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Cultivation of *Auricularia* species: a review of the history, health benefits, principles, practices, environmental conditions, research methods, and recent trends

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Auricularia species are edible mushrooms known as the Jew's ear, wood ear, jelly ear, black fungus, or by several other common names. Cultivated *Auricularia* species can be grown under a wide range of conditions, allowing for production volumes worldwide. The review provides a summary of the historical background of *Auricularia* cultivation which becomes a basis for cultivation practices. The principles of cultivating this genus are important in standardizing cultivation technology adaptable to certain regions, in Asia, Western countries (North America, Europe, and Australia), and Africa. Environmental conditions required in intensive cultivation are also dealt with such as the effect of temperature, humidity, light, and CO2. Some research approaches of *Auricularia* cultivation and recent trends in improving and harnessing the potential of *Auricularia* species are also included.

Keywords: Black ears, jew's ear, wood log cultivation, plastic bag cultivation, agricultural waste, submerged liquid cultivation, biological efficiency.

Global statistics on the production status of mushrooms and truffles show a huge disparity within the five-year production between Asia and the rest of the world (America, Oceania, Africa, and Europe) (FAO 2022). Production in Asia was millions of tons per year and increased even during the time of the Coronavirus crisis in 2020, while in the other continents production has remained the same and slightly decreased during the onset of the pandemic. China contributed about 95 % to the total worldwide production (FAO 2022). The second most widely grown mushroom in China is now *Auricularia* (Royse et al. 2017). *Auricularia auricula-judae* is one of the cultivated species and is produced in significant amounts (Royse 2014).

Auricularia spp. known as the Jew's ear, wood ear, jelly ear, black fungus, or by several other common names, are edible fungi accommodated in the order *Auriculariales*. The fruit bodies often have a distinctly earlike shape and purple brown, brown to blackish colour. They occur dispersed or in masses on dead or dying tree branches, trunks, rotting logs, *Auricularia* species are found worldwide; *A. nigricans (= A. polytricha)* (Woolly wood ear) occurs in both tropical and subtropical regions (Priya et al. 2016) while *A. auricula-judae* (Jew's ear or black wood ear) is a temperate species (Wang et al. 2016; Wu et al. 2015a, 2021). A total of 202 *Auricularia* taxa are listed Index Fungorum (www.indexfungorum.org, July 2023), out of these 48 now belong to other genera, 153 are still *Auricularia* spp., 53 species currently remain when synonymy is adjusted and when old, not recently confirmed taxa are left out. Several important species include diverse infraspecific taxa, e.g. *Auricularia auricula-judae, A. reflexa*, *A. caryophylla*, and *A. polytricha (=A. nigricans)*.

This review provides a summary of the cultivation history of *Auricularia*, its health benefits, principles of cultivating, and cultivation practices in Asia, Western countries (North America, Europe, and Australia), and Africa. Environmental conditions such as the effect of temperature, light, CO_2, some research methods, and recent trends in *Auricularia* cultivation are also included.

History of *Auricularia* mushroom cultivation

Intentional domestication of the *Auricularia* mushroom has been recorded through some historical accounts, mostly with references to its usage as a food and medicinal ingredient (Chang & Wasser 2017). As early as 300 to 600 BC, the Chinese collected in the wild and learned to cultivate wood ears (Cheng & Tu 1978, Chang 1993). In the 7th century, *Auricularia auricula-judae* was grown on wood logs according to writings in "Classical Chinese materia medica" a Chinese book during the Ming dynasty; as such it could be considered the earliest artificially cultivated mushroom (Chang 1977). An exemplar of Korean medicine (Donguibogam) dated 1613 written by Heo Jun, recorded seven medicinal mushrooms, one of them was *A. auricula*. Carolus Clusius recorded *Auricularia* spp. as a potential cure for sore throat (Roupas et al. 2012). In the early 17th century, European countries used *Auricularia* spp. in folk medicine but not as edible species. Herbalist John Gerard described a very detailed use of the wood ear (Sekara et al. 2015). From the 18th until 19th century, wood ears were used for the prevention of thrombosis recommended by Li Shih-Chen, the author of "Pen Tsao Kang Mu (Berch et al. 2007). They were consumed by Chinese populations as a traditional Chinese medicinal mushroom for treating jaundice and sore throats (Yao et al. 2019) and in Europe as medicinal and food supplement (Zięba et al. 2020). They were known to the early Hawaiians and became an export product to San Francisco during the late 1800s (Schenck & Dudley 1999) and were also exported from New Zealand (Stamets 2003). When dried, they shrivel to a much smaller size and may be shipped in that state and rehydrated for later use (Schenck & Dudley 1999). Within the last 30 years, the commercial production of *A. auricula-judae* developed rapidly in the rural areas of China (Sekara et al. 2015).

Health benefits of *Auricularia* mushroom

Cultivated *Auricularia* species can be grown under a wide range of conditions, allowing for production volumes worldwide (Bandara et al. 2019). Though this genus ranked fourth in popularity among the cultivated mushrooms (Raman et al. 2018), still domestication, production, and scientific studies rapidly increased, which is attributed to its contribution to the culinary industry (Sekara et al. 2015), nutritional composition (Kadnikova et al. 2015,Yao et al. 2019, Liang et al. 2019), and pharmacological properties, including antitumor, anticoagulant, cholesterol-lowering effects, anti-microbial and anti-viral, anti-inflammatory, anti-diabetic, anti-hyperlipidemic, anti-obesity, anti-thrombotic effect, anti-radiation, anti-cancer and anti-oxidant richness (Mau et al. 2001,Yoon et al. 2003, He et al. 2012, Sekara et. al. 2015, Avcı et al. 2016, Bandara et al. 2019, Islam et al. 2021).

The antioxidant properties of *Auricularia* spp. (Tab. 1) have promising applications in pharmaceuticals, in treating and managing different diseases (Mwangi et al. 2022) by showing stronger 1,1-Diphenyl-2-picrylhydrazyl (DPPH) scavenging activity than other mushroom species (Gąsecka et al. 2018, Hussein et al. 2015, Jagadish et al. 2009), as well as higher scavenging effect on hydroxyl free radicals (OH) (Zou et al. 2015, Zhang et al. 2015). DPPH radicals inhibit lipid oxidation and determine to which extent the free radicals are scavenged, while the elimination of hydroxyl radicals is an effective means to prevent cell damage in the body (Herraiz & Galisteo 2015, Hussein et al. 2015, Mwangi et al. 2022). Ferrous chelators are powerful pro-oxidants accelerating lipid peroxidation and are immediately extracted from the fruit body. The lower the values of chelated ferrous, the more powerful chelating capability the polysaccharide can possess (Cai et al. 2015, Ker et al. 2005, Zou et al. 2015). *Auricularia auricula-judae* polysaccharides exhibit stronger Fe^{2+} chelating activity than *Agaricus bisporus, A. brasiliensis, Ganoderma lucidum*, and *Phellinus linteus* fruit bodies (Kozarski et al. 2011). The antioxidant activity of mushrooms is linked to their phenolic component concentration which has been known for their function of stabilizing lipid oxidation, hence it can prevent oxidation damage and protect the human body (Izham et al. 2022, Ren et al. 2014). The different processing methods did influence *A. auricula-judae* and *A. nigricans'* total phenolic content such as a significant increase was observed when fruit bodies were oven dried, freeze-dried, cooked, and microwaved (Izham et al. 2022, Kho et al. 2009, Ng & Rosman 2019). Melanin is one of the main bioactive components in the fruit body of *A. auricula-judae*. Melanin from *A. auricula-judae* can be used as a safe and healthful colorant in the food industry (Wu et al. 2018) and this mushroom has a hepatoprotective effect by alleviating alcohol-induced liver damage in animal models (Hou et al. 2019). *Auricularia* could potentially be used as a natural antioxidant in the food, cosmetic and pharmaceutical industries (Wu et al. 2018)

The World Health Organization (WHO 2022) reported some risk factors for health such as malnu-

Tab. 1. Antioxidant potential of *Auricularia* species compared to some other mushroom species.

Antioxidant potential	Extraction method	Mushroom	Values	Reference
DPPH radical scavenging activity	Methanolic extraction EC50 of 0.08 mg/ml	*Auricularia auricula-judae*	93.33 %	Hussein et al. (2015)
		Polyporus tenuiculus	90.71 %	Hussein et al. (2015)
		Agaricus bisporus	85.44 %	Jagadish et al. (2009)
		Polyporus conchatus	46.53 %	Hussein et al. (2015)
	Methanolic extraction 1 mg/ml	*Auricularia auricula-judae*	100 %	Gasecka et al. (2018)
		Tremella fuciformis	94 %	Gasecka et al. (2018)
Hydroxyl radical scavenging	Polysaccharide extract	*Auricularia auricula-judae*	80 %	Zou et al. (2015)
		Gloeostereum incarnatum	56.23 %	Zhang et al. (2015)
Chelating ability on Fe2+ ions	Polysaccharide extract	*Auricularia auricula-judae*	0.43 mg/ml	Zou et al. (2015)
		Ganoderma lucidum	0.59 mg/ml	Kozarski et al. (2011)
		Phellinus linteus	0.91 mg/ml	
		Agaricus brasiliensis	2.04 mg/ml	
		Agaricus bisporus	7.8 mg/ml	
Water-soluble phenolic contents	Digested microwaved sample	*Auricularia polytricha*	156 %	Izham et al. (2022)
		Lentinula edodes	116 %	
		Agaricus bisporus	48 %	
		Pleurotus sajor-caju	60 %	

trition, obesity, anemia, and raised blood pressure (Tab. 2). The health benefits found in *Auricularia* spp. can provide an auspicious solution to address these health issues. Inventing novel drugs with low toxicity, high efficiency and few side effects are essential for chronic disease therapeutics. The more recent and attractive approach is mushroom polysaccharide treatment (Zhang et al. 2022). *Auricularia auricula-judae* polysaccharides (AAPs) have been accepted as one important biological constituent. Continuous development through *in vivo* and *in vitro* studies was done to improve biological activities and expand its application (Miao et al. 2020, Xia et al. 2019). Although these compounds have been elucidated, various complicated structures and their unclear mechanism of action still need to be further explored specifically in clinical studies (Islam et al. 2021). Importantly, cultivation practices and climatic and environmental factors may influence the production of these antioxidant compounds in *Auricularia* mushrooms (Ao & Deb, 2019, Mwangi et al. 2022)

Principles of mushroom cultivation and production

The cultivation of mushrooms ranges from a relatively primitive farming activity to a highly technological industry. In each case, however, continuous production of successful crops requires both practical experience and scientific knowledge (Chang & Wasser 2017). Cultivation of *Auricularia* spp. involves two important steps: spawn preparation and fruit body production (Priya et al. 2016). The most crucial factor in domesticating wild mushrooms is the development of appropriate technologies for spawn production (Stamets 2000). In nature, mushrooms use spores for generative multiplication. However, spores take time to germinate and competitor fungi might germinate and grow faster during that time. Therefore, traditionally a pure culture of the desired mycelium is added to the substrate to give it an advantage. This procedure is called spawning, and the pure culture is called spawn (Oei 2003). The spawn for *Auricularia nigrigans* has to be prepared from freshly prepared mother spawn – the same way as any cultivated species, raised from fresh fruit body cultures (Moreaux 2017).

The essential steps in spawn production are mother culture (also called stock culture, primary culture) on agar, inoculation cultures in Petri-dishes, mother spawn on grain in bottles, and final spawn on grain in a plastic bag (Oei 2003). Several culture media are currently used to cultivate *Auricularia*, i.e., Czapek-dox, Glucose Peptone, Malt Extract Agar (MEA), Mesangial Cell Medium (MCM), Potato Dextrose Agar (PDA), Yeast Extract

Tab. 2. Research findings of *Auricularia* products against health risk factors.

Risk factors for health	Findings	Reference
Stunted growth of children due to malnutrition	*Auricularia thailandica* rich in amino acids and minerals	Bandara et al. (2017)
Obesity	*Auricularia* polysaccharide extracts inhibit adipocyte differentiation	Park et al. (2018)
	Auricularia auricula-judae extract suppressed plasma glucose, total cholesterol, the weight of internal organs, epididymal fat, and the activity of hepatic enzymes	Choi et al. (2019), Ganesan & Xu (2018)
Anemia among woman	A novel *Auricularia auricula-judae* polysaccharide-iron (AAPS-iron(III)) show high efficiency on the treatment of iron deficiency	Liu et al. (2019)
Raised blood pressure	*Auricularia* extracts absorb glucose, reduce dialyzed glucose and inhibit the activity of alpha amylase, decrease chronic hyperglycemia	Liu et al. (2021), Wu et al. (2014)
	A dose of *Auricularia* polysaccharides led to reduction in total cholesterol and LDL levels and blood glucose compared to control diabetic rats	Hao (2014), Lu et al. (2018), Takeuchi et al. (2004), Zhang et al. (2020), Zhang & Riskowski (2020)

Agar (YEA), Yeast Mannitol Agar (YMA), and Leonian medium (Bandara et al. 2019, Jo et al. 2014, Yu et al. 2013). *Auricularia nigricans* cultured in Coconut Water Gelatin (CWG) had the fastest mycelial ramification and thick mycelial growth (Zurbano 2018). The method used for tissue culture of *Auricularia* fruit bodies was derived from Weber & Webster (2006), which involves preparation of culture media, pouring of culture media onto sterile Petri dishes under a laminar flow hood, rehydrating and sterilizing the fruit body, inoculating fruit bodies to culture media and incubating them under controlled environmental condition. Mycelia obtained from tissue culture were used to develop grain spawns. Paddy grain, Maize grain, and rubber sawdust were the best substrate for spawn run with a minimum of 16 and 18 days respectively required for fluffy growth of mycelium in the grains (Priya et al. 2016). Spawn media using millet, rye, and sorghum all support the formation of a vigorous and luxuriant mycelial mat (Stamets 2000). Supplementation with rice and wheat bran provides a protein-rich medium that can increase the rate of mycelia growth two-fold (Onyango et al. 2011). The next step in mushroom cultivation needs proper media for the vegetative and generative stages. Mushroom growers call the switch from mycelial extension to the production of mushroom primordia "pinning", the successive development of primordia into mushrooms "fruiting" (Kües & Liu 2000). The material on which the mycelium grows is called a fruiting substrate (Stamets 2000, Oei 2003). Non-composted substrates are also used in the cultivation of *Auricularia* species, (Suwannarach et al. 2022), these are often supplemented with carbohydrates and protein. The raw materials used for cultivation are usually wood wastes, cereal straws, grain hulls, coconut fibers, corncobs, coffee plant waste and coffee powder wastes, tea leaves, banana leaves, and seed hulls (Stamets 2000).

Within the cultivation process, pests and diseases may cause serious threats to *Auricularia* production (Rijal et al. 2021, Yang et al. 2022). Several common insect pests belonging to the order Diptera, including Phorid fly (*Megaselia halterata*) and Sciarid fly (*Lycoriella ingenua*) (Erler & Polat 2015, Meena 2021), as well as mites from the Pygmephorids (*Luciaphorus auriculariae* and *L. perniciosus*) and the Tyroglyphids (*Tyrophagus putrescentiae*) (Bussaman et al. 2011, Gulati & Anita 2017, Khaustov et al. 2018, Qu et al. 2015) infect mycelia and fruit bodies of *Auricularia*. Molds, mainly *Trichoderma* spp. (Dang et al. 2022), some gram-positive bacteria such as *Arthrobacter arilaitensis* and *Staphylococcus warneri* reduced yield and posed a risk of food poisoning or safety (Yang et al. 2022). The pathogenic fungus slippery scar disease (*Scytalidium auriculariicola*), was found in the cultivated bags used for growing *Auricularia nigricans* (Chen et al. 2019, Sun & Bian 2012). Substrates in the culture bags are sterilized or pasteurized (Suwannarach et al. 2022). For wood log cultivation, if during spawn run proper conditions were met, less than 10 % of the logs will be contaminated with wood fungi, e.g. *Schizophyllum commune* (Oei 2003).

Cultivation practices in Asia

Auricularia species are widely consumed in Asia (Thongklang et al. 2020). It is locally called „tengang daga" in the Philippines (Zurbano 2018), „Kulat telinga kera" in Malaysia (Lau et al. 2014), mù'ěr in China and Ki-kuragi in Japan (Sekara et al. 2015). *Auricularia nigricans (= A. polytricha)* and *A. auricula-judae* are cultivated, however, A. nigricans is commercially cultivated due to its adaptability to tropical and subtropical conditions (Oei & Nieuwenhuljzen 2005). *Auricularia delicata* may be a potential alternative to *A. nigricans* in commercial cultivation in the tropics (Zhang & Fevereiro, 2016). Currently, *A. cornea* and *A. heimuer* are commercially cultivated in China, Thailand, and Taiwan (Chang & Lee 2004, Duc 2005, Thongklang et al. 2020, Chen et al. 2021a).

Auricularia can be grown on both wood logs and on small plastic bags. Wood log cultivation in Taiwan as described by Oei (2003) begins with the selection of wood logs. During spawning, sawdust spawn is compressed into holes of the logs. Hot wax is used to cover the hole to prevent evaporation. Then logs are incubated and stacked in the laying yard for 1 month. To allow fruiting, logs are slanted against wooden bars and watered heavily to stimulate fruit body formation. The first primordia will form within 1 week. The Chinese distinguish five stages in the development of the fruit bodies: rice grain (1.5 days), coral (1.5 days), wood ear appearance (2 days), wood ear unfolding (1.5 days), and maturation (2 days). The duration of each stage can be achieved if the temperature is around 24 °C with 95 % relative humidity. However, the old method of boring holes is little utilized today due to major drawbacks such as cultivation requires the use of fresh wood as a growing substrate, a longer period of cultivation, a large area, and as well has a high probability of infection by other fungi (Duc 2005). Plastic bag cultivation technology in the Philippines (Oei & Nieuwenhuljzen 2005) uses substrate from dry sawdust (moisture content 15–18 %). There is a fermentation process and moistening period, where the prepared substrate (e.g. sawdust, $CaCO_3$, and fine rice bran) is piled into heaps and covered with plastic material for several days, then, filled

Tab. 3. Agricultural wastes used for cultivation of *Auricularia* mushroom.

Country	Species	Agricultural waste	Reference
China	*Auricularia* sp.	cotton residuals	Zhang et al. (2014)
	A. cornea	sawdust, maize straw	Chen et al. (2021b)
Philippines	*A. auricula-judae*	lumber sawdust, rice bran, rice hull, kakawati leaves, ipil-ipil leaves	Zurbano (2018), Quimio (1976), Khan et al. (1991)
Taiwan	*Auricularia* sp.	cotton waste, waste, rice straw, wood chips, and sawdust, grass plants (*P. repens* and *P. purpureum)*	Liang et al. (2019), Peng & Volvacea (2007)
India	*A. auricula-judae*	corn cobs, rice straw, broadleaf tree sawdust, and cottonseed bran with plaster stone, wheat bran, rice bran	Verma & Verma (2017) cited by Bandara et al. (2019), Ahila et. al. (2013)
Kenya	*A. auricula-judae*	sawdust, grass, sugarcane, bagasse, wheat straw, maize cobs, wheat bran	Onyango et al. (2013)
Nigeria	*A. auricula-judae*	oil palm waste (palm fronds, fallen palm trees, fruit bunch, decomposing palm litter	Osemwegie & Okhuoya (2009)
Thailand	*A. cornea*	rubber sawdust	Thongklang et al. (2020), Zhang & Riskowski (2020)
Indonesia	*A. polytricha*	*Mollucana* wood meal, *Shorea* sp.	Irawati (2012)
Malaysia	*A. polytricha*	oil palm empty bunch, palm pressed fibre, oil palm fronds, sago waste	Lau et al. (2014), Razak et. al. (2013)
Pakistan	*A. polytricha*	sawdust of *Acacia* and *Coffea arabica*, wheat grains	Khan et al. (1991)
Serbia	*A. auricula-judae*	plum sawdust, blackberry sawdust, wheat straw, oak sawdust	Galić et al. Zhang & Riskowski (2020)
Poland	*A. auricula-judae*	beech sawdust, birch sawdust	Siwulski et al. (2011)
	A. polytricha		
USA	*A. auricula-judae*	decayed pecan log	Zhang & Riskowski (2020)

into a desired plastic container before it undergoes heat treatment. Spawning is done afterwards. Spawn run takes about a month at 25–30 °C. Mycelial growth and fruit body formation are greatly affected by cultivation substrates. Different substrates were explored using agricultural wastes (Tab. 3) other than sawdust, due to a shortage of sawdust used by other industries, e.g. for fibreboards (Razak et al. 2013). Also, sawdust mixed up with chemicals used in the processing industries often harms mushroom growth and yield (Zurbano 2018). The freezing pre-treatment of the mycelium is a common method and key step of bag cultivation in northern China during the winter, done by putting outdoors for quick freezing. Freezing treatment can significantly improve the yield and harvest quality of *A. auricula-judae* (Li et al. 2021). Characteristics of harvested *A. nigricans* differ between wood log and straw bag cultivation in India. The abhymenial hairs are found longer, texture is tougher, color is less attractive, and production period is longer in wood log cultivation than in straw bag cultivation (Sharma et al. 2007).

Cultivation practices worldwide (America, Europe, Australia)

Cultivation technologies for growing *Auricularia* mushrooms have been developed independently in Europe and Asia. Asian countries have a longer cultivation tradition (using different technologies) and a different production profile compared to Europe and North America (Zieba et al. 2020). In Europe, and Australia, *Auricularia auricula-judae* is found throughout the year but is most prevalent in late summer and autumn (Li et al. 2021). For some reason, *Auricularia* has never been a popular food in Europe. However, in Hawaii, a ready market exists that could be supplied by commercial production in forest understory or by small farmers or backyard gardeners (Schenck & Dudley 1999). Hungary shows a gradual increase in exotic mushroom production (Bringye & Fekete-Farkas 2021). Cultivation of *Auricularia* species in Poland is marginal, mostly by amateurs of Asian culture (Mleczek et al. 2017). In Poland, Siwulski et al. (2011) used sawdust of beech and birch as growing substrate, supplemented with 20 % (w/w) of wheat bran and 0.2 % $CaCO_3$ and packed into a 2.5 kg capacity PP foil bag. Duncan (1972) examined different hardwood and conifer substrates of *Auricularia nigricans* in Europe, North America, and Australia.

Production of mushrooms in Africa in 2020 is approx. 30.8 thousand tons (FAO 2022). Records of *Auricularia* species occurring in Africa are *Auricularia auricula-judae, A. delicata, A. fuscoccinea, A. mesenterica, A. nigricans,* and *A. tenius* (Onyango et al. 2013, Bandara et al. 2020, Odamtten et al. 2022). *Auricularia nigricans* is the commonest among the jelly-like fungi in West Africa. Its fruit bodies are usually found in large numbers during late July (Jonathan et al. 2009). In Kenya, mushroom cultivation is not well developed, and only exotic species are grown for the hotel industry (Gateri et al. 2009). Wood ears have not been previously cultivated in Kenya, because they are protected by wildlife conservation laws (Odamtten et al. 2022). Regional agro-waste such as sawdust, grass, sugarcane, bagasse, wheat straw, maize cobs, and wheat bran were used as substrates in Kenya (Onyango et al. 2013). Onyango et al. (2013) cultivated *Auricularia* mushrooms in Nigeria utilizing palm substrates through the bag cultivation methods of Oei & Nieuwenhuljzen (2005).

Suitable environmental conditions for *Auricularia* cultivation

Environmental conditions play a crucial role for fruit body development. The optimum for mycelial growth and the subsequent fruiting is usually very distinct and fruit body development is often induced after drastically altering the environmental conditions (Kues & Liu 2000, Scrase & Elliott 1998). Every mushroom strain has its own set of climatic conditions under which it performs best. The objective is climate control during the successive phases of mushroom cultivation such as pasteurization, spawn run, induction of primordia, growth of mushrooms, and picking. Temperature, relative humidity of the air, CO_2 level, ventilation (fresh air and circulation air), and light are essential (Tab. 4).

Both, investments in climate control and energy costs can be high, if the mushroom requires a fruiting temperature that differs much from the prevailing temperatures. Lower costs are involved if the fruiting range is as close as possible to outside conditions (Oei 2003). The substrate temperature is an important parameter in both mycelial growth and fruit body formation. The substrate itself produces heat, the amount of which depends on the activity of microbes (including the mycelium of the cultivated mushroom) in the substrate. Higher substrate temperature (like in compost) than the ambient air temperature, can be desirable because it increases evaporation, which is necessary to transport nutrients from the mycelium inside the substrate to the fruit bodies (Oei 2003). High substrate temperature

Tab. 4. Growth parameters of *Auricularia* species (Stamets 2000).

Growth parameters	Spawn run	Primordia formation	Fruit body development
Temperature	24–30 °C	12–20 °C	21–30 °C
Relative Humidity	90–95 %	90–100 %	85–90 %
CO_2	>5000–20000 ppm	600–1000 ppm	2000–5000 ppm
Fresh air exchanges	0–1 per hour	5–8 per hour	4–5 per hour
Light requirements	Not needed	500–1000 lux	500–1000 lux
Duration	25–40 days	5–10 days	5–7 days

(>35 °C) can trigger thermophilic microorganisms and produce more heat, which increases the substrate temperature. In this way, the mycelium of the cultivated mushroom can also be damaged. *Auricularia nigricans* requires 23–28 °C for fruiting and suitable substrate technique applied are wood logs and sterilized substrate (Oei 2003). The growth response of three *Auricularia* species at seven different incubation temperatures indicated that both *A. delicata* and *A. nigricans* attained their maximum biomass production at 28 °C and *A. auricula-judae* at 30 °C after 10 days (Devi et al. 2015).

Air humidity is another important factor in the growing room conditions and it is strongly dependent on the air temperature. The warmer the air, the more water it can contain maximally. Air humidity of at least 80 % is required to prevent the wood ears from shriveling (Oei 2003). For pepeiao (wood ear) production in Hawaii, logs were kept at 24–30 °C with 90–100 % relative humidity and adequate air circulation. Once the wood has been colonized, a lower temperature (12–20 °C) is needed to initiate fruiting (Schenck & Dudley 1999). The wild strain of *A. cornea* produced fruit bodies under 75–85 %

Tab. 5. Common parameter in cultivation studies of *Auricularia* mushroom.

Component	Parameter	Reference
Species identification	Morphological characteristics Microscopic Macroscopic	Bandara et al. (2017), Looney et al. (2013), Musngi et al. (2005, Thongklang et al. (2020), Wu et al. (2015ab)
	Molecular analyses	Bandara et al. (2017), Malysheva & Bulakh (2014), Wu et al. (2015)
	Phylogenetic analyses	Zhou & Dai (2013), Wu et al. (2021)
Agronomic (growth and yield)	For mycelial growth Mycelial growth rate, density and color, mycelial thickness, biological efficiency (BE), incubation period	Jo et al. (2014), Razak et al. (2013), Zhang & Fevereiro (2016), Chen et al. (2021a), Ibrahim & Shaharudin (2021)
	For spawn Days for spawn run	Ahila et al. (2013)
	For fruit bodies Days for pin head formation (DFPF), Days for first harvest (DFFH), Days to complete two harvests, Total cropping period) and Total yield, biological efficiency	Ahila et al. (2013), Bandara et al. (2020)
Substrate quality	Physical properties (particle size, volume weight, density, porosity, and water-holding capacity), Chemical Properties (quantities of holocellulose, α-cellulose, Klason lignin, and ash), C/N ratio	Razak et al. (2013), Ibrahim & Shaharudin (2021)
Nutrient composition analysis of fruit bodies	Proximate analysis Moisture, crude ash, crude fat, crude fiber, crude protein content, total soluble sugar, total energy, total polysaccharide, phenolic content, antioxidant capacity	AOAC International (1995), Hung & Nhi (2012), Liang et al. (2019), Bandara et al. (2020)

humidity and was cultivated on rubber sawdust (Thongklang et al. 2020)

Carbon dioxide is another important environmental factor affecting growth and morphogenesis of Basidiomycetes. Excess CO_2 inhibits fruiting; especially fruit body development and sometimes causes abnormal fruit body development in Basidiomycetes (Seo & Suzuki 2004). All cultivated mushrooms are aerobic organisms. They require O_2 for their metabolism and produce CO_2. Mycelium growth benefits from increasing O_2 and CO_2 levels up to a certain optimum, and then it suffers disadvantages. Too high concentrations are lethal (Royse et al. 2017). During the spawn run, high CO_2 levels do not cause a problem up to a certain degree of the colonization. However, during fruiting, many mushrooms are sensitive to high CO_2 levels (Oei 2003). Airflow over a mushroom bed will increase the water evaporation rate. If the airflow is non-uniform, some beds will become drier than others. Fresh air can be blown in the growing rooms to reduce CO_2 levels, adjust the desired temperature and humidity inside the growing room. Stagnant air will cause fruit bodies of *Auricularia* to rot and become deformed (Oei 2003).

Light is important in the fruit body formation of *Auricularia* spp. The mycelium not only requires an amount of diffuse light but also some directly radiated light. A light intensity of 500 lux is reported to be optimal for fruit body formation.

Research approaches in cultivation

Continuous production of successful crops requires both practical experience and scientific knowledge (Chang & Wasser 2017). Table 5 presents some of the methods used to improve cultivation practices of *Auricularia* mushrooms. Identification of *Auricularia* strain (e.g., *A. auricula-judae*) is crucial, particularly if introducing them to different regions. Incorrectly labelled strains can result in economic loss and wasted breeding programs (Tang et al. 2010). Molecular and phylogenetic analyses can prevent misidentification of diverse *Auricularia* strains (Zięba et al. 2020). For instance, the Chinese *Auricularia* strain named "Maomuer", widely cultivated for over a century in Southern China, proved to be *A. cornea*; and *A. polytricha*, originally from Jamaica, has been shown to be a synonym of *A. nigricans* (Looney et al. 2013). *Auricularia auricula-judae* mushrooms are commercially marketed worldwide, and precise identification and classification are of prime importance to Chinese exporters (Zięba et al. 2020). In domesticating wild mushrooms, appropriate technologies for spawn production (Stamets 2000) and fruit bodies (Kües & Liu 2000) should be considered. Another important parameter is the Biological Efficiency (BE) defined as the ratio of the weight of the fresh fruit body (g) per dry weight of substrate (g), expressed in percentage (Chen et al. 2021a, Liang et al. 2019). This calculates the effectiveness of mushroom strain and substrate combination for cultivating (Tab. 6). The substrate quality is enhanced through a well-balanced carbon and nitrogen ratio in the substrate, while an imbalanced C/N ratio hinders growth (Razak et al. 2013). According to Stamets (2000), physical properties such as homogeneity in particle size of the substrate are crucial in all stages up to and through spawn generation. In fruit body formation a substrate with a mixture of fine and large particles is considered ideal (Razak et al. 2013). The nutritional composition (proximate analysis) should be considered when conducting cultivation studies because different substrates can affect the nutritional qualities of fruit bodies. For example, Yao et al. (2019) show the effect of sawdust and cornstalk substrate on melanin composition, an important secondary metabolite of black ear mushroom.

Recent trends in cultivating *Auricularia* species

Spent mushroom substrate (SMS) is the efficient recycling and utilization of a by-product. SMSs have high potential in a wide range of applications, including recycling as the substrate for the new cultivation cycle of mushrooms, biofertilizer and soil amendment, animal feed, renewable energy production, and pollution bioremediation (Leong et al. 2022). Spent mushroom sawdust wastes (SMSWs) could be a promising alternative substrate to cultivate other mushrooms. Wu et al. (2020) found that it was possible to use spent sawdust wastes of *Pleurotus eryngii* and *P. cystidiosus* for the cultivation of *A. nigricans*.

Non-food usage of *Auricularia* spp.

Mushroom-based materials have potential as substitutes of leather and textiles. In addition, an enzyme produced by *Auricularia auricula-judae* has been identified for plastic degradation, however, no distinct degradation effects were achieved by the pure enzyme, thus, current ongoing research is focused on mycelium-based degradation (whole cell degradation) (Meyer et al. 2020). The potential of reducing environmental pollution as a source of biofuel was explored (Wu et al. 2020, 2021b). Wang et al. (2022) found *Auricularia auricula-judae* biomass

Tab. 6. Biological efficiency of fruit bodies of *Auricularia* species using different substrates.

Substrate	Species	Biological efficiency (%)	Reference
Sawdust + oil palm frond	*A. polytricha*	289.9	Razak et al. (2013)
Sawdust + empty fruit bunch	*A. polytricha*	260.7	Razak et al. (2013)
Sawdust + 60 % *Panicum repens* stalk	*A. polytricha*	148.12	Liang et al. (2019)
Sawdust + 30 % corn stalk	*A. polytricha*	145.05	Liang et al. (2019)
Corn straw + coarse sawdust + fine sawdust	*A. cornea*	130	Chen et al. (2021a)
Rubber sawdust	*A. cornea*	72.46+11.23	Thongklang et al. (2020)
Corn cobs + wheat bran	*A. auricula-judae*	70.3	Onyango et al. (2011)
P. eryngii (PES) + *P. cystidiosus* spent sawdust	*A. polytricha*	58.85	Wu et al. (2020)
Paddy straw + wheat bran	*A. polytricha*	58.20	Ahila et al. (2013)
Rubberwood sawdust + empty fruit bunch	*A. polytricha*	37.4	Lau et al. (2014)
Rubberwood sawdust + rice bran	*A. polytricha*	34.3	Lau et al. (2014)
Lumber sawdust + rice bran + lime	*A. polytricha*	30.79	Zurbano (2018)
Falcataria moluccana wood meal	*A. polytricha*	15.6	Irawati et al. (2012)

feasible as feedstock for biochar preparation, an excellent carrier material controlling the release of pesticides and fertilizers. Melanin extracted from *Auricularia* can be a natural ingredient for the cosmetic industry (Sun et al. 2016).

Concluding remarks

The cultivation of *Auricularia* mushroom from history moving to the future is becoming more profound. Its potential does not solely provide an umami mouthfeel to culinary enthusiasts but also a source of nutrients such as protein enzymes benefiting not only human's health but also animals as a source of potent feedstock. Pharmacological and therapeutic applications are well studied and new interesting discoveries continually unfold. Its application on non-food products is brighter, such as in the biopolymer industry, fashion industry, and bio-based circular economy that produces biofuels with a reduced carbon footprint. The ability of this mushrooms to degrade lignocellulosic materials found in agricultural wastes is an essential solution to pressing environmental waste management concerns. Thus, cultivation studies of *Auricularia* species are still significant.

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