PLANT SCIENCE TODAY
Vol 13(sp5): 1–17
https://doi.org/10.14719/pst.16511

eISSN 2348-1900

REVIEW ARTICLE

Cyclocybe aegerita (syn. Agrocybe aegerita)-Black poplar mushroom: Cultivation biology, nutritional profiling and bioactive potential for sustainable commercial production

R Kalpana Devi[1], G Thiribhuvanamala[1]*, P Mahalakshmi[1], M Senthilkumar[2], S P Thamarai Selvi[3] & N Bharathi[4]

[1]Department of Plant Pathology, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[2]Department of Agricultural Microbiology, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[3]Department of Floriculture and Landscape Architecture, Horticultural College and Research Institute , Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[4]Department of Plant Molecular Biology and Bioinformatics, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

*Correspondence email - thiribhuvanamala.g@tnau.ac.in

Received: 03 July 2026; Accepted: 24 August 2026; Available online: Version 1.0: 21 September 2026

Cite this article: Kalpana DR, Thiribhuvanamala G, Mahalakshmi P, Senthilkumar M, Thamarai SSP, Bharathi N. *Cyclocybe aegerita (syn. Agrocybe aegerita)*-Black poplar mushroom: Cultivation biology, nutritional profiling and bioactive potential for sustainable commercial production. Plant Science Today. 2026; 13(sp5): 1-17. https://doi.org/10.14719/pst.16511

Abstract

Cyclocybe aegerita (V. Brig.) Vizzini, previously reported as *Agrocybe aegerita* and *Agrocybe cylindracea* is an edible and medicinal mushroom species with high farming potential, nutritional and bioactive value, with the emergence of several works on its production, cultivation and nutritional benefits. This review highlights its taxonomy, cultivation needs, substrates, nutrient composition and its key bioactive compounds as well as reported nutraceutical and pharmaceutical properties. Based on the literature reviewed, mycelial growth was found to be best at pH 5.5–7.0 and 25–28 °C, while the initiation and fruiting of primordia appear to be best at lower temperatures of 15–20 °C and under high relative humidity levels with controlled light and carbon dioxide (CO_2) levels. Typical values of biological efficiency are 32–68 %, while optimised strain-substrate combinations are greater than 100 % and up to 179–194 % in some studies. Based on the nutritional studies carried out, the mushroom is a source of protein, dietary fibre, minerals, phenolics, unsaturated fatty acids and the identified bio actives in the mushroom are polysaccharides, lectins, terpenoids, steroids, peptides, ergosterol derivatives, ergothioneine and glutathione. Activities that have been reported through experimentation consist of antioxidant, anti-aging, anti-tumour, anti-microbial, anti-quorum sensing, anti-biofilm and immunomodulatory, with most of the pharmacological evidence being pre-clinical. The integration of cultivation and bioactivity data allows the identification of the most suitable production conditions, the identification of points of consensus and divergence in the literature and the identification of priorities for future improvements of strains, substrates and for the translation of bioactive compounds.

Keywords: bioactive compounds; *Cyclocybe aegerita*; growth condition; pharmaceutical properties; substrates

Introduction

The usage of mushrooms as health supplements has been in the cultures of ancient Greece, Rome, China, India and they have been part of the traditional medicine of Eastern Asia for centuries (1). Lion's Mane (*Hericium erinaceus)*, Reishi (*Ganoderma lucidum*) and Giant Oyster (*Pleurotus giganteus)* are types of medicinal mushrooms that are grown around the world for their nutritional benefits and use in health supplements (2). Since ancient times, mushrooms have played diverse roles in human civilisation, serving as sustenance, medicine, psychoactive substances and symbols of religious significance (3). Pioppino, scientifically known as *Cyclocybe aegerita* (V. Brig.) Vizzini, is previously reported as *Agrocybe aegerita* and *Agrocybe cylindracea*, one of the most delicious and aromatic medicinal mushrooms grow best in warm, temperate forests and are often found naturally on trees like cottonwoods, willows, poplars, maples, box elders and tea oil trees. This nutrient rich and therapeutic mushroom is widely grown in several Asian and European countries (4, 5).Although *C. aegerita* is valued for its unique flavour, nutritional profile and medicinal value, its cultivation is often limited by low yields. Renowned for its anti-cancer attributes, aesthetic enhancements, anti-diarrheal abilities, strengthening effects on the spleen and diuretic properties, this mushroom has been crowned with the title "Chinese God Mushroom" (6). Mushrooms are enjoyed as food and are also valued for their health benefits, often described as "food that also cures". As basidiomycetous fungi, mushrooms contain a variety of compounds that are greatly prized for their medicinal properties, as well as for their use in flavouring and making perfumes (7). Medicinal mushrooms are an excellent source of several antioxidant; thus, they can be utilised for pharmaceutical purposes (8). The protein content of *C. aegerita* is high, making up about 25–30 % of its weight (9). Throughout history, Asian populations, particularly those in China, have utilised this fungus as a traditional remedy to promote urination and enhance the function

of the spleen, both of which are linked to managing uric acid concentrations in the body (10). Earlier studies examining the fruiting body of *C. aegerita* have identified the presence of various substances, including palmitic acid, linoleic acid, ergosterol, mannitol and trehalose (11). Furthermore, the genus *Cyclocybe* is recognised for containing various biologically active substances. These include indole derivatives and phenols with antioxidant qualities, polysaccharides that demonstrate blood sugar-lowering effects and agrocybin, a peptide that exhibits anti-fungal properties. Usage of these bioactive compounds may result in the identification of novel drugs to combat anti-biotic resistance, addressing the critical challenge of microorganisms becoming resistant to existing drugs (12, 13). In recent years, mushroom bioactive components have gained significant interest due to their various biological functions like antioxidant, anti-microbial, anti-inflammatory and immune-modulating properties. Researchers have devised several extraction techniques grounded in diverse principles to extract these bioactive components including hot water extraction, hot alkaline extraction, ultrasound-assisted extraction, microwave-assisted extraction, superheated water extraction and enzymatic extraction (14). Therefore, this review will highlight the importance of *C. aegerita* mushroom cultivation and its numerous salutary properties aiding in human health.

Review methodology

The literature survey for this review was provided from major scientific databases such as Google Scholar, Scopus, Web of Science, PubMed and ScienceDirect covering publications up to March 2026. The following combinations of the proposed keywords were used for the search: Medicinal mushrooms, *Agrocybe* species, *C. aegerita*, *A. aegerita*, *A. cylindracea*, black poplar mushroom, cultivation methodologies, substrate, biological efficiency, nutritional composition, bioactive compounds, human health, plant health antioxidant, anti-tumour, anti-inflammatory, consumption dose, toxicity, human trials and anti-microbial. Only original research articles, reviews and book chapters that provided relevant information about taxonomy, cultivation biology, nutrient composition, metabolites and biological activities were considered. Peer-reviewed studies presenting experimental data were preferred over older basic references that were important in taxonomy, cultivation history, or first reports of major compounds and/or activities.

Taxonomy and Nomenclature

The genus *Agrocybe* was originally classified within the Bolbitiaceae family. However, a recent study using rDNA sequence data for phylogenetic analysis led to its reclassification to the family *Strophariaceae*. Consequently, it was transferred to the renewed genus *Cyclocybe* and its current valid scientific name is *C. aegerita* (V. Brig.) Vizzini (15).

Super Kingdom	:	Eukaryota
Kingdom	:	Fungi
Subkingdom	:	Dikarya
Phylum	:	Basidiomycota
Subphylum	:	Agaricomycotina
Class	:	Agaricomycetes
Order	:	Agaricales
Family	:	Strophariaceae
Genus	:	*Cyclocybe*

Taxonomy of *Cyclocybe aegerita*

Current name: *Cyclocybe aegerita* (V. Brig.) Vizzini. The other edible mushrooms of the genus *Cyclocybe* are *Cyclocybe dura*, *Cyclocybe pediades, Cyclocybe praecox* and *Cyclocybe striatipes* (16).

Cultivation biology of *Cyclocybe aegerita*

Cultural physiological requirements for mycelial growth of *Cyclocybe aegerita*

Culture medium is the primary substrate supporting mycelial development in mushroom. Various media have been evaluated to optimise and accelerate mycelial growth, thereby shortening the overall cultivation cycle. The agar media conducive for mycelium growth of *C. aegerita* are potato dextrose agar (PDA) and malt extract agar (MEA) (17). On investigating the growth of *C. aegerita*, on solid and semi solid medium, significant growth was observed in Walksman solid agar medium facilitating a diameter of 77 mm and on examining semi-solid mediums, Czapek Dox solution was more favourable, fostering a growth rate of 6.7 mg/mL (18). On wheat and oatmeal agar media with a pH of 6.0, *C. aegerita* mycelium exhibited peak growth rates between 3.2–6.4 mm per day (19). The growth-promoting effects of gibberellic acid (GA), a phytohormone and pyridoxine, a vitamin, resulted in enhanced mycelial growth of the mushrooms (20). A significant increase in *C. aegerita* mycelial growth was observed with GA at 20 ppm and naphthaleneacetic acid (NAA) at 50 ppm, highlighting the potential of hormonal supplementation in enhancing fungal proliferation (18). The differences between the reports, however, indicate that neither of the media is at present entirely satisfactory for all strains or conditions of growth. Growth regulators like GA, pyridoxine and NAA can induce mycelial growth but they are strained and condition dependent and should be confirmed by standardised comparative trials before being recommended for cultivation practice.

The potential of hydrogen (pH) of the growth medium influences the mushroom's ionic environment, physiological processes, structural characteristics and fruiting body formation. This acidity or alkalinity level impacts various aspects of mushroom development and the surrounding medium (21). Consequently, determining the pH level of the growth medium is crucial for enhancing mycelial development. The effects of pH modification on *C. aegerita* growth were examined, revealing a notable increase in radial growth rate with a modified pH of MEA from 4.7–6.0 (22). It thrives in alkaline environments, with optimal growth observed at a pH of 9 (18). Further investigation of the pH requirements revealed a maximum dry mycelial weight at pH 7 (84.05 mg/25 mL) (23). Similarly, a better mycelial growth was seen at pH range of 5–7 (24). In the various studies reviewed, the most consistent pH range for growth of *C. aegerita* mycelia was found in the slightly acidic to neutral range of pH 5.5–7.0, with some studies reporting good growth at pH 6.0–7.0. While one study indicated an optimum of pH 9, this value does not seem to be representative of the wider literature and may reflect the behaviour of the specific strain or specific experimental conditions used in the study.

Growth conditions required for spawn run and fruiting body induction of *Cyclocybe aegerita*

The cultivation of mushrooms requires specific environmental conditions influenced by various physical elements. These elements encompass the temperature of the substrate, the surrounding air temperature, atmospheric moisture content and the levels of carbon dioxide (CO_2) present in the environment (25). Mushroom

mycelial growth is significantly affected by the crucial environmental factor of temperature (26). The ideal growth of mushrooms necessitates specific temperature conditions. For instance, the button mushroom thrives within a temperature range of approximately 20–25 °C for vegetative growth, which enhances mycelial growth. Deviating from the optimal range, either towards lower or higher temperatures, can impede or completely halt mycelial growth and may also promote contamination from other organisms competing for resources (27). *Cyclocybe aegerita* exhibited optimal growth at a temperature of 25 °C, with growth ceasing entirely at higher temperatures, notably 35 °C (95 °F) (18, 28). Mycelial growth reached its peak at 28 °C, while no growth was detected at temperatures of 34 °C and 37 °C over a two-week incubation period (19). The highest dry mycelial weight was observed at 25 °C (84.50 mg/25 mL) followed by 20 °C (78.30 mg/25 mL) (23). A temperature of 25 °C was ideal for mycelial growth on the substrate, whereas a cooler temperature of 15–17 °C was necessary for primordial formation (29–31). An air temperature of 16–18 °C promotes fruiting body production (5). An ambient temperature of 10–25 °C was conducive to good mycelial colonisation (32). The temperature range of 20–27 °C was suitable for spawn running, while a slightly decreased temperature of 20–25 °C was required for fruiting body induction (6, 33). Primordia development was observed at a cooler temperature of 18–20 °C lower than the temperature required for spawn running (4, 34).

A controlled environment with a temperature of 18 °C, 90 % humidity, 700 lux of light for 12 hr and low levels of CO_2 (< 1200 ppm) was optimal for fruiting body induction (35). A two-phase cultivation method was introduced involving two different environmental conditions, initially incubating the mushroom culture in a sawdust-wheat bran substrate under specific conditions (65 % RH, 25 °C, darkness) and then transferring it to a well-illuminated environment with a reduced temperature (15 °C) to promote fruiting (36). The relative air humidity required for colonisation of mushroom bags was around 75 % and for fruiting bodies induction were found when placed under a controlled condition involving 90 % RH and 400 lux of light for 12 hr (37). Maintaining a relative humidity of 85–90 % in air-conditioned bottles were optimal for mycelial growth, while a slightly higher humidity of 85–95 % with 500 lux of light for 10 hr per day and the CO_2 level below 1000 ppm was necessary for basidiocarp production (29, 30). A relative humidity of 67 ± 2 % and a CO_2 level of 1200 ± 150 ppm were identified as ideal conditions for mycelial growth (31). Fruiting bodies induction was observed at a setting involving high humidity (90–93 %), increased CO_2 levels (1300 ppm) and adequate lighting (500–600 lux) (5). After complete colonisation, increasing the humidity to 80–90 % and providing light for 2–4 hr facilitated fruiting body production (32). For successful mushroom production, increasing the relative humidity from 60 % during mycelial growth to 85–95 % during fruiting is crucial (6, 33). The cultivation area required specific environmental conditions for the initial growth stages. These included a relative humidity between 80–85 %, a CO_2 level of 2000 ppm and illumination at 5000 lux. These parameters were essential to maintain until the first primordia emerged (34). Optimal conditions for the development of fruiting bodies include a temperature between 18–20 °C, relative humidity ranging from 70–80 % and a photoperiod consisting of 9 hr of illumination followed by 15 hr of darkness (4). Available studies indicate that *C. aegerita* grows best in a two-stage culture system, vegetative growth takes place at moderate temperatures and fruiting takes place under cooler more humid and light conditions. The temperature range suitable for mycelial colonisation is 25–28 °C, the relative humidity is 75–90 % and the level of CO_2 is low to moderate. The effects of lower temperatures (15–20 °C), light exposure (400–700 lux), higher relative humidity (85–95 %) and CO_2 (1000–1200 ppm) have been more reproducibly linked to fruiting body initiation. When summarising the evidence, temperature seems to be the most important factor for developmental stage, whereas humidity, light and CO_2 were of secondary importance and sufficient evidence exists to confirm cooler temperatures for primordia formation and fruiting and warmer temperatures for spawn running. Table 1 summarises the optimal cultivation parameters reported for mycelial growth and fruiting of *C. aegerita* under different experimental conditions. Fig. 1. represents the integrated overview of culture condition, two phase cultivation and substrate selection for cultivation of *C. aegerita*.

Selection of substrates for obtaining higher yield of *Cyclocybe aegerita*

Cultivation of *C. aegerita* has proven successful on a diverse range of agricultural and forestry byproducts. These include cereal straws like barley and wheat, fruit remnants such as orange peel and grape stalks, aquatic plants like reeds, grain processing leftovers like rice husks, oilseed residues such as sunflower seeds and wood industry waste from willow trees in the form of sawdust (35, 38). Table 2 summarises the substrates, supplementation strategies, yield outcomes and biological efficiency reported for *C. aegerita* across the available studies. There is considerable variation among studies in substrate performance, however, there are some commonalities. Wheat straw, sawdust-based substrates and wheat straw or sawdust supplemented with bran are systems which have been repeated most successfully; less successful substrates include olive press cake and less successful substrates with lower levels of colonisation or productivity. Biological efficiency reported is very variable (32–68 % on several conventional straw or sawdust formulations and above 100 % in optimised and supplemented systems; as high as 179 and 194 % respectively, under certain strain-substrate combinations). As the values are high, they should be interpreted with care as they are greatly influenced by genotype, type of supplements and cultivation format. Overall, the evidence favours the use of wheat straw or sawdust-based substrates that have been supplemented with bran or other nutrients for practical cultivation. However, due to factors such as limited availability and reduced cost-effectiveness of this substrate, the cultivation of this mushroom has been hindered.

Nutrient composition of *Cyclocybe aegerita*

As a nutrient-dense food source, mushrooms offer a well-rounded diet comprising proteins, carbohydrates, minerals and vitamins. They are particularly abundant in various essential elements, including potassium, phosphorus, magnesium, calcium, copper, zinc, iron, manganese and sodium (47). These essential nutrients are crucial for key physiological processes, such as skeletal maintenance, supporting muscular function, enabling neural signalling, enhancing immune response and contributing to the energy production mechanisms. The precise mineral composition of mushrooms may differ based on factors such as mushroom species, cultivation environment and substrate. However, including mushrooms in the diet can be a beneficial strategy to improve overall mineral intake and enhance overall health and well-being. The mineral composition of *C. aegerita* mushroom consists of total

Table 1. Optimal cultural conditions for mycelial growth, spawn running, primordia formation and fruiting of *Cyclocybe aegerita*

Medium/substrate	pH	Temperature (°C)	Relative humidity (%)	CO_2 (ppm)	Light	Reference
Growth stage: Mycelial growth						
Potato dextrose agar (PDA) and malt extract agar (MEA)	5.5–6.5	25–28				(17, 22)
Wheat agar, oatmeal agar	6.0	28				(19)
Walksman solid agar and Czapek Dox semi-solid medium	9	25				(18)
Medium supplemented with GA (20 ppm) and NAA (50 ppm)	-	25				(20)
Liquid medium	7.0	25	-	-	Darkness	(23)
Varied growth medium	5–7	25–28				(22–24)
Growth stage: Spawn running						
Sawdust + wheat bran	-	25	65	-	Darkness	(36)
Lignocellulosic substrates	-	20–27	60–75	-	Darkness	(6, 33, 37)
Growth stage: Primordia formation						
Colonised sawdust substrate	-	15–17	85–90	< 1200	12hr, 400–700 lux	(29, 30, 35, 37)
Colonised substrate	-	18–20	80–90	-	2–4 hr light	(32, 34)
Growth stage: Fruiting body development						
Controlled environment	-	16–18	90–93	1300	500–600 lux	(5)
Cultivation room	-	18–20	70–80	-	9 hr light/15 hr darkness	(4)
Colonised substrate	-	15–20	85–95	< 1000	10–12 hr, 500 lux	(29, 30)
Controlled chamber	-	18	90	< 1200	12hr, 700 lux	(35)

GA: gibberellic acid; NAA: naphthaleneacetic acid.

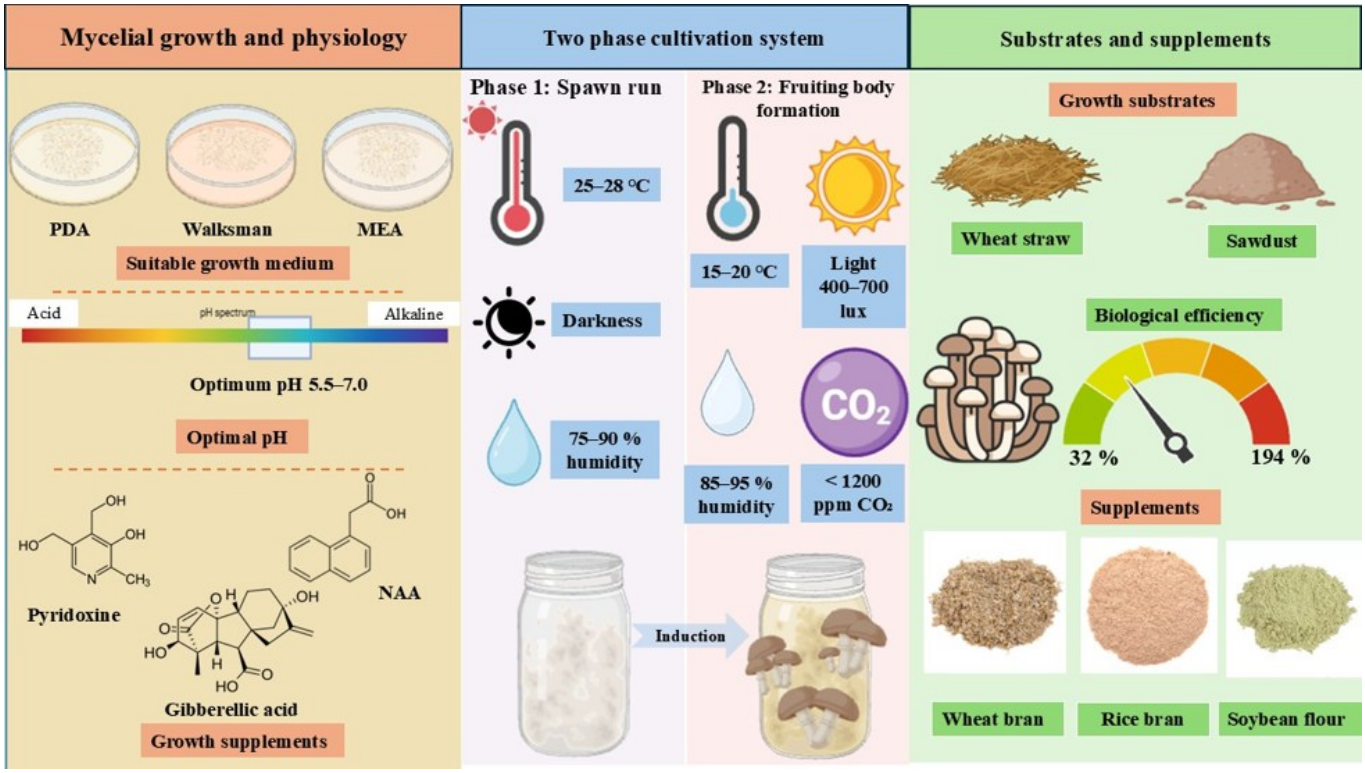


Fig. 1. Integrated overview of cultural conditions, two phase cultivation and substrate selection for cultivation of *Cyclocybe aegerita*.

PDA: potato dextrose agar; MEA: malt extract agar; NAA: naphthaleneacetic acid.

Table 2. Substrates, supplementations, yield and biological efficiency reported for *Cyclocybe aegerita*

Substrates	Supplements	Yield	Biological efficiency (%)	Salient findings	Reference
Individual substrates					
Wheat straw	-		60	Superior substrate for long term cultivation	(18)
	Black tea pomace	-	36	Tea waste supported moderate production	(37)
	Rolled oats or soybean flour	-	54.5–72.4	Supplements increased BE by 0.5–1.2 fold	(4)
	Soybean flour	-	179	Highest BE reported for a strain-substrate combination	
Paddy straw	Rice bran (10 %)	Highest yield	-	Rice bran significantly enhanced productivity	(39)
	Wheat bran (10 %)	-	36.4	Wheat bran improved biological efficiency	(32)
Cotton waste	-	136.6 g	34.88	Highest yield among agricultural wastes	(35)
Peanut shell	-	34.81 g	10.15	Poor substrate for cultivation	
Wheat straw	-	150.5 g	49.80	Highest yield among agricultural wastes	
Sawdust	-	-	67.66	Highest BE among tested conventional substrates	(40)
Beech wood sawdust	Corn meal (15 %) or wheat bran (15 %)	-	-	Fastest colonisation (20 days)	(19)
Sawdust	$CaCO_3$ (8 g/100 g substrate)	72.81 g	-	Highest yield, polysaccharide content and shortest spawn run	(30)
Wood chips	Wheat bran	-	-	Earliest fruiting (29 days)	(41)
Culture substrate	Selenium (Se)	-	-	Enhanced phenolics, flavonoids and antioxidant activity without reporting BE	(42)
Korshinsk peashrub (40 %)	-	-	-	Produced high-quality mushrooms; increased crude protein and polysaccharides (6.60 %)	(6)
Bottle substrate ("Sanggang" strain)	-	134 g/850 mL bottle	-	High yield with 13-day shelf life	(28)
Combination of substrates					
Wheat straw (78 %) + wheat bran (20 %)	-	-	194	Highest BE reported under optimised conditions	(34)
Wood chips + wheat bran + cottonseed + wheat seed	-	-	123	Lower BE than non-woody substrate	
Sawdust + paddy straw	-	-	32.1	Moderate biological efficiency	(43)
Wheat straw (70–80 %) + solid waste (10–20 %)	-	770.5 g	-	Highest fresh mushroom yield	(44)
Solid waste (10–20 %) + millet (10 %)	-	642.9 g	-	High productivity	
Sawdust (beech + alder + birch)	-	-	-	Most suitable sawdust combination	(17)
Miscanthus, switchgrass, flax and hemp	-	-	-	Suitable alternative lignocellulosic substrates	(29)
Sawdust + spent *Pleurotus ostreatus* substrate	Wheat bran + gypsum + sucrose	76.5 g/bag	-	High fruiting body production	(45)
Straw (30 %) + sawdust (52.2 %)	Rice bran (8 %) + corn bran (8 %) + $MgSO_4$ + $CaCO_3$	-	35	Good mycelial growth and fruiting after 35–40 days	(46)

BE: biological efficiency; $CaCO_3$: calcium carbonate; $MgSO_4$: magnesium sulfate.

dietary fibre (TDF)-11.43, ash content-11.97, pure dietary fibre (PDF)-10.06, carbon content-40.00, nitrogen content-5.92 and hydrogen content-6.31 using Heneberg and Stochman method (48). Research examining the proximate and mineral content of *C. aegerita* mushrooms found them to be high in water content (92.36 %), while containing minimal amounts of fat (0.20 mg/100 g), crude fibre (8.05 mg/100 g) and ash (1.22 mg/100 g) (39). The *C. aegerita* mushrooms contain high levels of crude proteins (38.3 %), crude fats (3.0 %) and ashes (8.2 %), with potassium and phosphorus content exceeding that of other minerals. Additionally, the mushrooms were found to have significant amounts of total phenolics and flavonoids (49). The composition of *C. aegerita* includes substantial amounts of carbohydrates (84.51 g/100 g dw), proteins (6.68 g/100 g dw) and ash (6.69 g/100 g dw). It also contains polyunsaturated fatty acids, with linoleic acid being predominant (78.40 %). This fatty acid profile contributes to the unique flavour of *C. aegerita* (50). The addition of 40 % Korshinsk peashrub to the substrate resulted in an improved nutritional composition, with increases of 6.60 % in crude protein and 4.46 % in polysaccharide content (6). *Cyclocybe aegerita* contained heavy metal contents (µg/g dry weight) of silver-0.030, aluminium-5.6, arsenic-0.08, cadmium-0.019, chromium-0.46, nickel -0.20, lead-0.016 and strontium-0.74 and essential and minor element (µg/g dry weight) contents of boron-0.16, calcium-45.7, cobalt-0.032, copper-0.24, iron-19.6, gallium-0.018, indium-0.08, potassium-84.8, lithium-0.130, magnesium-18.8, manganese-0.84, sodium-5.9, phosphorus-84.5, selenium-0.02, thallium-0.11,

Table 3. Proximate composition and mineral profile of *Cyclocybe aegerita*

Research	Moisture	Protein	Fat	Fibre	Ash	Minerals	Reference
Proximate composition (fresh mushroom)	92.36 %	-	0.20 g/100 g	8.05 g/100 g	1.22 g/100 g	-	(39)
	900 g/kg	20.5 g/kg	5.1 g/kg	-	-	Magnesium (0.593 g/kg), potassium (3.3 g/kg) and sodium content (0.004 g/kg)	(11)
	-	38.3 %	3.0 %	-	8.2 %	Potassium and phosphorus predominant	(49)
Nutritional profile (dry weight)	-	6.68 g/100 g	PUFA-rich (linoleic acid 78.4 %)	-	6.69 g/100 g	-	(50)
Dietary fibre analysis	-	-	-	TDF: 11.43%; PDF: 10.06%	11.97 %	carbon: 40.00 %; nitrogen: 5.92 %; hydrogen: 6.31 %	(48)
Mineral composition	-	-	-	-	-	Potassium (84.8), phosphorus (84.5), calcium (45.7), iron (19.6), magnesium (18.8), sodium (5.9), zinc (0.82), manganese (0.84), copper (0.24), cobalt (0.032), selenium (0.02) µg/g DW; Silver (0.030), aluminium (5.6), arsenic (0.08), cadmium (0.019), chromium (0.46), nickel (0.20), lead (0.016), strontium (0.74) µg/g DW	(51)

PUFA: poly unsaturated fatty acid; TDF: total dietary fibre; PDF: pure dietary fibre.

vanadium-0.13 and zinc-0.82 (51). The black poplar mushroom contains moisture content of 900 g/kg, protein (20.5 g/kg), fats (5.1 g/kg), ascorbic acid (0.082 g/kg) and minerals viz., magnesium (0.593 g/kg), potassium (3.3 g/kg) and sodium content (0.004 g/kg) (11). Table 3 summarises the overall mineral composition reported for *C. aegerita* across the available studies.

Bioactive compounds of *Cyclocybe aegerita*

Mushrooms are celebrated not just for their taste but also for their wide-ranging biological benefits. These include effects that are anti-diabetic, antioxidant, anti-tumour, anti-fungal, anti-bacterial, anti-viral and anti-inflammatory in nature (52). These biological functions are attributed to the existence of numerous potent bioactive components. The compounds responsible include proteins, dietary fibre, lectins, polysaccharides, phenolic and polyphenolic substances, terpenoids, ergosterols and volatile organic compounds (53, 54). Fig. 2 represents the major biological activities exhibited by *C. aegerita*. The major classes of bioactive compounds and their reported biological activities are summarised in Table 4.

Polysaccharides

Mushrooms offer various health advantages due to their active biological components. Among these components are polysaccharides, which primarily consist of β-glucan. This compound is characterised by its β1,3/1,6 glycosidic bond structure (76). This unique bonding increases the resistance potential against the α-1,4-amylase enzyme in humans, making β-glucan indigestible. Compared to other sources, mushroom polysaccharides have a lower molecular weight, which enhances their absorption and utilisation by the human body (77). Clinical studies have shown promising results for several commercial

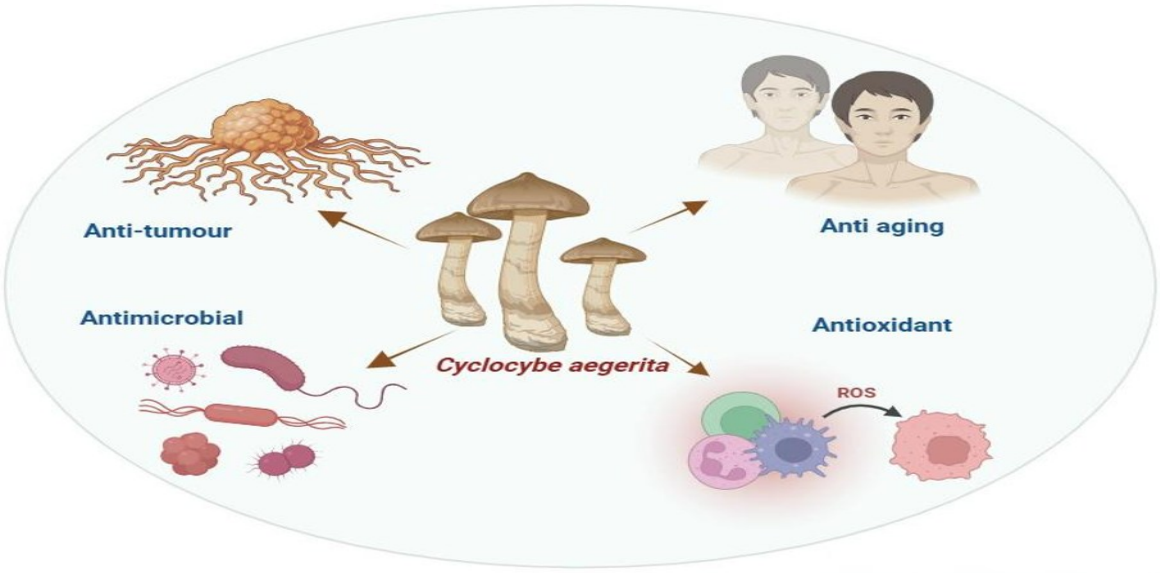


Fig. 2. Overview of biological activities reported from *Cyclocybe aegerita.*

ROS: reactive oxygen species.

Table 4. Bioactive compounds identified in *Cyclocybe aegerita* and reported biological activities

Bioactive compounds	Compound group	Activity	Reference
Agrocybin	Peptide	Anti-fungal	(12)
p-Hydroxybenzoic acid, *p*-coumaric acid and cinnamic acid	Phenolic acid	Antioxidant	(42)
Peptides	Peptides	Antioxidant	(55)
Mycelial polysaccharides-Arabinose, fucose, galactose, glucose and mannose	Polysaccharides	Antioxidant; anti-aging and organ protection	(56)
AAPS- Rhamnose, fucose, arabinose, xylose, mannose, glucose and galactose	Polysaccharides	Antioxidant, anti-aging	(56)
Phenolic compounds, flavonoids, tocopherols and ascorbic acid	Phenols	Antioxidant	(50)
Methanolic extract	Phenols	Antimicrobial activities and the antiqourum effect on *Pseudomonas aeruginosa*	(57)
Benzoic acid	Phenolic acid	Antioxidant and anti-biofilm	(58)
Aegerolysin	Protein	Hemolytic proteins that help in development of fungal bodies	(59)
Lectin	Protein	Anti-viral tobacco mosaic virus (TMV)	(60)
Lectin	Protein	Anti-tumour effects via apoptosis-inducing and DNase activities	(61)
Lectin	Protein	Anti-viral (influenza virus)	(62)
Ageritin (vacuolar ribonuclease)	Ribotoxin protein	Anti-fungal properties against *Penicillium digitatum*	(63)
Met-ageritin (isoform of ageritin)	Ribotoxin protein	Anti-fungal	(64)
Ageritin	Ribotoxin protein	Anti-proliferative, induction of apoptosis and anti-fungal	(65)
Ageritin	Ribotoxin protein	Cytotoxic, anti-fungal, anti-bacterial, entomotoxic and nematotoxic	(66)
Protein nanocomposite AANL-SeNP	Protein nanocomposite	Anti-lung cancer	(67)
Lectin	Protein	Hemagglutination activity	(68)
Ergosterol	Sterol	Anti-inflammatory	(69)
5,8-epidioxy-ergosta-6,22-dien-3β-ol	Sterol	Anti-inflammatory; antioxidant	
Glutathione and ergothioneine	Low molecular weight antioxidants	Antioxidant	(70)
Ceramide	Lipids	Anti-tumour	(71)
Lectin, serine proteinase, triethylene glycol, α-bisabolol and *n*-hexadecanoic acid	Protein, enzyme, small molecule mixture	Anti-tumour	(72)
Deoxyribonuclease (AAD)	Enzymes	Anti-proliferative-anti-tumour applications	(73)
Ubiquitin-conjugating enzyme	Enzyme	Anti-tumour	(74)
Fibrinolytic enzyme	Enzyme	Anti-coagulant and anti-thrombolytic	(75)

AAPS: *Agrocybe aegerita* polysaccharide fraction; AANL-SeNP: nanocomposite of *Agrocybe aegerita* lectin with selenium nanoparticles.

medications derived from mushroom polysaccharides. These include schizophyllan, lentinan, trifolin and complexes of polysaccharide-peptide and polysaccharide-protein (78). Polysaccharides from the genus *Cyclocybe* are reported to be involved in regulating the immune system, lowering blood sugar levels, preventing cell damage, fighting cancer, reducing aging and acting as antioxidants (79). *Cyclocybe aegerita* fruiting bodies and mycelium contain substantial amounts of various polysaccharides, including glucose, fructose, galactose, mannose, rhamnose, fucose, arabinose and xylose, which possess anti-tumour properties (80), anti-aging, antioxidant (56, 79, 81) and immunomodulatory activity (82).

Lectins

Proteins known as lectins can specifically attach to carbohydrates found on cell surfaces, resulting in cell aggregation. Within this group, lectins derived from mushrooms have been extensively studied due to their diverse biological activities. Studies have demonstrated that these proteins possess various properties, including the capacity to stimulate cell division, inhibit cell growth, target and attack cancer cells, combat viruses and enhance immune system function (83). Lectins have been extracted from both the reproductive structures and vegetative filaments of certain edible fungal species including *Tricholoma mongolicum, P. ostreatus* and *C. aegerita* (84). The molecular weights of these lectins have been determined to range from 12–68 kilodaltons (67). The lectins obtained from *C. aegerita* had good activity and stability at 60 °C and in the extreme acidic pH of 2.42 or alkaline pH of 12.22 environments, which are unsuitable for the lectins grabbed from other sources (60).

Steroids

Steroids are a significant component of fungi, most are ergosterol and their derivatives. Fungi primarily contains ergosterol as their main sterol, which is essential for maintaining the flexibility and structure of cell membranes. Furthermore, ergosterol serves important immunological purposes (85). These compounds play a significant role as secondary metabolites of the genus *Cyclocybe*. The seven steroid compounds (1–7) have been observed to date (69, 86–88). Components 1 and 2 had the ability to reduce inflammation and had antioxidant potential (69). Components 3–7 from *Cyclocybe chaxingu* effectively reduced the activity of osteoclasts, the cells responsible for breaking down bone tissue, which could potentially be used to prevent or control osteoporosis (87). Compound 8 exhibited anti-microbial effects against several

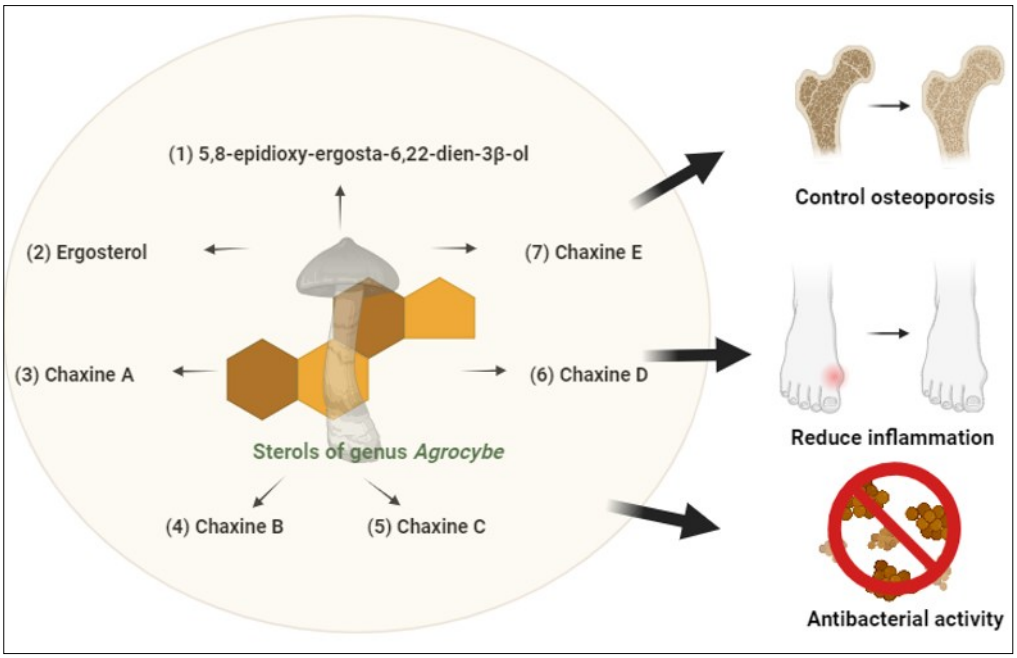


Fig. 3. Steroidal compounds reported from *Cyclocybe aegerita* and related taxa, with major reported activities (69, 86–89).

bacterial species (89). Representative steroidal compounds reported from *C. aegerita* and related *Cyclocybe* species are shown in Fig. 3.

Terpenoids

Terpenoids comprise a diverse group of naturally occurring compounds with varied structures. Their versatility is demonstrated by their applications in pharmaceuticals, therapeutic products, dietary supplements and as components in flavours and fragrances. During the development of *C. aegerita* fruiting bodies, researchers identified a total of 22 different volatile sesquiterpenes (90, 91). Four terpenoids were reported under submerged culture conditions of *C. aegerita* viz., bovistol, bovistol derivatives B and C and pasteurestin C (92).

Nutraceutical properties of *Cyclocybe aegerita*

Nutritional composition and functional food potential

Previous analyses of the fruiting bodies collected from the natural environment and cultures, it was found that there is a high content of macronutrients (mainly proteins and dietary fibres) and palmitic acid, linoleic acid, ergosterol, mannitol and trehalose (71). Comparative nutritional and anti-radical-capacity studies have been made of *C. aegerita* in comparison to *Agaricus bisporus* (J.E. Lange) Imbach for macronutrients, free and protein-bound amino acids and fatty-acid content and the possibility of using it in functional foods, e.g., antioxidant-enriched cream cheese (50).

Flavour compounds

In the area of sensory characteristics, *C. aegerita* stands out prominently for its umami taste, a sensation recognised as the fifth basic taste by humans, distinguished by its pleasant, savoury, or meaty essence. Amongst the five proteases used, the optimum protease for enzymatic hydrolysis of *C. aegerita* was protamex that produced the highest sensory score for umami (7.03) and equivalent umami concentration (EUC) (1039.475 ± 2.673 g, monosodium glutamate (MSG)-eq/100 g). The protamex-treated hydrolysate had the highest umami sensory score, EUC value and acceptability, with the most low-molecular-weight peptides (< 1 kDa) and soluble sugars, correlating positively with umami intensity (93). An earlier study identified eleven distinct aromatic compounds in the fruiting bodies of *C. aegerita* (90). These included hexane and octan-3-one, which provide a grassy scent; oct-1-en-3-one and oct-1-en-3-ol, contributing floral and rose-like notes; acetic acid, reminiscent of vinegar; benzaldehyde, offering an almond fragrance; (E)-oct-2-en-1-ol, characterised by a rancid smell; butanoic acid, isovaleric acid and pentanoic acid, all imparting cheese-like flavours; and 2-phenylethanol, which produces a rose-like scent.

A comprehensive analysis of taste components, including free amino acids, 5'-nucleotides and organic acids, was performed, with a particular emphasis on their EUC as a key taste indicator. *Cyclocybe aegerita* showed marked growth-stage variation in taste compounds. Glycine, isoleucine, leucine, threonine and valine were higher in mycelia, whereas fruit bodies had greater total free amino acids. Umami-enhancing 5'-nucleotides ranged from 0.36–0.98 mg/g across stages. Malic acid, succinic acid and total organic acids were more abundant in fruit bodies, while primordium showed higher tartaric and oxalic acid than either mycelia or fruit bodies. Sensory EUC values rose sharply across development 19.20, 66.19 and 322.42 g/100 g for mycelia, primordium and fruit bodies respectively highlighting *C. aegerita*'s potential as a functional food and flavour enhancer (94). Previous research also indicated that organic acids contribute to the flavour profile of alcoholic beverages like wine and sake, suggesting potential applications as safer food flavouring additives from mushrooms (95).

The culinary flavour is enhanced by the presence of MSG component and it was reported to be present in the black poplar mushrooms ranging from 10.9–11.9 mg/g dw (96). The composition of total amino acids in black poplar mushrooms, with glutamic acid + glutamine (Glx) comprising 16 % and higher essential amino acids at a rate of 5.3 g/kg (11). These findings underscore the diverse nutritional and sensory attributes of various mushroom species, providing insights into their potential applications in culinary and functional food industries.

Antioxidant activity

The methanolic, ethanolic and aqueous extracts of *C. aegerita* fruiting bodies and mycelium exhibits dose-dependent radical scavenging activity in 2,2-diphenyl-1-picrylhydrazyl (DPPH), 2,2'-azino-bis (3-ethylbenzothiazoline-6-sulfonic acid) (ABTS), ferric reducing antioxidant power (FRAP), oxygen radical absorbance

capacity (ORAC) and nitric-oxide assays due to the presence of phenolic acids (gallic acid, quinic acid) and sterols (50, 57, 58, 71, 97). *In vivo*, the polysaccharide fractions produced by mycelium (Ac-MPS, Al-MPS, En-MPS) reversed this activity in aged mice induced by D-galactose, by restoring the activities of superoxide dismutase (SOD), catalase (CAT) and glutathione peroxidase (GPX), which are three enzymes related to the defence against lipid peroxidation and reducing the levels of malondialdehyde (MDA), a marker of this lipid peroxidation (56, 79).

The optimal extraction method for polysaccharides from *C. aegerita* was determined using accelerated solvent extraction combined with response surface methodology (ASE-RSM). This approach was employed due to the known antioxidant properties of mushroom polysaccharides. The study identified the ideal extraction parameters as follows: 6.5 min of extraction duration, 71 °C extraction temperature and 3 extraction cycles. Under these optimised conditions, the yield of crude polysaccharides was 19.77 ± 0.12 % (98). Similarly, the ideal conditions for generating peptides with maximum antioxidant properties were also determined. The optimal parameters were determined to be a temperature of 51.1 °C, a pH of 8.5 and an enzyme-to-substrate ratio of 3 %. Under these specific parameters, researchers identified five new antioxidant peptides. This discovery underscores the potential use of *C. aegerita* protein hydrolysates as natural antioxidants in both functional foods and food processing applications (55).

Anti-aging and gut microbiota effects

Mushrooms are well-known for their rich content of antioxidants, including selenium, vitamins C and E, polyphenols, glutathione and ergothioneine. These protective compounds function in unison to counteract oxidative stress and inflammation, thus lowering the likelihood of developing chronic diseases such as cardiovascular disorders, cancer and degenerative neurological conditions. Incorporating a diverse range of mushrooms into one's diet can offer a broad spectrum of antioxidants, promoting overall health and wellness. A dedicated polysaccharide fraction-*Agrocybe aegerita* polysaccharide fraction (AAPS) extended the lifespan and reduced oxidative stress in *Drosophila melanogaster*, as well as decreased oxidative damage and changed gut microbiota composition (increasing the firmicutes/bacteroidetes ratio and the abundance of *Lactobacillus*) in D-galactose-aged mice (99). A second study, which compared the effects of AAPS with *Bifidobacterium lactis* Bb-12, a probiotic, found that AAPS had synergistic effects in the attenuation of aging-related oxidative stress and in restoring gut microbiota, suggesting it plays a prebiotic role as well (100).

Researchers successfully extracted a unique melanin pigment from *C. aegerita*. This naturally occurring melanin exhibits structural similarities to synthetic tyrosine melanin, specifically belonging to the 3,4-dihydroxyphenylalanine category. The pigment demonstrates remarkable stability across a broad spectrum of conditions, maintaining its integrity at temperatures ranging from 20–100 °C and in environments with pH levels between 11–14 (101). The robust antioxidant capabilities of *C. aegerita* can be attributed to its high concentrations of ergothioneine and glutathione, which are present at levels of 2.56 and 1.92 (mg/g dry weight) respectively (70).

Anti-diabetic potential

Hypoglycemic polysaccharides were described at genus level for *Cyclocybe* species (71) and species-specific studies of extracts of *C. aegerita* from Serbia indicated α-amylase inhibitory activity, a commonly used *in vitro* model of anti-diabetic activity (97), no *in vivo* glucose tolerance nor diabetic-model data for this species was found.

Pharmaceutical properties of *Cyclocybe aegerita*

Anti-tumour/cytotoxicity activity

Mushrooms have attracted interest due to their potential as anti-tumour agents, attributed to the diverse bioactive compounds they possess. *Cyclocybe aegerita* stands out as one of the widely recognised mushrooms celebrated for its anti-tumour effects. The best-characterised anti-cancer principle is the *Agrocybe aegerita* lectin (AAL), a 15.8 kDa homodimer galectin first purified from fruiting bodies. *Agrocybe aegerita* lectin inhibited the proliferation of mouse S-180 sarcoma cells, HeLa, SW480, SGC-7901, MGC-803, BGC-823 and HL-60 tumour cells *in vitro*, induced apoptosis (assessed by staining with Hoechst 33258 dye, mitochondrial-potential assays, flow cytometry and terminal deoxynucleotidyl transferase dUTP nick-end labelling (TUNEL) assays of excised tumour tissue) and exhibited DNase activity which is suggested as a component of its mechanism of action. *In vivo*, AAL inhibited the growth of S-180 tumour in mice (61). It also reduced lung metastasis in a 4T1 mouse model of breast cancer along with characterising its pharmacokinetic profile in a later study (102). A variant of AAL that recognises GlcNAc was then crystallised and structurally characterised (103). In human tissue, AAL-histochemistry has been employed as a probe of glycophenotype: AAL-reactive glycoconjugates were found to be much more prevalent in colorectal-cancer tissue than in normal adjacent tissue and were seen to be associated with the depth of invasion and tumour-node-metastasis (TNM) stage in a 59-patient series; this is the closest available evidence to a human-tissue/clinical correlate for this species (72). A ceramide isolated from the fruiting body inhibited proliferation of stomach, breast and central nervous system (CNS) cancer cell lines by 26.9–39.1 % at 100 µg/mL (71). In addition, polysaccharides fractions derived from the fruiting bodies and mycelia of *Agrocybe aegerita* (AAP) and *Agrocybe cylindracea* (ACP) inhibited MGC-803 gastric cancer cell proliferation *in vitro* and suppressed S180 sarcoma and S180 ascites tumours *in vivo* (100). A fucoglucogalactan from the closely related *A. cylindracea* was shown to induce lysosome-mediated apoptosis in colorectal cancer cells via H3K27ac-regulated cathepsin D, though this finding has not yet been confirmed in *C. aegerita* itself (104).

A novel nanocomposite called AANL-SeNPs, developed through oxidation-reduction (REDOX) showed a significant reduction in the cell inhibition rate by approximately half and the average tumour volume was reduced by about 79 % in lung cancer. Additionally, they observed that AANL-SeNPs exerted an anti-lung cancer effect by upregulating the expression of CLK2 (67). The edible mushroom galectin *C. aegerita* lectin (AAL/AAGL), has shown anti-tumour properties by inducing apoptosis *in vitro*. It was further supported by the observed correlation between the AAL/AAGL's efficacy and the ratio of GAL3ST2 (enzyme responsible for 3'-sulfo-TF expression) to ST3GAL1 (competing enzyme) within cancer cell lines. Overexpression of GAL3ST2 significantly enhanced the growth inhibitory effect of AAL/AAGL, highlighting the importance of 3'-sulfo-TF antigen as a target ligand (105). Two DNase-active anti-tumour proteins (AAL and AAL-2) were purified from *C. aegerita*, as DNase-active enzymes are reported to have promise as anti-cancer agents (103) and ageritin induced apoptosis in COLO 320, HeLa and Raji cells (63).

Anti-microbial and anti-biofilm activity

Ageritin obtained from *C. aegerita* was found to be toxin against the bacteria *Micrococcus lysodeikticus* at a concentration of 5.3 µM with growth inhibition of 50 % (66). Agrocybin, a ~9 kDa anti-fungal peptide, inhibited the plant-pathogenic fungus *Mycosphaerella arachidis* (IC50 125 µM) but showed no activity against a panel of Gram-positive and Gram-negative bacteria and no anti-proliferative activity toward HepG2 cells (12). An ethanolic mycelial extract inhibited quorum-sensing-regulated virulence factors and biofilm formation in *Pseudomonas aeruginosa* PAO1 in a dose-dependent manner, alongside confirmed antioxidant activity in the same extract (58). Similarly, an extract of *C. aegerita* showed anti-biofilm activity by 84.24 % at a concentration of 0.5 minimum inhibitory concentration (MIC) and anti-quorum sensing activity at concentrations ranging from 7.70–10.30 mm in the bacteria *P. aeruginosa* (57). A compound known as fucogalactan, extracted from *C. aegerita* substrates, demonstrated the ability to reduce arginase enzymatic activity by 60.5 % when present at a concentration of 10 µmol/L. This inhibition of arginase of *Leishmania* sp. was found to be effective in treatment of leishmaniasis (82). This suggests that the compounds in *C. aegerita* mushrooms show promise for combating fungal and bacterial infections.

Anti-fungal activity

Ageritin, a ribotoxin-like ribosome-inactivating protein (RIP) that cleaves a single phosphodiester bond in the sarcin–ricin loop of large rRNA, inhibited the phytopathogenic fungi *Botrytis cinerea* (57 %) *Colletotrichum truncatum* (42%) and *Alternaria alternata* (57 %) in plate assays, while sparing the beneficial fungus *Trichoderma harzianum*; its anti-fungal action was linked to ribosome-damaging ribonuclease activity (106). Earlier phytochemical work identified agrocybenine (anti-fungal alkaloid) and cylindan (reported anti-cancer activity) among the mushroom's bioactive secondary metabolites (107). A ribonuclease found in *C. aegerita* mushrooms, known as ageritin, targets rRNA in the α-sarcin/ricin stem-loop (SRL), establishing a novel ribotoxin family within basidiomycetes. This compound demonstrated anti-fungal activity against *Penicillium digitatum* (63).

Anti-viral activity

The lectin compound AAL, extracted from *C. aegerita*, demonstrated significant anti-viral activity. When applied at a concentration of 200 µg/mL, it reduced the number of lesions by 84.3 %. Further analysis revealed that AAL's half-maximal inhibitory concentration (IC50) against tobacco mosaic virus (TMV) infection in *Nicotiana glutinosa* leaf assays ranged between 30–40 µg/mL (60). No other scientific evidence of anti-viral activity on humans or animals has been reported.

Anti-inflammatory activity

A ceramide isolated from the fruiting body inhibited cyclooxygenase-1 (43 %) and cyclooxygenase-2 (92.3 %) at 25 µg/mL, with an IC50 of 5.3 µg/mL against COX-2 comparable in the same assay system to reference non-steroidal anti-inflammatory drugs (NSAIDs) tested at much lower concentrations (71). Two sterols, ergosterol and 5α,8α-epidioxy-(22E,24R)-ergosta-6,22-dien-3β-ol, showed weaker but measurable COX-1/COX-2 inhibition and antioxidant activity at 100 µg/mL (69). These are enzyme-inhibition data; no whole-animal inflammation model specific to *C. aegerita* was identified.

Pore-forming proteins (aegerolysins) and insecticidal potential

The founding sequence of the aegerolysin protein family, Aa-Pri1, was cloned from *C. aegerita* as a primordium-specific gene (108). Aegerolysins are small (13–20 kDa) lipid-binding proteins that, in the homologous *Pleurotus* system, co-assemble with the MACPF-domain protein pleurotolysin B to form 13-meric transmembrane pores in cholesterol/sphingomyelin or ceramide-phosphoethanolamine-rich membranes, conferring insecticidal activity against western corn rootworm and Colorado potato beetle, as well as reported anti-tumoural, anti-proliferative and anti-bacterial effects across the protein family (109, 110). Direct functional bioactivity data for the *C. aegerita* protein itself remains limited compared with the well-characterised *Pleurotus* homologues.

Other specific activities

The ethanol and water extracts derived from *C. aegerita* demonstrated promising results in lowering serum uric acid levels in mice with hyperuricemia, bringing these levels closer to normal. This effect was attributed to two mechanisms: the inhibition of hepatic xanthine oxidase (XOD) activities and the increase in renal organic anion transporter 1 (OAT1), which likely facilitated the excretion of uric acid (10). A novel lectin *Cyclocybe cylindracea* lectin (CCL) protein (molecular weight > 35 kDa) with two chemically identified subunits and potential hemagglutination activity was discovered (68). A fibrinolytic enzyme of the serine protease type was discovered and characterised from the fruiting bodies of *C. aegerita*. This enzyme could break down fibrinogen and act as an anti-coagulant agent by hindering thrombin activity (75).

Safety profile and hepatotoxicity

A pharmacological profile is incomplete without its safety data. Aqueous fruiting-body extract produced a median lethal dose of 8.77 g/kg in mice and 25–250 mg/kg/day dosing for six days caused marked hepatic injury in BALB/c-Bagg albino model mice; liquid chromatography-mass spectrometry (LC-MS/MS) identified AAL the same lectin responsible for the anti-tumour and anti-viral activities above as the principal hepatotoxic component and it was found resistant to digestive-enzyme degradation (111). It is concluded that correct preparation/consumption is important for avoiding this risk, but the relevance of these experimental doses to normal culinary intake of cooked *C. aegerita* has not been established.

The major bioactive compounds and their reported pharmacological activities are summarised in Table 5. Overall, the pharmacological properties present in the mushrooms provide a promising scope for development of novel anti-microbial treatments, dietary supplements and functional foods but lacks in human clinical evidence. These developments could have significant effects on therapeutic and preventive measures for emerging diseases.

Economic significance, cultivation challenges and sustainability of *Cyclocybe aegerita* production

Cyclocybe aegerita has emerged as a commercially valuable crop, with its distinctive aroma, crisp texture and high protein content and is gaining popularity in the fresh market and in the production of canned, sauced and dried product lines for export markets (113). According to market analyses, the global *C. aegerita* trade is valued in the billions of US dollars and the Asian market is the largest producer while North America, Europe and East Asia are the fastest-growing consumer markets, as demand for natural, functional and minimally processed foods grows (114). But a series

Table 5. Pharmacological activities of *Cyclocybe aegerita*

Compound	Activity	*In vitro*	*In vivo* (Animal)	Human evidence	Limitations	Reference
Lectin (AAL)		Growth inhibition of HeLa, SW480, SGC-7901, MGC80-3, BGC-823, HL-60; apoptosis induction; DNase activity	Inhibited S-180 sarcoma in BALB/c mice; suppressed 4T1 breast-cancer lung metastasis, altered pharmacokinetics	AAL-histochemistry used as a prognostic glycophenotype marker in colorectal-cancer tissue detection	*Ex vivo* tissue biomarker only, not a treatment trial; AAL is also the compound behind the mushroom's hepatotoxicity	(61, 72, 102, 103)
Ceramide, linoleic acid, glucopyranosides	Anti-tumour/ cytotoxic	26.9–39.1 % inhibition of stomach, breast and CNS cancer cell proliferation at 100 µg/mL	Not reported	Not reported	Single concentration screen, no dose-response or mechanism beyond COX linkage	(71)
Protein/selenium nanocomposite		The average tumour volume was reduced about 79 % after treated by AANL-seNPs in lung cancer	Suppressed transplanted S180 sarcoma and S180 ascites tumours in mice	Not reported	Structure-activity relationships incompletely resolved, most *in vivo* data from the sister taxon *Agrocybe cylindracea*, not confirmed in *Cyclocybe aegerita* specifically	(67)
Polysaccharides	Antioxidant / anti-ageing	DPPH scavenging up to 85 %, hydroxyl-radical scavenging up to 69 %	Restored SOD/CAT/GPX activity and lowered MDA in D-galactose-induced aging mice, prolonged *Drosophila* lifespan, reshaped gut microbiota (higher firmicutes/ bacteroidetes, more *Lactobacillus*)	Not reported	Aging-mouse and fly models only, no human biomarker or lifespan data	(58, 79, 99, 100)
Phenolic acids, gallic acid and rutin		DPPH/ABTS/FRAP activity, gallic acid quantified at 27.9 mg/100 g extract, ORAC and ferricyanide assays positive	Not reported	Not reported	*In vitro* assays only, antioxidant capacity strongly extraction-solvent dependent, limiting cross-study comparison	(42, 50, 97)
Ceramide (1), ergosterol and 5α,8α-epidioxy-ergosta-6,22-dien-3β-ol	Anti-inflammatory	Ceramide inhibited COX-1 (43 %) and COX-2 (92.3 %) at 25 µg/mL, IC50 5.3 µg/mL against COX-2; the two sterols inhibited COX-1 (57 %, 19 %) and COX-2 (22 %, 28 %) at 100 µg/mL	Not reported	Not reported	Enzyme-inhibition assay only, no whole -cell or animal inflammation model, no comparison of oral bioavailability	(69, 71)
Polysaccharides	Anti-diabetic / hypoglycaemic	α-Amylase inhibitory activity demonstrated for Serbian *Cyclocybe aegerita* extracts, genus-level polysaccharides reported hypoglycaemic	Not reported for *Cyclocybe aegerita* specifically (hypoglycaemic polysaccharide activity reported for the genus)	Not reported	Single-enzyme *in vitro* assay, no glucose-tolerance or diabetic-animal data specific to this species	(71, 97)
Crude and purified mycelium/fruiting-body	Immunomodulatory	Not the main focus, enzyme/ antioxidant assays used as proxy	Improved immune parameters in tumour-bearing mice as chemotherapy adjuvant (genus-level evidence), enhanced antioxidant enzyme activity in D-galactose-aged mice	Not reported	Immunomodulatory claims for *Cyclocybe aegerita* rest largely on analogy with other mushroom polysaccharides rather than dedicated immune-endpoint studies	(79, 112)

Agrocybin (anti-fungal peptide)	Anti-microbial / anti-biofilm	Dose-dependent inhibition of *Pseudomonas aeruginosa* quorum-sensing and biofilm formation, agrocybin inhibited the plant pathogen *Mycosphaerella arachidis* (IC50 125 µM) but was inactive against tested bacteria	Not reported	Not reported	Narrow pathogen panel, agrocybin activity not confirmed against clinically relevant bacterial pathogens	(57, 106)
Ageritin and Agrocybin	Anti-fungal (against phytopathogens)	Ageritin (200 µg/plug) inhibited *Botrytis cinerea* (57 %) *Colletotrichum truncatum* (42%) and *Alternaria alternata* (57 %) by rRNA-cleaving ribotoxin activity, agrocybenine and cylindan reported with anti-fungal/anti-cancer activity in earlier phytochemical work	Not reported	Not reported	Plate-based plant-pathogen assays, no data on human-pathogenic fungi or systemic exposure	(12, 106)
Lectin (AAL)	Anti-viral (plant virus)	AAL bound tobacco mosaic virus (TMV) particles and inhibited TMV infection in *Nicotiana glutinosa* leaf assays	Not reported (plant infectivity assay only)	Not reported	Demonstrated against a plant virus, not a human/animal pathogen, mechanism of anti-viral binding not resolved	(60)
Aa-Pri1 (Aegerolysin)	Insecticidal / defence-related pore-forming proteins	Aa-Pri1 is the founding sequence of the aegerolysin protein family, related *Pleurotus* aegerolysin/pleurotolysin-B complexes form membrane pores and show insecticidal and anti-tumoural/anti-bacterial activity	Insecticidal activity against western corn rootworm and Colorado potato beetle demonstrated for *Pleurotus*-derived aegerolysins, not yet shown for the *Cyclocybe aegerita* protein itself	Not reported	Direct functional/ bioactivity data for the *Cyclocybe aegerita* protein (Aa-Pri1) itself are limited, most functional pore-forming and insecticidal evidence comes from the homologous *Pleurotus* proteins	(108–110)
Lectin	Safety / hepatotoxicity	LC-MS/MS identified AAL as the hepatotoxic component, AAL resistant to digestive-enzyme degradation	LD50 8.77 g/kg in mice, 25–250 mg/kg/day for 6 days caused marked hepatic injury in BALB/c mice	Not reported (no human poisoning case series identified)	High-dose/parenteral-style exposure in mice, relevance to normal culinary consumption of cooked mushroom not established	(111)

AAL: *Agrocybe aegerita* lectin; CNS: central nervous system; COX: cyclooxygenase; DPPH: 2,2-diphenyl-1-picrylhydrazyl; SOD: superoxide dismutase; CAT: catalase; GPX: glutathione peroxidase; MDA: malondialdehyde; ABTS: 2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid); FRAP: ferric reducing antioxidant power; ORAC: oxygen radical absorbance capacity; LC-MS/MS: liquid chromatography-mass spectrometry.

of enduring production problems limit this economic capacity. *Cyclocybe aegerita* is grown in enclosed and humid substrate culture systems and thus is highly susceptible to microbial contamination; surveys of *C. aegerita* production facilities in Korea have recovered a large proportion of *Trichoderma* spp. (as well as *Aspergillus* spp., *Mucor* spp. and *Penicillium* spp.) as pathogens associated with *C. aegerita* fruiting bodies and composts (115). In addition, mushroom crops across the globe are experiencing significant losses due to the mycoparasitic diseases dry bubble, cobweb, wet bubble and green mold, with strains of these pathogens becoming resistant to a limited range of fungicides, highlighting the need for an integrated approach to disease management, rather than chemical control alone (116, 117).

Quality control is also critical after harvest: deterioration during storage and transport-caused by moisture loss, membrane damage, changes in antioxidant enzyme activity and surface bacterial growth-directly affects shelf life and market value (113). Such pressures make sustainability a key issue for the industry, because, like other cultivated mushroom species, *C. aegerita* is cultivated on low-value or burned agricultural residues, such as straw, sawdust, cottonseed hull, etc., which are used as nutrient sources for the crop and result in a nutrient-rich spent mushroom substrate, which can be recycled as animal feed, biofertiliser or compost in a circular-economy system (6, 118). Because this waste-to-food model reduces pressure on arable land, conserves water relative to conventional protein sources and aligns with sustainable production and responsible consumption targets, biocontrol and microbiome-based disease management strategies rather than expanded fungicide use are increasingly framed as the pathway that allows economic expansion of *C. aegerita* cultivation to proceed without compromising its environmental credentials (119).

Commercial development and industrial relevance

Cyclocybe aegerita has notable industrial relevance as a choice of edible mushroom, a useful functional food and also a model mushroom system for mushroom development and metabolite research. It is also quite successful as a commercial crop because it can be grown on agricultural residues and more recently, yield has been enhanced by methods of cultivation in controlled environments. But the large-scale production is limited by the

strain-dependent performance, variable biological efficiency and the requirement of proper control of substrate composition, temperature, humidity and post-harvest handling. Hence, the species is potentially good for niche and value-added markets, but more standardisation is required before it can compete with the more established commercial mushrooms.

Research gaps and future directions

Despite the nutritional and bioactive benefits of *C. aegerita*, there are still some research gaps that need to be filled before its potential for cultivation and commercialisation can be realised. Previous studies were hindered by strain-to-strain variability, variable growth substrate performance and lack of uniformity in the cultivation protocol throughout the growth stages. Furthermore, most of these health-related effects reported are based upon *in vitro* or animal studies and there is limited human evidence. The strain improvement, comparative optimisation of substrate, precise environment management, post-harvest management and intensive translation research should therefore be in the focus of future work, not only to ensure the industrial feasibility but also to ensure the safe utilisation of the strains.

Conclusion

Cyclocybe aegerita is a nutritionally valuable edible mushroom with notable potential for sustainable cultivation and high-value utilisation. The literature reviewed, however, suggests that its production ability is significantly affected by strain selection, substrate composition and environmental control and that there is still significant variation in biological efficiency between production systems. Concurrently, the species has been demonstrated to be rich in various bioactive compounds possessing antioxidant, anti-microbial, anti-inflammatory, immunomodulatory and anti-tumour properties with most evidence limited to preclinical studies. Therefore, *C. aegerita* poses potential as a mushroom crop, but needs further optimisation of mushroom culture protocols, optimisation of mushroom strain performance and testing for safety and translation to prove its commercial and biomedical potential.

Acknowledgements

The authors sincerely acknowledge the Department of Plant Pathology, Tamil Nadu Agricultural University, Coimbatore, for providing necessary support and facilities for the preparation of this manuscript.

Authors' contributions

RKD contributed to the conceptualisation, literature collection, manuscript drafting and manuscript editing. GT contributed to supervision and critical review of the manuscript. PM, MS, SPTS and NB contributed to literature validation, data compilation and manuscript revision. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

References

1. TorrestGómez M. Human medicinal mushroom use. In: Therapeutic mushrooms for diabetes mellitus. Apple Academic Press; 2023. p. 35–66. https://doi.org/10.1201/9781003332046-3
2. Singh A, Saini RK, Kumar A, Chawla P, Kaushik R. Mushrooms as nutritional powerhouses: A review of their bioactive compounds, health benefits and value-added products. Foods. 2025;14(5):741. https://doi.org/10.3390/foods14050741
3. Winkelman M. Introduction: Evidence for entheogen use in prehistory and world religions. Journal of Psychedelic Studies. 2019;3(2):43–62. https://doi.org/10.1556/2054.2019.024
4. Uhart M, Piscera JM, Albertó E. Utilization of new naturally occurring strains and supplementation to improve the biological efficiency of the edible mushroom *Agrocybe cylindracea*. Journal of Industrial Microbiology and Biotechnology. 2008;35(6):595–602. https://doi.org/10.1007/s10295-008-0321-1
5. Stamets P. Growing gourmet and medicinal mushrooms. Ten Speed Press; 2011.
6. Li Z, Zhou Y, Zhao G, Xu C, Pan J, Li H, et al. Impacts of yield, nutritional value and amino acid contents during short-term composting for the substrate for *Agrocybe aegerita*. Horticulturae. 2024;10(3):234. https://doi.org/10.3390/horticulturae10030234
7. Kües U, Liu Y. Fruiting body production in basidiomycetes. Applied Microbiology and Biotechnology. 2000;54(2):141–52. https://doi.org/10.1007/s002530000396
8. Mwangi RW, Macharia JM, Wagara IN, Bence RL. The antioxidant potential of different edible and medicinal mushrooms. Biomedicine & Pharmacotherapy. 2022;147:112621. https://doi.org/10.1016/j.biopha.2022.112621
9. Petrović J, Glamočlija J, Danijel DM, Ana D, Steva L, Slađana PS, et al. Comparative chemical analysis and bioactive properties of aqueous and glucan-rich extracts of three widely appreciated mushrooms: *Agaricus bisporus* (JE Lange) Imbach, *Laetiporus sulphureus* (Bull.) Murill and *Agrocybe aegerita* (V. Brig.) Vizzini. Pharmaceuticals. 2024;17(9):1153. https://doi.org/10.3390/ph17091153
10. Yong T, Chen S, Xie Y, Shuai O, Li X, Chen D, et al. Hypouricemic effects of extracts from *Agrocybe aegerita* on hyperuricemia mice and virtual prediction of bioactives by molecular docking. Frontiers in Pharmacology. 2018;9:498. https://doi.org/10.3389/fphar.2018.00498
11. Landi N, Pacifico S, Ragucci S, Di Giuseppe AMA, Iannuzzi F, Zarrelli A, et al. Pioppino mushroom in southern Italy: An undervalued source of nutrients and bioactive compounds. Journal of the Science of Food and Agriculture. 2017;97(15):5388–97. https://doi.org/10.1002/jsfa.8428
12. Ngai PHK, Zhao Z, Ng TB. Agrocybin, an antifungal peptide from the edible mushroom *Agrocybe cylindracea*. Peptides. 2005;26(2):191–6. https://doi.org/10.1016/j.peptides.2004.09.011
13. Lo KM, Cheung PCK. Antioxidant activity of extracts from the fruiting bodies of *Agrocybe aegerita* var. alba. Food Chemistry. 2005;89(4):533–9. https://doi.org/10.1016/j.foodchem.2004.03.006
14. Nadar SS, Rao P, Rathod VK. Enzyme assisted extraction of biomolecules as an approach to novel extraction technology: A review. Food Research International. 2018;108:309–30. https://doi.org/10.1016/j.foodres.2018.03.006
15. Niveiro N, Uhart M, Albertó E. Revision of the genera *Agrocybe* and *Cyclocybe* (Strophariaceae, Agaricales, Basidiomycota) in Argentina. Rodriguésia. 2020;71:e02272018. https://doi.org/10.1590/2175-7860202071038
16. Li J, Yang W, Ren J, Cao B, Zhu X, Lin L, et al. A new species *Agrocybe*

striatipes, also a newly commercially cultivated mushroom with highly nutritional and healthy values. Journal of Fungi. 2023;9(3):383. https://doi.org/10.3390/jof9030383

17. Jasińska A, Siwulski M, Sobieralski K. Mycelium growth and yielding of black poplar mushroom-*Agrocybe aegerita* (Brig.) Sing. on different substrates. Journal of Agricultural Science and Technology A. 2012;2(9):1040–7.
18. Sharma VP, Sharma SR, Satish Kumar SK. Physiological requirements and cultivation of *Agrocybe aegerita*. 2004.
19. Solomko EF, Lomberg ML. Effect of cultural conditions on mycelial growth and fruiting of *Agrocybe aegerita*. International Journal of Medicinal Mushrooms. 2007;9(3/4):352.
20. Dulay RMR, Cabrera EC, Kalaw SP, Reyes RG, Hou CT. Nutritional requirements for mycelial growth of three *Lentinus* species from the Philippines. Biocatalysis and Agricultural Biotechnology. 2020;23:101506. https://doi.org/10.1016/j.bcab.2020.101506
21. Dulay RMR, Cabrera EC, Kalaw SP, Reyes RG. Optimization of submerged culture conditions for mycelial biomass production of fourteen *Lentinus* isolates from Luzon Island, Philippines. Biocatalysis and Agricultural Biotechnology. 2021;38:102226. https://doi.org/10.1016/j.bcab.2021.102226
22. Bilay VT, Solomko EF, Buchalo AS, editors. Growth of edible and medicinal mushrooms on commercial agar. 2000.
23. Sakthivel K, Prakasam V, Thiribhuvanamala G, Madhavan S. Nutritional, temperature and pH requirements for the mycelial growth of black poplar mushroom, *Agrocybe aegerita*. Madras Agricultural Journal. 2023;99(10–12):1.
24. Song AiRong SA, Liu TongBao LT. Effects of KH_2PO_4 on submerged culture of *Agrocybe aegerita* under different pH values. 2004.
25. Wachowicz E, Woroncow L. Comprehensive model of processes proceeding at a mushroom-growing celler. Technical Sciences. 2010;13:30–9. https://doi.org/10.2478/v10022-010-0004-9
26. Kalaw SP, Alfonso DO, Dulay RMR, De Leon AM, Undan JQ, Undan JR, et al. Optimization of culture conditions for secondary mycelial growth of wild macrofungi from selected areas in Central Luzon, Philippines. Curr Res Environ Appl Mycol. 2016;6(4):277–87. https://doi.org/10.5943/cream/6/4/5
27. Munshi NA, Dar GH, Ghani MY, Kauser S, Mughal N. Button mushroom cultivation. Communication and Publication Centre SKUAST-K. 2010;1:1–33.
28. Zervakis G, Philippoussis A, Ioannidou S, Diamantopoulou P. Mycelium growth kinetics and optimal temperature conditions for the cultivation of edible mushroom species on lignocellulosic substrates. Folia Microbiologica. 2001;46(3):231–4. https://doi.org/10.1007/BF02818539
29. Jasińska A, Siwulski M, Sobieralski K, Majtkowski W, Rogalski J, Ohga S. Comparative study of mycelial growth and carpophore yield of *Agrocybe aegrerita* (Brig.) Sing. on selected agricultural and textile industry wastes as a cultivation substrate. 2014. https://doi.org/10.5109/1434373
30. Jasińska A, Siwulski M. Impact of substrate supplemented with $CaCO_3$ on mycelial growth, yield, morphological features and storability of fruiting bodies of black poplar mushroom *Agrocybe cylindracea* (DC.) Marie. International Journal of Horticultural Science. 2021;27:76–86. https://doi.org/10.31421/ijhs/27/2021/5432
31. Bandura I, Kulyk AS, Makohon SV, Tsyz OM, Khareba OV, Khareba VV, et al. Qualitative characteristics of the fungus *Cyclocybe aegerita* strains 2229, 2230, 2231 IBK under industrial cultivation conditions. Plant and Soil Science. 2021;12(3):85–99. https://doi.org/10.31548/agr2021.03.085
32. Sood B, Sh K. Assessing the potential of lignocellulosic agro-wastes for high yield of *Agrocybe aegerita* (Brig.) Singer under Punjab climatic conditions. International Journal of Science and Nature. 2016;7(1):104–11.
33. Sharma V, Sharma S, Kumar S. Cultivation of least-exploited commercial mushrooms. Mushroom Biology and Biotechnology. 2007;213:167.
34. Rezaeian SH, Pourianfar HR, Shahtahmasbi SH. Cultivation of black poplar mushroom, *Cyclocybe aegerita*, on woody and non-woody lignocellulosic substrates with a high biological efficiency. Asian Journal of Mycology. 2022;5(1):31–9. https://doi.org/10.5943/ajom/5/1/3
35. Philippoussis A, Zervakis G, Diamantopoulou P. Bioconversion of agricultural lignocellulosic wastes through the cultivation of the edible mushrooms *Agrocybe aegerita*, *Volvariella volvacea* and *Pleurotus* spp. World Journal of Microbiology and Biotechnology. 2001;17(2):191–200. https://doi.org/10.1023/A:1016685530312
36. Shim SM, Kim SB, Kim HY, Rho HS, Lee HS, Lee MW, et al. Genes expressed during fruiting body formation of *Agrocybe cylindracea*. Mycobiology. 2006;34(4):209–13. https://doi.org/10.4489/MYCO.2006.34.4.209
37. Kleofas V, Sommer L, Fraatz MA, Zorn H, Rühl M. Fruiting body production and aroma profile analysis of *Agrocybe aegerita* cultivated on different substrates. Natural Resources. 2014;5(6):233. https://doi.org/10.4236/nr.2014.56022
38. Nicolini L, Von Hunolstein C, Carilli A. Solid state fermentation of orange peel and grape stalks by *Pleurotus ostreatus*, *Agrocybe aegerita* and *Armillariella mellea*. Applied Microbiology and Biotechnology. 1987;26(1):95–8. https://doi.org/10.1007/BF00282155
39. Muthu N, Shanmugasundaram K. Proximate and mineral compositions of edible mushroom *Agrocybe aegerita*. Journal of Pharmacognosy and Phytochemistry. 2016;5(1):116.
40. Sharma VP, Sharma SR. Molecular identification and cultivation of the black poplar culinary-medicinal mushroom *Agrocybe aegerita* (V. Brig.) Singer (Agaricomycetideae). International Journal of Medicinal Mushrooms. 2009;11(1). https://doi.org/10.1615/IntJMedMushr.v11.i1.100
41. Sadegh SH, Ramezan D, Pirnia M, Aran M, Sarani S. Evaluation of yield and total polysaccharide amounts of the basidiocarp of Iranian isolates of *Agrocybe aegerita* and *Hypsizygus ulmarius* mushroom produced on various substrates. Journal of Microbial Biology. 12(45):1–17.
42. Gąsecka M, Mleczek M, Siwulski M, Niedzielski P, Kozak L. Phenolic and flavonoid content in *Hericium erinaceus*, *Ganoderma lucidum* and *Agrocybe aegerita* under selenium addition. Acta Alimentaria. 2016;45(2):300–8. https://doi.org/10.1556/066.2016.45.2.18
43. Sarker NC, Shaheen M, Amin SMR, Khan AS. Domestication and cultivation of *Agrocybe aegerita* on straw and sawdust substrate. Bangladesh J Mushroom. 2008;2:73–9.
44. Isikhuemhen OS, Mikiashvili NA, Kelkar V. Application of solid waste from anaerobic digestion of poultry litter in *Agrocybe aegerita* cultivation: Mushroom production, lignocellulolytic enzymes activity and substrate utilization. Biodegradation. 2009;20(3):351–61. https://doi.org/10.1007/s10532-008-9226-y
45. Zhao ZG, Gong ZJ, Chen H. *Agrocybe aegerita* and *Auricularia auricula* fruit body yields on cultivation substrates containing different amounts of spent *Pleurotus ostreatus* substrate. Acta Edulis Fungi. 2009;16(3):36–8.
46. Hằng NTB. A study of the influence of the medium on the growth, development and biological efficiency of *Agrocybe aegerita* in Da Nang City. Tạp chí Khoa học và Công nghệ-Đại học Đà Nẵng. 2016:146–50.
47. Kalac P. Mineral composition and radioactivity of edible mushrooms. Academic Press; 2019. https://doi.org/10.1016/B978-0-12-817565-1.00005-4
48. Bauer Petrovska B, Kulevanova S, Jordanoski B, Stefov V.

Investigation of dietary fibre in some edible mushrooms from Macedonia. Nutrition & Food Science. 2001;31(5):242–6. https://doi.org/10.1108/00346650110396664

49. Seo SY, Ahn MS, Choi SR, Song EJ, Choi MK, Kim YS. Analysis of nutritional compositions and biological activity of *Agrocybe aegerita*. Journal of Mushroom. 2011;9(3):116–22.

50. Petrović J, Glamočlija J, Stojković D, Ćirić A, Barros L, Ferreira ICFR, et al. Nutritional value, chemical composition, antioxidant activity and enrichment of cream cheese with chestnut mushroom *Agrocybe aegerita* (Brig.) Sing. Journal of Food Science and Technology. 2015;52(10):6711–8. https://doi.org/10.1007/s13197-015-1783-6

51. Konuk M, Afyon A, Yagiz D. Minor element and heavy metal contents of wild growing and edible mushrooms from western Black Sea region of Turkey. Fresenius Environmental Bulletin. 2007;16(11A):1359.

52. Du B, Zhu F, Xu B. An insight into the anti-inflammatory properties of edible and medicinal mushrooms. Journal of Functional Foods. 2018;47:334–42. https://doi.org/10.1016/j.jff.2018.06.003

53. Kalač P. A review of chemical composition and nutritional value of wild-growing and cultivated mushrooms. Journal of the Science of Food and Agriculture. 2013;93(2):209–18. https://doi.org/10.1002/jsfa.5960

54. Zhu F, Du B, Bian Z, Xu B. Beta-glucans from edible and medicinal mushrooms: Characteristics, physicochemical and biological activities. Journal of Food Composition and Analysis. 2015;41:165–73. https://doi.org/10.1016/j.jfca.2015.01.019

55. Song R, Liang T, Shen Q, Liu J, Lu Y, Tang C, et al. The optimization of production and characterization of antioxidant peptides from protein hydrolysates of *Agrocybe aegerita*. LWT. 2020;134:109987. https://doi.org/10.1016/j.lwt.2020.109987

56. Jing H, Li J, Zhang J, Wang W, Li S, Ren Z, et al. The antioxidative and anti-aging effects of acidic-and alkalic-extractable mycelium polysaccharides by *Agrocybe aegerita* (Brig.) Sing. International Journal of Biological Macromolecules. 2018;106:1270–8. https://doi.org/10.1016/j.ijbiomac.2017.08.138

57. Petrović J, Glamočlija J, Stojković D, Nikolić M, Ćirić A, Fernandes A, et al. Bioactive composition, antimicrobial activities and the influence of *Agrocybe aegerita* (Brig.) Sing on certain quorum-sensing-regulated functions and biofilm formation by *Pseudomonas aeruginosa*. Food & Function. 2014;5(12):3296–303. https://doi.org/10.1039/C4FO00819G

58. Bains A, Chawla P, Inbaraj BS. Evaluation of *in vitro* antimicrobial, antioxidant and anti-quorum sensing activity of edible mushroom (*Agrocybe aegerita*). Foods. 2023;12(19):3562. https://doi.org/10.3390/foods12193562

59. Berne S, Križaj I, Pohleven F, Turk T, Maček P, Sepčić K. *Pleurotus* and *Agrocybe* hemolysins, new proteins hypothetically involved in fungal fruiting. Biochimica et Biophysica Acta (BBA)-General Subjects. 2002;1570(3):153–9. https://doi.org/10.1016/S0304-4165(02)00190-3

60. Sun H, Zhao CG, Tong X, Qi YP. A lectin with mycelia differentiation and antiphytovirus activities from the edible mushroom *Agrocybe aegerita*. BMB Reports. 2003;36(2):214–22. https://doi.org/10.5483/BMBRep.2003.36.2.214

61. Zhao C, Sun H, Tong X, Qi Y. An antitumour lectin from the edible mushroom *Agrocybe aegerita*. Biochemical Journal. 2003;374(2):321–7. https://doi.org/10.1042/bj20030300

62. Ma L, Xu B, Huang M, Sun L, Yang Q, Chen Y, et al. Adjuvant effects mediated by the carbohydrate recognition domain of *Agrocybe aegerita* lectin interacting with avian influenza H9N2 viral surface glycosylated proteins. Journal of Zhejiang University-SCIENCE B. 2017;18(8):653–61. https://doi.org/10.1631/jzus.B1600106

63. Citores L, Ragucci S, Ferreras JM, Di Maro A, Iglesias R. Ageritin, a ribotoxin from poplar mushroom (*Agrocybe aegerita*) with defensive and antiproliferative activities. ACS Chemical Biology. 2019;14(6):1319–27. https://doi.org/10.1021/acschembio.9b00291

64. Ragucci S, Landi N, Russo R, Valletta M, Citores L, Iglesias R, et al. Effect of an additional N-terminal methionyl residue on enzymatic and antifungal activities of Ageritin purified from *Agrocybe aegerita* fruiting bodies. International Journal of Biological Macromolecules. 2020;155:1226–35. https://doi.org/10.1016/j.ijbiomac.2019.11.090

65. Baglivo I, Ragucci S, D'Incecco P, Landi N, Russo R, Faoro F, et al. Gene organization, expression and localization of ribotoxin-like protein ageritin in fruiting body and mycelium of *Agrocybe aegerita*. International Journal of Molecular Sciences. 2020;21(19):7158. https://doi.org/10.3390/ijms21197158

66. Ragucci S, Landi N, Russo R, Valletta M, Pedone PV, Chambery A, et al. Ageritin from pioppino mushroom: The prototype of ribotoxin-like proteins, a novel family of specific ribonucleases in edible mushrooms. Toxins. 2021;13(4):263. https://doi.org/10.3390/toxins13040263

67. Zhang Y, Chen Y, Wang B, Cai Y, Zhang M, Guo X, et al. A novel selenium nanocomposite modified by AANL inhibits tumor growth by upregulating CLK2 in lung cancer. Bioorganic Chemistry. 2024;148:107459. https://doi.org/10.1016/j.bioorg.2024.107459

68. Toumi ME, Kebaili FF, Rebai R, Derardja I, Toumi M, Calogero GS, et al. Purification and biochemical characterization of novel galectin from the black poplar medicinal mushroom *Cyclocybe cylindracea* (Agaricomycetes) strain MEST42 from Algeria. International Journal of Medicinal Mushrooms. 2024;26(2). https://doi.org/10.1615/IntJMedMushrooms.2023051925

69. Zhang Y, Mills GL, Nair MG. Cyclooxygenase inhibitory and antioxidant compounds from the fruiting body of an edible mushroom, *Agrocybe aegerita*. Phytomedicine. 2003;10(5):386–90. https://doi.org/10.1078/0944-7113-00272

70. Kalaras MD, Richie JP, Calcagnotto A, Beelman RB. Mushrooms: A rich source of the antioxidants ergothioneine and glutathione. Food Chemistry. 2017;233:429–33. https://doi.org/10.1016/j.foodchem.2017.04.109

71. Diyabalanage T, Mulabagal V, Mills G, DeWitt DL, Nair MG. Health-beneficial qualities of the edible mushroom, *Agrocybe aegerita*. Food Chemistry. 2008;108(1):97–102. https://doi.org/10.1016/j.foodchem.2007.10.049

72. Liang Y, Liu HH, Chen YJ, Sun H. Antitumor activity of the protein and small molecule component fractions from *Agrocybe aegerita* through enhancement of cytokine production. Journal of Medicinal Food. 2014;17(4):439–46. https://doi.org/10.1089/jmf.2013.2846

73. Chen Y, Jiang S, Jin Y, Yin Y, Yu G, Lan X, et al. Purification and characterization of an antitumor protein with deoxyribonuclease activity from edible mushroom *Agrocybe aegerita*. Molecular Nutrition & Food Research. 2012;56(11):1729–38. https://doi.org/10.1002/mnfr.201200316

74. Qi C, Li DF, Feng L, Hou Y, Sun H, Wang DC, et al. Biochemical and structural characterization of a novel ubiquitin-conjugating enzyme E2 from *Agrocybe aegeria* reveals Ube2w family-specific properties. Scientific Reports. 2015;5(1):16056. https://doi.org/10.1038/srep16056

75. Li G, Liu X, Cong S, Deng Y, Zheng X. A novel serine protease with anticoagulant and fibrinolytic activities from the fruiting bodies of mushroom *Agrocybe aegerita*. International Journal of Biological Macromolecules. 2021;168:631–9. https://doi.org/10.1016/j.ijbiomac.2020.11.118

76. Rosdan Bushra SM, Nurul AA. Bioactive mushroom polysaccharides: The structure, characterization and biological functions. Journal of Liquid Chromatography & Related Technologies. 2022;45(13–16):174–90. https://doi.org/10.1080/10826076.2023.2182317

77. Hyder MS, Dutta SD. Mushroom-derived polysaccharides as

antitumor and anticancer agent: A concise review. Biocatalysis and Agricultural Biotechnology. 2021;35:102085. https://doi.org/10.1016/j.bcab.2021.102085

78. Ren L, Perera C, Hemar Y. Antitumor activity of mushroom polysaccharides: A review. Food & Function. 2012;3(11):1118–30. https://doi.org/10.1039/c2fo10279j

79. Jing H, Zhang Q, Liu M, Zhang J, Zhang C, Li S, et al. Polysaccharides with antioxidative and antiaging activities from enzymatic-extractable mycelium by *Agrocybe aegerita* (Brig.) Sing. Evidence-Based Complementary and Alternative Medicine. 2018;2018 (1):1584647. https://doi.org/10.1155/2018/1584647

80. Ji Y, Zheng MF, Ye SG, Wu XB, Chen JY. *Agrocybe aegerita* polysaccharide combined with chemotherapy improves tumor necrosis factor-α and interferon-γ levels in rat esophageal carcinoma. Diseases of the Esophagus. 2013;26(8):859–63. https://doi.org/10.1111/j.1442-2050.2012.01397.x

81. Liu X, Liu D, Chen Y, Zhong R, Gao L, Yang C, et al. Physicochemical characterization of a polysaccharide from *Agrocybe aegirita* and its anti-ageing activity. Carbohydrate Polymers. 2020;236:116056. https://doi.org/10.1016/j.carbpol.2020.116056

82. Motoshima RA, Rosa TdF, Mendes LdC, da Silva EV, Viana SRF, do Amaral BS, et al. Inhibition of *Leishmania amazonensis* arginase by fucogalactan isolated from *Agrocybe aegerita* mushroom. Carbohydrate Polymers. 2018;201:532–8. https://doi.org/10.1016/j.carbpol.2018.08.109

83. Singh RS, Bhari R, Kaur HP. Mushroom lectins: Current status and future perspectives. Critical Reviews in Biotechnology. 2010;30(2):99–126. https://doi.org/10.3109/07388550903365048

84. Singh SS, Wang H, Chan YS, Pan W, Dan X, Yin CM, et al. Lectins from edible mushrooms. Molecules. 2014;20(1):446–69. https://doi.org/10.3390/molecules20010446

85. Rodrigues ML. The multifunctional fungal ergosterol. mBio. 2018;9 (5):10–1128. https://doi.org/10.1128/mBio.01755-18

86. Kawagishi H, Akachi T, Ogawa T, Masuda K, Yamaguchi K, Yazawa K, et al. Chaxine A, an osteoclast-forming suppressing substance, from the mushroom *Agrocybe chaxingu*. Heterocycles. 2007;69(1):253–8. https://doi.org/10.3987/COM-06-S(O)25

87. Choi JH, Ogawa A, Abe N, Masuda K, Koyama T, Yazawa K, et al. Chaxines B, C, D and E from the edible mushroom *Agrocybe chaxingu*. Tetrahedron. 2009;65(47):9850–3. https://doi.org/10.1016/j.tet.2009.09.064

88. Yajima A, Kagohara Y, Shikai K, Katsuta R, Nukada T. Synthesis of two osteoclast-forming suppressors, demethylincisterol A3 and chaxine A. Tetrahedron. 2012;68(6):1729–35. https://doi.org/10.1016/j.tet.2011.12.057

89. Chen M, Wang KL, Liu M, She ZG, Wang CY. Bioactive steroid derivatives and butyrolactone derivatives from a Gorgonian-derived *Aspergillus* sp. fungus. Chemistry & Biodiversity. 2015;12 (9):1398–406. https://doi.org/10.1002/cbdv.201400321

90. Orban A, Hennicke F, Rühl M. Volatilomes of *Cyclocybe aegerita* during different stages of monokaryotic and dikaryotic fruiting. Biological Chemistry. 2020;401(8):995–1004. https://doi.org/10.1515/hsz-2019-0392

91. Zhang C, Chen X, Orban A, Shukal S, Birk F, Too HP, et al. *Agrocybe aegerita* serves as a gateway for identifying sesquiterpene biosynthetic enzymes in higher fungi. ACS Chemical Biology. 2020;15(5):1268–77. https://doi.org/10.1021/acschembio.0c00155

92. Surup F, Hennicke F, Sella N, Stroot M, Bernecker S, Pfütze S, et al. New terpenoids from the fermentation broth of the edible mushroom *Cyclocybe aegerita*. Beilstein Journal of Organic Chemistry. 2019;15(1):1000–7. https://doi.org/10.3762/bjoc.15.98

93. Yang F, Fu A, Meng H, Liu Y, Bi S. Non-volatile taste active compounds and umami evaluation of *Agrocybe aegerita* hydrolysates derived using different enzymes. Food Bioscience. 2024;58:103772. https://doi.org/10.1016/j.fbio.2024.103772

94. Wang WK, Zhu Y, Tang Y, Lu N, Song JL, Yuan WD, et al. Non-volatile taste components of different cultivated mushrooms at mycelia, primordium and fruit body cultivation stages. International Journal of Food Properties. 2016;19(9):1938–48. https://doi.org/10.1080/10942912.2015.1089891

95. Pereira DM, Valentão P, Andrade PB. Organic acids of plants and mushrooms: Are they antioxidants. Functional Plant Science and Biotechnology. 2009;3:103–13.

96. Mau J. The umami taste of edible and medicinal mushrooms. International Journal of Medicinal Mushrooms. 2005;7(1/2):119. https://doi.org/10.1615/IntJMedMushr.v7.i12.120

97. Rašeta M, Berežni S, Bauer R, Krstic S. Mycochemical profile and biological activity of edible mushroom species *Cyclocybe aegerita* (V. Brig.) Vizzini 2014. Planta Medica. 2022;88(15):P–205. https://doi.org/10.1055/s-0042-1759181

98. Du B, Peng F, Xie Y, Wang H, Wu J, Liu C, et al. Optimization extraction and antioxidant activity of crude polysaccharide from chestnut mushroom (*Agrocybe aegerita*) by accelerated solvent extraction combined with response surface methodology (ASE-RSM). Molecules. 2022;27(8):2380. https://doi.org/10.3390/molecules27082380

99. Liu X, Wu L, Tong A, Zhen H, Han D, Yuan H, et al. Anti-aging effect of *Agrocybe aegerita* polysaccharide through regulation of oxidative stress and gut microbiota. Foods. 2022;11(23):3783. https://doi.org/10.3390/foods11233783

100. Liu X, Feng Y, Zhen H, Zhao L, Wu H, Liu B, et al. *Agrocybe aegerita* polysaccharide combined with *Bifidobacterium lactis* Bb-12 attenuates aging-related oxidative stress and restores gut microbiota. Foods. 2023;12(24):4381. https://doi.org/10.3390/foods12244381

101. Chen BoWen CB, Zhang XiaoLin ZX, Sun XiaoRui SX, Luo Yan LY, Du HongXia DH, Meng JunLong MJ, et al. Extraction, characterization, stability and antioxidative capacity of *Agrocybe aegerita* melanin. 2017.

102. Yang Q, Yin Y, Pan Y, Ye X, Xu B, Yu W, et al. Anti-metastatic activity of *Agrocybe aegerita* galectin (AAL) in a mouse model of breast cancer lung metastasis. Journal of Functional Foods. 2018;41:163–70. https://doi.org/10.1016/j.jff.2017.12.058

103. Jiang S, Chen Y, Wang M, Yin Y, Pan Y, Gu B, et al. A novel lectin from *Agrocybe aegerita* shows high binding selectivity for terminal N-acetylglucosamine. Biochemical Journal. 2012;443 (2):369–78. https://doi.org/10.1042/BJ20112061

104. Wang Z, Chen K, Zhang K, He K, Zhang D, Guo X, et al. *Agrocybe cylindracea* fucoglucogalactan induced lysosome-mediated apoptosis of colorectal cancer cell through H3K27ac-regulated cathepsin D. Carbohydrate Polymers. 2023;319:121208. https://doi.org/10.1016/j.carbpol.2023.121208

105. Li Y, Li Y, Xia J, Yang Q, Chen Y, Sun H. 3'-Sulfo-TF antigen determined by GAL3ST2/ST3GAL1 is essential for antitumor activity of fungal galectin AAL/AAGL. ACS Omega. 2021;6(27):17379–90. https://doi.org/10.1021/acsomega.1c01544

106. Ragucci S, Castaldi S, Landi N, Isticato R, Di Maro A. Antifungal activity of ageritin, a ribotoxin-like protein from *Cyclocybe aegerita* edible mushroom, against phytopathogenic fungi. Toxins. 2023;15(9):578. https://doi.org/10.3390/toxins15090578

107. Koshino H, Lee IK, Kim JP, Kim WG, Uzawa J, Yoo ID. Agrocybenine, novel class alkaloid from the Korean mushroom *Agrocybe cylindracea*. Tetrahedron Letters. 1996;37(26):4549–50. https://doi.org/10.1016/0040-4039(96)00900-8

108. Fernandez Espinar MT, Labarère J. Cloning and sequencing of the Aa-Pri1 gene specifically expressed during fruiting initiation in the edible mushroom *Agrocybe aegerita* and analysis of the predicted amino-acid sequence. Current Genetics. 1997;32(6):420–4. https://doi.org/10.1007/s002940050297

109. Panevska A, Hodnik V, Skočaj M, Novak M, Modic Š, Pavlic I, et al. Pore-forming protein complexes from *Pleurotus* mushrooms kill western corn rootworm and Colorado potato beetle through targeting membrane ceramide phosphoethanolamine. Scientific Reports. 2019;9(1):5073. https://doi.org/10.1038/s41598-019-41450-4

110. Frangež R, Šuput D, Molgó J, Benoit E. Ostreolysin a/pleurotolysin b and equinatoxins: Structure, function and pathophysiological effects of these pore-forming proteins. Toxins. 2017;9(4):128. https://doi.org/10.3390/toxins9040128

111. Jin Y, Che T, Yin Y, Yu G, Yang Q, Liu W, et al. Lethal protein in mass consumption edible mushroom *Agrocybe aegerita* linked to strong hepatic toxicity. Toxicon. 2014;90:273–85. https://doi.org/10.1016/j.toxicon.2014.08.066

112. Zhang L, Yan M, Liu C. A comprehensive review of secondary metabolites from the genus *Agrocybe*: Biological activities and pharmacological implications. Mycology. 2024;15(2):162–79. https://doi.org/10.1080/21501203.2023.2292994

113. Yang C, Yang J, Zhou Y, Ou Y, Wang Z, Qi W, et al. Biochemical characterization and bacterial diversity of *Agrocybe aegerita* during postharvest storage. Frontiers in Microbiology. 2025;16:1596093. https://doi.org/10.3389/fmicb.2025.1596093

114. Data Insights Market. Comprehensive insights into *Agrocybe aegerita*: Trends and growth projections 2025–2033. 2025. https://www.datainsightsmarket.com/reports/agrocybe-aegerita-395631

115. Choi IY, Choi JN, Sharma PK, Lee WH. Isolation and identification of mushroom pathogens from *Agrocybe aegerita*. Mycobiology. 2010;38(4):310–5. https://doi.org/10.4489/MYCO.2010.38.4.310

116. Gea FJ, Navarro MJ, Santos M, Diánez F, Carrasco J. Control of fungal diseases in mushroom crops while dealing with fungicide resistance: A review. Microorganisms. 2021;9(3):585. https://doi.org/10.3390/microorganisms9030585

117. Gajanayake AJ, Jayawardena RS, Hyde KD, Luangharn T, Liyanage WKK, Caige L, et al. Fungal threats to global mushroom cultivation: Diseases, competitor molds and management strategies-a review. Mycosphere. 2025;16(1):3130–76. https://doi.org/10.5943/mycosphere/16/1/22

118. Grimm D, Wösten HAB. Mushroom cultivation in the circular economy. Applied Microbiology and Biotechnology. 2018;102(18):7795–803. https://doi.org/10.1007/s00253-018-9226-8

119. Viriato V, Carvalho SADd, Santoro BdL, Bonfim FPG. A business model for circular bioeconomy: Edible mushroom production and its alignment with the sustainable development goals (SDGs). Recycling. 2024;9(4):68. https://doi.org/10.3390/recycling9040068

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

Copyright: © The Author(s). This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution and reproduction in any medium, provided the original author and source are credited (https://creativecommons.org/licenses/by/4.0/)

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.