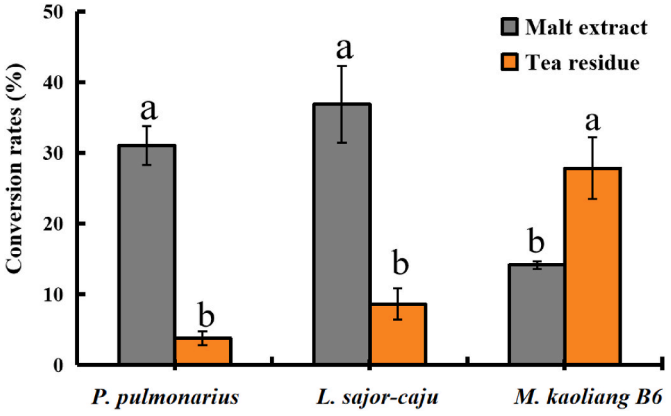

Fig. 3. Biological conversion rates of different edible fungi in malt extract and tea residue liquid media.

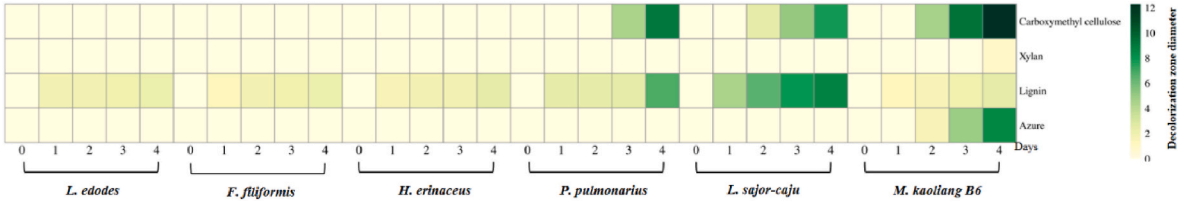

Fig. 2. Heatmap of decolorization zone diameter of edible fungi on different culture media.

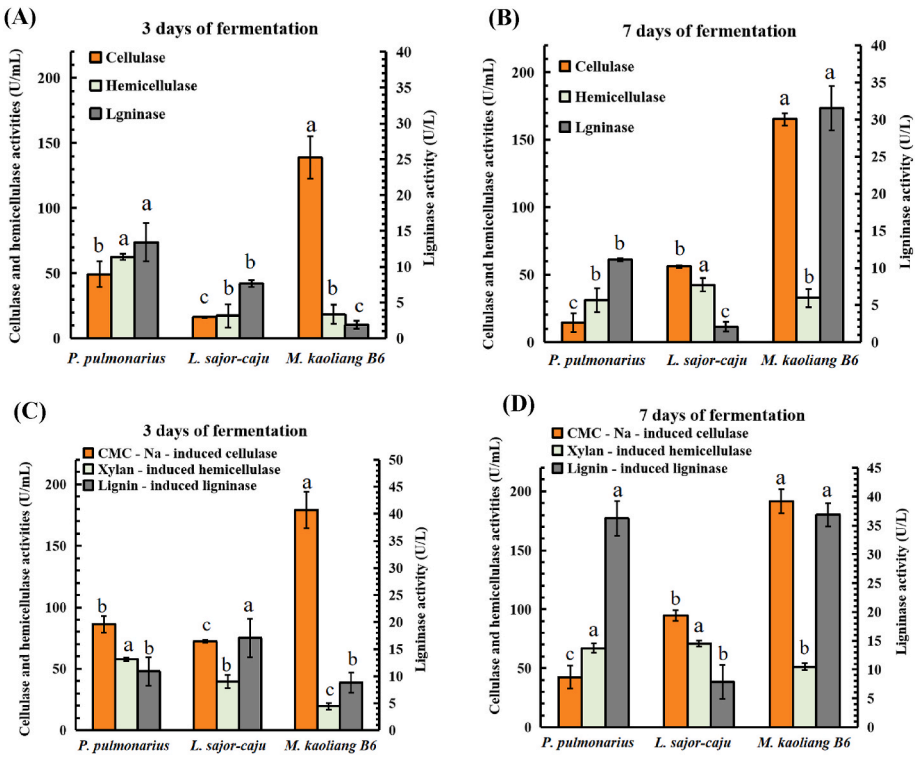

Fig. 4. Cellulase, hemicellulase, and ligninase activities of strains in (A) 3 d of fermentation in malt extract medium; (B) 9 d of fermentation in malt extract medium; (C) 3 d of fermentation in malt extract medium supplemented with additional carboxymethyl cellulose sodium (CMC-Na), xylan, or lignin; and (D) 9 d of fermentation in malt extract medium supplemented with additional CMC-Na, xylan, or lignin.

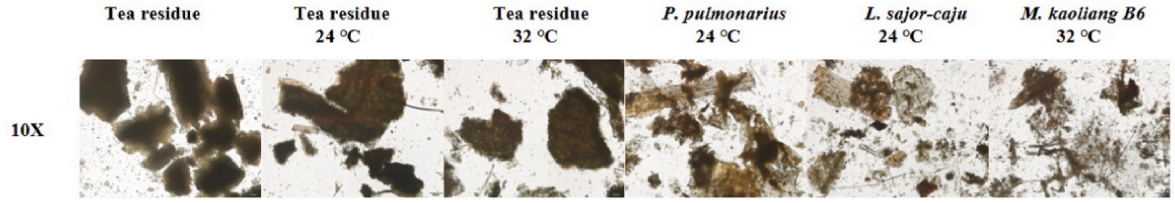

Fig. 5. Changes in the structure of tea residue before and after 9-day fermentation with different edible fungi.

3.3. Growth and enzyme production of edible fungi in tea residue or malt extract media

3.3.1. Fungal conversion efficiency of culture media

Fig. 3 shows the conversion rates of *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6* in malt extract and tea residue liquid media after 9 d of cultivation. When malt extract was used as the medium, *L. sajor-caju (Fr.)* exhibited the highest conversion rates of 36.9%, while *P. pulmonarius* showed a relatively lower rate of 31.0%, and *M. kaoliang B6* exhibited the lowest rate of 14.1%. When tea residue was used as the medium, the conversion rate of *M. kaoliang B6* significantly increased to 27.8%, whereas the conversion rates of *P. pulmonarius* and *L. sajor-caju (Fr.)* both significantly decreased to 8.6% and 3.8%, respectively. A significant difference in the conversion rates of the three fungi was observed between malt extract and tea residue media (Fig. 3). The growth status of *M. kaoliang B6* on solid tea residue plates was inferior to that of *P. pulmonarius* and *L. sajor-caju (Fr.)* (Fig. 1 and Table 1). This phenomenon might be attributed to the fact that *P. pulmonarius* and *L. sajor-caju (Fr.)* mainly used agar as a nutrient source (Chen et al., 2020; Smiderle et al., 2012), while *M. kaoliang B6* mainly used substances in tea residue (such as cell wall polysaccharides and polyphenols) for growth (Long et al., 2023; Shi et al., 2022). In addition, *M. kaoliang B6* experienced increased exposure to tea residue in liquid media, which stimulated the secretion of (hemi) cellulases and ligninases (Fig. 2), thereby enhancing its ability to degrade tea residue.

3.3.2. Differences in activities of cellulases, hemicellulases, and ligninases

To further analyze the cell wall degradation ability of *P. pulmonarius*, *P. sajor-caju*, and *M. kaoliang B6*, cellulase, hemicellulase, or ligninase activities were determined after fermentation in malt extract medium supplemented with additional CMC-Na, xylan, or lignin.

As shown in Fig. 4A and B, after fermentation in malt extract medium, *M. kaoliang B6* exhibited relatively higher cellulase activity in the broth, while *P. pulmonarius* exhibited higher hemicellulase and ligninase activities. After 3 d of fermentation, the cellulase activity in *M. kaoliang B6* fermentation broth peaked at 139 U•mL^{-1}, approximately 3 times that of *P. pulmonarius* and 9 times that of *L. sajor-caju (Fr.)*. The hemicellulase activity in *P. pulmonarius* fermentation broth peaked at 62.5 U•mL^{-1}, approximately 3.5 times those of *L. sajor-caju (Fr.)* and *M. kaoliang B6*. The ligninase activity in *P. pulmonarius* was 13.4 U•L^{-1}, which was twice those of *L. sajor-caju (Fr.)* and *M. kaoliang B6*. However, the enzymatic activities of *P. pulmonarius* showed a negative correlation with fermentation time. This phenomenon might be attributed to the rapid growth of *P. pulmonarius*, resulting in smaller surface area contact between mycelium balls and the medium.

In the media supplemented with CMC-Na, xylan, or lignin, the

Table 2
Weight hanges in nutrient composition of tea residue, mycelium, and fermentation broth before and after fermentation by edible fungi (mg•g^{-1}).

Fermentation time (d)	Strain	Tea residue sediment					Mycelium sediment					Fermentation broth				
		Total dry weight	Protein content	Total sugar content	Pectin content	Other	Total dry weight	Protein content	Total sugar content	Pectin content	Other	Total dry weight	Protein content	Total sugar content	Pectin content	Other
0	Control-24/32	770	239	250	34	246	0.0	0.0	0.0	0.0	0.0	230	31	59	52	151
	P. pulmonarius						8.3	1.8	4.2	0.4	1.3	222	34	100	50	106
	L. sajor-caju						8.7	1.5	5.3	0.5	1.0	221	34	90	50	116
	M. kaoliang B6						10.3	2.6	6.6	0.2	0.7	220	34	69	49	136
1	Control-24	771	230	249	33	259	0.0	0.0	0.0	0.0	0.0	229	31	64	61	136
	Control-32	769	215	256	34	265	0.0	0.0	0.0	0.0	0.0	231	31	78	64	120
	P. pulmonarius	752	200	245	31	276	10.0	2.2	5.1	0.4	1.6	238	32	97	56	116
	L. sajor-caju	679	199	194	26	260	42.0	7.4	25.6	7.4	1.1	278	32	133	59	118
	M. kaoliang B6	622	172	154	24	272	68.1	16.8	43.3	1.3	4.6	310	33	82	62	199
5	Control-24	769	233	265	33	237	0.0	0.0	0.0	0.0	0.0	231	31	65	70	127
	Control-32	770	195	261	33	281	0.0	0.0	0.0	0.0	0.0	230	31	74	73	114
	P. pulmonarius	683	195	213	27	247	49.6	12.5	21.5	2.4	9.1	268	18	47	55	184
	L. sajor-caju	550	143	82	20	305	88.7	23.5	40.5	7.4	12.0	361	23	68	54	263
	M. kaoliang B6	410	84	41	15	269	259.1	64.1	154.7	4.9	24.5	331	33	74	78	213
9	Control-24	769	204	268	34	263	0.0	0.0	0.0	0.0	0.0	231	30	82	70	109
	Control-32	768	170	265	33	301	0.0	0.0	0.0	0.0	0.0	232	30	81	69	111
	P. pulmonarius	635	150	198	24	264	49.6	10.9	25.2	2.1	7.9	316	18	50	47	237
	L. sajor-caju	538	133	102	21	282	108.0	18.1	62.3	5.7	15.1	354	20	62	35	276
	M. kaoliang B6	375	65	58	13	239	305.7	75.6	194.2	5.8	20.8	319	36	72	76	207

cellulase, hemicellulase, and ligninase activities were enhanced (Fig. 4C and D). After 3 d of fermentation, *M. kaoliang B6* exhibited the highest cellulase activity of 179 U•mL^{-1}, which was twice those of *P. pulmonarius* and *L. sajor-caju (Fr.)*. The hemicellulase activity in *P. pulmonarius* peaked at 57.8 U•mL^{-1}, which was 6 times higher than that of *M. kaoliang B6*. *L. sajor-caju (Fr.)* exhibited the highest ligninase activity of 22.0 U•L^{-1}, followed by *P. pulmonarius* (17.1 U•L^{-1}), which were both higher than that of the pure malt extract fermentation. On day 7, *M. kaoliang B6* maintained the highest cellulase activity of 191 U•mL^{-1}, which increased by 26 U•mL^{-1} compared with pure malt extract fermentation. The hemicellulase activities in *P. pulmonarius* and *L. sajor-caju (Fr.)* peaked at 67.1 and 70.9 U•mL^{-1}, respectively, showing enhancements compared with malt extract fermentation. Ligninase activities in *P. pulmonarius* and *M. kaoliang B6* peaked at 36.2 and 36.9 U•L^{-1}, respectively, which were approximately 4 times higher than the values observed on day 3 and surpassing levels in malt extract fermentation on day 7. This phenomenon indicated that the addition of CMC-Na, xylan, or lignin stimulated the production of corresponding degrading enzymes by the strains (Kannan et al., 1990; Lu et al., 2023a).

The higher conversion efficiency of *M. kaoliang B6* could be attributed to its superior cellulase and lignin enzyme activities, which effectively degraded the lignocellulosic structure in the tea residue cell walls, leading to nutrient release and utilization. Although *P. pulmonarius* and *L. sajor-caju (Fr.)* exhibited the highest hemicellulase activities, hemicellulose was less abundant in tea residue than cellulose (Pang et al., 2021) and was not its primary structural component of the cell wall. Therefore, its degradation alone was insufficient for effective nutrient release.

3.4. Fermentation of *P. pulmonarius, L. sajor-caju (Fr.), and M. kaoliang B6* in tea residue liquid medium

3.4.1. Tea residue changes under optical microscope

Fig. 5 shows the electron microscopy results of tea residue fermented by *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6* after 9 d. The original tea residue had low transparency and a smooth surface, remaining unchanged after 9 d in a shaker at a constant temperature. Both control groups exhibited minimal structural changes, indicating that incubation at a constant temperature did not significantly damage the tea residue. Tea residue fermented by *P. pulmonarius* and *L. sajor-caju (Fr.)* showed increased transparency, grooved surfaces with wrinkles, and thinning. The mycelia of *M. kaoliang B6* intertwined with the tea residue, leading to noticeable fragmentation into small pieces, increased transparency, hollow structures, reduced surface flesh, and depressions. This phenomenon was attributed to the production of various enzymes, such as cellulases, pectinases, and proteases, by strains during fermentation. These enzymes acted on the tea residue surface, thus disrupting its structure. Comparing the degree of tea residue destruction, *M. kaoliang B6* exhibited a strong enzyme production ability in tea residue medium and a robust capacity to use tea residue, aligning with its higher biological conversion rate among the three strains (Fig. 3).

3.4.2. Analysis of component transformation in tea residue medium

Tea residue liquid medium was separately fermented by *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6*, and Table 2 shows the composition changes in tea residue, mycelium, and fermentation broth. During fermentation, all three strains showed a decrease in the dry weight of tea residue and an increase in the dry weight of mycelium. Among them, the changes in tea residue dry weight and mycelium dry weight after fermentation by *M. kaoliang B6* were the most significant, decreasing by 395 mg g^{-1} and increasing by 306 mg g^{-1}, respectively. The total sugar content in the tea residue after it was fermented by *M. kaoliang B6* decreased the most by 192 mg g^{-1}, followed by protein, which decreased by 181 mg g^{-1}, approximately 3 times that of *P. pulmonarius* and twice that of *L. sajor-caju (Fr.)*. At the same time, the protein and total sugar content in the mycelium of *M. kaoliang B6*

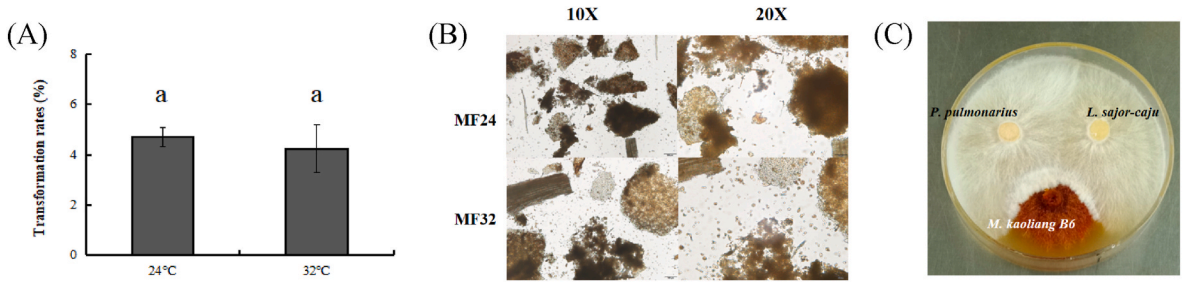

Fig. 6. (A) Biological conversion rates of combined fermentation at different temperatures in tea residue medium; (B) changes in tea residue structure before and after combined fermentation at different temperatures (0, 9: fermentation time 0, 9 days; MF24: combined fermentation group at 24 °C; and MF32: combined fermentation group at 32 °C); and (C) compatibility of strains.

increased to 76 and 194 mg g^{-1}, respectively, which were approximately 7 times that of *P. pulmonarius* and 4 times that of *L. sajor-caju (Fr.)*, corresponding to the decrease in protein and total sugar content in the tea residue. The increase in the mycelium of *M. kaoliang B6* among the three strains was the highest at 73 mg g^{-1}, which was 8 times that of *P. pulmonarius* and 4.4 times that of *L. sajor-caju (Fr.)*. *Monascus kaoliang B6* could effectively degrade the cell wall of tea residue and fully use its biomass for growth during liquid-state fermentation of tea residue. Although *M. kaoliang B6* exhibited the highest yield and protein content in tea residue liquid medium, along with the ability to produce red pigment, its application might be influenced by toxicity concerns. It could only serve as a substitute for hemoglobin as a colorant for meat analogues.

During the 9-day fermentation, all three strains exhibited an increase in the dry weight of the fermentation broth. The most substantial increased in dry weight (133 mg g^{-1}) was observed in the fermentation broth of *L. sajor-caju (Fr.)*, followed by *P. pulmonarius* and *M. kaoliang B6*, which increased by 94 and 99 mg g^{-1}, respectively. The total sugar and pectin content in both *L. sajor-caju (Fr.)* and *M. kaoliang B6* initially increased in the fermentation broth and decreased, with pectin increasing by 9 and 29 mg g^{-1}, respectively. This phenomenon might be attributed to the active cellulase and lignin peroxidase enzyme systems of *M. kaoliang B6*, which facilitated cellulose degradation and nutrient utilization in the tea residue. Furthermore, the early-stage cellulose degradation by *L. sajor-caju (Fr.)* and *M. kaoliang B6* increased polysaccharides and pectin contents in the fermentation broth (Awafo et al., 1995; Salis et al., 2009), followed by rapid strain growth, sugar absorption, and preferential utilization of proteins and sugars by *M. kaoliang B6*, primarily targeting monosaccharides (Wang et al., 2023a).

Additionally, the concentrations of other substances in the fermentation broth of the three strains significantly increased. The highest increase in the concentration of other substances was observed (160 mg g^{-1}) in *L. sajor-caju (Fr.)* fermentation broth, followed by *P. pulmonarius* fermentation broth (131 mg g^{-1}), and the smallest increase of 71 mg g^{-1} was observed in *M. kaoliang B6* fermentation broth. This phenomenon might be attributed to the presence of polyphenolic substances in the fermentation broth; thus, supplementary experiments were conducted (see Table A.1 in Supplementary). However, the results showed that on day 5 of fermentation, the polyphenol contents in the fermentation broth of *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6* were only 9.57, 5.65, and 4.57 mg g^{-1}, respectively. These results might be attributed to the oxidation of tea polyphenols into quinones or some active substances during the fermentation process, or they were metabolized by the strains to synthesize other substances (Bei et al., 2018), thus decreasing polyphenol content. In summary, *M. kaoliang B6* had the best fermentation effect on tea residue, with a significant decrease in tea residue dry weight and a significant increase in mycelium dry weight after fermentation. The protein and pectin contents in the fermentation broth also increased.

Fungal fermentation broke down the complex lignocellulosic structure in tea residue, facilitating the conversion of proteins, polysaccharides, and other nutrients into fungal protein and valuable nutritional components. Utilizing these fungi promoted environmental sustainability by recycling agricultural waste into useful products, reducing reliance on chemical processing and minimizing waste disposal. For instance, *Aspergillus tubingensis* was utilized for the conversion of waste lignocellulosic biomass, such as palm empty fruit bunches, into fungal lipids. This process effectively removed lignin and hemicellulose while minimizing the generation of waste biomass (Intasit et al., 2023).

To further improve the nutrient conversion from tea residue and reduce biomass waste, the three selected strains was used for combined fermentation to explore the potential benefits of co-growth in optimizing nutrient utilization.

3.4.3. *Fermentation effects of three mixed edible fungi on tea residue*

Fig. 6A shows the conversion rates of *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6* or their combination used for fermentation in tea residue liquid medium for 9 d at 24 °C and 32 °C. When the three strains were used for fermentation at 24 °C or 32 °C, their conversion rates of tea residue were 4.73% and 4.24%, respectively, which are relatively low. Fig. 6B shows the electron microscope results of the co-fermentation of *P. pulmonarius*, *L. sajor-caju (Fr.)*, and *M. kaoliang B6* in tea residue after 9 d. The results revealed a slight decrease in tea residue transparency, but the surface remains relatively smooth without significant degradation. As shown in Fig. 6C–*P pulmonarius* and *L. sajor-caju (Fr.)* were dense and exhibit outstanding growth rates. Their mycelia could intertwine and grow without antagonistic lines, enabling co-fermentation. However, the colonies of *M. kaoliang B6* were covered by those of *P. pulmonarius* and *L. sajor-caju (Fr.)*, and the colony radius in the covered area was significantly smaller than on the other side without antagonistic strains. This phenomenon indicated that *P. pulmonarius* and *L. sajor-caju (Fr.)* were dominant species in the co-cultured system and inhibited the growth of *M. kaoliang B6*. The dominance of *P. pulmonarius* and *L. sajor-caju (Fr.)* might be attributed to their rapid growth, thus competing for growth resources with *M. kaoliang B6*. *Monascus kaoliang B6* was not suitable for co-cultivation with *P. pulmonarius* and *L. sajor-caju (Fr.)*.

4. Conclusion

Using tea residue as a medium, *P. pulmonarius* and *L. sajor-caju (Fr.)* grew fastest in plate, with colony radii of 33.1 and 28.5 mm after 8 dads. *M. kaoliang B6* exhibited significant degradation of cellulose, hemicellulose, and lignin, with decolorization radii of 12.2, 0.9, and 8.5 mm. Thereby these strains had potential to covert tea residue. After liquid fermentation, *P. pulmonarius* and *L. sajor-caju (Fr.)* produced 108 and 50 mg g^{-1} mycelium, which could be served as raw materials for meat analogues. *M. kaoliang B6* demonstrated the highest conversion efficiency of 27.8%, attributed to its exceptional cellulase (191 U•mL^{-1}) and lignin enzyme activity (36.9 U•L^{-1}), allowing effective degradation

of cell walls and nutrient release. Co-fermentation of these three strains had little effect on the improvement of conversion efficiency that a further optimization or screen of more strains might further improve the fermentation efficiency. Generally, utilizing tea residue for edible fungi fermentation was a sustainable process for biowaste treatment, enabling efficient nutrient conversion under mild conditions without adding chemicals.

CRediT authorship contribution statement

Yufei Zhang: Data curation, Formal analysis, Writing – original draft. **Yanyin Lu:** Investigation, Validation. **Dandan Pan:** Methodology, Validation. **Yanyan Zhang:** Writing – review & editing. **Chen Zhang:** Conceptualization, Writing – original draft, Funding acquisition. **Zexin Lin:** Supervision, Project administration, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was supported by Department of Science and Technology of Fujian Province Foreign Cooperation Project (2023I0006) and Good Food Institute under GFI grant number 22-CM-CN-DG-1-348. We thank LetPub (www.letpub.com) for its linguistic assistance during the preparation of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.crfs.2024.100907.

Data availability

Data will be made available on request.

References

Araújo, N.L., Avelino, K.V., Halabura, M.I.W., Marim, R.A., Kassem, A.S.S., Linde, G.A., Colauto, N.B., do Valle, J.S., 2021. Use of green light to improve the production of lignocellulose-decay enzymes by Pleurotus spp. in liquid cultivation. Enzym. Microb. Technol. 149, 109860.

Arora, D.S., Sharma, R.K., 2010. Ligninolytic fungal laccases and their biotechnological applications. Appl. Biochem. Biotechnol. 160 (6), 1760–1788.

Avelino, F., 2024. Chapter 9 - ferric reducing antioxidant power (FRAP). In: Avelino, F. (Ed.), Antioxidant Methods. Academic Press, pp. 123–133.

Awafo, V.A., Chahal, D.S., Charbonneau, R., 1995. Effect of irradiation, as a pretreatment, on bioconversion of corn stover into protein-rich mycelial biomass of Pleurotus sajor-caju. Radiat. Phys. Chem. 46 (4), 1299–1302, 2.

Barr, C.J., Mertens, J.A., Schall, C.A., 2012. Critical cellulase and hemicellulase activities for hydrolysis of ionic liquid pretreated biomass. Bioresour. Technol. 104, 480–485.

Bei, Q., Chen, G., Lu, F., Wu, S., Wu, Z., 2018. Enzymatic action mechanism of phenolic mobilization in oats (Avena sativa L.) during solid-state fermentation with Monascus anka. Food Chem. 245, 297–304.

Bizzani, M., William Menezes Flores, D., Alberto Colnago, L., David Ferreira, M., 2020. Monitoring of soluble pectin content in orange juice by means of MIR and TD-NMR spectroscopy combined with machine learning. Food Chem. 332, 127383.

Bonatti, M., Karnopp, P., Soares, H.M., Furlan, S.A., 2004. Evaluation of Pleurotus ostreatus and Pleurotus sajor-caju nutritional characteristics when cultivated in different lignocellulosic wastes. Food Chem. 88 (3), 425–428.

Cano y Postigo, L.O., Jacobo-Velázquez, D.A., Guajardo-Flores, D., Garcia Amezquita, L. E., García-Cayuela, T., 2021. Solid-state fermentation for enhancing the nutraceutical content of agrifood by-products: recent advances and its industrial feasibility. Food Biosci. 41, 100926.

Chai, W.Y., Krishnan, U.G., Sabaratnam, V., Tan, J.B.L., 2021. Assessment of coffee waste in formulation of substrate for oyster mushrooms Pleurotus pulmonarius and Pleurotus floridanus. Future Foods 4, 100075.

Chaudhary, V., Katyal, P., Kaur, J., Bhatia, S., Singh, S., Poonia, A.K., Puniya, A.K., Raposo, A., Yoo, S., Han, H., Alturki, H.A., Kumar, A., 2024. Bioactive activity and safety analysis of Monascus red biopigment. Food Biosci. 57, 103523.

Chen, F., Xiong, S., Sundelin, J., Martín, C., Hultberg, M., 2020. Potential for combined production of food and biofuel: cultivation of Pleurotus pulmonarius on soft- and hardwood sawdusts. J. Clean. Prod. 266, 122011.

Debnath, B., Haldar, D., Purkait, M.K., 2021. Potential and sustainable utilization of tea waste: a review on present status and future trends. J. Environ. Chem. Eng. 9 (5), 106179.

Dedousi, M., Melanouri, E.-M., Karayannis, D., Kaminarides, E.-I., Diamantopoulou, P., 2024. Utilization of spent substrates and waste products of mushroom cultivation to produce new crops of Pleurotus ostreatus, Pleurotus eryngii and Agaricus bisporus. Carbon Res. Conv. 7 (2), 100196.

Duan, Y., Guo, F., Li, C., Xiang, D., Gong, M., Yi, H., Chen, L., Yan, L., Zhang, D., Dai, L., Liu, X., Wang, Z., 2024. Aqueous extract of fermented Eucommia ulmoides leaves alleviates hyperlipidemia by maintaining gut homeostasis and modulating metabolism in high-fat diet fed rats. Phytomedicine 128, 155291.

El-Debaiky, S.A., 2017. Antagonistic studies and hyphal interactions of the new antagonist Aspergillus piperis against some phytopathogenic fungi in vitro in comparison with Trichoderma harzianum. Microb. Pathog. 113, 135–143.

Gupta, A., Sharma, S., Saha, S., Walia, S., 2013. Yield and nutritional content of Pleurotus sajor caju on wheat straw supplemented with raw and detoxified mahua cake. Food Chem. 141 (4), 4231–4239.

Huang, H., Chen, J., Chen, Y., Xie, J., Liu, S., Sun, N., Hu, X., Yu, Q., 2021. Modification of tea residue dietary fiber by high-temperature cooking assisted enzymatic method: structural, physicochemical and functional properties. Lebensm. Wiss. Technol. 145, 111314.

Huang, Z.-R., Chen, M., Guo, W.-L., Li, T.-T., Liu, B., Bai, W.-D., Ai, L.-Z., Rao, P.-F., Ni, L., Lv, X.-C., 2020. Monascus purpureus-fermented common buckwheat protects against dyslipidemia and non-alcoholic fatty liver disease through the regulation of liver metabolome and intestinal microbiome. Food Res. Int. 136, 109511.

Hussain, S., Anjali, K.P., Hassan, S.T., Dwivedi, P.B., 2018. Waste tea as a novel adsorbent: a review. Appl. Water Sci. 8 (6), 165.

Intasit, R., Cheirsilp, B., Louhasakul, Y., Thongchul, N., 2023. Enhanced biovalorization of palm biomass wastes as biodiesel feedstocks through integrated solid-state and submerged fermentations by fungal co-cultures. Bioresour. Technol. 380, 129105.

Ju, M., Zhang, J., Mai, T., Li, L., Gu, T., Liu, Y., Gao, M., 2023. Co-culture of Rhodotorula mucilaginosa and Monascus purpureus increased the yield of carotenoids and Monascus pigments. Lebensm. Wiss. Technol. 183, 114949.

Kannan, K., Oblisami, G., Loganathan, B.G., 1990. Enzymology of ligno-cellulose degradation by Pleurotus sajor-caju during growth on paper-mill sludge. Biol. Waste 33 (1), 1–8.

Kayode, R.M.O., Olakulehin, T.F., Adedeji, B.S., Ahmed, O., Aliyu, T.H., Badmos, A.H.A., 2015. Evaluation of amino acid and fatty acid profiles of commercially cultivated oyster mushroom (Pleurotus sajor-caju) grown on gmelina wood waste. Niger. Food J. 33 (1), 18–21.

Kurt, S., Buyukalaca, S., 2010. Yield performances and changes in enzyme activities of Pleurotus spp. (P. ostreatus and P. sajor-caju) cultivated on different agricultural wastes. Bioresour. Technol. 101 (9), 3164–3169.

Lechner, B.E., Papinutti, V.L., 2006. Production of lignocellulosic enzymes during growth and fruiting of the edible fungus Lentinus tigrinus on wheat straw. Process Biochem. 41 (3), 594–598.

Leite, P., Sousa, D., Fernandes, H., Ferreira, M., Costa, A.R., Filipe, D., Gonçalves, M., Peres, H., Belo, I., Salgado, J.M., 2021. Recent advances in production of lignocellulolytic enzymes by solid-state fermentation of agro-industrial wastes. Curr. Opin. Green Sustainable Chem. 27, 100407.

Leyva, A., Quintana, A., Sánchez, M., Rodríguez, E.N., Cremata, J., Sánchez, J.C., 2008. Rapid and sensitive anthrone–sulfuric acid assay in microplate format to quantify carbohydrate in biopharmaceutical products: method development and validation. Biologicals 36 (2), 134–141.

Lin, Y.-J., Huang, C.-Y., Tsai, B.C.-K., Kumar, K.A., Hsieh, D.J.-Y., Chiu, P.-L., Chang, Y.-M., Ho, T.-J., Kuo, W.-W., Ju, D.-T., 2023. Alcoholic Hericium erinaceus mycelia extract induces SIRT-1/ERK-1/2 mediated autophagy to prevent accumulation and spreading of alpha-synuclein and amyloid-beta peptide on the A53T transgenic mice. J. Funct.Foods 110, 105874.

Lin, Z., Wei, H., Zhang, Y., Liu, P., Liu, Y., Huang, Z., Lv, X., Zhang, Y., Zhang, C., 2022. Improving emulsification properties of alkaline protein extract from green tea residue by enzymatic methods. Curr. Res. Food Sci. 5, 1235–1242.

Liu, Y., Zhao, G., Ren, J., Zhao, M., Yang, B., 2011. Effect of denaturation during extraction on the conformational and functional properties of peanut protein isolate. Innovat. Food Sci. Emerg. Technol. 12 (3), 375–380.

Long, M., Pei, X., Lu, Z., Xu, D., Zheng, N., Li, Y., Ge, H., Cao, W., Osire, T., Xia, X., 2023. Effective degradation of anthraquinones in Folium Sennae with Monascus fermentation for toxicity reduce and efficacy enhancement. Heliyon 9 (8), e18735.

Lu, X., Tong, S., Liu, P., 2023a. Enhanced α-glucosidase inhibition activity of exopolysaccharides fractions from mycelium of Inonotus obliquus under addition of birch sawdust lignocellulose component. Int. J. Biol. Macromol. 242, 124699.

Lu, X., Zhao, Y., Li, F., Liu, P., 2023b. Active polysaccharides from Lentinula edodes and Pleurotus ostreatus by addition of corn straw and xylosma sawdust through solid-state fermentation. Int. J. Biol. Macromol. 228, 647–658.

Moonmoon, M., Shelly, N.J., Khan, M.A., Uddin, M.N., Hossain, K., Tania, M., Ahmed, S., 2011. Effects of different levels of wheat bran, rice bran and maize powder supplementation with saw dust on the production of shiitake mushroom (Lentinus edodes (Berk.) Singer). Saudi J. Biol. Sci. 18 (4), 323–328.

Pang, B., Huang, L., Teng, J., Zhang, J., Xia, N., Wei, B., 2021. Effect of pile fermentation on the cells of Chinese Liupao tea: the first record of cell wall of Liupao tea on transmission electron microscope. Food Chem. 361, 130034.

Pradeep Kumar, V., Sridhar, M., Ashis Kumar, S., Bhatta, R., Steven, B., 2023. Elucidating the role of media nitrogen in augmenting the production of lignin-depolymerizing enzymes by white-rot fungi. Microbiol. Spectr. 11 (5).
Reddy, G.V., Ravindra Babu, P., Komaraiah, P., Roy, K.R.R.M., Kothari, I.L., 2003. Utilization of banana waste for the production of lignolytic and cellulolytic enzymes by solid substrate fermentation using two Pleurotus species (P. ostreatus and P. sajor-caju). Process Biochem. 38 (10), 1457–1462.
Saini, S., Sharma, K.K., 2021. Fungal lignocellulolytic enzymes and lignocellulose: a critical review on their contribution to multiproduct biorefinery and global biofuel research. Int. J. Biol. Macromol. 193, 2304–2319.
Salis, A., Pisano, M., Monduzzi, M., Solinas, V., Sanjust, E., 2009. Laccase from Pleurotus sajor-caju on functionalised SBA-15 mesoporous silica: immobilisation and use for the oxidation of phenolic compounds. J. Mol. Catal. B Enzym. 58 (1), 175–180.
Sherwood, M.B., De Beer, E.J., 1947. Discrepancy in analysis of penicillin in blood by the Oxford cup method as revealed by the paper disc technique. Science (New York, N. Y.) 105 (2729), 414, 414.
Shi, R., Luo, Q., Liu, Y., Meng, G., Chen, W., Wang, C., 2022. Effect of γ-butyrolactone, a quorum sensing molecule, on morphology and secondary metabolism in Monascus. Lebensm. Wiss. Technol. 172, 114225.
Smiderle, F.R., Olsen, L.M., Ruthes, A.C., Czelusniak, P.A., Santana-Filho, A.P., Sassaki, G.L., Gorin, P.A.J., Iacomini, M., 2012. Exopolysaccharides, proteins and lipids in Pleurotus pulmonarius submerged culture using different carbon sources. Carbohydr. Polym. 87 (1), 368–376.
Villares, A., Mateo-Vivaracho, L., García-Lafuente, A., Guillamón, E., 2014. Storage temperature and UV-irradiation influence on the ergosterol content in edible mushrooms. Food Chem. 147, 252–256.
Wang, M., Zhao, R., 2023. A review on nutritional advantages of edible mushrooms and its industrialization development situation in protein meat analogues. J. Future Foods 3 (1), 1–7.
Wang, W.-j., Li, Y., Li, F.-h., Zeng, K.-f., Ming, J., 2022. Polypropylene crisper and 1-MCP delay the softening, lignification and transcription levels of related enzyme genes of golden needle mushrooms (Flammulina velutipes). J. Integr. Agric. 21 (1), 249–260.
Wang, Y., Gao, C., Long, P., Hu, Z., Zhu, L., Wang, L., Shao, Y., Wang, B., He, Y., 2023a. Dynamic changes of active substances of rice, Pueraria and yam fermentation by Monascus ruber. Lebensm. Wiss. Technol. 183, 114925.
Wang, Y., Ye, F., Zhou, B., Liang, Y., Lin, Q., Lu, D., Zhou, X., Liu, J., 2023b. Comparative analysis of different rice substrates for solid-state fermentation by a citrinin-free Monascus purpureus mutant strain with high pigment production. Food Biosci. 56, 103245.
Xu, Q., Yang, Y., Hu, K., Chen, J., Djomo, S.N., Yang, X., Knudsen, M.T., 2021. Economic, environmental, and emergy analysis of China's green tea production. Sustain. Prod. Consum. 28, 269–280.
Xu, Z., Zheng, Z., Cai, G., Chen, B., Yang, H., 2024. Improving the hypoglycemic activity of phenolic extracts from Dendrobium officinale leaves using the solid-state fermentation of edible fungi. Food Biosci. 58, 103828.
Ye, X., Zhang, M., Gong, Z., Jiao, W., Li, L., Dong, M., Xiang, T., Feng, N., Wu, Q., 2024. Inhibition of polyphenols on Maillard reaction products and their induction of related diseases: a comprehensive review. Phytomedicine 128, 155589.
Zhang, C., Bozileva, E., van der Klis, F., Dong, Y., Sanders, J.P.M., Bruins, M.E., 2016. Integration of galacturonic acid extraction with alkaline protein extraction from green tea leaf residue. Ind. Crop. Prod. 89, 95–102.
Zhang, C., Wu, X., Chen, J., Zhou, J., 2024. Novel fungal alternative proteins from Penicillium limosum for enhancing structural and functional properties of plant-based meat analogues. Food Chem. 444, 138627.