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Influence of low-intensity artificial light on the fatty acid profile of the biotechnologically important culinary mushroom *Pleurotus eryngii* in vitro

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Abstract

Background The problem of searching for environmentally friendly regulators of the biosynthetic activity of edible and medicinal mushrooms is crucial for creating highly effective biotechnologies. One such regulator is light. This study aimed to compare and evaluate the fatty acid profile and fat quality indices of lipids from the mycelial mass of *Pleurotus eryngii* under various light-emitting diode (LED) and laser light irradiation regimes.

Methods To determine the effect of artificial light on the biosynthetic activity of *P. eryngii*, an artificial lighting system based on LED matrices with wavelengths of 470 nm (blue), 530 nm (green), and 650 nm (red), as well as an argon gas laser as a coherent visible light source at 488 nm, was used. For all experimental variants, the energy density on the surface of the samples was set to the same, providing an energy dose of 240 mJ/cm^2. Irradiation was carried continuously.

Results Twenty-seven fatty acids were identified in the studied *P. eryngii* mycelial mass samples, including nine saturated fatty acids (SFAs), eight monounsaturated fatty acids (MUFAs) and ten polyunsaturated fatty acids (PUFAs). The control sample (without irradiation) contained the lowest number of fatty acids (fourteen). With irradiation in all modes, a decrease in the amount of SFA and the formation of new MUFA and PUFA with a chain length of C20-C24, which were absent in the control, were observed. Blue light stimulated the synthesis of significant amounts of α-linolenic acid (C18:3ω-3). The ratios of ΣPUFA/ΣSFA, ΣPUFA/ΣMUFA and ΣPUFAω-6/ω-3 in the mass of mycelium irradiated with blue light were within the optimal values for the human diet.

Conclusions The selected mycelial photoactivation modes using low-intensity laser and LED light of different spectral composition and coherence may have potential in the biotechnology of submerged cultivation of *P. eryngii* to obtain mycelial mass with an improved fatty acid profile, which can be considered as a useful source of lipids.

Keywords Fungi, LED, Laser, Pure culture, Fatty acids

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Introduction

One of the priority areas of modern biotechnology is the development and implementation of innovative methods for cultivating edible and medicinal macromycetes to obtain a wide range of commercially valuable biotechnological products [1–3]. Modern research confirms that edible and medicinal macromycetes can synthesise many biologically active substances with high biomedical potential [1, 4, 5]. Based on the mycelial mass and culture liquid of medicinal macromycetes, functional food products, nutraceuticals, new-class drugs—the so-called "fungal medicinal products"—biopreparations with fungicidal and bactericidal activity, and cosmetics are being developed [2, 6, 7]. One such biotechnologically valuable or culinary mushroom species is *P. eryngii*, also known as the king oyster mushroom. Due to its high protein and dietary fiber content and the presence of water-soluble vitamins, minerals, essential fatty acids, and amino acids, this species is a high-quality and low-calorie food and an alternative deputy to meat, fish, and vegetables [8–11]. Moreover, in the fruiting bodies and mycelia of *P. eryngii*, bioactive components, such as polysaccharides [12–14], sterols [15], polyphenols, terpenes [15, 16], which have antioxidant, antihyperlipidemic, antidiabetic, anti-inflammatory and immunostimulating activities have been identified [14, 17, 18]. Given its beneficial effects on human health, the fruiting bodies and mycelial mass of *P. eryngii* can be used as potential sources for the development of functional foods or nutraceuticals [9, 11, 15, 16].

Advances in mushroom biotechnology, particularly in the mushroom cultivation industry, focus on optimizing the use of mushroom resources to drive economic growth and enhance human well-being [1, 19]. When cultivating producers of biologically active metabolites, it is important to focus efforts on establishing parameters for obtaining the desired final product. The search for eco-friendly regulators of the biosynthetic activity of macromycetes remains a relevant task. One of such regulatory factors can be considered low-intensity laser and LED light. While significant progress has been made in using artificial light in plant growing, the bioregulatory effect of this factor on the biosynthetic activity of macromycetes remains insufficiently studied, and the choice of optimal modes of their use requires further justification. Understanding the effects of artificial low-intensity light on fungal metabolism may positively impact the development of bioprocesses that focus on the targeted synthesis of specific bioactive compounds. Several researchers have studied the spectral sensitivity of *P. eryngii* for fruiting and the antioxidant activity of fruiting body extracts [20, 21]. However, growing mushroom fruiting bodies requires a relatively long period, resources, and labor. An alternative approach is submerged fermentation, which enables the rapid and cost-effective production of the final product while also being more environmentally sustainable [22]. Replacing edible mushroom fruiting bodies with cultured mycelia obtained through submerged cultivation holds significant potential for food production applications [3].

Modern research confirms the potential of artificial light to enhance the efficiency of edible and medicinal mushroom cultivation technologies [23–27]. However, its primary application has been to increase fruiting body yield, while its use in submerged cultivation remains largely unexplored. In natural environments, fungi adapt to light exposure through metabolic changes, particularly in fatty acid composition. In this context, unsaturated fatty acids play a critical role, potentially influencing fungi's photoreception ability [28]. However, the effect of artificial light on the lipid composition of the cultivated mycelial mass remains insufficiently studied. In this aspect, the study of the effect of LED and laser light on the metabolism of *P. eryngii* seems to be a promising task for the targeted regulation and intensification of the cultivation process of this valuable fungus species.

Currently, there are no available data in the literature on the specific influence of LED and laser light on the fatty acid profile of *P. eryngii* under submerged culture conditions. Meanwhile, consumer interest in the fatty acid composition of various food products is steadily increasing. Since the human body requires essential fatty acids that cannot be synthesized internally and must be obtained through diet, edible and medicinal mushrooms are emerging as promising candidates for the development of functional foods, nutraceuticals, and dietary supplements [9, 29, 30]. Along with protein, lipids play an important role in nutrition, and their value increases with increasing polyunsaturated fatty acid content. It is well-known that polyunsaturated fatty acids with chain lengths of C_{18} to C_{22} play an important role in basic metabolism and have a high potential for beneficial effects on the human body [31, 32].

In this context, investigating the factors that regulate the fatty acid profile of edible mushrooms is highly relevant. The fat content of mushrooms is low. According to several authors [31, 32], the lipid content in the mycelium of cultivated mushrooms can reach no more than 15%. However, they contain unsaturated fatty acids, which account for more than 70% of the total fatty acid content. The lipids of basidiomycetes contain the same fatty acids that are found in other eukaryotic organisms. The fatty acid composition of lipids is represented by a homologous series of saturated and unsaturated acids. The predominant unsaturated fatty acids, as a rule, are linoleic ($C_{18:2\omega-6}$) (from 30 to 40% or more of the total fatty acids) and oleic acid ($C_{18:1\omega-9}$) (10–20%), which are necessary for the synthesis of prostaglandins, and among the saturated fatty acids, such as palmitic acid ($C_{16:0}$) (20–30%

of the total fatty acids). Other acids are found in smaller amounts [33–35].

Considering the nutritional and pharmacological value of *P. eryngii* and its potential for developing of functional food products, we conducted a study to explore the possibility of regulating the fatty acid composition of its mycelial mass through photoregulation.

The current study aimed to investigate the impact of LED and laser light on the qualitative and quantitative composition of fatty acids, as well as the quality indices of lipids in the mycelial mass of the biotechnologically important mushroom species *P. eryngii*.

Materials and methods

Mushroom sample and cultivation conditions

The subject of the research was a pure culture of the edible basidiomycete *P. eryngii var. ferula* IBK 2035, which is preserved in the Mushroom Culture Collection at the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine (acronym IBK) (occurrence dataset available: https://www.gbif.org/occurrence/2580369484, accessed on March 30, 2024). The taxonomic status of *P. eryngii var. ferula* IBK 2035 has been confirmed at the species level using molecular genetic methods and deposited in the NCBI database available at GenBank (accession number: MN646251.1) (https://www.ncbi.nlm.nih.gov/nuccore/MN646251.1). According to the Index Fungorum database, *P. eryngii var. ferulae* is considered a synonym of *P. eryngii* (http://www.indexfungorum.org, accessed on March 30, 2024). In addition, in previous studies, we established the main cultural and morphological characteristics of the IBK 2035 strain, which can be used to control its purity in the vegetative stage of growth at all stages of cultivation [36].

Cultivation of the mycelial mass was carried out in 0.5 L Erlenmeyer flasks, containing 100 mL of the liquid medium glucose-peptone-yeast (GPY), g/L: glucose – 25.0; peptone – 3.0; yeast extract – 2.0; KH_2PO_4 – 1.0; K_2HPO_4 – 1.0; $MgSO_4 \cdot 7H_2O$ – 0.25; pH 6.0. Cultivation in submerged culture conditions by shaking on an orbital shaker at 120 rpm at 26 °C for 12 days in darkness.

The impact of artificial low-intensity irradiation using leds and laser on the fatty acid composition of mycelial mass

The effect of artificial low-intensity irradiation on the fatty acid composition of *P. eryngii* IBK 2035 mycelia was studied following a previously described procedure [37]. The graphical scheme of the investigations is presented in Fig. 1. To investigate the effect of LED light on the biosynthetic activity of *P. eryngii* mycelium, including its fatty acid profile, an artificial lighting system based on light-emitting diode matrices developed by the Institute of Physics of the National Academy of Sciences of Ukraine (Kyiv, Ukraine) was used in combination with an LHN-106M1 argon ion laser [37]. LEDs emitting light with wavelengths of $\lambda = 470$ nm (blue), $\lambda = 530$ nm (green), and $\lambda = 650$ nm (red) were used as LED sources.

As a source of coherent visible light, an LHN-106M1 argon ion laser was used, and wavelength selection was achieved through a Litrow prism. This allowed the laser to generate monochromatic radiation at 488 nm. In all variants of experiments, the conditions of equal energy doses of light effects on the vegetative mycelium were chosen so that for all light sources, the energy density on the surface of the sample was the same and amounted to

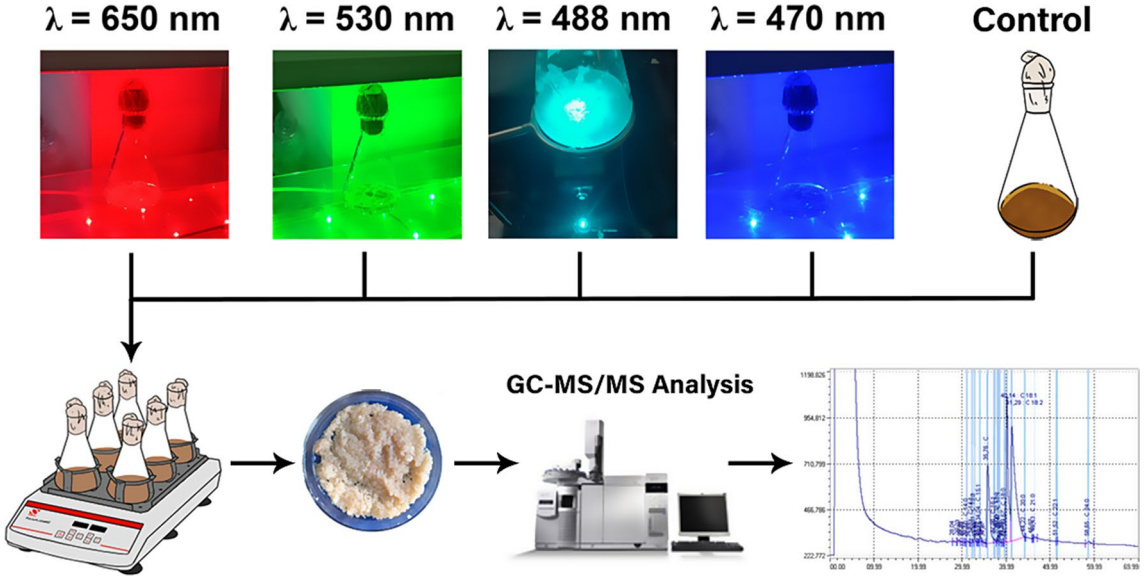

Fig. 1 Graphical visualization of the main steps carried out in the investigations

240 mJ/cm^2 in our experiments. The calculated parameters of the lighting system are given in the Supplementary Materials (Supplementary Table 1). Flasks with mycelia were irradiated continuously. When choosing the exposure time, we assumed that a possible mechanism responsible for the biological activity of light is initiated by the absorption of a single photon of the LED and laser radiation with a disruption of the biological system. Taking this into account, the exposure time was chosen so that the number of falling photons was practically the same when treating the mycelium with light of different wavelengths. Nonirradiated (control) and irradiated mycelium were used to study the effect of light on fatty acids and aromatic compounds. After irradiation, the mycelia were sown in an amount of 10% by volume in an Erlenmeyer flask containing 100 mL of the liquid medium GPY. After 12 days of cultivation, four grams of mycelial mass was taken for the determination of the fatty acid profile and the aromatic components.

Determination of fatty acid composition of mycelial mass

Extraction of fatty acids from the lipid fraction of the crushed mycelial mass *P. eryngii* was carried out with a mixture of chloroform/methanol/water 2:2:1.8 (v/v/v) according to the Bligh and Dyer method. After extraction, the lipid fraction was dissolved in 1 mL of hexane and subjected to methylation using 3–5 drops of a 30% solution of sodium methoxide in methanol. Chromatography of fatty acid methyl esters was carried out on a "Kristalyuks-4000 M" gas chromatograph with a flame-ionization detector (FID). The separation of the substances under study was carried out on a Zebron ZB-WAX capillary column with a stationary phase of 100% polyethylene glycol (length 30 m, internal diameter 0.32 mm, stationary phase layer (0.25 μm). The chromatography conditions were as follows: the column temperature ranged from 50 to 220 °C at a rate of 4 °C/min; the evaporator temperature was 230 °C, the detector temperature was 250 °C, the inlet pressure of the special purity nitrogen column was 0.8 atm, the blowing rate onto the detector was 30 cm^3/min, the discharge rate from the column was 10 cm^3/min, the volumetric flow rate of air was 300 cm^3/min, and the hydrogen flow rate was 30 cm^3/min. Chromatographic information was processed using the Netchromwin program.

Calculation of fat quality indices

Fat quality indices, including the ΣPUFA/ΣSFA, ΣPUFA/ΣMUFA, and ΣPUFA *ω-6/ω-3* ratios, atherogenic index (AI) [38], nutritive value index (NVI), thrombogenic index (TI) [39], and hypocholesterolemic (h)/hypercholesterolemic (H) fat acids, were calculated based on the results of fatty acid profiling of the mycelial mass under different irradiation regimes [40]. They were calculated according to the following equations: AI was calculated using Eq. 1, NVI was calculated using Eq. 2, TI was calculated using Eq. 3, h/H was calculated using Eq. 4:

$$\mathrm{AI} = \frac{(C12:0 + 4 \times C14:0 + C16:0)}{\Sigma MUFA + \Sigma PUFA} \quad (1)$$

$$\mathrm{NVI} = \frac{(\mathrm{C18:0} + \mathrm{C18:1})}{\mathrm{C16:0}} \quad (2)$$

$$\mathrm{TI} = \frac{(C14:0 + C16:0 + C18:0)}{\left[\begin{array}{c}(0.5 \times MUFA) + (0.5 \times \Sigma\omega - 6) \\ + (3 \times \Sigma\omega - 3) + (\Sigma\omega - 3/\Sigma\omega - 6)\end{array}\right]} \quad (3)$$

$$h/H = \left[\begin{pmatrix} C_{18:1\omega-9} + C_{18:1\omega-7} \\ + C_{18:2\omega-6} + C_{18:3\omega-6} \\ + C_{18:3\omega-3} + C_{20:3\omega-6} \\ + C_{20:4\omega-6} + C_{20:5\omega-3} \\ + C_{22:4\omega-6} + C_{22:5\omega-3} \\ + C_{22:6\omega-3} \end{pmatrix}\right] / (C_{14:0} + C_{16:0}) \quad (4)$$

Statistical analysis

The cultivation, sampling, and analysis were performed in triplicate. The results of the quantitative content of fatty acids in the mycelium samples were considered the average value between the three replicates. Factor analysis was used to identify the basic structure of the fatty acid profile of the mycelial mass of the edible medicinal mushroom and to identify important factors. Factor analysis was performed via principal component analysis using the interactive web computing platform Jupyter Notebook.

Results

Fatty acid composition and fat quality indices

A comparative analysis of lipid fractions of the mycelial mass of *P. eryngii* made it possible to establish variations and differences in the fatty acid profile depending on the irradiation mode (Table 1). The chromatograms of the fatty acid composition of the mycelial mass *P. eryngii* under various irradiation modes are presented in Supplementary Tables 2–6.

A total of twenty-seven fatty acids were identified in the studied samples of *P. eryngii* mycelial mass, of which nine were SFAs, eight were MUFAs, and ten were PUFAs (Table 1). Fourteen fatty acids were identified in the control sample (without irradiation). It should be noted that there was a general tendency that for all irradiation modes used, an increase in the amount of fatty acids was observed relative to the control. Twenty fatty acids were identified in the mycelium sample irradiated with blue light, twenty-five fatty acids were identified with green light, and twenty-four fatty acids were identified with red light irradiation (Table 1).

Table 1 Fatty acid composition of the mycelial mass of *Pleurotus eryngii* under different modes of irradiation with LED and laser light

No.	Fatty acids	Irradiation modes, nm				
		Control	LED			Laser
			λ = 470	λ = 530	λ = 650	λ = 488
Saturated Fatty Acids (SFA), content %						
1.	Myristic acid ($C_{14:0}$)	ND	0.794*	0.241*	0.352*	ND
2.	Pentadecanoic acid ($C_{15:0}$)	ND	ND	0.8534*	0.254*	0.342*
3.	**Palmitic acid ($C_{16:0}$)**	**14.03**	**12.82**	**12.38**	**13.16**	**14.25**
4.	Margaric acid ($C_{17:0}$)	0.1310	0.769	0.173	0.094	0.642
5.	Stearic acid ($C_{18:0}$)	9.183	1.919	1.513	5.44	1.148
6.	Arachidic acid ($C_{20:0}$)	4.429	ND▲	1.801	3,801	1.416
7.	Behenic acid ($C_{22:0}$)	ND	ND	1.9598*	ND	ND
8.	Tricosanoic acid ($C_{23:0}$)	1.865	1.569	1.527	1.840	ND▲
9.	Lignoceric acid ($C_{24:0}$)	ND	ND	0.3221*	0.990*	0.502*
Monounsaturated Fatty Acids (MUFA), content %						
10.	Myristoleic acid ($C_{14:1\ \omega-5}$)	ND	0.999*	ND	0.269*	ND
11.	*cis-10*-pentadesenoic acid ($C_{15:1}$)	ND	1.078*	1.160*	1.654*	ND
12.	Palmitoleic acid ($C_{16:1\omega-7}$)	0.7182	4.640	2.735	4.389	5.426
13.	*cis-10*- heptadecenoic acid ($C_{17:1}$)	1.357	1.231	1.218	1.054	1.886
14.	**Oleic acid ($C_{18:1\omega-9}$)**	**18.79**	**24.99**	**21.24**	**22.19**	**21.12**
15.	Gondoic acid ($C_{20:1\omega-9}$)	ND	0.651*	0.382*	1.186*	0.249*
16.	Erucic acid ($C_{22:1\omega-9}$)	ND	1.873*	1.495*	1.054*	1.634*
17.	*cis*-15-tetracosenoic acid ($C_{24:1\omega-9}$)	ND	0.220*	0.142*	0.2154*	0.452*
Polyunsaturated Fatty Acids (PUFA), content %						
18.	**Linoleic acid ($C_{18:2\omega-6}$)**	**39.03**	3.315	**40.06**	**33.88**	1.688
19.	γ-linolenic acid ($C_{18:3\omega-6}$)	2.036	2.819	3.311	2.355	2.868
20.	**α-linolenic acid ($C_{18:3\omega-3}$)**	5.70	**36.32**	1.643	1.056	**41.51**
21.	Eicosadienoic acid ($C_{20:2\omega-6}$)	ND	1.264*	1.572*	1.441*	1.811*
22.	Arachidonic acid ($C_{20:4\omega-6}$)	ND	0.649*	0.921*	ND	0.014*
23.	*cis*-5,8,11,14,17-eicosapentaenoic acid ($C_{20:5\omega-3}$)	ND	ND	0.766*	ND	1.149*
24.	*cis*-11,14,17-eicosatrienoic acid ($C_{20:3\omega-3}$)	1.016	ND▲	1.463	1.291	ND▲
25.	*cis*-8,11,14-eicosatrienoic acid ($C_{20:3\omega-6}$)	1.152	ND▲	0.843	0.141	1.263
26.	*cis-13,16*-docosadiendienoic acid ($C_{22:2\omega-6}$)	0.458	0.4137	0.224	0.485	0.554
27.	*cis-4,7,10,13,16,19*- docosahexaenoic acid ($C_{22:6\omega-3}$)	ND	1.331*	ND	1.405*	ND

Notes: ND – not determined. «*» – newly formed fatty acids compared to the control. «▲» – fatty acids lost compared to the control

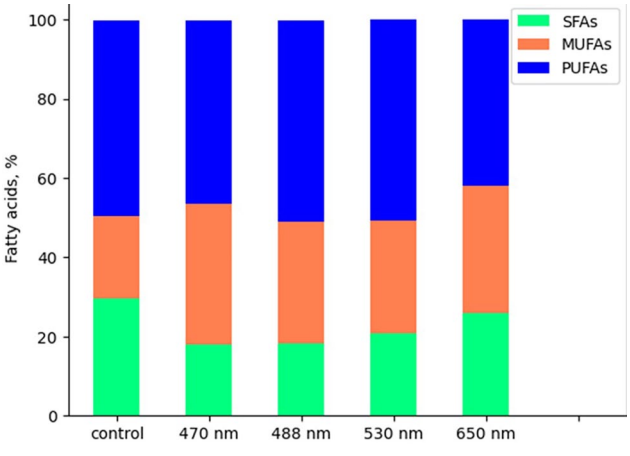

Fig. 2 The total content of saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs), and polyunsaturated fatty acids (PUFAs) in the mycelia of *Pleurotus eryngii* IBK 2035 under different irradiation modes

The content of SFA was highest in the control sample (without irradiation) and reached 29.63%. Under all the tested irradiation modes, the number of SFAs decreased; the lowest value of 17.87% was recorded for mycelial mass irradiated with blue light, and the highest value of 25.93% was recorded for mycelial mass irradiated with red light (Fig. 2).

The main component of SFA in all variants of the studied samples was palmitic acid, and its amount varied from 12.38% when the samples were irradiated with blue LED light to 14.25% when the samples were irradiated with laser light. SFA lauric acid ($C_{12:0}$) and myristic acid ($C_{14:0}$) are among the most atherogenic agents contributing to hypercholesterolemia. In all studied samples, these SFAs were not detected or were present at low concentrations ($C_{14:0}$: 0.352–0.794%), which can be considered a positive factor when consuming the mycelial mass of *P. eryngii* as a food product.

In the mycelium of *P. eryngii* MUFAs and PUFAs make up the majority of the total amount of fatty acids (Table 1). Analysing the increase in the amount of fatty acids under different irradiation modes, it should be noted that there is a significant difference in the qualitative composition the formation of new MUFAs with a chain length of C_{20}–C_{24} under all irradiation modes. In the mycelial mass after irradiation, ω-9 MUFAs, oleic acid ($C_{18:1ω-9}$), gondoic acid ($C_{20:1ω-9}$), and erucic acid ($C_{22:1ω-9}$), which are essential fatty acids, were identified. It should be noted that the amount of oleic acid increased under all irradiation modes; the maximum amount was recorded when the sample was irradiated with blue LED light (24.99%). Gondoic acid and erucic acid were absent in the control samples but were synthesized under all irradiation modes. Linoleic acid ($C_{18:2ω-6}$) and α-linolenic acid ($C_{18:3ω-3}$) were the main PUFAs in the studied samples. Blue light induced the synthesis of a significant amount of α-linolenic acid ($C_{18:3ω-3}$) in the mycelial mass and inhibited the formation of linoleic acid ($C_{18:2ω-6}$) relative to the control and other modes used (Table 1). In addition, irradiation under all modes contributed to the enrichment of the qualitative composition of PUFAs. The following PUFAs were synthesized under all irradiation modes: eicosadienoic acid ($C_{20:2ω-6}$), arachidonic acid ($C_{20:4ω-6}$), *cis*-5,8,11,14,17 eicopentaenoic acid ($C_{20:5ω-3}$), and *cis*-4,7,10,13,16,19-docosahexaenoic acid ($C_{22:6ω-3}$), which were absent in the control samples. Two PUFAs *cis*-11,14,17-eicosatrienoic acid ($C_{20:3ω-3}$) and *cis*-8,11,14-eicosatrienoic acid ($C_{20:3ω-6}$), were lost upon irradiation with blue light compared to the control.

The ratios ΣPUFA/ΣSFA, ΣPUFA/ΣMUFA, and ΣPUFAω-6/ω-3 are commonly used parameters to evaluate the nutritional value and healthfulness of a food product for human consumption. A balanced dietary intake of ΣPUFAs and ΣSFAs is important for regulating serum cholesterol levels. In general, ΣPUFA/ΣSFA values greater than 0.45 are recommended for use in the human diet to prevent the development of cardiovascular disease and some chronic diseases. In the studied mycelial mass samples, this indicator ranged from 1.62 (650 nm) to 2.7 (488 nm) (Table 2), so this parameter, regardless of the irradiation mode, fell within the recommended range.

Table 2 Fat quality indices of lipids obtained from the mycelial mass *Pleurotus eryngii* IBK 2035

Item	Control	470 nm	530 nm	650 nm	488 nm
ΣSFAs	29.63[a]	17.87	20.77	25.93	18.30
ΣMUFAs	20.87[b]	35.68[a]	28.37	32.01	30.77
ΣPUFAs	49.39	46.11	50.80	42.05[b]	50.85[a]
ΣPUFA/ΣSFA	1.67	2.58	2.4	1.62[b]	2.7[a]
ΣPUFA/ΣMUFA	2.4[a]	1.29[b]	1.79	1.3	1.65
PUFAω-3	6.72	37.65	3.87[b]	3.75	43.21[a]
PUFAω-6	42.68	8.46	46.53[a]	38.30	7.64[b]
ΣPUFAω-6/ω-3	6.35	0.22	12.12[a]	10.21	0.17[b]
NVI	2.0	2.1	1.8	2.1	1.6
AI	0.19[a]	0.19[a]	0.17[b]	0.19[a]	0.17[b]
TI	0.45[a]	0.26	0.29	0.41	0.1[b]
h/H	4.83	4.64	5.5[a]	4.62[b]	4.89

Note: Values are the means of three determinations. ΣSFAs: total saturated fatty acids; ΣMUFAs: total monounsaturated fatty acids; ΣPUFAs: total polyunsaturated fatty acids; NVI: nutritive value index; AI: atherogenic index; TI: thrombogenic index; h/H: ratio of hypocholesterolemic (h)/hypercholesterolemic (H) index fatty acids. A and b within a row represent the highest and lowest significant ($p < 0.05$) values, respectively

When considering the ΣPUFA indicator in the diet balance, it is necessary to take into account such important indicators as ΣPUFAω-3 and ΣPUFAω-6. A high proportion of ΣPUFAs is not necessarily beneficial for health unless it is balanced for Σω-6/ω-3 PUFAs. This ratio is an indicator of the hypocholesterolemic index. ΣPUFAsω-3 play a major role in the regulation of the thrombogenic index (TI), whereas ΣPUFAω-6 dominate the atherogenic index (AI). The AI, TI, and h/H indices are well-known indicators of the atherogenic, thrombogenic, and hypo- or hypercholesterol potential of fatty acids, respectively, and they are widely used to assess the nutritional quality of the lipid fraction of foods [32, 39].

A healthy food product should be characterized by low AI and TI values and a high h/H index. In the diet, a ΣPUFAω-6/ω-3 ratio less than 4.0 indicates desirable amounts of ω-3 and ω-6 fatty acids and a reduced risk of cardiovascular disease. In our study, the ratio of ΣPUFAω-6/ω-3 corresponded to such standards only for mycelia irradiated with blue light (Table 2). This is because blue light stimulated the synthesis of α-linolenic acid ($C_{18:3ω-3}$), which significantly affected the ΣPUFAω-6/ω-3 index. The lowest AI value (0.17) was recorded when the samples were irradiated with green and laser light. The AI in the control and when irradiated with blue LED and red light did not differ (0.19).

TI indicates the relationship between the sum of the main SFAs and the sum of the main classes of MUFAs, with the former considered pro-atherogenic (promoting the adhesion of lipids to the cells of the circulatory system) and the latter inhibiting plaque aggregation and reducing the level of esterified fatty acids and cholesterol. In the mycelium samples studied, a decrease in TI values was observed under all irradiation modes relative to the control; the lowest values were recorded for mycelia irradiated with blue light.

The h/H index reflects the effect of certain fatty acids on cholesterol metabolism. Higher h/H values in terms of nutritional value are considered beneficial for human health. The h/H indices obtained in this study ranged from 4.62 to 5.5, with maximum values recorded under blue and green light.

Thus, the analysis of the results obtained shows that when the mycelium is irradiated, the main indicators shift within the limits of optimal values for the human

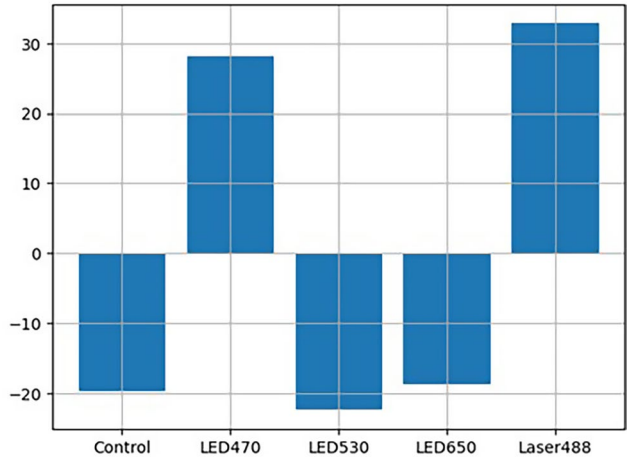

Fig. 3 Graphical representation of the estimates for PC1 under various irradiation modes

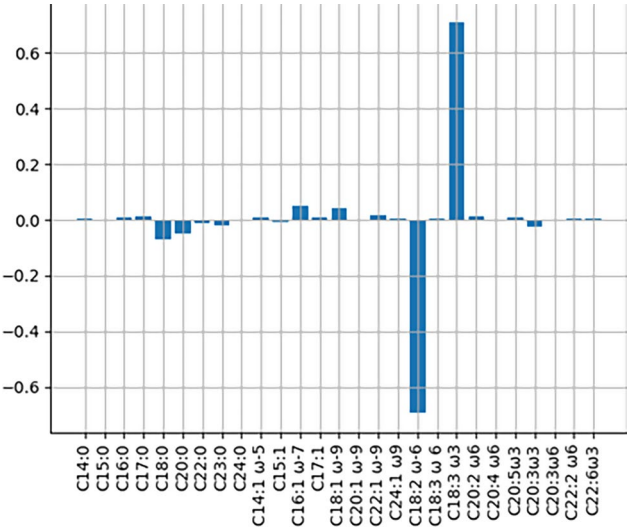

Fig. 4 Graphical representation of the estimates for the fatty acid profile of the mycelial mass in factor loadings

diet; the samples irradiated with blue light were the most effective. The highest NVI value was typical for mycelia irradiated with blue and red light (Table 2). Therefore, we can conclude that irradiation with low-intensity LED light and a laser affects the fatty acid profile of the *P. eryngii* mycelial mass. Changes occurred in both the quantitative and qualitative composition of the components. The results obtained confirm that the mycelial mass of *P. eryngii* obtained from all tested regimes can be considered beneficial in terms of the fatty acid profile and healthy lipid composition indicators.

The saturated fatty acids $C_{12:0}$ and $C_{14:0}$, which contribute to hypercholesterolemia, were not detected or were present at low concentrations, which indicates that mushroom mycelia consumption is a positive factor. The ΣPUFAω-6/ω-3 ratios in our studies for irradiated mycelium were close to the recommended values. The ΣPUFA/SFA, ΣPUFA/MUFA, and ΣPUFAω-6/ω-3 indices of the mycelial mass irradiated with blue light are within the optimal values for the human diet.

Principal component analysis (PCA)

PCA extracts data that distinguish different groups and simplifies the estimation procedure by eliminating irrelevant data. As a result of performing a factor analysis using the principal component method, it was established that the first principal component provides a 96.7% representation of the variability of the fatty acid profile of *P. eryngii* under various modes of irradiation with LEDs and laser light. Therefore, there is no need to consider the following main components. A graphical representation of the first principal component is shown in Fig. 3, Supplementary Table 7).

According to the analysis shown in Fig. 3, blue light, both LED and laser, had the greatest effect on the fatty acid profile of the mycelial mass of *P. eryngii*. In addition, Fig. 4 shows the contribution of each fatty acid to factor loadings under the most effective irradiation modes.

By analysing the fatty acid profile of the mycelial mass using PCA, we can confidently state that blue light, both laser and LED, induced the synthesis of a significant amount of α-linolenic acid ($C_{18:3\ \omega-3}$) in the mycelial mass and inhibited the formation of linoleic acid ($C_{18:2\ \omega-6}$) relative to the control and other modes used (Fig. 4). Based on the obtained PCA data, it can be concluded that assessing the variability of the fatty acid profile of this mushroom, it is sufficient to control the content of only these two fatty acids.

A significant increase in the amount of α-linolenic acid ($C_{18:3\omega-3}$) and a decrease in the amount of linoleic acid ($C_{18:2\omega-6}$) in the mycelial mass of the mushroom significantly influenced the ΣPUFAω-6/ω-3 index. In our study, the ratio of ΣPUFAω-6/ω-3 corresponded to the standards of optimal values for the human diet for mycelium irradiated with blue light (Table 2). Additionally, the ΣPUFA/SFA, ΣPUFA/MUFA, and ΣPUFAω-6/ω-3 indices of the mycelial mass irradiated with blue light are within the optimal values for the human diet.

Discussion

Currently, solving problems associated with obesity and metabolic disorders in a significant part of the population remains relevant. In this regard, edible mushrooms, including *P. eryngii*, can be considered potential candidates for the development of functional food products and nutraceuticals [8, 41–43]. One of the environmentally friendly regulators of morphogenesis and metabolic pathways in fungi is light [44].

During evolution, fungi have formed a photoregulatory system, mycochrome, which is characterized by the

dependence of several stages of morphogenesis and physiology on the duration and intensity of light exposure [45]. For most macromycetes, light is an important source of both temporal and spatial information regarding environmental changes [46]. Additionally, light can serve as an indicator of various environmental stresses, such as exposure to genotoxic ultraviolet (UV) radiation, oxidative stress, increasing temperature, or decreasing humidity [47, 48]. The photoreception of various fungi has been studied for over 150 years, and it has been established that fungi's responses to light can be both rapid, such as phototropism, and long-term. The mechanisms of light perception by fungi are considered by several researchers as an effective tool for increasing the functional activity of fungal cells [44, 49]. Despite the significant variability of photobiological responses in fungi, researchers have identified universal mechanisms of photostimulation [44, 50–52]. It has been demonstrated that short-term exposure to laser and LED light (from several seconds to tens of minutes) can significantly increase the functional activity of cells of both animal and plant origin [44, 53]. At the same time, the long-term effects of light exposure depend mainly on genetic reprogramming of the fungal genome and involve changes in gene expression patterns. A key question is how such coordinated activation and repression of hundreds of genes is achieved [51, 54]. The issue of photoreception of light energy in the mycelium and the mechanisms of reactions occurring after absorption of light photons remains complex and continues to be intensively studied. It is known that fungal light sensors are chromoproteins - low-molecular compounds that absorb light in certain parts of the spectrum and initiate protein reactions. Some specialized photoreceptive proteins or protein complexes with diverse structures, mechanisms of action, and photosensitivity have been identified in fungi [27].

Photoreceptors detect light and generate a signal that propagates within the cell and stimulates a cellular response. Their light-absorbing cofactors, known as chromophores, are heterocyclic organic molecules that can capture photons of light [51, 55]. Fungal photoreceptors often contain multiple protein domains that perform different functions. Typically, a photoreceptor domain is either attached or located close to a chromophore and can chemically interact with it when exposed to light [56]. The first step in the perception of light by a fungal organism is a physical reaction: the absorption of photons by an organic chromophore molecule. This initiates a light-dependent signalling pathway that causes conformational changes in the protein and subsequent signal transduction into biochemical reactions that affect gene expression [51]. To date, photoreactions of more than 100 fungal species belonging to different taxonomic groups have been studied. Particular attention is paid to studying the perception of light signals by fungi and their transformation into morphological, physiological and metabolic reactions [20, 23–25, 27, 57–60].

The mechanisms of perception of blue, near UV, green and red light by fungi have been studied [44, 50]. It has been established that the processes of spore germination, mycelial development and growth, formation of anamorphic and teleomorphic stages, as well as changes in the chemical composition of the mycelium and fruiting bodies, can be regulated by certain light regimes [44, 50, 61, 62]. It is now known that fungi perceive light signals in a wide range of wavelengths using various photoreceptors. Fungi can perceive near ultraviolet, blue, green, red, and far-red light due to the presence of up to 11 photoreceptors and corresponding signalling cascades that control a significant part of the genome. These mechanisms allow fungal organisms to adapt to changes in environmental conditions [48]. To date, the following types of blue light receptors have been identified: White Collars (WC), Vivid (VVD), Cryptochrome and Photolyase [44, 56]. WC proteins are the most studied fungal light receptors. The second group of blue light photoreceptors - Vivid protein (VVD), which is widespread in the fungal kingdom. The third group of blue light receptors is represented by specialized proteins of the Cryptochrome and Photolyase families, discovered only in the 1990s. Their functions are still less studied in detail compared to WC and VVD [56].

Blue light photoreceptors such as White Collar-1 and White Collar-2 (WC-1/2) have been experimentally shown to regulate gene expression and globally restructure cellular metabolism in fungi [48, 63–66]. Proteins similar to WC-1 and WC-2 have been identified in the genomes of many species of ascomycetes, basidiomycetes, and zygomycetes. They are responsible for the photoresponse of fungi to light. It is suggested that WC complexes arose early in the evolution of fungi, acting as both photoreceptors and transcription factors [51, 55].

Genes responsible for blue light photoreception have been identified in basidiomycetes such as *Coprinus cinereus* and *Lentinula edodes* [64, 66]. Kanda et al. (2007) identified photoregulatory genes controlling tyrosinase enzymatic activity in macromycetes such as *Agaricus bisporus*, *L. edodes*, and *Polyporus arcularius* [67]. Nakano et al. (2010) first identified 15 genes with upregulated and 13 genes with downregulated expression in response to blue light in the vegetative mycelium of *Pleurotus ostreatus* [68]. Fungal genomes also contain genes for other photoreceptors. Red light perception is mediated by phytochromes, molecules that until recently were thought to be unique to plants [45, 46]. Phytochromes responsible for red and far-red light perception were first discovered in *Aspergillus nidulans* and *Neurospora crassa*. They are high-molecular proteins containing multiple domains for light reception and signal transduction.

A unique feature of phytochromes is their absence in vertebrates, while they are widespread in plants, bacteria, and fungi [56, 69]. Recently, retinal-based opsin systems have been discovered whose biological functions require further study. Opsins are membrane-bound proteins with seven transmembrane helices responsible for the perception of green light [48, 56]. They are essential components of vision in vertebrates, including humans, but their role in fungal photoreception remains poorly understood. Spectral sensitivity analysis suggests that flavin-related compounds are present in the photoreceptors of *Schizophillum commune*, *Coprinopsis congregatus* and *P. ostreatus* [70, 71]. However, identification of the different types of photoreceptors and their mechanisms of action in macromycetes requires further in-depth molecular and biochemical studies. In this way, the question of the structure, physicochemical properties and functionality of light-sensing biomolecules remains open. The diversity of photoreactions in different fungal species indicates the existence of a wide range of photoreceptor molecules, which explains the different photosensitivity among species and taxonomic groups.

Thus, the analysis of experimental works aimed at studying the mechanisms of photoreception in fungi confirms that light can be an effective tool for targeted regulation of morphogenesis and biological activity of fungi, which certainly opens up opportunities for the development of new environmentally friendly intensive technologies for their cultivation. Therefore, when cultivating the fruiting bodies of some species of edible macromycetes, blue light is used to stimulate growth and initiate the formation of fruiting bodies [72–75]. Research on the photoresponse mechanisms of *P. eryngii* under blue light exposure was carried out by a group of researchers [76]. Three main metabolic pathways have been identified that regulate the formation and growth of fruiting bodies when exposed to blue light, namely, the carbon metabolism, glycolysis/gluconeogenesis, and amino acid biosynthesis pathways [76]. Similar results for photostimulation of primary cells via blue light metabolic pathways were found in *P. ostreatus* [77]. This allows us to conclude that metabolic pathways are photostimulated in response to light exposure.

It is currently known that the magnitude of the final effect of short-term low-intensity laser radiation depends on the initial physiological state of the irradiated object, which is determined by its redox potential (a shift towards a more oxidized state is associated with stimulation of cell activity, and a shift towards a more reduced state is associated with its suppression). Due to light exposure, the redox potential of the cell is normalized [78]. The more pronounced the irradiation effect is, the more the redox potential of the cell is shifted to the reduced side. Moreover, one of the important components of the cell's redox system is the cell's unsaturated fatty acids, which are the substrate for the additional creation of free radicals in the cell under the influence of radiation.

Based on the above, we can assume that one of the mechanisms that ensures the ability of fungi to photoreceive different types of light is the corresponding changes in their fatty acid profile and the degree of unsaturation of cellular lipids. To understand the biological phenomena associated with the photoresponse of edible mushrooms, it is critical to precisely control both the wavelength and intensity of light. However, conventional light sources such as fluorescent lamps have a wide range of wavelengths, making it difficult to determine the effect of a specific wavelength range.

Advances in red, green, and blue LED technology have made it possible to use specific portions of the optical spectrum with precise control of the emission intensity. Additionally, when assessing the biochemical impact of light on mushrooms, it is necessary to consider the energy of the light quantum, the intensity of the light flux, the dose, and the spectral composition of light. From this point of view, LEDs can provide, even at low and medium intensities, spectral density (energy per single frequency interval) that is not available to other sources. With LED light, efficient irradiation can be achieved by suppressing unnecessary wavelengths and reducing energy costs by reducing unnecessary heat generation [72, 79].

Recently, the photobiological effect of LEDs on the biosynthetic activity of some species of edible mushrooms has been experimentally studied in vitro [58, 80–82]. In previous studies, we investigated the effect of LED and laser light at doses of 45–230 mJ/cm^2 on the morphogenesis and biosynthetic activity of some biotechnologically important species [83–85].

According to the literature, the fruiting bodies of *P. eryngii* are characterized by a high content of unsaturated fatty acids. Fifteen fatty acids have been identified in the fruiting bodies, of which ten are SFAs and five are MUFAs and PUFAs. For the fruiting bodies of *P. eryngii*, the PUFAs/SFAs and PUFAs/MUFAs ratio ranged from 4.05 to 6.84 respectively, indicating the high nutritional value of this species [86]. In our study, 27 fatty acids were identified in the mycelial mass samples of *P. eryngii*, including nine SFAs, eight MUFAs, and ten PUFAs. The control sample (without irradiation) contained the lowest number of fatty acids (fourteen). For the cultured mycelium, the maximum PUFA/SFA ratio did not exceed 2.8, and the PUFA/MUFA ratio was within 1.7, recorded during blue light irradiation (Table 2).

Previous publications have investigated the effects of LEDs and laser light on the growth characteristics and biosynthetic activity of valuable species of the culinary and medicinal mushrooms in vitro: *L. edodes* [37] and *Hericium erinaceus* [87]. The irradiation of the mycelia

of the studied species with blue (λ = 470 nm, λ = 488 nm) and red (λ = 650 nm) light significantly impacted the mushroom growth characteristics. Light inoculum treatment led to a reduction in the lag phase and an increase in the strain's growth rate. The highest biomass yield was recorded when irradiated with blue light. In addition, irradiation of mycelia with blue (470 nm; 488 nm), green (530 nm), and red (650 nm) light increased the synthesis of both extra- and intracellular polysaccharides. The most effective irradiation modes for all species were blue LED and laser light.

A comparative analysis of the lipid fraction of the mycelial mass of all studied species made it possible to establish a general positive trend in changes in the fatty acid profile under LED and laser irradiation. It should be noted that when the mycelia were irradiated in all modes, the qualitative composition of the mycelial mass improved, and the SFAs content decreased. At the same time, the amount of newly formed PUFAs and MUFAs increased.

These fluctuations in the content of SFAs, MUFAs, and PUFAs can be considered the result of inducible enzymatic reactions. In response to the influence of an external factor—irradiation—fungal cells synthesize inducible enzymes, in this case, desaturases, which catalyze the conversion of single bonds between carbon atoms in acyl chains (C–C) into double bonds (C = C).

For the *L. edodes* culture, a significant difference was noted in the qualitative composition of the mycelial mass: irradiation with red light produced short-chain acids C_6–C_{12}, while irradiation with green light induced the synthesis of long-chain acids C_{20}–C_{24} [37]. In addition, the greatest changes in the aromatic profile of the mycelial mass and culture liquid were recorded upon irradiation with green light. The content of aromatic components increased by 24.6 times in the mycelial mass and by 38.5 times in the culture liquid. The results obtained suggest the possibility of using low-intensity LED light for targeted regulation of the biosynthetic activity of biotechnologically important species of edible and medicinal mushrooms to improve their consumer characteristics [37].

In the context of global efforts toward sustainable development, culinary and medicinal mushrooms are becoming promising producers for creating functional foods, nutraceuticals, dietary supplements, and designer foods, including probiotics and prebiotics. However, realizing their full potential requires a deeper understanding of how various factors, including low-intensity artificial light, affect their morphogenesis, growth characteristics, and metabolic processes. Considering that light is an eco-friendly source that can be used to regulate various stages of biotechnological processes, further research on the intricate relationship between light and fungal physiology is necessary.

According to Sande [32], the fatty acid profile of *P. eryngii* fruiting bodies has a low SFA content (215.2–382.8 mg/100 g dry weight) and high MUFA and PUFA levels (127.3–68.4 mg/100 g dry weight and 870.1–1344.1 mg/100 g dry weight, respectively). In addition, indicators of the nutritional quality of the lipid fraction (AI was 0.17–0.19; TI was 0.34–0.49; h/H was 6.47–5.52).

The presence of a significant amount of PUFAs, including essential ones, in the mycelial mass of *P. eryngii* allows it to be classified as a useful source of lipids. According to the literature, the consumption of unsaturated fatty acids, especially long-chain polyunsaturated fatty acids, is necessary to reduce blood cholesterol levels and to regulate cellular physiology [88, 89]. Several fatty acids, such as oleic, linoleic, α-linolenic, and arachidonic acids, contained in the mycelial mass are essential for human metabolism [90]. In addition, the mycelial mass of *P. eryngii* contains various pharmacologically active compounds that can significantly enhance the nutraceutical effect of this species [91–93].

Thus, the results of the photoreaction studies in *P. eryngii* indicate the possibility of implementing the use of LEDs and laser light of a certain wavelength to regulate biosynthetic activity to obtain mycelium with an increased content of unsaturated fatty acids. However, further studies are needed to establish effective irradiation modes.

Conclusions

Environmentally friendly methods for targeted regulation of the fatty acid profile of the mycelial mass of the commercially important edible mushroom *P. eryngii* using low-intensity LEDs and laser light of varying coherence and spectral composition are proposed. Short-term low-intensity irradiation in the visible region of the spectrum stimulates the synthesis of monounsaturated and polyunsaturated fatty acids and improves the nutritional quality of the lipid fraction of the mycelial mass of *P. eryngii*.

The selected photostimulation modes can be used for submerged cultivation of king oyster mushrooms. By studying the photosensitivity of *P. eryngii*, new scientifically based experimental results were obtained, which together complement and expand our understanding of the photoreception processes of macromycetes.

Supplementary Information

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Supplementary Material 1

Supplementary Material 2

Supplementary Material 3

Supplementary Material 4

Supplementary Material 5

Supplementary Material 6

Supplementary Material 7

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Author contributions
O.M. and N.P. planned the work, contributed to the concept of the article, wrote and edited the manuscript, and conducted the study of the effect of low-intensity light on the fatty acid profile of mycelium mass under submerged culture conditions. M.L. performed a literature review, translated the manuscript into English, and prepared mycelium samples. A.N. determined the design of the light source and its operating modes, calculated the irradiation doses of the inoculum, irradiated it, discussed the effects of irradiation, and participated in the preparation of the article. A.B. performed the principal component analysis (PCA) and prepared the figures and tables. All authors contributed to the revision of the manuscript and read and approved the submitted version.

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Data availability
Data is provided within the manuscript or supplementary information files.

Declarations

Ethics approval and consent to participate
This research does not involve any ethical issues.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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References

1. Badalyan SM, Zambonelli A. The potential of mushrooms in developing healthy food and biotech products. Fungi Fungal Prod Hum Welf Biotechnol. 2023. p. 307–44. https://link.springer.com/chapter/10.1007/978-981-19-8853-0_11.
2. Badalyan S, Rapior S. Perspectives of biomedical application of macrofungi. Curr Trends Biomedical Eng Biosci. 2020;19(5):556024. https://doi.org/10.19080/CTBEB.2020.19.556024.
3. Berovic M, Boh B, Gregori A. Medicinal mushroom biotechnology. Anat Physiol Biochem Int J. 2024;7(4):555719. https://doi.org/10.19080/APBIJ.2024.07.555719.
4. Deshmukh SK, Sridhar KR, Badalyan SM. Fungal biotechnology: Prospects and avenues. 1st ed. CRC Press; 2022. https://doi.org/10.1201/9781003248316.
5. Badalyan SM, Borhani A. Medicinal, nutritional, and cosmetic values of macrofungi distributed in Mazandaran province of Northern Iran (Review). Int J Med Mushrooms. 2019;21:1099–106. https://doi.org/10.1615/IntJMedMushrooms.2019032743.
6. Kour H, Kour D, Kour S, Singh S, Jawad Hashmi SA, Yadav AN, et al. Bioactive compounds from mushrooms: Emerging bioresources of food and nutraceuticals. Food Biosci. 2022;50:102124. https://doi.org/10.1016/j.fbio.2022.102124.
7. Badalyan SM, Barkhudaryan A, Rapior S. Medicinal macrofungi as cosmeceuticals: A review. Int J Med Mushrooms. 2022;24:1–13. https://doi.org/10.1615/IntJMedMushrooms.2022043124.
8. Amerikanou C, Tagkouli D, Tsiaka T, Lantzouraki DZ, Karavoltsos S, Sakellari A, et al. *Pleurotus eryngii* chips—chemical characterization and nutritional value of an innovative healthy snack. Foods. 2023;12(2):353. https://doi.org/10.3390/foods12020353.
9. Mayirnao H-S, Sharma K, Jangir P, Kaur S, Kapoor R. Mushroom-derived nutraceuticals in the 21st century: An appraisal and future perspectives. J Future Foods. 2025;5:342–60. https://doi.org/10.1016/j.jfutfo.2024.07.013.
10. Raman J, Jang KY, Oh YL, Oh M, Im JH, Lakshmanan H, et al. Cultivation and nutritional value of prominent *Pleurotus* spp.: An overview. Mycobiology. 2020;49:1–14. https://doi.org/10.1080/12298093.2020.1835142.
11. Teniou S, Bensegueni A, Hybertson BM, Gao B, Bose SK, McCord JM, et al. Bio-driven investigation of the wild edible mushroom pleurotus eryngii revealing unique properties as functional food. J Funct Foods. 2022;89:104965. https://doi.org/10.1016/j.jff.2022.104965.
12. Chen SY, Ho KJ, Liang CH, Tsai CH, Huang LY, Mau JL. Preparation of culinary-medicinal King oyster mushroom pleurotus eryngii-fermented products with high ergothioneine content and their taste quality. Int J Med Mushrooms. 2012;14:85–93. https://doi.org/10.1615/IntJMedMushr.v14.i1.90.
13. Zhang B, Li Y, Zhang F, Linhardt RJ, Zeng G, Zhang A. Extraction, structure and bioactivities of the polysaccharides from pleurotus eryngii: A review. Int J Biol Macromol. 2020;150:1342–7. https://doi.org/10.1016/j.ijbiomac.2019.10.144.
14. Battaglia V, Sorrentino R, Verrilli G, del Piano L, Sorrentino MC, Petriccione M, et al. Potential use of carduncullus biomass on *Pleurotus eryngii* production: Heteroglycans content and nutritional properties (preliminary results). Foods. 2023;12(1):58. https://doi.org/10.3390/foods12010058.
15. Kikuchi T, Isobe M, Uno S, In Y, Zhang J, Yamada T, Strophasterols E. Rearranged ergostane-type sterols from pleurotus eryngii. Bioorg Chem. 2019;89:103011. https://doi.org/10.1016/j.bioorg.2019.103011.
16. Kikuchi T, Kitaura K, Katsumoto A, Zhang J, Yamada T, Tanaka R. Three bisabolane-type sesquiterpenes from edible mushroom pleurotus eryngii. Fitoterapia. 2018;129:108–13. https://doi.org/10.1016/j.fitote.2018.06.021.
17. Devi PV, Islam J, Narzary P, Sharma D, Sultana F. Bioactive compounds, nutraceutical values and its application in food product development of oyster mushroom. J Future Foods. 2024;4:335–42. https://doi.org/10.1016/J.JFUTFO.2023.11.005.
18. Xu J, Xu D, Hu Q, Ma N, Pei F, Su A, et al. Immune regulatory functions of biologically active proteins from edible fungi. Front Immunol. 2023;13. https://doi.org/10.3389/fimmu.2022.1034545.
19. Berovic M, Zhong JJ. Biochemical engineering and biotechnology of medicinal mushrooms. Springer Cham. 2023. https://doi.org/10.1007/978-3-031-36950-6.
20. Miyazaki Y, Masuno K, Abe M, Nishizawa H, Matsumoto T, Kunitomo S et al. Light-stimulative effects on the cultivation of edible mushrooms by using blue LED. In: Proceedings of the 7th International Conference on Mushroom Biology and Mushroom Products; Arcachon, France. Mushroom biology and mushroom products: Volume 2, Poster session. 2011. p. 58–67.
21. Yue Z, Zhang W, Liu W, Xu J, Liu W, Zhang X. Effect of different light qualities and intensities on the yield and quality of facility-grown *Pleurotus eryngii*. J Fungi. 2022;8(12):1244. https://doi.org/10.3390/jof8121244.
22. Berovic M, Zhong JJ. Advances in pilot-scale stirred bioreactors in solid-state and submerged cultivations of medicinal mushrooms. In: Berovic M, Zhong JJ, editors. Biochemical engineering and biotechnology of medicinal mushrooms. Advances in biochemical engineering/biotechnology, vol 184. Cham: Springer; 2022. p. 163–85. https://link.springer.com/chapter/10.1007/10_2021_196
23. Ha SY, Jung JY, Yang JK. Effect of light-emitting diodes on cordycepin production in submerged culture of Paecilomyces japonica. J Korean Wood Sci Technol. 2020;48:548–61. https://doi.org/10.5658/WOOD.2020.48.4.548.
24. Tiniola RC, Pambid RC, Adonis S, Bautista AS, Dulay RMR. Light-emitting diode enhances the biomass yield and antioxidant activity of Philippine wild mushroom Lentinus swartzii. Asian J Agric Biol. 2021;202008435. https://doi.org/10.35495/ajab.2020.08.435.

25. Akkan T, Çetin M, Akkan LÖ. The effect of different light wavelengths and lighting duration on the yield and quality of Pleurotus ostreatus mushroom. Ege Üniversitesi Ziraat Fakültesi Dergisi. 2024;61:437–47. https://doi.org/10.20289/zfdergi.1480768.
26. Chao SC, Chang SL, Lo HC, Hsu WK, Lin WT, Hsu TH. Enhanced production of fruiting body and bioactive ingredients of *Cordyceps militaris* with LED light illumination optimization. JAST. 2019;21:451–62. http://jast.modares.ac.ir/article-23-14310-en.html.
27. Galindo LJ, Milner DS, Gomes SL, Richards TA. A light-sensing system in the common ancestor of the fungi. Curr Biol. 2022;32:3146–e31533. https://doi.org/10.1016/j.cub.2022.05.034.
28. Corrochano LM. Fungal photoreceptors: Sensory molecules for fungal development and behaviour. Photochemical and Photobiological sciencesphotochem. Photobiol Sci. 2007;6:725–36. https://doi.org/10.1039/b702155k.
29. Navarro-Simarro P, Gómez-Gómez L, Ahrazem O, Rubio-Moraga Á. Food and human health applicationhnol. 2024;81:43–56. https://doi.org/10.1016/j.nbt.2024.03.003
30. Niego AG, Rapior S, Thongklang N, Raspé O, Jaidee W, Lumyong S, et al. Macrofungi as a nutraceutical source: Promising bioactive compounds and market value. J Fungi. 2021;7:397. https://www.mdpi.com/2309-608X/7/5/397/htm
31. Reis FS, Barros L, Martins A, Ferreira ICFR. Chemical composition and nutritional value of the most widely appreciated cultivated mushrooms: An inter-species comparative study. Food Chem Toxicol. 2012;50(2):191–7. https://doi.org/10.1016/J.FCT.2011.10.056.
32. Sande D, de Oliveira GP, Moura MAF, Martins B de A, Lima MTNS, Takahashi JA. Edible mushrooms as a ubiquitous source of essential fatty acids. Food Res Int. 2019;125:108524. https://doi.org/10.1016/J.FOODRES.2019.108524
33. Kalač P. A review of chemical composition and nutritional value of wild-growing and cultivated mushrooms. J Sci Food Agric. 2013;93(2):209–18. https://doi.org/10.1002/jsfa.5960.
34. Ragunathan R, Swaminathan K. Nutritional status of pleurotus spp. Grown on various agro-wastes. Food Chem. 2003;80(3):371–5. https://doi.org/10.1016/S0308-8146(02)00275-3.
35. Ulziijargal E, Mau J-L. Nutrient compositions of culinary-medicinal mushroom fruiting bodies and mycelia. Int J Med Mushrooms. 2011;13(4):343–9. https://doi.org/10.1615/INTJMEDMUSHR.V13.I4.40.
36. Bisko N, Lomberg M, Mykchaylova O, Mytropolska N, Kutovenko V, Gryganskyi A. Biology, morphology, and phylogeny of some strains of the *Pleurotus eryngii* species complex. Arch Biol Sci. 2022;74(3):271–81. https://doi.org/10.2298/ABS220524026B.
37. Mykchaylova O, Dubova H, Negriyko A, Lomberg M, Krasinko V, Gregori A, et al. Photoregulation of the biosynthetic activity of the edible medicinal mushroom lentinula edodes in vitro. Photochem Photobiol Sci. 2024;23:435–49. https://doi.org/10.1007/s43630-023-00529-8.
38. Ulbricht TLV, Southgate DAT. Coronary heart disease: Seven dietary factors. Lancet. 1991;338(8773):985–92. https://doi.org/10.1016/0140-6736(91)91846-M.
39. Wołoszyn J, Haraf G, Okruszek A, Wereńska M, Goluch Z, Teleszko M. Fatty acid profiles and health lipid indices in the breast muscles of local Polish goose varieties. Poult Sci. 2020;99(2):1216–24. https://doi.org/10.1016/J.PSJ.2019.10.026.
40. Fernandes CE, Vasconcelos MADS, De Almeida Ribeiro M, Sarubbo LA, Andrade SAC, Filho ABDM. Nutritional and lipid profiles in marine fish species from Brazil. Food Chem. 2014;160:67–71. https://doi.org/10.1016/J.FOODCHEM.2014.03.055.
41. Włodarczyk A, Krakowska A, Sułkowska-Ziaja K, Suchanek M, Zięba P, Opoka W, et al. *Pleurotus* spp. mycelia enriched in magnesium and zinc salts as a potential functional food. Molecules. 2021;26:162. https://doi.org/10.3390/MOLECULES26010162.
42. Bell V, Silva CRPG, Guina J, Fernandes TH. Mushrooms as future generation healthy foods. Front Nutr. 2022;6(9):1050099. https://doi.org/10.3389/FNUT.2022.1050099.
43. Xiaofeng D, Minaxi S, Jieyin C. Fungi in sustainable food production. Dai X, Sharma M, Chen J, editors. 2021. https://link.springer.com/10.1007/978-3-030-64406-2
44. Corrochano LM. Light in the fungal world: From photoreception to gene transcription and beyond. Annu Rev Genet. 2019;53:149–70. https://doi.org/10.1146/annurev-genet-120417-031415.
45. Rodriguez-Romero J, Hedtke M, Kastner C, Müller S, Fischer R. Fungi, hidden in soil or up in the air: Light makes a difference. Annu Rev Microbiol. 2010;64(1):585–610. https://doi.org/10.1146/annurev.micro.112408.134000.
46. Wang Z, Li N, Li J, Dunlap JC, Trail F, Townsend JP, et al. The fast-evolving phy-2 gene modulates sexual development in response to light in the model fungus Neurospora crassa. mTurgeon BG, editor. mBio. 2016;7(2). https://doi.org/10.1128/mbio.02148-15
47. Fuller KK, Dunlap JC, Loros JJ. Fungal light sensing at the bench and beyond. Adv Genet. 2016;96:1–51. https://doi.org/10.1016/bs.adgen.2016.08.002.
48. Yu Z, Fischer R. Light sensing and responses in fungi. Nat Rev Microbiol. 2019;17(1):25–36. https://doi.org/10.1038/S41579-018-0109-X.
49. Corrochano LM, Galland P. 11 Photomorphogenesis and gravitropism in fungi. Growth, differentiation and sexuality. 2016;235–66. https://link.springer.com/chapter/10.1007/978-3-319-25844-7_11
50. Corrochano LM, Galland P. Photomorphogenesis and gravitropism in fungi. In: Kües, Fischer, editors Growth, Differentiation and Sexuality. 2006;233–59. https://doi.org/10.1007/3-540-28135-5_13
51. Fischer R, Aguirre J, Herrera-Estrella A, Corrochano LM. The complexity of fungal vision. In: The Fungal Kingdom. 2017;441–61. https://doi.org/10.1128/9781555819583.ch20.
52. Idnurm A, Verma S, Corrochano LM. A glimpse into the basis of vision in the kingdom Mycota. Fungal Genet Biol. 2010;47(11):881–92. https://doi.org/10.1016/j.fgb.2010.04.00953.
53. Tisch D, Schmoll M. Light regulation of metabolic pathways in fungi. Appl Microbiol Biotechnol. 2010;85(5):1259–77. https://doi.org/10.1007/s00253-009-2320-1.
54. Purschwitz J, Müller S, Kastner C, Fischer R. Seeing the Rainbow: Light sensing in fungi. Curr Opin Microbiol. 2006;9(6):566–71. https://doi.org/10.1016/j.mib.2006.10.011.
55. Herrera-Estrella A, Horwitz BA. Looking through the eyes of fungi: Molecular genetics of photoreception. Mol Microbiol. 2007;64(1):5–15. https://doi.org/10.1111/j.1365-2958.2007.05632.x.
56. Bayram ÖS, Bayram Ö. An anatomy of fungal eye: Fungal photoreceptors and signalling mechanisms. J Fungi. 2023;9(5):591. https://doi.org/10.3390/jof9050591.
57. Castrillo M, García-Martínez J, Avalos J. Light-dependent functions of the Fusarium fujikuroi CryD DASH cryptochrome in development and secondary metabolism. Appl Environ Microbiol. 2013;79(8):2777–88. https://doi.org/10.1128/aem.03110-12.
58. Kho CH, Kan SC, Chang CY, Cheng HY, Lin CC, Chiou PC, et al. Analysis of exopolysaccharide production patterns of Cordyceps militaris under various light-emitting diodes. Biochem Eng J. 2016;112:226–32. https://doi.org/10.1016/j.bej.2016.04.028.
59. Frayco JG, Maata AY, Pepito EMT, Quirante MM, Veras GY, Vigonte CT. Duration of light exposure using white light-emitting diode (LED) on the performance of white oyster mushroom (Pleurotus ostreatus L). Asian J Agricultural Hortic Res. 2024;11:115–23. https://doi.org/10.9734/ajahr/2024/v11i4346.
60. Kim SY, Son J, Lo YM, Lee C, Moon B. Effects of light-emitting diode (LED) lighting on the ergosterol content of beech mushrooms (Lyophyllum ulmarium). J Food Process Preserv. 2014;38:1926–31. https://doi.org/10.1111/jfpp.12165.
61. Igbalajobi O, Yu Z, Fischer R. Red-and blue-light sensing in the plant pathogen Alternaria alternata depends on phytochrome and the white-collar protein LreA. Di Pietro, ed. Mbio. 2019;10(2). https://doi.org/10.1128/mbio.00371-19
62. Yu Z, Streng C, Seibeld RF, Igbalajobi OA, Leister K, Ingelfinger J, et al. Genome-wide analyses of light-regulated genes in Aspergillus nidulans reveal a complex interplay between different photoreceptors and novel photoreceptor functions. PLoS Genet. 2021;17(10):e1009845. https://doi.org/10.1371/journal.pgen.1009845.
63. Sano H, Kaneko S, Sakamoto Y, Sato T, Shishido K. The basidiomycetous mushroom Lentinula edodes white collar-2 homolog PHRB, a partner of putative blue-light photoreceptor PHRA, binds to a specific site in the promoter region of the L. edodes tyrosinase gene. Fungal Genet Biol. 2009;46(4):333–41. https://doi.org/10.1016/j.fgb.2009.01.001.
64. Sano H, Narikiyo T, Kaneko S, Yamazaki T, Shishido K. Sequence analysis and expression of a blue-light photoreceptor gene, Le.phrA from the basidiomycetous mushroom Lentinula edodes. Biosci Biotechnol Biochem. 2007;71(9):2206–13. https://doi.org/10.1271/bbb.70170.
65. Kuratani M, Tanaka K, Terashima K, Muraguchi H, Nakazawa T, Nakahori K, et al. The dst2 gene essential for photomorphogenesis of coprinopsis cinerea encodes a protein with a putative FAD-binding-4 domain. Fungal Genet Biol. 2010;47(2):152–8. https://doi.org/10.1016/j.fgb.2009.10.00.
66. Terashima K, Yuki K, Muraguchi H, Akiyama M, Kamada T. The dst1 gene involved in mushroom photomorphogenesis of Coprinus cinereus encodes a

putative photoreceptor for blue light. Genetics. 2005;171(1):101–8. https://doi.org/10.1534/genetics.104.040048.
67. Kanda S, Masumoto S, Nakano K, Morinaga T, Aimi T, Kitamoto Y, et al. Photoregulated tyrosinase gene in Polyporus arcularius. Mycoscience. 2007;48(1):34–41. https://doi.org/10.1007/s10267-006-0327-3.
68. Nakano Y, Fujii H, Kojima M. Identification of blue-light photoresponse genes in oyster mushroom mycelia. Biosci Biotechnol Biochem. 2010;74(10):2160–5. https://doi.org/10.1271/bbb.100565.
69. Navarro E, Peñaranda A, Hansberg W, Torres-Martínez S, Garre V. A White Collar 1-like protein mediates opposite regulatory functions in mucor circinelloides. Fungal Genet Biol. 2013;52:42–52. https://doi.org/10.1016/j.fgb.2012.12.003.
70. Durand R, Furuya M. Action spectra for stimulatory and inhibitory effects of UV and blue light on fruit-body formation in coprinus congregatus. Plant Cell Physiol. 1985;26(6):1175–83. https://doi.org/10.1093/oxfordjournals.pcp.a077013.
71. Richartz G, Maclellan AJ. Action spectra for hyphal aggregation, the first stage of fruiting, in the basidiomycete pleurotus ostreatus*. Photochem Photobiol. 1987;45(S1):815–20. https://doi.org/10.1111/j.1751-1097.1987.tb07888.x.
72. Huang MY, Lin KH, Lu CC, Chen LR, Hsiung TC, Chang WT. The intensity of blue light-emitting diodes influences the antioxidant properties and sugar content of oyster mushrooms (Lentinus sajor-caju). Sci Hortic. 2017;218:8–13. https://doi.org/10.1016/J.SCIENTA.2017.02.014.
73. Arjona D, Aragón C, Aguilera JA, Ramírez L, Pisabarro AG. Reproducible and controllable light induction of in vitro fruiting of the white-rot basidiomycete pleurotus ostreatus. Mycol Res. 2009;113(5):552–8. https://doi.org/10.1016/J.MYCRES.2008.12.006.
74. Idnurm A, Heitman J. Light controls growth and development via a conserved pathway in the Fungal Kingdom. PLoS Biol. 2005;3(4):e95. https://doi.org/10.1371/JOURNAL.PBIO.0030095.
75. Yi ZL, Huang WF, Ren Y, Onac E, Zhou GF, Peng S, et al. LED lights increase bioactive substances at low energy costs in culturing fruiting bodies of Cordyceps militaris. Sci Hortic. 2014;175:139–43. https://doi.org/10.1016/j.scienta.2014.06.006.
76. Xie C, Gong W, Zhu Z, Yan L, Hu Z, Peng Y. Comparative transcriptomics of Pleurotus eryngii reveals blue-light regulation of carbohydrate-active enzymes (CAZymes) expression at primordium differentiated into fruiting body stage. Genomics. 2018;110(3):201–9. https://doi.org/10.1016/J.YGENO.2017.09.012.
77. Kojima M, Kimura N, Miura R. Regulation of primary metabolic pathways in oyster mushroom mycelia induced by blue light stimulation: Accumulation of Shikimic acid. Sci Rep. 2015;5:8630. https://doi.org/10.1038/srep08630.
78. Karu T. Photobiology of low-power laser effects. Health Phys. 1989;56(5):691–704. https://pubmed.ncbi.nlm.nih.gov/2651364/.
79. Jang MJ, Lee YH, Ju YC, Kim SM, Koo HM. Effect of color of light emitting diode on development of fruit body in Hypsizygus marmoreus. Mycobiology. 2013;41(1):63–6. https://doi.org/10.5941/MYCO.2013.41.1.63.
80. Dong JZ, Liu MR, Lei C, Zheng XJ, Wang Y. Effects of selenium and light wavelengths on liquid culture of Cordyceps militaris link. Appl Biochem Biotechnol. 2012;66(8):2030–6. https://doi.org/10.1007/S12010-012-9628-5.
81. Araújo NL, Avelino KV, Halabura MIW, Marim RA, Kassem ASS, Linde GA, et al. Use of green light to improve the production of lignocellulose-decay enzymes by *Pleurotus* spp. In liquid cultivation. Enzyme Microb Technol. 2021;149.109860. https://doi.org/10.1016/j.enzmictec.2021.109860.
82. Halabura MIW, Avelino KV, Araújo NL, Kassem ASS, Seixas FAV, Barros L, et al. Light conditions affect the growth, chemical composition, antioxidant and antimicrobial activities of the white-rot fungus *Lentinus crinitus* mycelial biomass. Photochem Photobiol Sci. 2023;22(3):669–86. https://doi.org/10.1007/s43630-022-00344-7.
83. Poyedinok N, Mykchaylova OB, Tugay N, Tugay A, Negriyko A, Dudka I. Effect of light wavelengths and coherence on growth, enzymes activity, and melanin accumulation of liquid-cultured inonotus obliquus (Ach.:Pers.) Pilát. Appl Biochem Biotechnol. 2015;176(2):333–43. https://doi.org/10.1007/s12010-015-1577-3.
84. Poyedinok N, Negriyko A, Mykchaylova O. Effects of light wavelengths and coherence on basidiospores germination. JMBFS. 2015;4(4):352–7. https://doi.org/10.15414/jmbfs.2015.4.4.352-357.
85. Poyedinok NL, Mykhailova OB, Shcherba VV, Buchalo AS, Negriyko AM. Light regulation of growth and biosynthetic AcCurt.: Fr.) P. Karst. (Aphyllophoromycetideae), in pure culture. Int J Med Mushrooms. 2008;10(4):369–78. https://doi.org/10.1615/IntJMedMushr.v10.i4.100.
86. Saini RK, Rauf A, Khalil AA, Ko EY, Keum YS, Anwar S, et al. Edible mushrooms show significant differences in sterols and fatty acid compositions. S Afr J Bot. 2021;141:344–56. https://doi.org/10.1016/J.SAJB.2021.05.022.
87. Mykchaylova O, Dubova H, Lomberg M, Negriyko A, Poyedinok N. Influence of low-intensity light on the biosynthetic activity of the edible medicinal mushroom Hericium erinaceus (Bull.: Fr.) Pers. in vitro. Arch Biol Sci. 2023;75(4):489–501. https://doi.org/10.2298/ABS230821040M.
88. Hossain S, Hashimoto M, Choudhury EK, Alam N, Hussain S, Hasan M, et al. Dietary mushroom (Pleurotus ostreatus) ameliorates atherogenic lipid in hypercholesterolaemic rats. Clin Exp Pharmacol Physiol. 2003;30(7):470–5. https://doi.org/10.1046/J.1440-1681.2003.03857.X.
89. Parikh P, McDaniel MC, Ashen MD, Miller JI, Sorrentino M, Chan V, et al. Diets and cardiovascular disease: An evidence-based assessment. J Am Coll Cardiol. 2005;45(9):1379–87. https://doi.org/10.1016/j.jacc.2004.11.068.
90. Mokochinski JB, López BGC, Sovrani V, Dalla Santa HS, González-Borrero PP, Sawaya ACHF, et al. Production of agaricus brasiliensis mycelium from food industry residues as a source of antioxidants and essential fatty acids. Int J Food Sci Technol. 2015;50(9):2052–8. https://doi.org/10.1111/IJFS.12861.
91. Liang CH, Huang LY, Ho KJ, Lin SY, Mau JL. Submerged cultivation of mycelium with high ergothioneine content from the culinary-medicinal king oyster mushroom pleurotus eryngii (higher Basidiomycetes) and its composition. Int J Med Mushrooms. 2013;15(2):153–64. https://doi.org/10.1615/IntJMedMushr.v15.i2.40.
92. Liang CH, Ho KJ, Huang LY, Tsai CH, Lin SY, Mau JL. Antioxidant properties of fruiting bodies, mycelia, and fermented products of the culinary-medicinal king oyster mushroom, pleurotus eryngii (higher Basidiomycetes), with high ergothioneine content. Int J Med Mushrooms. 2013;15(3):267–75. https://doi.org/10.1615/intjmedmushr.v15.i3.40.
93. Chen J, Mao D, Yong Y, Li J, Wei H, Lu L. Hepatoprotective and hypolipidemic effects of water-soluble polysaccharidic extract of Pleurotus eryngii. Food Chem. 2012;130(3):687–94. https://doi.org/10.1016/j.foodchem.2011.07.110.

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