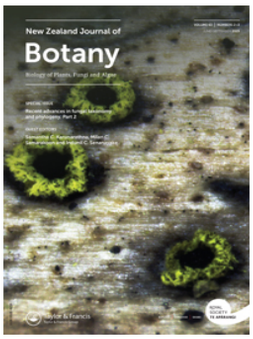

New Zealand Journal of Botany

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/tnzb20

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To cite this article: Samantha C. Karunarathna, Nimesha M. Patabendige, Siril Wijesundara, Steven L. Stephenson, He Jun & Kalani K. Hapuarachchi (23 Apr 2025): Cultivation of *Ganoderma*: methodologies and hurdles, New Zealand Journal of Botany, DOI: 10.1080/0028825X.2025.2488393

To link to this article: https://doi.org/10.1080/0028825X.2025.2488393

NEW ZEALAND JOURNAL OF BOTANY
https://doi.org/10.1080/0028825X.2025.2488393

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REVIEW ARTICLE

Cultivation of *Ganoderma*: methodologies and hurdles

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ABSTRACT

Ganoderma, a prized medicinal mushroom renowned for its therapeutic properties, has a rich history of traditional use. As demand for this valuable fungus continues to rise, cultivation emerges as a sustainable solution to meet market needs. This review explores the intricate methodologies and challenges associated with cultivating *Ganoderma*. Successful cultivation hinges upon meticulous substrate selection, efficient spawn production, and precise management of cultivation parameters. By optimising these factors, cultivators can achieve high yields with consistent quality. However, the cultivation of *Ganoderma* is challenging. Contamination control poses a significant challenge, necessitating rigorous protocols to maintain purity and prevent unwanted microbial growth. Genetic variability within strains of *Ganoderma* presents complexities that require careful management to ensure uniformity and desired traits in cultivated populations. To overcome these challenges and further enhance cultivation efficiency, the adoption of biotechnological approaches holds considerable promise. Harnessing advancements in biotechnology can facilitate targeted improvements in *Ganoderma* cultivation, from optimising growth conditions to enhancing strain resilience and productivity. This review provides an in-depth exploration of *Ganoderma* cultivation techniques, highlighting key considerations and recent advancements. By addressing challenges and leveraging innovative strategies, *Ganoderma* cultivation is poised to meet the growing demand for this esteemed medicinal mushroom.

ARTICLE HISTORY
Received 10 September 2024
Accepted 18 March 2025

HANDLING EDITOR
Sajeewa Maharachchikumbura

KEYWORDS
Biotechnological approaches; contamination control; medicinal mushrooms; spawn production; substrate selection

Introduction

Ganoderma is a highly valued medicinal mushroom with a long history of use in traditional medicine (Konara et al. 2022; Ekiz et al. 2023; Gafforov et al. 2023a; 2023b). Its therapeutic properties and potential health benefits have led to an increased

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/0028825X.2025.2488393

interest in cultivating this mushroom. *Ganoderma* cultivation offers a sustainable solution to meet the rising demand for its bioactive compounds, industrial uses, and medicinal applications (Anusiya et al. 2021; Bhambri et al. 2022; Zahuri et al. 2024). Its popularity is growing due to increasing interest in its beneficial medicinal properties (Oke et al. 2022; Arshadi et al. 2023). This mushroom is known for its bioactive compounds, including polysaccharides, triterpenoids, and other secondary metabolites, which exhibit a range of health-promoting effects (Blundell et al. 2023; Galappaththi et al. 2023). These effects include antioxidant, anti-inflammatory, immunomodulatory, antitumour, and hepatoprotective activities (Cör Andrejč et al. 2022; Johra et al. 2023). The medicinal potential of *Ganoderma* has been demonstrated in various studies, showing its efficacy against conditions such as cancer, cardiovascular diseases, diabetes, and liver disorders (Chan et al. 2021; Chugh et al. 2022; Swallah et al. 2022; Badalyan et al. 2023).

Ganoderma cultivation involves several key techniques that contribute to successful production. Substrate selection and preparation play a crucial role, as *Ganoderma* species have specific substrate preferences such as logs from trees, sawdust, or agricultural residues (Amiri-Sadeghan et al. 2022; Atila 2022; Seethapathy et al. 2023; Pradhan et al. 2024). The choice of substrate affects the growth, yield, and quality of *Ganoderma* mushrooms (Diamantopoulou et al. 2021; Sun et al. 2024a). Different substrate formulations and supplementation strategies have been explored to optimise the cultivation process and enhance the production of bioactive compounds (Tang et al. 2010; Zhou 2017; Du et al. 2019; Suwannarach et al. 2022). Spawn production is another critical step in *Ganoderma* cultivation, providing the inoculum required for mycelial growth is essential. Various methods, including grain spawn and sawdust spawn, have been employed to produce high-quality inoculum (Zhou et al. 2012; Rashad et al. 2019; Ofodile et al. 2022). The selection of a suitable strain or species for cultivation is essential to ensure the desired medicinal properties and optimal yield (Seethapathy et al. 2023; Nguyen et al. 2023a). In addition, the cultivation of *Ganoderma* has notable impacts on the composition of the microbial community associated with it (Ren et al. 2020; Yao et al. 2023a).

Controlling cultivation conditions is vital for maximising the growth and development of *Ganoderma*. Parameters such as temperature, humidity, light, and air circulation are carefully managed to create an optimal environment for mycelial growth and fruiting body formation (Zhou 2017). In addition, the use of advanced technologies such as bioreactors has shown potential for improving productivity and standardising cultivation practices (Salmon et al. 2016; Abdullah et al. 2022; Berovic and Zhong 2023; Supramani et al. 2023). The cultivation of *Ganoderma* mushrooms offers tremendous opportunities in the fields of medicine, nutraceuticals, and agriculture (Hapuarachchi et al. 2018; Ise et al. 2021; Oke et al. 2022). With ongoing advancements in cultivation techniques, understanding of genetic variability, and exploration of biotechnological tools, the future of *Ganoderma* cultivation looks promising. This progress paves the way for increased production, standardisation of quality, and accessibility of *Ganoderma*-derived products for global health and well-being (Wen et al. 2010; Bijalwan et al. 2020; Konara et al. 2022). This review provides a comprehensive overview of *Ganoderma* cultivation, highlighting its significance, cultivation techniques, challenges, and future prospects.

Global distribution of *Ganoderma* species

Species of *Ganoderma* have been extensively studied worldwide, with a particular focus on this type of research in China (Teng 1934; Wang et al. 2012). Teng (1934) was among the first to document *Ganoderma* species in China, identifying four species and one variety, including "*G. lucidum*." This species, originally described by Patouillard (1907) from tropical regions of China, was later recognised as an important edible and medicinal mushroom in Chinese culture, commonly referred to as "Lingzhi" (Teng 1963; Liu 1974; Tai 1979; Ying et al. 1987; Mao 1998; Zhao and Zhang 2000). In China alone, an impressive number of species of *Ganoderma* have been reported. Tai (1979) documented approximately 86 species belonging to the genera *Ganoderma*, *Amauroderma, Haddowia*, and *Humphreya* within the Ganodermataceae. Zhao and Zhang (2000) further expanded this list to include 98 species. Notably, a significant number of new species of *Ganoderma* have been described based on Chinese collections, with Wu and Dai (2005) and Wasser et al. (2006) adding 58 new species to the Ganodermataceae, including 10 species under *Amauroderma* and 48 under *Ganoderma*. Wang et al. (2012) distinguished 13 laccate species of *Ganoderma* from those widely cultivated in China. The classification and identification of *G. lucidum* have undergone revisions and clarifications.

Moncalvo et al. (1995) initially proposed that *G. lucidum* sensu stricto is distributed in Europe and extends to China. However, subsequent molecular analysis by Pegler and Yao (1996) revealed that collections of *G. lucidum* from China were often not conspecific with their European counterparts. Wang et al. (2012) conducted morphological and phylogenetic analyses, confirming that the Chinese *G. lucidum* is conspecific with *G. sichuanense*, originally described from Sichuan, southwestern China. Furthermore, Wang (2009) identified a misnaming issue with *G. lucidum* distributed in tropical Asia, proposing *G. multipileum* D. Hou as the earliest valid name for this species in that region. They emphasised that *G. multipileum* is distinct from both the European *G. lucidum* and the true species of *Ganoderma* found in East Asia. Hawksworth (2005) suggested the introduction of a new name for the European *G. lucidum* while preserving the well-known Chinese *Ganoderma*.

Apart from *G. lucidum*, several other morphologically similar species have been described, including *G. multipileum* (Hou, 1950), *G. sichuanense* (Zhao et al., 1983), and *G. lingzhi* (Cao et al., 2013) from China, as well as *G. resinaceum* (Patouillard, 1889) from Europe and *Ganoderma* Murrill, *G. sessile*, *G. tsugae*, and *G. zonatum* (Murrill, 1902, 1908) from the USA (Cao and Yuan 2013; Zhou et al. 2014). It is important to note that many members of *Ganoderma* have not undergone systematic studies, leading to incorrect recordings and misidentifications in China and around the world (Wang et al. 2012). Overall, the worldwide distribution of species of *Ganoderma* is extensive, with their presence documented in various countries across different continents. Ongoing research efforts continue to uncover new species and expand our understanding of the distribution patterns. These findings have important implications for ecological studies, conservation efforts, and the utilisation of *Ganoderma* for medicinal and industrial purposes.

Exploring the cultivation potential of undervalued species of *Ganoderma*: unlocking promising opportunities

Species of *Ganoderma* have been revered for centuries in traditional medicine for their purported health benefits (Ekiz et al. 2023; Kou et al. 2023). As their popularity grew,

many *Ganoderma* species have been successfully cultivated and commercialised for various applications (Badalyan and Zambonelli 2023). However, there remain several lesser-known species of *Ganoderma* with untapped potential for cultivation on a global scale. The cultivation and exploration of these species could lead to the development of novel medicinal products, contributing to global health and well-being. The next part of this chapter aims to highlight some of these promising species, shedding light on their unique characteristics and potential benefits that make them attractive candidates for future cultivation endeavours.

The cultivation of *Ganoderma* species through outdoor methods was first reported in 1621, utilising spawn inoculum on the substrate (Chang and Miles 2004a). This technique gained significant popularity in China during the 1970s, leading to widespread cultivation (Tai 1979; Zhao 1989; Zhao and Zhang 2000). Subsequent attempts at artificial cultivation of *Ganoderma* were made by Mayzumi et al. (1997), while Henmi in 1937 pioneered the cultivation of fruiting bodies on solid substrates in Japan (Mizuno et al. 1996). It was not until the 1970s that Yukio Naoi successfully achieved mass production of mature *Ganoderma* fruiting bodies on an artificial sawdust substrate (Naoi, 1997). During the 1980s and 1990s, *Ganoderma lucidum* emerged as the most extensively cultivated species (Wang et al. 2012).

The taxonomy of *Ganoderma* is vast, with over 498 reported taxonomic names worldwide (Index Fungorum 2025). Notably, several species of *Ganoderma* have been successfully domesticated on a global scale, including *G. tsugae, G. amboinense, G. australe, G. tropicum, G. neojaponicum, G. gibbosum, G. lucidum, G. applanatum, G. leucocontextum*, and *G. resinaceum* (Luangharn et al., 2021; Konara et al., 2022). Moreover, some species of *Ganoderma* have been evaluated for their optimal mycelial growth and have shown potential for cultivation aimed at producing supplements enriched with trace elements such as selenium (Se), copper (Cu), and zinc (Zn) (Table 1) (Rzymski et al. 2016). However, species of *Ganoderma* such as *Ganoderma sinense, Ganoderma annulare, Ganoderma colossum, Ganoderma oregonense*, and *Ganoderma weberianum* have demonstrated potential for cultivation and exploitation. These species possess unique properties such as immunomodulatory effects, antioxidant potential, antimicrobial and antiviral activities, anticancer properties, and benefits for metabolic disorders and diabetes. Cultivation efforts targeting these species could lead to the development of novel therapeutic agents and meet the demand for natural products with diverse health benefits (Roberts 2004; Papp et al. 2017; Kumar et al. 2022; Nguyen et al. 2023b).

Ganoderma cultivation methods

The artificial cultivation of *Ganoderma* has witnessed significant progress, requiring specific conditions for successful growth. Proper identification and classification of *Ganoderma*, as well as the selection of suitable cultivation sources for industrial and commercial purposes, are crucial. The production of *Ganoderma* varies depending on environmental factors and cultivation location, with both indoor and outdoor methods being utilised. The cultivation of *Ganoderma* has been driven by the continuous improvement of cultivation techniques, aiming to achieve substantial economic value (Wagner et al. 2003; Lai et al. 2004; Zhou 2017), while the current state of knowledge

Table 1. Different species of *Ganoderma* used in cultivation studies.

Fungal species	References
Ganoderma amboinense	Hiroo (2008)
G. applanatum	Boh et al. (2004), Jo et al. (2006), Jo et al. (2009), Jeong et al. (2009), Zhou et al. (2015), Jo et al. (2023)
G. adspersum	Zhou et al. (2015)
G. australe	Papaspyridi et al. (2009), Papaspyridi et al. (2011), Goh et al. (2016), Luangharn et al. (2017)
G. boninense	Nawawi and Ho (1990), Kok et al. (2013), Goh et al. (2016)
G. bonsai	Chen and Miles (1996)
G. capense	Liu (1999)
G. dianzhongense	He et al. (2023)
G. esculentum	He et al. (2023)
G. gibbosum	Zhiqun and Ziwu (2011), Luangharn et al. (2021)
G. japonicum	Hsieh and Yeh (2004)
G. leucocontextum	Luangharn et al. (2021), Niu et al. (2022)
G. lingzhi	Goh et al. (2016), Hennicke et al. (2016)
G. capense	Liu (1999)
G. lucidum	Cho et al. (1982), Adaskaveg and Gilbertson (1986), Triratana et al. (1991), Lin (1996), Mizuno et al. (1996), Chen and Chao (1997), Cha and Yoo (1997), Yang and Liau (1998), Chen (1999), Mayzumi et al. (1997), Chinh and Cong (1999), Tham et al. (1999), Biley et al. (2000), Hong et al. (2001), Jiang (2001), Gonzales-Matute et al. (2002), Wagner et al. (2003), Chen (2004), Kapoor and Sharma (2014), Lai et al. (2004), Boh et al. (2004), Zhang et al. (2004), Gao et al. (2023), Jayasinghe et al. (2008), Erkel (2009), Hossain et al. (2009), Hou and Liao (2009), Peksen and Yakupoglu (2009), Cong (2010), Yan (2010), Zhang and Wang (2010), Zhou et al. (2010), Peksen et al. (2011), Azizi et al. (2012), Chen (2012), Gurung et al. (2012), Wang et al. (2012), Kamra and Bhatt (2013), Magday et al. (2014), Roy et al. (2015), Hennicke et al. (2016), Li et al. (2016b), Liu et al. (2017a,2017b), Zhou (2017), Jandaik and Gupta (2022), Vasmatkar (2022), Subedi et al. (2021)
G. neo-japonicum	Cha and Yoo (1997), Hsieh and Yeh (2004), Jo et al. (2010), Jo et al. (2011), Tan et al. (2015)
G. orbiforme	Wannasawang et al. (2023)
G. resinaceum	Hafiz et al. (2007), El-Fallal et al. (2015), Chen et al. (2017), Luangharn et al. (2021), Hassan and Al-Qiassi (2022)
G. sichuanese	Wannasawang et al. (2023)
G. sinense	Nguyen et al. (2023a)
G. tropicum	Liu et al. (2009)
G. tsugae	Adaskaveg and Gilbertson (1986)
G. zonatum	Hsieh and Yeh (2004), Jo et al. (2009)

for developing economical large-scale processes is lacking (Wagner et al. 2003, 2004; Wang et al. 2012; Li et al. 2016b).

Chang and Miles (2004b) reported the most readily recognised process of producing *Ganoderma* fruiting bodies, which can be divided into two major stages. The first stage involves the preparation of the fruiting culture, stock culture, mother spawn, and planting spawn, and the second stage is growing substrates for mushroom cultivation. *Ganoderma* cultivation involves several methods aimed at providing optimal conditions for the growth and development of species of *Ganoderma*. These methods can be categorised into two main approaches: indoor cultivation and outdoor cultivation (Wang et al. 2018).

Indoor cultivation of *Ganoderma* is typically carried out in controlled environments such as greenhouses or dedicated cultivation facilities. This method allows for precise control over environmental factors such as temperature, humidity, light, and air circulation (Zhou 2017; Cortina-Escribano et al. 2020; Nguyen et al. 2023b). Various techniques are employed in indoor cultivation, including substrate-based cultivation, liquid culture fermentation, and bioreactor systems (Asadollahzadeh et al. 2023). The substrate-based method involves growing *Ganoderma* on specific substrates such as logs from trees, sawdust, or agricultural byproducts to produce fruiting bodies (supplementary files,

Figure 4), spores, and mycelial biomass, while the liquid culture focuses solely on producing mycelia and subsequent production of biomass and bioactive compounds (Supplementary files, Figure 5). These methods are used for commercial production of various *Ganoderma* products (Chang and Miles 2017; Liu et al. 2017a). Bioreactor systems provide a controlled environment for large-scale cultivation of *Ganoderma*, with the ability to monitor and regulate various parameters (Liu et al. 2017a, 2017b).

Outdoor *Ganoderma* cultivation takes advantage of natural resources and conditions for growth. This method involves selecting suitable cultivation sites, preparing the substrate materials, and providing favourable weather conditions (Wasser 2017; Wang et al. 2018). Common substrates used in outdoor cultivation include logs from trees and agricultural residues. Outdoor cultivation is often practiced in shaded areas to protect the growing *Ganoderma* from direct sunlight and extreme weather conditions (Paterson 2006; Boh et al. 2007).

Regardless of the cultivation method, several factors play a crucial role in successful *Ganoderma* cultivation. These include the selection of suitable strains or species, proper substrate preparation, maintaining optimal environmental conditions, managing pests and diseases, and implementing appropriate cultivation techniques (Rani and Lal 2019; Singh et al. 2021). Continuous research and development in cultivation methods are essential for improving the efficiency and sustainability of *Ganoderma* cultivation. This includes exploring new substrates, optimising growth parameters, and developing innovative technologies to enhance the yield and quality of *Ganoderma* biomass and bioactive compounds (Guo et al. 2023; Jin et al. 2020). Hence, *Ganoderma* cultivation encompasses a range of methods tailored to provide the ideal conditions for the growth and development of species of *Ganoderma*. Indoor cultivation offers controlled environments and various techniques such as substrate-based cultivation and liquid culture fermentation. Outdoor cultivation utilises natural resources and weather conditions (Ramesh et al. 2020). Both approaches require careful consideration of factors such as strain selection, substrate preparation, environmental control, and cultivation techniques to achieve successful cultivation outcomes (Ramarathnam et al. 2013; Rahman et al. 2021).

Indoor cultivation

Ganoderma indoor cultivation refers to the controlled cultivation of species of *Ganoderma* in indoor environments, providing optimal conditions for their growth and development (Zhou 2017). This method allows for year-round cultivation, ensuring a consistent supply of *Ganoderma* biomass and bioactive compounds. Several key factors are considered for successful indoor cultivation, including substrate selection, environmental control, and cultivation techniques (Ji et al. 2024).

Substrates used for *Ganoderma* indoor cultivation can vary, with commonly employed materials including logs from trees, sawdust, agricultural residues, or synthetic substrates (Hassan and Saadi 2023). The choice of substrate influences mycelial growth, fruiting body formation, and the quality of bioactive compounds produced. Environmental control plays a crucial role in indoor cultivation to create favourable conditions for *Ganoderma* growth. Parameters such as temperature, humidity, light intensity, and air circulation are carefully regulated to mimic the natural habitat requirements of species of

Ganoderma (Cha and Yoo 2009). Proper environmental control ensures optimal growth and development throughout the cultivation cycle. Various cultivation techniques are employed in indoor *Ganoderma* cultivation, including bag cultivation, bottle cultivation, tray cultivation, or stacked bed systems (Jandaik and Gupta 2022).

Each technique offers advantages in terms of space utilisation, ease of handling, and scalability. Recent advancements in indoor *Ganoderma* cultivation have focused on optimising cultivation parameters and techniques to improve productivity and bioactive compound content. Studies have explored the effects of different cultivation parameters, such as substrate composition, light conditions, and ventilation, on *Ganoderma* growth and metabolite production. These efforts aim to enhance biomass yield, improve product quality, and develop efficient cultivation systems. However, indoor cultivation of *Ganoderma* provides a controlled and efficient approach to ensure consistent production of biomass and bioactive compounds (Supramani et al. 2023; Cruz-Félix et al. 2024). Substrate selection, environmental control, and cultivation techniques play vital roles in achieving successful cultivation outcomes (Chen 1999). Ongoing research and optimisation efforts in indoor cultivation techniques contribute to the advancement of sustainable and reliable production of *Ganoderma* biomass and bioactive compounds.

Outdoor cultivations

Outdoor cultivation of *Ganoderma* refers to the cultivation of species of *Ganoderma* in open-air environments, utilising natural resources and conditions for their growth (Aimi et al. 2018). This method offers several advantages, including large-scale production, cost-effectiveness, and utilisation of natural sunlight (Kavishree et al. 2017). Successful outdoor cultivation of *Ganoderma* involves careful selection of cultivation sites, appropriate substrate materials, and favourable weather conditions (Chang and Miles 2004a). Selection of the cultivation site is crucial for outdoor *Ganoderma* cultivation. Factors such as climate, temperature, humidity, sunlight exposure, and air quality play significant roles in determining the success of cultivation (Lin 2019). Suitable sites with favourable environmental conditions are chosen to ensure optimal growth and development of *Ganoderma*. The choice of substrate material is important in outdoor cultivation. Commonly used substrates include logs from trees, tree stumps, or agricultural waste materials like straw or sawdust (Rashad et al. 2019). These substrates provide a suitable environment for *Ganoderma* mycelial growth and fruiting body formation. Weather conditions, especially temperature and humidity, greatly influence outdoor *Ganoderma* cultivation. The optimal temperature range for *Ganoderma* growth varies among species, typically ranging from 20°C to 30°C. Adequate humidity levels, usually around 80% to 90%, are required to facilitate mycelial growth and fruiting body development (Nguyen et al. 2019).

Proper maintenance and management of the cultivation site are essential for successful outdoor *Ganoderma* cultivation. Regular monitoring of temperature, humidity, and rainfall helps optimise cultivation conditions (Rukhiran et al. 2023). Control measures for pests, diseases, and weeds are also implemented to ensure the healthy growth of *Ganoderma*. Research on outdoor *Ganoderma* cultivation has focused on improving cultivation techniques, substrate utilisation, and cultivation site selection. Studies have explored the effects of different cultivation parameters and environmental factors on

Ganoderma growth and metabolite production (Ji et al. 2024). These efforts aim to enhance productivity, optimise resource utilisation, and promote sustainable outdoor cultivation practices.

Mushrooms collection, morphological characteristic examination, and isolation of the pure culture

During extensive fieldwork, the fruiting bodies of *Ganoderma* are photographed in their natural habitat and collected for further examination (Kornerup and Wanscher 1978; Núñez and Ryvarden 2000; Lodge et al. 2004; Rathnayaka et al. 2024). In the laboratory, the macroscopic details, including colour, texture, smell, and the dominant host/substrate, are described while the specimens are fresh. They are then dried at 40°C until all moisture is eliminated (Hu et al. 2022). Detailed micro-morphology of the specimens is recorded based on the dry material, following the methods outlined by Lodge et al. (2004). Colour information is recorded using the system described by Ridgeway (1912). The dried samples are carefully stored in sealed plastic bags with dehydrated silica gel as a desiccant to prevent moisture absorption and are deposited as voucher collections in internationally recognised herbaria for future studies. Microscopic features are examined using dried materials through hand sections. Basidiospores can be rehydrated and observed by mounting them in sterile distilled water or 3–5% potassium hydroxide (KOH) along with drops of 1–3% Congo red, Melzer's reagent, and Cotton blue to highlight different tissues (Kreisel and Schauer 1987).

Internal details are observed under a compound microscope and documented. Dimensions of microscopic characteristics are measured using Image Frame Work software (Tarosoft®, v0.9.7). The spore shape quotient (Q = L/W) is calculated based on the mean values of lengths and widths of at least 30 basidiospores. Each specimen's basidiospore size is provided in the species description. Fungal identification is performed using taxonomic keys (Zhao et al. 1983; Núñez and Ryvarden 2000). Mycelia are isolated under aseptic conditions following the method described by Stamets (2000). Cleaned sections of internal sterile tissue from fresh mushroom fruiting bodies are transferred to potato dextrose agar (PDA) culture plates. The culture plates are then incubated at temperatures ranging from 25 to 30°C for 7–10 days (Chang and Miles 2004b; Kapoor and Sharma 2014; Liu et al. 2017b). This provides a suitable physical structure for colony development, to which the species of *Ganoderma* are adapted. Once the agar surface is fully covered with *Ganoderma* mycelia, stock pure cultures are deposited in the culture collection for preservation and future reference.

Ganoderma cultivation parameters

Ganoderma growth encompasses various stages, including mycelium, primordium, and mature fruiting bodies, each with specific nutritional and environmental needs. Factors like carbon and nitrogen sources, along with parameters like temperature, humidity, light, and oxygen levels, are important for the successful artificial cultivation of *Ganoderma*. Furthermore, cultivation conditions significantly affect biomass and polysaccharide production in *Ganoderma*. The synthetic medium with specific composition and pH, along with optimal aeration and inoculum density, resulted in peak production of

biomass and polysaccharides (Simonic et al. 2008; Zhou et al. 2012; Habijanic et al. 2013; Zhou 2017; Subedi et al. 2021; Nguyen et al. 2023a).

Primordial development is a crucial stage in mushroom cultivation (Stamets 2000; Jandaik et al. 2013; Zhou 2017; Jandaik and Gupta 2022). Dense networks of mycelia on the substrate progress into primordia, which then mature into young fruiting bodies, with notable pore development visible under their surfaces. *Ganoderma* mycelia typically emerge on the substrate between 7 and12 days after inoculation (Chang and Miles 2004b; Klaus and Wan 2022; Pilotti and Bridge 2023), although some strains may show white mycelial growth as early as 3–5 days. Within 15–20 days, a thick layer of mycelia covers the substrate (Kapoor and Sharma 2014; Luangharn et al. 2017). These substrates are then moved to growth houses, placed on shelves, and the plastic ring (bottleneck) is opened slightly to allow airflow. The environment is controlled at temperatures of 24–28°C and relative humidity between 70 and 90%, with regular misting of the growing bags (Peksen and Yakupoglu 2009). Daily ventilation combined with water spraying for 15–20 min ensures the development of mature fruiting bodies.

Nutritional factors

Media

Ganoderma primarily undergoes its life cycle stages within the mycelial phase (Chinh and Cong 1999; Jo et al. 2009; Du et al. 2019). The choice of culture media significantly impacts various aspects of mycelial growth, colony morphology, sporulation, and exobiopolymer production (Yang and Liau 1998; Kim et al. 2002; Sharma and Pandey 2010). The composition of media, including mineral salts and inorganic elements, plays a crucial role in shaping the flavour profile and amino acid composition of mycelia. Typically, pure cultures of *Ganoderma* are isolated from sterile internal tissues using Potato Dextrose Agar (PDA) (Stamets 2000; Lai et al. 2004; Erkel 2009; Bellere 2018) and subsequently transferred to different media types based on the specific species. Notably, PDA generally promotes extensive radial growth and high mycelial density, followed by Malt Extract Agar (MEA) and Yeast Malt Agar (YMA) (Biley et al. 2000; Jiang 2001; Jayasinghe et al. 2008; Jo et al. 2009; Luangharn et al. 2017, 2019; Nussbaum et al. 2023). Alternative media like Oil Palm Extract Agar (OPEA), Coconut Extract Agar (CEA), Coconut Extract Medium (CEM), and Glucose Peptone have also been investigated (Goh et al. 2013; Kok et al. 2013; Kachrimanidou et al. 2023). Bioactivity evaluations encompass not only fruiting bodies but also submerged mycelial cultures, with several studies conducted in liquid synthetic media to facilitate biomass production for bioactive compound analyses (Yang and Liau 1998; Berovič et al. 2003; Zhou et al. 2012; Tan et al. 2015; Li et al. 2016b; Liu et al. 2017a, 2017b; Habijanic et al. 2015; Cruz-Félix et al. 2024). Various species of *Ganoderma* have been scrutinised to identify optimal culture media for mycelial growth (Hsieh and Yeh 2004; Roberts 2004; Jo et al. 2006; Roy et al. 2015; Zhou et al. 2015; Li et al. 2016b; Luangharn et al. 2017; Liu et al. 2017b; Nguyen et al. 2019). Factors such as strain selection, media composition, growth conditions, and environmental variables influence productivity (Yang and Liau 1998; Wachtel-Galor et al. 2011; Fraga et al. 2014; Magday et al. 2014; Hassan and Saadi 2023; Supramani 2019). The specific

nutritional requirements of different fungal species dictate the choice of culture media, ultimately shaping colony characteristics and growth outcomes.

Nutrients

Microorganisms, including basidiomycetes such as species of *Ganoderma*, are dependent on carbon and nitrogen sources for their growth and development (Shih et al. 2006; Elisashvili et al. 2009; Krupodorova et al. 2021). These essential nutrients are typically incorporated into the growth media or substrate along with inorganic salts to facilitate mycelial growth. Glucose is often favoured over other carbon sources by tropical macrofungi (Zhou et al. 2012; Suberu et al. 2013; Klaus and Wan 2022; Nguyen et al. 2023a). Substrates utilised for *Ganoderma* cultivation are commonly supplemented with carbon sources like sugars; glucose, maltose, arabinose, mannose, starch, celluloses and molasses, as well as nitrogen sources such as yeast extract, peptone, meat extract, malt extract, and corn powder to augment mycelial growth (Wagner et al. 2004; Han et al. 2008; Jayasinghe et al. 2008; Jeong et al. 2009; Ueitele et al. 2014; Krupodorova et al. 2021; Klaus and Wan 2022). Nitrogen sources typically employed for cultivating fruiting bodies encompass wheat bran, rice bran, corn powder, ammonium sulphate, urea, and other nitrogen-containing compounds (Seo and Kitamoto 1999; Zhou et al. 2012). Specific species of *Ganoderma*, like *G. japonicum* and *G. zonatum*, exhibit a preference for glucose as a carbon source, while others such as *G. lucidum* display preferences for different carbon sources like dextrin, galactose, and fructose, alongside specific nitrogen sources (Hsieh and Yeh 2004; Jayasinghe et al. 2008; Nguyen et al. 2023a). The C:N ratio of substrates is crucial for *Ganoderma* cultivation and the growth and maturation of *Ganoderma* rely on an appropriate proportion of carbon and nitrogen sources. When the medium maintains a carbon-to-nitrogen ratio ranging from 15 to 45:1, *Ganoderma* mycelium demonstrates regular growth, with the optimum ratio being 20:1. For *G. lucidum*, optimal growth, and sporulation occur within a carbon-to-nitrogen ratio of 30–40:1 (Zhou and Deng 1996; Zhou et al. 2012; Sudheer et al. 2019). Optimisation of the nutrient composition in the medium for submerged cultivation of *G. lucidum* has been demonstrated to significantly enhance mycelial growth, resulting in increased yields and shortened cultivation periods (Avtonomova et al. 2006; Liu and Zhang 2018).

In addition, the enzyme system of *G. lucidum* is influenced by factors such as plant cell wall composition, with submerged cultivation in oak sawdust yielding the highest enzyme activities, particularly in certain strains (Sitarz et al. 2013; Ćilerdžić et al. 2014, 2016; Stajić et al. 2022). Essential inorganic elements like potassium, sodium, calcium, magnesium, phosphorus, sulphur, and zinc are vital for *Ganoderma* growth, with phosphorus, potassium, and magnesium being particularly important. Calcium sulphate is commonly added to media to adjust pH, improve substrate ventilation, fix nitrogen, and increase calcium and sulphur levels (Wachtel-Galor et al. 2011; Zhou 2017). Growth factors such as vitamins B1, B2, B6, and biotin play crucial roles in the metabolic processes of *Ganoderma* during its growth and development. Typically required in small amounts (around 10 mg/L), these substances are often naturally present in substrates, making additional supplementation unnecessary (Zhou 2017; Khorsheed 2023; Pradhan et al. 2024). Maintaining substrate moisture at 60–65% is optimal for *Ganoderma* cultivation, ensuring proper mycelial growth and oxygen levels. However, for

looser substrates like bagasse, moisture content should be raised to 70% (Zhou et al. 2012; Subedi et al. 2021; Wannasawang et al. 2023).

Environmental factors

pH

The optimal pH serves as a pivotal factor in mushroom cultivation, with varying pH levels influencing the development of different mushroom strains (Yang and Liau 1998; Wagner et al. 2003; Khan et al. 2013; Bellettini et al. 2019; Suwannarach et al. 2022). Generally, mushrooms thrive at pH levels close to neutral (Khan et al. 2013; Yadav and Chandra 2014; Bhambri et al. 2022). Species of *Ganoderma* have been examined to determine the pH range conducive to mycelial growth, demonstrating robust growth across a broad pH spectrum, particularly favouring alkaline conditions (Jayasinghe et al. 2008; Jeong et al. 2009; Magday et al. 2014; Luangharn et al. 2017; Subedi et al. 2021). Several researchers emphasised the significance of pH and light in *G. lucidum* mycelial growth, with pH adjustment typically achieved using HCl for acidity and KOH or NaOH for alkalinity (Yang and Liau 1998; Kapoor and Sharma 2014; Nguyen et al. 2023a). Jayasinghe et al. (2008) noted that Korean *G. lucidum* thrives within a wide pH range, particularly excelling at pH 5, mirroring findings reported for Philippine *G. lucidum* strains by Magday et al. (2014), albeit some strains can tolerate pH levels ranging from 3 to 11 (Kapoor and Sharma 2014). *Ganoderma zonatum* demonstrates optimal growth at pH 4.6, while *G. applanatum* thrives within the pH range of 6–9 (Jo et al. 2009; Luangharn et al. 2017; Subedi et al. 2021). Consequently, different *Ganoderma* strains exhibit preferences for varying pH conditions, typically gravitating towards neutrality. pH regulation profoundly affects cell growth and exopolysaccharide (EPS) production in *Ganoderma lucidum* cultivation. Modulating pH to 3 and 6 enhances growth and EPS production, respectively. The bistage pH control technique effectively boosts EPS production while preserving cell growth, morphology, and broth properties, rendering it suitable for large-scale fermentation (Lee et al. 1999).

Temperature

Temperature is the primary attribute that must be regulated, it's a very important environmental factor that indicated for the growth and reproduction especially for enzymatic reactions during the development process of the mycelia and fruiting bodies, and view toward possible mushroom cultivation (Akinyele and Adetuyi 2005; Kurtzman 2010; Sakamoto 2018; Bellettini et al. 2019; Wang et al. 2024a). It also affects the pileus colour, mycelium density, colony diameter, and colony pigment (Lee et al. 2010). Most fungi prefer a temperature range of 25–30°C for mushroom production (Cartwright and Findlay 1934; Cho et al. 1982; Wagner et al. 2003; Daza et al. 2006; Jo et al. 2010; Gurung et al. 2012; Zhou et al. 2012; Luangharn et al. 2017; Zhou 2017; Carrasco et al. 2021), while in tropical areas, the optimal temperatures range between 21 and 26°C or higher are suitable for mushroom growing (Thawthong et al. 2014; Subbiah and Balan 2015; Jarial et al. 2024). The optimal temperature range for fruiting body production is narrower than mycelial growth (Chang and Miles 2004b; Thuy and Suzuki 2019). Mswaka and Magan (1999) reported the optimum temperature for wood-decaying

fungi from temperate regions is between 25 and 30°C. Several studies have reported that the optimal temperature for mycelium growth of species of *Ganoderma* is between 25 and 30°C (Lai et al. 2004; Jayasinghe et al. 2008; Jeong et al. 2009; Elisashvili 2012; Zhou et al. 2012; Lisiecka et al. 2015; Luangharn et al. 2017, 2019; Nguyen et al. 2023a, 2023b; Wei et al. 2024), nevertheless Taiwan *G. lucidum* shows that the optimal growth temperature for mycelial growth is 30–35°C, the growth decreases rapidly above and below these temperature values (Yang and Liau 1998; Liu et al. 2023a), while Vietnam strain of *G. lucidum* does not grow in 35°C (Cong 2010; Liu et al. 2023a; Nguyen et al. 2023a, 2023b). When the temperature is below 20 °C, the fruiting body will become yellow and rigid, while it will easily die when the temperature is above 35 °C (Zhou 2017). It is clear from the studies published that the optimal conditions for different *Ganoderma* strains are different, and the mycelial growth and fruiting body production also depend on different factors.

Humidity

Humidity for *Ganoderma* cultivation is measured in terms of the amount of water vapour in the air or in the substrate, such as the different developmental states requiring different moisture. According to Zhou et al. (2012) reported the optimal substrates moisture content is between 60 and 65%. The relative humidity (RH) for the mycelial running is 60–70%, within 85–90% for primordial initiation, and the humidity level in the environmental air for fruiting bodies development is 70–85% (Chang and Miles 2004b; Tan et al. 2015). Tan et al. (2015) reported the relative humidity to stimulate enzymatic hydrolysis processes during mycelia growth of *G. neo-japonicum* is maintained at 70%.

Air

Air quality and composition play crucial roles in the controlled cultivation of species of *Ganoderma*, especially in environments where conditions are optimised to replicate natural growth settings. One of the most important aspects of growing mushrooms is air exchange; hence, good ventilation is necessary for full mycelium colonisation on the substrate and fruiting bodies development (Ji et al. 2024). The substrate bag should remove its cover on top to air exchange to occur through the semipermeable membrane (Stamets 2000), furthermore, without proper air input and distribution, there is a little chance of obtaining consistently mature fruiting bodies (Chang and Miles 2004a). Ventilation should be done through the slow diffusion of gases to free air exchange into the cultivation room (two times daily). *Ganoderma*, a high temperature aerobic fungus, requires different rates of oxygen and carbon dioxide and also good ventilation for the fructification period (Zhou et al. 2012). It does not grow under high carbon dioxide (CO2) concentrations. However, branching of the stipe is achieved by raising the level of CO2, and the dim light also enhances the length of the stipe (Chen and Miles 1996; Zhou and Lin 1999; Zhou et al. 2012). If the CO_2 concentration is lower than 0.1% (1000 ppm), the fruiting bodies would be abnormal, while if CO2 is higher than 0.1%, that indicates the fruiting bodies are growing and have a normal developed (Stamets 2000; Zhou et al. 2012; Zhou 2017).

Light

Light is influenced by the colour, size, and texture of the fruiting bodies. It plays the phototropic responses of reproductive structures for fungi (Seo et al. 1995; Chang and Miles 2004b; López-Peña et al. 2019; Jin et al. 2023). Without light, the fruiting bodies would be malformed (Stamets 2000). *Ganoderma* does not require light during incubation of the substrate media (Kapoor and Sharma 2014; Luangharn et al. 2017). Weak light exposure needs to stimulate fruiting body formation. *Ganoderma* primordial initiation requires light at about 500–1000 lux to support an increased oxygen level to fruiting bodies form (Arya 2007; Islam et al. 2011; Zhou 2017), while 750–1500 lux are needed to stimulate fruiting bodies development (Chang and Miles 2004b). *Ganoderma* cultures showed the greatest sensitivity to blue and red light and the intense lighting causes the delay of mycelial growth or stopped (Poyedinok et al. 2008; Zapata et al. 2009; Zhou et al. 2012; Alcazar et al. 2021), and absence of light affect to the formation of pigments (Chen and Miles 1996).

Mother spawn preparation and spawn production

Spawn is a substrate into which mushroom mycelium has been impregnated and developed; they have many types, including natural virgin pure spawn, brick spawn, flake spawn, liquid spawn, and pure culture spawn (Chang and Miles 2004a). Mother spawn production usually uses several raw materials as the substrate (Chen 1999; Quimio 2002). Cereal grains frequently used include millet, wheat, corn, rice, barley and sorghum (Quimio 2002; Nwanze et al. 2005; Barreto et al. 2008; Elhami and Ansari 2008; Luangharn et al. 2014, 2017), while sawdust spawn is also evaluated (Chang and Miles 2004b). Cereal grain substrate is not only a vehicle for evenly distributing the mycelium, but also nutritional supplements, used for *Pleurotus ostreatus* (Hoa and Wang 2015), *Lentinus subnudus* (Kadiri and Arzai 2004), *Laetiporus sulphureus* (Luangharn et al. 2014), and *Ganoderma lucidum* (Chen 1999; Chi 2005; Jayasinghe et al. 2008; Hossain et al. 2009).

Spawn production is done from different kinds of grain-based media. It is produced by inoculating a sterile grain medium with the pure culture of a particular mushroom species. The spawn media are prepared by washing the grains and soaking them for 12–18 h (Klomklung et al. 2012; Luangharn et al. 2014), water drains off, and washed until clean for a soft grain, while hard grains are boiled for 15–20 min and cool it down at room temperature. Before being placed into the bottles, the grains-based media can be mixed with the other ingredients to stimulate mycelia growth and compact mycelial, and then autoclave at 121°C for 15 min (Luangharn et al. 2014) and let to cool. The active mycelia from a pure culture were cut and inoculated into the grain media. All bottle spawns are incubated for spawn running at 25–30°C in darkness (Luangharn et al. 2017). After incubation, the mushroom mycelium expands as a linear extension of cells and covers the grain media surface (Supplementary files, Figure 3). In the overview of previous publications, many methods have been described for *Ganoderma* spawn preparation (Chi 2005; Han et al. 2008; Singh et al. 2015; Tan et al. 2015; Joshi and Sagar 2016; Li et al. 2016b; Hassan and Saadi 2023). The quality grain media should not have water left and not clumping before inoculating the active mycelia. For small-scale, organically grown rye or wheat grain are used for spawn

preparation (Chang and Miles 2004b). However, the substrates are chosen to prepare the mushroom spawn depending on the readily availability, and inexpensive. Moisture content plays a critical role in mycelial colonisation; the ideal should be 50% for *Ganoderma* sp.

Ganoderma cultivation

Ganoderma grows on a wide variety of dead or dying trees in nature, e.g. deciduous trees (Ellis and Ellis 1990). Because natural *Ganoderma* has limited distribution, it has great difficulty properly controlling fruiting body quality in nature. Thus, it must grow under a controlled environment. It can be cultivated on the sawdust of many more trees than for shiitake (Erkel 2009). In artificial *Ganoderma* cultivation, only four species were successfully cultivated, which are *G. lucidum* (Leyss. Ex. Fr.) Karst, *G. lucidum* (Leyss. Ex. Fr) Karst vat., *G. japonicum* (Fr.) Lloyd, and *G. capense* (Lloyd) Teng (Zhou and Lin 1999), while nowadays the main cultivated species are *G. lingzhi, G. lucidum*, *G. sinense*, *G. tsugae,* and *G. leucocontextum* (Chen et al., 2017; Luangharn et al., 2020), although 77 species are distributed worldwide (Supplementary files, Figure 1–3). It is estimated that 200,000 farmers in China are cultivating *Ganoderma*, and its cultivars differ in different regions, such as Northeast China (Jilin, Liaoning province), East China (Anhui, Jiangsu, and Zhejiang province), South China (Hainan, Fujian province), and Southwest China (Sichuang, Yunnan province) (Li et al. 2016b), while in Northwest China (Tibet) *G. leucocontextum* is cultivated (Li et al. 2014). Currently, the various adopted methods are widely derived as a substituted raw material for *Ganoderma* cultivation such as sawdust of hardwood, logs from trees, wood segment, tree stump, seed hull, and alternative agricultural wastes from farm crops (Zhang et al. 2004; Chi 2005; Hou and Liao 2009; Peksen and Yakupoglu 2009; Zhang and Wang 2010; Zhou et al. 2010; Skalicka-Wozniak et al. 2012; Roy et al. 2015), while most large scale cultivations are conducted on logs from trees, bags or bottles, either indoor or outdoor cultivation (Li et al. 2016b). However, logs are not adopted in production practice (Zhou et al. 2012).

Substrate-based cultivation

Substrate-based cultivation is a common method used for growing species of *Ganoderma*, providing an environment suitable for mycelial growth and subsequent fruiting body formation (Amiri-Sadeghan et al. 2022). Various types of substrates have been employed in this cultivation method, including logs from trees, sawdust, silver grass, and agricultural byproducts (Liu et al. 2023b). Logs from trees are widely used as substrates for *Ganoderma* cultivation (Oei 2018). The logs provide a natural habitat for the growth of the fungus and serve as a nutrient source. Oak, poplar, and *Eucalyptus* logs are among the commonly used types. The logs are typically prepared by sterilisation or pasteurisation to eliminate competing microorganisms and create a favourable environment for *Ganoderma* growth (Yao et al. 2013). Sawdust is another common substrate employed in *Ganoderma* cultivation. It offers advantages such as uniform particle size and high nutrient availability. Sawdust-based substrates are prepared by mixing the sawdust with supplements such as wheat bran or rice bran to enhance nutrient content and promote mycelial growth (Patel et al. 2020). Agricultural byproducts, including rice

straw, wheat straw, and corn cobs, have also been utilised as substrates for *Ganoderma* cultivation. These materials provide an eco-friendly option for substrate preparation and can contribute to waste recycling (Kumar et al. 2021). To initiate cultivation, *Ganoderma* spores or mycelial culture are inoculated onto the prepared substrates. The substrates are then placed in a controlled environment with specific temperature, humidity, and light conditions to support mycelial growth. As the mycelium colonises the substrate, it forms a network and eventually develops fruiting bodies under suitable conditions (Stamets 2005). It is worth noting that the cultivation techniques and conditions can vary depending on the specific species of *Ganoderma* and desired outcomes. Detailed protocols and specific references can be found in research papers and publications dedicated to *Ganoderma* cultivation. A general overview of some common methods used for *Ganoderma* cultivation is as follows.

Sawdust bags cultivation

Sawdust is accepted as the preferable main ingredient used as a basic substrate for sawdust bags cultivated for the commercial-scale mushroom productions (Royse 1996; Smith et al. 2002; Pathmashini et al. 2008). This method is popular worldwide for *Ganoderma* and many species of mushrooms (Jiang 2001; Olei 2003; Okhuoya et al. 2005; Jo et al. 2010; Moonmoon et al. 2010; Azizi et al. 2012; Hwang et al. 2015; Roy et al. 2015). *Ganoderma* is widely cultivated by using hardwood sawdust to improve the quality of fruiting bodies, and the surface of fruiting bodies become hard (Zhou 2017), but it is considered a risk for contamination (Li et al. 2016b). *Ganoderma* is usually cultivated on different types of hardwood sawdust such as *Acacia* sp. (wattles), *Artocarpus heterophyllus* (jackfruit), *Alnus* spp. (alder), *Brachystagia nigerica* (miombo), *Carya* spp. (pecan), *Corylus* spp. (hazel), *Dalbergia sissoo* (North Indian rosewood), *Dipterocarpus turbinatus* (gurjun oil tree), *Gmelina arborea* (beachwood), *Hevea brasiliensis* Mull-Arg. (para rubber), *Magnolia* spp., *Mangifera indica* (mango), *Melia dubia* (malabar neemwood), *Michelia champaca* (champak), *Populus* sp. (Poplar), *Prunus* spp. (plum), *Quercus* spp. (oak), *Swietenia mahagoni* (mahogany), *Tectona grandis* (teak), and *Triplochiton scleroxylon* (African hardwood) (Chen and Chao 1997; Chen 1999; Stamets 2000; Rani et al. 2015; Roy et al. 2015; Ihayere et al. 2017; Jeewanthi et al. 2017; Zarzoliana et al. 2020; Ofodile et al. 2022; Wang et al. 2024b). Gurung et al. (2012) reported that sawdust of *Alnus* could give a high yield of *G. lucidum*, while for *G. australe* para rubber could give a good yield (Luangharn et al. 2017), and oak is suitable for *G. neo-japonicum* production (Jo et al. 2010). However, the type of supplements depends on the development process of fruit bodies as they differ from different cultivation methods or raw materials (Chen 1999; Roy et al. 2015).

Sawdust substrates (sifting or mixing materials) are widely used as a raw material for growing mushrooms. In order to optimise the media substrate formula, initially, sawdust is enriched with a proper organic and inorganic additive (carbon and nitrogen sources), and supplements are added to the substrate to stimulate the mycelial growth. All components are mixed thoroughly with water and gradually added until the moisture content is around 60–75% (Peksen and Yakupoglu 2009; Gurung et al. 2012); however, water content below 40% does not activate the mycelial growth on the substrate (Luangharn et al. 2017). The correct water content can be checked by pressing the medium manually by hand. The proper sawdust substrates are filled into polypropylene

bags; for example, 6.50 × 12.50 in. of polypropylene bag are used for 800 grams of sawdust, compact packed into each bag, and punched to make holes, and a plastic ring (bottleneck) is used to seal the top. The sawdust substrate bags are sterilised under high pressure and temperature at 15 psi and 121°C for 30 min or 90–95°C for 5–8 h (Chang and Miles 2004b), after sterilisation, the sawdust bags are allowed to cool down at room temperature before use. The appropriate amount of 5–10 grams of spawn is used to inoculate into the hole of each sawdust bag and cover under sterile conditions. After inoculation, the sawdust bags are incubated at 26 ± 1°C in darkness, 60–70% moisture content for spawn running (Luangharn et al. 2017; Zhou 2017) and to produce the fruiting bodies. In addition, the fruiting can be encouraged by casing the substrate with sterile soil after the mycelial colonises the substrate to provide moisture in a humid microclimate for primordial initiation and fruiting body development (Stamets and Chilton 1983; Chen 2012).

Natural log cultivation

The historical method of cultivation of medicinal mushrooms is still practiced mainly in Asia, on logs from hardwood trees or short wood segments (Mayzumi et al. 1997; Chang and Buswell 1999; Smith et al. 2002; Gurung et al. 2012). Log cultivation is the widely used method for the cultivation of *Ganoderma*, and it is a simple natural method for growing saprobic fungi by absorbing the organic matter of wood in nature to develop into fruiting bodies. This method gives higher quality, greater active constituent contents (Chen et al. 2001; Chen 2002; Li et al. 2016b). *Ganoderma* primordia are usually formed 1–2 months after spawning (Chen 2004), and to harvest the fruiting bodies produced it takes about 6 months to 2 years for the first flush produce, and it continues to produce for 4–5 years (Stamets 2000), it takes much labour for harvesting as it is time-consuming to harvest, but quick turnover enables high yield within a shorter time (Li et al. 2016b). Recently, *Ganoderma* cultivation using logs from trees has not been adopted in production practice (Chen 2004). *Ganoderma* can be grown on logs of broadleaf species of trees, such as pecan, elder, choke, cherry, and plum in China (Chen and Chao 1997; Chen 1999), while sugar maple and white oak are proven to be superior substrate species (Chen 1999). In Thailand, mulberry logs were suitable for *G. lucidum* cultivation (Poomsing et al. 2013). *Ganoderma lucidum* is successfully grown on hardwood logs and stumps in Louisiana and humid southeastern United States (Stamets 2000). In China, *G. lucidum* is widely grown on oaks, maple groves, Platycarya, and other local species of hardwood tree (Erkel 2009; Qiu et al. 2023), *G. tsugae* grows on hemlocks, and *G. oregonense*, is found on a variety of conifers (Stamets 2000).

Log substrates should be in high quality from healthy living trees, without signs of decay or invasion of other organisms (Li et al. 2016b). The season for felling the trees is also very important; the late autumn and early spring are the ideal periods to cut and inoculate (Mudge 2013). Sapwood is considered to contain high sugar levels, and the bark is tighter, which affects the rate of mycelial growth (Chen 1999). Mostly, the entire long or short logs, tree trunks, and tree branches are used, while the short logs are more commonly used (Stamets 2000; Chen 2012). Before the logs are used, the log tree should be cut 3 weeks before spawning (Chen and Chao 1997; Mudge 2013). Log lengths vary from 0.9 to 1.2, 1 m long, and 5 to 13 cm in diameter, are easy to handle, and are the most productive (Tong et al. 2020). In China, the standard log size is 15

cm in diameter and 15–24 cm long (Chen 2004). Temperatures are 25–30°C; if the water content of the dry log is less than 40%, it should be soaked for 1–3 days or until the desired moisture level is reached. For the drill series, an appropriate 8 cm from the end of the log is marked, drill 12–20 cm down the length until the other butt end is reached, and 8 cm in diameter with 2.5 cm deep for dowel spawn (Chang and Miles 2004a). Using short log segments is a part of natural log cultivation; it provides for the short growing cycle, higher biological efficiency, and good quality of fruiting bodies, consequently, and superior economical (Chang and Buswell 1999). It involves the use of sterilised short logs about 12 cm in diameter and approximately 15 cm long which allow for optimum mycelial running. To inoculum the spawn, an appropriate amount of spawn (10 g) is inoculated into each hole, and the ends of logs and each hole are sealed with hot wax to prevent drying and contaminations, label the name of the species of mushroom, and stacked on the nursery pots or arrange in laying yard for their production lifetime (Chen 1999; Jandaik and Gupta 2022; Pradhan et al. 2024). The moisture should be controlled by water spraying. The short log segment cultivation then is buried in the soil base for fruiting bodies production (Chang and Buswell 1999), while the forced fruiting bodies method of log cultivation is soaked in cold and clean water for 18–24 h, within 3–4 days, primordia emerge from the log substrate and grow to mature mushrooms in 5–7 days and result in fruiting bodies form more evenly (Stamets 2000; Chang and Miles 2004b). Although it can grow using both indoor and outdoor methods, the outdoor method requires less maintenance, and the first flush of mushrooms is often delayed than indoor methods (Stamets 2000). A cultivation protocol has been developed using poplar billets, utilising readily available side branch pieces from pruned poplar trees in North India. The economic viability and profitability of *G. lucidum* cultivation have also been assessed (Sona et al. 2014).

Agricultural wastes

The substituted cultivation technology is defined as using cultivation techniques on the solid state of several types of agricultural wastes (Malarvizhi et al. 2003; Erkel 2009; Zhou et al. 2012). To determine the substrate substitutes, carefully select the raw materials, and should be fresh and not moldy before use (Chang and Miles 2004b), the appropriate ratio of rice bran in the mixture for *Ganoderma* should be 10–20% (Royse and Bahler 1986; Tham et al. 1999; Olei 2003), and all ingredients should be mixed well. Sawdust is usually mixed with a suitable substrate as those are cheap and readily available in the local areas, it includes rice husks, rice, wheat bran, wheat straw, paddy straw, corncobs, sugarcane bagasse, coconut fibre, peanut hulls, olive by products, oak leaf, cotton seed husk, cotton stalks, foot materials of farm crops, whey permeate, crop stalks, diaper waste and animal manure for cultivation of *Ganoderma* (Triratana et al. 1991; Gonzales-Matute et al. 2002; Huiping et al. 2005; Song et al. 2007; Peksen and Yakupoglu 2009; Yan 2010; Zhang and Wang 2010; Zhou et al. 2010; Veena and Pandey 2011; Manavalan et al. 2012; Ćilerdžić et al. 2014; Ueitele et al. 2014; De Carvalho et al. 2015; Cilerdzic et al. 2018; Koutrotsios et al. 2019; Rashad et al. 2019; Baktemur et al. 2022; Khoo et al. 2022), while tea waste was found as a new additive supplement for cultivation of *G. lucidum* (Peksen and Yakupoglu 2009; Zhou et al. 2012; Bulam et al. 2019). Wheat bran was reported as the best substrate for growth of *G. lucidum* (Peksen and Yakupoglu 2009; Yang et al. 2003), and it agrees with those obtained by Erkel (2009) that stated the

highest yield and biological efficiency (BE) were obtained from wheat bran and corn bran, while rice bran, ground corn, and ground sorghum gave the lowest yield. Ground rice tends to decrease mycelial growth rate (Yang et al. 2003). Triratana et al. (1991) showed that rice bran, ground corn, and ground sorghum give a high yield. Cotton seed hulls give high yields but poor quality (Zhou 2017).

Liquid culture fermentation

Liquid culture fermentation is a commonly employed method for the cultivation of species of *Ganoderma* (Li et al. 2021). In this technique, *Ganoderma* mycelium is grown in a liquid medium containing nutrients (Li et al. 2016a). The use of liquid culture allows for faster mycelial growth and provides better control over cultivation conditions (Guo et al. 2023). To enhance oxygen supply and nutrient distribution, the liquid culture is often agitated (Li et al. 2016a). This technique offers advantages such as controlled growth conditions, high product yield, and scalability (Guo et al. 2022). In recent years, significant progress has been made in optimising the liquid culture fermentation process of *Ganoderma*, leading to improved production of biomass and bioactive compounds (Li et al. 2021).

The choice of a suitable liquid culture medium is crucial for successful fermentation. Various formulations have been developed to support the growth and metabolite production of *Ganoderma* (Du et al. 2024). For example, Zhou et al. (2020) investigated the use of different carbon and nitrogen sources in the medium, including glucose, fructose, and peptone, and found that glucose and peptone combination resulted in the highest mycelial growth and ganoderic acid production in *G. lucidum*. Similarly, Yang et al. (2019) studied the effects of different nitrogen sources, such as yeast extract and ammonium nitrate, on biomass and polysaccharide production in *G. lucidum*, and reported that yeast extract significantly enhanced polysaccharide synthesis. Furthermore, optimising the fermentation conditions, including temperature, pH, aeration, and agitation, is essential for achieving optimal growth and metabolite production in *Ganoderma* liquid culture Wang et al. (2021) investigated the influence of temperature and pH on the mycelial growth and triterpenoid production of *G. lucidum*. They found that a temperature of 28°C and a pH of 5.5 were favourable for both mycelial growth and triterpenoid accumulation.

To improve the fermentation process and enhance product yields, various strategies have been employed. Submerged fermentation using bioreactors allows for precise control of environmental parameters, such as dissolved oxygen levels and nutrient availability. Bioreactor systems, including stirred tank reactors, airlift reactors, and bubble column reactors, have been utilised in *Ganoderma* cultivation (Ravindran et al. 2021). These systems facilitate efficient mass transfer and provide a homogeneous environment for fungal growth. Recent studies have focused on optimising liquid culture fermentation techniques to improve *Ganoderma* cultivation. These include strategies such as medium composition optimisation, bioreactor design optimisation, and process parameter optimisation to enhance biomass yield and bioactive compound production. These advancements contribute to the development of efficient and sustainable methods for large-scale production of *Ganoderma* biomass and bioactive compounds.

Hence, liquid culture fermentation has emerged as a valuable method for the cultivation of species of *Ganoderma*. Optimisation of the culture medium composition, fermentation conditions, and the use of bioreactor systems have contributed to improved biomass and bioactive compound production (Wu et al. 2024). Further research in this area is essential to enhance the efficiency and sustainability of *Ganoderma* liquid culture fermentation. Liquid culture fermentation is a widely used method for the cultivation of species of *Ganoderma*, offering several variations depending on the specific requirements of the fungus (Guo et al. 2023). Here are some common types of liquid culture fermentation methods employed for *Ganoderma* cultivation.

Submerged fermentation

In submerged fermentation, the *Ganoderma* mycelium is grown in a liquid medium with optimal nutrient composition. This method provides better control over environmental factors such as pH, temperature, and oxygen supply, resulting in enhanced mycelial growth and efficient production of bioactive compounds such as enzymes, ganoderic acids, and polysaccharides (Fang and Zhong 2002a, 2002b; Zhang and Tang 2008; Cui et al. 2015; Rodrigues et al. 2019; Yang et al. 2021; Pessoa et al. 2023; Cruz-Félix et al. 2024; Sun et al. 2024b).

Shake flask fermentation

Shake flask fermentation involves the cultivation of *Ganoderma* mycelium in small-scale glass or plastic flasks. The flasks are agitated on a shaker to ensure proper aeration and nutrient distribution. This method is commonly used for preliminary studies and small-scale production of *Ganoderma* biomass and secondary metabolites (Wan et al. 2016; Girmay et al. 2018; Feng et al. 2019; Mao et al. 2020; Sun et al. 2021).

Bioreactor fermentation

Bioreactor fermentation involves the use of specialised vessels known as bioreactors to cultivate *Ganoderma* mycelium on a larger scale. Bioreactors provide precise control over environmental parameters, such as agitation, aeration, and nutrient supplementation. This method allows for higher biomass production and scalability, making it suitable for commercial cultivation (Tang and Zhong 2003; Zhang et al. 2014a; Esmaelifar et al. 2021; Supramani et al. 2023; Kianirad et al. 2024).

Fed-batch fermentation

Fed-batch fermentation involves the gradual addition of nutrients to the culture medium during the cultivation process. This method allows for better control of nutrient availability, leading to improved productivity and enhanced production of bioactive compounds in *Ganoderma* cultivation (Tang and Zhong 2002; Kim et al. 2006; Tang et al. 2009, 2011; Zhu et al. 2010; Wei et al. 2016; Supramani et al. 2023; Cruz-Félix et al. 2024; Qiong et al. 2021; Rosales-López et al. 2022).

Breeding techniques

Breeding techniques in *Ganoderma* cultivation are vital for enhancing the desired traits of this valuable fungus. Traditional methods like selective breeding involve choosing

individual *Ganoderma* specimens with favourable characteristics, such as rapid growth or high medicinal potency, and breeding them to produce offspring with similar attributes (Zhou et al. 2012; Zhou 2017). In the selective breeding technique, tissue and single-spore isolation are used to develop superior strains. This method is particularly useful for *Ganoderma* since its spores are difficult to germinate. The process typically involves isolating tissue, screening clones, purifying and rejuvenating the strain, conducting cultivation trials, and finally selecting the superior strain (Karadeniz et al. 2013; Zhou 2017; Xie et al. 2023).

Crossbreeding has been utilised since 1983 to produce hybrid strains through genetic recombination, achieved by pairing monosporic cultures (Gani 2017). This method aims to amalgamate desirable traits from different strains. However, the application is limited in *Ganoderma* due to challenges in germinating *Ganoderma* spores and obtaining the necessary monokaryotic strains for breeding (Zhou et al. 2012; Zhou 2017; Dong et al. 2022). Mutation breeding offers a more effective approach by inducing genetic mutations to develop strains with enhanced qualities such as higher yield and temperature resistance. This method involves selecting a strain, treating it with mutagens, and then screening for desired mutations (Zhang et al. 2014b, 2014c). Protoplast fusion is a technique used to merge cell protoplasts from different strains, facilitating genetic mixing that overcomes compatibility barriers. This method has been key in generating new strains with improved traits, including temperature tolerance and year-round production capability (Chiu et al. 2005; Singh et al. 2007; Raman et al. 2021; Tang et al. 2023; Li et al. 2023b). Genetic engineering uses recombinant DNA technology to alter genetic material, allowing for the transfer of beneficial traits from one organism to another. This has enabled the creation of transgenic mushrooms with improved yields and qualities (Konka and Khanna 2022). However, this technique faces challenges such as low rates of DNA integration and expression, and instability in the new strains. Modern genetic engineering techniques allow for precise manipulation of *Ganoderma*'s genetic makeup, enabling the introduction of specific genes to enhance traits like disease resistance or medicinal compound production. Through these breeding methods, growers can develop *Ganoderma* strains that meet diverse needs, whether it be for commercial cultivation, medicinal use, or environmental adaptation (Shi et al. 2012; Wang et al. 2020; Tan et al. 2023; Azi et al. 2024).

Fruiting body development management, harvesting and preparation of the next crop

The development of *Ganoderma* fruiting bodies involves distinct stages and requires careful management practices (Zhou 2017). Adequate ventilation, high humidity, and diffused dim light are crucial during pileus differentiation (Sakamoto 2018). Growers must choose between sawdust synthetic log cultivation and natural log cultivation, with most preferring soil-buried log cultivation indoors (Chen 2002; Bandaranayake et al. 2011; Berovic et al. 2022). Primordia develop into stalks and caps in controlled environmental conditions, typically emerging within 7–14 days under optimal temperatures (Roberts 2004; Zhou et al. 2012; Luangharn et al. 2020). Temperature control is essential for quality fruiting body formation, with the ideal range being 25–35°C. Management strategies include water spray, aeration, light regulation, disease and insect

prevention, harvesting, and drying (Feng et al. 2016; Zhang et al. 2023). The differentiation process in *Ganoderma* demands constant temperature conditions to prevent abnormalities (Zhou 2017). Regular inspection and pruning ensure quality control, while harvesting involves cutting the stalk with a 2 cm stub and air drying for 2–3 days. Proper drying methods are vital for preserving product quality (Sadiq et al. 2021; Jandaik and Gupta 2022).

Ganoderma fruiting bodies are harvested manually at various stages of maturation, which vary depending on the species, consumer preferences, and market demands (Chang and Miles 2004b). Different cultivators have developed a range of techniques for harvesting the fruiting bodies. Typically, the mature fruiting bodies are identified when the white margin of the pileus (cap) disappears. These are harvested by hand, using clean knives to carefully detach them from their growing medium before the application of water spray. After harvesting, the fruiting bodies are weighed and dried at a temperature of 60°C (Royse 1996). The usual harvesting period for species of *Ganoderma* spans approximately 90 days (Peksen and Yakupoglu 2009). However, certain species can be harvested in a slightly shorter timeframe of 70–80 days (Erkel 2009; Azizi et al. 2012; Luangharn et al. 2017). It has been observed that the yield of fruiting bodies is highest during the first cycle of growth, with subsequent cycles showing a gradual decline in productivity (Chang and Buswell 1999) and reaffirmed in later studies. To initiate subsequent fruiting cycles, the substrate bags are left to ventilate daily without water spray or light exposure for a period of 3–7 days (Luangharn et al. 2017). After this resting phase, the bags require an additional 1–2 weeks to absorb more nutrients from the substrate, which helps to sustain the production of new fruiting bodies in the following cycles. This cyclical process ensures the continuous cultivation of *Ganoderma*, optimising both yield and quality over time.

In *Ganoderma* cultivation, "flushes" can refer to either the timing of harvests or the number of harvest cycles. Typically, growers continue cultivation under optimal conditions for second and third flushes, even though yields tend to decrease, particularly in the third flush (Melanouri et al. 2022). During the initial harvest, it's crucial to carefully add water or a nutrient solution to aid in spawn running. After a two-week period of spawn running, the second flush can be harvested. *Ganoderma* can usually be harvested for two flushes in substitute cultivation (Gurung et al. 2012). The process from the formation of primordia to the harvestable fruiting bodies takes approximately 25–30 days. With effective management, 1 kg of dry substrate can yield 100–120 g of dry *Ganoderma* fruiting bodies (Bijalwan et al. 2021). Extending the harvesting time is facilitated by utilising unused substrate, promoting mycelial metabolism with nutritional supplements, facilitating nutrient transfer and accumulation by adding water, and promoting primordial differentiation to enhance nutrient absorption (Jandaik and Gupta 2022).

Equipment systems for substrate preparation, mechanisation, and automation control

The substrate preparation system for cultivating *Ganoderma* involves various mechanical tools designed to streamline the intensive and laborious process. This includes machinery for slicing wood or agricultural residues, reducing these into finer particles, and mixing the base and supplemental ingredients with water (Cotter 2014; Zhou 2017; Guo et al.

2023). Once mixed, the substrates are packed into specialised bags using a bagging machine. Sterilisation, a crucial step to prevent contamination, employs both physical methods like heat, fermentation, and ultraviolet light using devices such as steam sterilisers and UV lamps (Gurung et al. 2012; Du et al. 2019; Jandaik and Gupta 2022; Pradhan et al. 2024). The preparation of fungal strains involves specific equipment for isolating and cultivating the strains, including inoculation boxes, cultivation frames, and equipment for strain preservation like freeze dryers. After harvest, the produce is handled using dryers and vacuum packaging machines to ensure quality and longevity (Poomsing et al. 2013; Rashad et al. 2019; Sadiq et al. 2021).

Ganoderma production has evolved from traditional methods to more technologically advanced approaches (Li et al. 2019; Mawar et al. 2020; Morat 2024). Historically, methods ranged from manual, garden-style to wood-log cultivation, reflecting a shift from small-scale farming to industrialised setups (Sona et al. 2014; Bijalwan et al. 2021; Li et al. 2023a). Currently, a mix of methods is used worldwide, all adhering to the growth requirements of *Ganoderma* growth (Zhou et al. 2012; Du et al. 2019). Modern production primarily utilises mechanical and automated systems. Mechanical modes involve machines for substrate mixing, bagging, and environment control like air conditioning, fans, and humidifiers (Biswas et al. 2011; Zhou 2017; Keshamma et al. 2022). These processes are predominantly manually managed, with some use of intelligent controls for precision in environmental factors like temperature, humidity, and CO_2 levels (Jandaik and Gupta 2022; Nuansoi et al. 2022). In contrast, the automated model integrates advanced intelligent systems for environmental monitoring and control within mushroom houses and spawn rooms This setup allows for precise adjustments based on pre-set parameters, managing all aspects of production from substrate preparation to harvest (Bulaclac and Caluag 2023). Machinery such as inoculation devices and conveyor belts streamline operations, while automated systems ensure optimal growth conditions, demonstrating a significant move towards fully mechanised *Ganoderma* production.

Bioreactors, also known as fermentation tanks, serve as vessels where specific microorganisms thrive, leading to fermentation and the production of valuable substances (Wagner et al. 2003). In modern biotechnology, a range of bioreactors is employed to produce *Ganoderma* biomass or bioactive metabolites like polysaccharides and ganoderic acid (Hu et al. 2018; Supramani et al. 2023; Kianirad et al. 2024). These bioreactors are typically classified into suspension systems and immobilisation systems (Zhong 2010). Among the suspension systems, Stirred Tank Reactors (STRs) and airlift reactors (ARs) are extensively utilised in *Ganoderma* fermentation (Lee et al. 2007; Habijanic et al. 2013). Stirred tank reactors, comprising tanks, mixers, and control devices, are particularly favoured for their versatility in controlling fermentation parameters such as dissolved oxygen concentration, pH, temperature, and nutrient supplementation (Papaspyridi et al. 2011; Rosales-López et al. 2022). On the other hand, airlift reactors differ fundamentally in design and structure from STRs (Tang et al. 2007; Berovič and Popovic 2018). While research on large-scale *Ganoderma* fermentation is limited, both liquid-state fermentation (LSF) and solid-state fermentation (SSF) show promising potential for industrial production (Zhou 2017). Despite most studies being conducted on a smaller scale, recent efforts have demonstrated the feasibility of scaling up *Ganoderma* fermentation processes to larger volumes, paving the way for increased production of *Ganoderma* biomass and metabolites.

Diseases in *Ganoderma* cultivation

Diseases can significantly impact the cultivation of species of *Ganoderma*, leading to reduced yield and compromised quality of the harvested mushrooms. Understanding and managing these diseases is crucial for sustainable *Ganoderma* cultivation. Several diseases have been reported in *Ganoderma* cultivation, affecting both the mycelium and the fruiting bodies (Cao et al. 2022; Kredics et al. 2022).

One common disease in *Ganoderma* cultivation is the green mold disease caused by species of *Trichoderma* like *T. asperellum*, *T. citrinoviride*, *T. ganodermatigerum, T. guizhouense*, *T. hamatum*, *T. harzianum*, *T. Koningiopsis T. paratroviride*, and *T. virens*, on *G. sichuanense* (An et al. 2022, Li et al. 2023c), *T. Longibrachiatum, T. Hengshanicum* on *G. lingzhi* (Zhang et al. 2019, Cai et al. 2020). *Trichoderma* spp. are aggressive competitors that can overgrow *Ganoderma* mycelium, leading to a decline in growth and productivity (Naher et al. 2018). Another fungal pathogen, *Ganoderma* brown blotch, caused by *Phellinus noxius*, can cause brown discolouration and rotting of the *Ganoderma* fruiting bodies. In addition, bacterial diseases, such as soft rot caused by *Pseudomonas* spp., can result in the decay of the fruiting bodies (Gill and Tsuneda 1997). Viral infections have also been reported in *Ganoderma* cultivation. For instance, the *Ganoderma boninense* basidiomycete virus (GbBV) has been identified in species of *Ganoderma*, causing severe deformities in the fruiting bodies. Other viral pathogens, such as the *Ganoderma* green spot virus (GGSV), have been associated with discolouration and abnormal growth of *Ganoderma* mushrooms. To manage these diseases, various control measures can be implemented. Good hygiene practices, including regular sanitation of cultivation facilities and tools, can help reduce the spread of pathogens (Rathore et al. 2023). Proper substrate sterilisation and the use of disease-free spawn can minimise the introduction of pathogens into the cultivation system (Joshi and Sagar 2016). Moreover, biological control agents, such as *Trichoderma* species or beneficial bacteria, can be applied to suppress the growth of pathogenic organisms (Yao et al. 2023b).

Research efforts are ongoing to develop disease-resistant strains of *Ganoderma* through breeding and genetic engineering approaches. By identifying genes associated with disease resistance, breeders aim to develop cultivars with enhanced resistance to common pathogens (Wang et al. 2018). Hence, diseases pose a significant challenge to *Ganoderma* cultivation, affecting both the mycelium and the fruiting bodies. Proper disease management practices, including sanitation measures, use of disease-free materials, and biological control agents, are essential for maintaining healthy *Ganoderma* cultivation systems. Continued research and development of disease-resistant cultivars are crucial for sustainable and successful *Ganoderma* cultivation. Some common diseases of *Ganoderma* have been discussed in the following section.

The *Ganoderma* diseases can be caused by pathogens in most fungi and bacteria. They affect the mycelial running and development to fruiting bodies stages. Physiological diseases can be observed on the substrate media (Colavolpe et al. 2014). A cause huge loss of mushroom contamination is mostly from the sterilisation process, growing process, physical and environment (Velázquez-Cedeño et al. 2004; Colavolpe et al. 2014). *Aspergillus*, *Penicillium*, *Trichoderma*, and *Rhizopus* are the main sources of biological contamination. This fungus is often observed in the early stages of the process with a

green mold layer on the substrate (Colavolpe et al. 2014; Wang et al. 2022). It occurs a few days after inoculation, especially during spawning and cropping phases, and finally causes huge losses in mushroom crops (Jandaik and Guleria 1999). It infects fruiting bodies (stipe and pileus) and mycelium tubes, with allochroic patches appearing on the pileus, leading to gradual rot and producing a pale green mildew-like layer (Lu et al. 2016). Furthermore, yellow rot, the most destructive disease of cultivated *Ganoderma lucidum* in Korea, has been attributed to the yellow rot pathogen (YRP). *Xylogone ganodermophthora* and *Scytalidium ganodermophthorum* were identified as the teleomorph and anamorph of YRP, respectively. However, only *Xylogone ganodermophthora* was found to cause disease in *Ganoderma lucidum* (Kang et al. 2010). In addition, *Xylogone sphaerospora* has also been identified as causing disease in *G. lucidum* (Lee et al. 1996). Bacteria are also the microorganism that usually causes the disease during mushroom cultivation state. Water spaying results in high humidity, and, further, non-flow ventilation in the cultivation area nourishes the growth of bacteria (Upadhyay et al. 1991). To prevent contaminations and diseases from mushroom cultivation, it should maintain a clean and hygienic growing area with the proper physical environment (Chang and Buswell 1999; Chang and Miles 2004b; Patel 2013).

Leading companies in *Ganoderma* cultivation and ınnovation

Several companies worldwide have successfully pioneered large-scale *Ganoderma* cultivation, contributing to both medicinal and commercial applications. DXN Holdings Bhd (dxn2u.com) in Malaysia is a global leader in organic *Ganoderma* production, offering a diverse range of health products. In the United States, Aloha Medicinals (alohamedicinals.com) specialises in biotechnological advancements for large-scale medicinal mushroom cultivation. Japan's Hokuto Corporation (hokto-kinoko.co.jp) has developed innovative mushroom biotechnology methods, ensuring sustainable and efficient cultivation. In addition, Chinese companies such as Beijing Luyuan Qiuzheng Technology Development Co., Ltd., Jiangzhong Pharmaceutical Co., Ltd., and Wuyishan Yuanshengtai Biological Technology Co., Ltd. have made significant advancements in *Ganoderma* cultivation and product development (Patsnap). These companies exemplify successful *Ganoderma* cultivation efforts, setting industry standards for quality and innovation.

Biotechnology and genetic variability in enhancing *Ganoderma* cultivation

The cultivation of *Ganoderma*, can be significantly improved through biotechnology and genetic research (Feng et al. 2024; Wang et al. 2024a, 2024b). Tissue culture techniques and liquid fermentation allow for mass propagation and controlled production of bioactive compounds (Wang et al. 2024a, 2024b). Genetic engineering tools like CRISPR-Cas9 and RNA interference (RNAi) facilitate targeted modifications, enhancing traits such as polysaccharide and triterpenoid production (Wang et al. 2020; Zou et al. 2021; Tarafder et al. 2024). Selective breeding and marker-assisted selection (MAS) help develop high-yield, stress-resistant strains (Xie et al. 2023; Zhou et al. 2024; Li et al. 2024a, 2024b). Genetic variability plays a crucial role in optimising *Ganoderma*

cultivation by influencing growth rate, environmental adaptability, and bioactive compound synthesis (Sun et al. 2024; Yu et al. 2024; Azi et al. 2025). Understanding genetic factors affecting stress tolerance, substrate utilisation, and metabolite biosynthesis enables the development of superior strains with enhanced medicinal properties (Wang et al. 2024a, 2024b; Xu et al. 2025). Biotechnology also aids in formulating nutrient-enriched substrates and co-cultivation with beneficial microbes, further improving growth efficiency (Azi et al. 2024; Kianirad et al. 2024; Li et al. 2025; Liu et al. 2025). However, challenges such as regulatory concerns, strain stability, and public acceptance must be addressed. Future research should focus on functional genomics, transcriptomics, and metabolic engineering to optimise *Ganoderma* production. Integrating biotechnological advancements with traditional cultivation methods can ensure sustainable, high-quality mushroom production, benefiting both commercial and medicinal applications.

Recommendations

Ganoderma, a medicinal mushroom with rich metabolites, has gained widespread recognition. It is cultivated not only for health purposes but also for its valuable bioactive compounds. Cultivators strive to optimise various factors, including substrates, methods, processes, and environmental conditions, to achieve high yields and quality. This report provides a summary of the essential processes and factors involved in *Ganoderma* cultivation, highlighting critical parameters for mycelial growth and fruiting body production. Factors such as media composition, temperature, relative humidity, water content, ventilation, light intensity, and substrate formulation significantly influence the growth of *Ganoderma* under both field and laboratory conditions. Large-scale cultivation relies on proper selection of substrates and their formulations, taking into account biological efficiency. In addition, the yield of *Ganoderma* mushrooms is influenced by strain selection, cultivation processes, geographical locations, climatic conditions, and the inherent genetic characteristics of individual species. It should be noted that different species of *Ganoderma* require specific growth conditions.

Challenges and future prospects

Despite the potential benefits of *Ganoderma* cultivation, several challenges need to be addressed. Changes in log composition and soil microbiota during continuous cultivation of *Ganoderma* are problematic (Zhang et al. 2022; Yao et al. 2023a). Fruiting body development is hindered in cultivated soil due to colonisation by non-*G. lucidum* fungi. *Trichoderma* and *Muc*or are dominant antagonistic fungi found during *G. lucidum* cultivation. Waterlogging sanitation effectively reduces fungal colonies, improving *G. lucidum* fruiting body development and spore yield. Hence, effective sanitation methods are essential for successful *G. lucidum* cultivation (Tong et al. 2020). Contamination control is crucial to prevent the growth of competing microorganisms and maintain the purity of the cultivated *Ganoderma*. Strict sterilisation protocols, cleanroom facilities, and proper hygiene practices are necessary to minimise contamination risks. Genetic variability within species of *Ganoderma* poses challenges in terms of strain selection and maintaining desirable characteristics. Advances in

molecular markers and genetic studies have aided in strain identification, preservation, and selection of superior strains for cultivation. In addition, the use of genetic engineering and breeding techniques holds promise for enhancing the production of bioactive compounds and developing strains with improved characteristics. The scalability of *Ganoderma* cultivation from small-scale to commercial production is a significant consideration. Optimisation of cultivation processes, including substrate utilisation, spawn production, and environmental management, is crucial for achieving high yields and cost-effectiveness. Furthermore, the development of sustainable cultivation practices, such as recycling agricultural residues and waste materials, can contribute to the economic and environmental sustainability of *Ganoderma* cultivation.

Conclusions

Ganoderma, renowned for its copious metabolites, stands as a cornerstone in medicinal mushroom lore, boasting a rich reservoir of bioactive compounds with profound therapeutic implications. Beyond its conventional health applications, *Ganoderma* harbours a plethora of biologically active constituents, elevating its status as a potent source of complementary medicinal attributes. Your diligent efforts as cultivators to optimise *Ganoderma* growth through meticulous refinement of substrates, methodologies, processes, and environmental parameters are crucial in attaining maximal yield and quality. This comprehensive report delineates the pivotal processes and factors indispensable for successful *Ganoderma* cultivation, emphasising critical parameters governing mycelial proliferation and fruiting body development. Notably, *Ganoderma* exhibits a protracted growth cycle relative to other domesticated mushrooms, underscoring the imperative for meticulous media selection and temperature modulation to foster optimal culture conditions.

Augmenting the cereals grain media (spawn) and sawdust substrate with additive nutrients, encompassing carbon–nitrogen and organic–inorganic sources, constitutes a customary prelude to sterilisation, enriching the growth milieu. Integral to mycelial propagation and spawn running is the meticulous regulation of relative humidity (RH), complemented by judicious management of water content, ventilation, and light intensity throughout the mycelial development phase, crucial for augmenting fruiting body yields. These multifaceted environmental factors profoundly influence fungal growth dynamics across field and laboratory settings, underscoring their indispensability in cultivation endeavours. The scale-up of *Ganoderma* cultivation hinges upon the judicious selection of sawdust substrates and their nuanced formulations, wherein distinct substrates manifest varying degrees of biological efficiency (BE). While preliminary studies and laboratory-scale trials suggest promising scalability, further validation through field-scale implementation and case studies would be beneficial to confirm the reproducibility of these techniques in diverse cultivation settings. Consequently, formulation refinement, initially piloted on a laboratory scale, remains a crucial step in ensuring seamless replication and adoption by mushroom cultivators worldwide. The choice of strain and substrate composition are key factors in *Ganoderma* cultivation, as they significantly impact the final yield and quality of the mushrooms. Consequently, initially piloted on a laboratory scale, formulation refinement assumes paramount significance, facilitating seamless replication and adoption by mushroom cultivators worldwide.

Ultimately, attaining optimal mushroom yields depends on various factors, including strain selection, substrate composition, cultivation methodologies, geographical locale, climatic exigencies, and inherent genetic predispositions. Given the inherent variegation among species of *Ganoderma*, bespoke cultivation strategies tailored to specific species profiles emerge as imperative for sustained success.

Acknowledgments

Samantha C. Karunarathna thanks the National Natural Science Foundation of China (No. 32260004), Yunnan Revitalisation Talents Support Plan (High-End Foreign Experts and Young Talents Programmes), and the Key Laboratory of Yunnan Provincial Department of Education of the Deep-Time Evolution on Biodiversity from the Origin of the Pearl River.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the National Natural Science Foundation of China [grant number 32260004]; the Key Laboratory of Yunnan Provincial Department of Education of the Deep-Time Evolution on Biodiversity from the Origin of the Pearl River; and Yunnan Revitalization Talents Support Plan (High-End Foreign Experts Programs).

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