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RESEARCH ARTICLE

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Effects of Blue Light on Fruiting Body Production and Ergothioneine Content During Sawdust Cultivation of Shiitake (*Lentinula edodes*)

Min-Jun Kim, Yeonsug Jeong, Mi-Jeong Park, Yeongseon Jang and Kang-Hyeon Ka

Forest Microbiology and Application Division, Department of Forest Bioresources, National Institute of Forest Science, Suwon, Republic of Korea

ABSTRACT

The cultivation period of shiitake (*Lentinula edodes*) is approximately 120–150 d, which is longer than that of other edible mushrooms. The development of fruiting bodies in shiitake is affected by light exposure. In this study, we investigated the effects of blue light on the production and ergothioneine contents of shiitake mushrooms. Fruiting body production (yield) on the medium irradiated with blue light increased in both cultivars (L808, 555 ± 60 g/3 kg medium; Sanbackhyang, 1090 ± 106 g/3 kg medium). Additionally, blue light increased the ergothioneine contents and antioxidative activities, and the ergothioneine content of L808 (about 2.8 mg/g) was higher than that of Sanbackhyang (about 1.2 mg/g). These results suggest that blue light is effective in shortening the cultivation period and increasing ergothioneine contents during shiitake cultivation.

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Blue light; ergothioneine; fruiting body; *Lentinula edodes*

1. Introduction

Lentinula edodes (shiitake) occupies a high share in global mushroom market, and it is the second most cultivated edible mushroom worldwide [1,2]. Shiitake contains several bioactive compounds, including dietary fibers and antioxidants, that can maintain good health and prevent diseases [3]. Among these, ergothioneine is gaining attention for its powerful antioxidant properties and its role in cellular protection against oxidative stress and inflammation [4,5]. Since humans cannot synthesize ergothioneine [6], dietary sources, such as shiitake mushrooms are particularly valuable.

Shiitake is typically cultivated on a sawdust medium, and the sawdust medium turns white when the mycelium completely grows. In this state, the sawdust medium is used for browning and fruiting body generation. If browning of the medium is incomplete, it is considered infected by other contaminants, and large production cannot be expected. Once browning is complete, even if the medium comes into contact with external air, it does not get contaminated by other bacteria, and moisture evaporation within the medium is suppressed, thereby improving mushroom development. In shiitake cultivation, the sawdust medium is cultured for 100–150 d for its browning; this is an excessively long cultivation period compared to those of other mushrooms, such as *Pleurotus* spp. [7,8].

Light is a crucial factor for morphogenesis in fungi [9]. Filamentous fungi use light as a cue for their physiological and morphological responses [10]. Light irradiation at various wavelengths affects mycelial growth. Among visible lights, blue light induces an increase in mycelial biomass of *Ganoderma lucidum* [11]. Irradiation of blue light during the fruiting body formation processing leads to efficient production of the characteristic fruiting bodies in *Pholiota nameko* and *Pleurotus eryngii*, and high intensity of blue light in the primordial stage of *Grifola frondosa* results in high fruiting body production [12]. Irradiation with blue light from light-emitting diodes (LED) during the growth of fruiting bodies of oyster mushroom *(Lentinus sajor-caju)* increases its radical scavenging potential compared to that after usual irradiation [13]. Recent study has shown that blue light exposure can stimulate biosynthetic pathways in *L. edodes*, influencing secondary metabolites and other biochemical markers under controlled, *in vitro* conditions [14]. However, these findings primarily address *in vitro* conditions, and there is limited understanding of how blue light affects shiitake mushrooms in full-cycle cultivation settings, particularly in terms of yield and morphological characteristics during sawdust-based cultivation. In this study, we investigated the effects of three different

CONTACT Yeongseon Jang idjys@korea.kr

cultivation conditions on fruiting body production, morphological characteristics, antioxidant compounds, and antioxidant activities of two shiitake cultivars.

2. Materials and methods

2.1. Spawn preparation

Two cultivars, Sanbackhyang and L808, stored at the National Institute of Forest Science were used. Sanbackhyang is the cultivar developed by the National Institute of Forest Science [15]. L808 is the cultivar that has been cultivated in China [16] and it is imported to Korea as spawn. They were inoculated onto potato dextrose agar (PDA; Difco, Detroit, MI) medium and incubated at 25 °C for 14 d to confirm their conditions. They were subcultured on PDA medium and incubated for 14 d. Each cultivar was inoculated into a 1-L plastic bottle filled with 650 g medium composed of 80% oak sawdust and 20% wheat bran (w/w) with 55–60% moisture content, and incubated at 23 °C for 30 d.

2.2. Cultivation conditions and induction of fruiting bodies

The medium was comprised 85% oak sawdust and 15% (w/w) wheat bran. The moisture content was adjusted to 55–60%. Cylindrical bags were filled with 3 kg of the medium and were autoclaved. Approximately, 10 g sawdust spawn was inoculated into four inoculation holes of the medium, and the inoculated area was sealed with tape to prevent contamination. The inoculated medium was incubated at 23 °C and 60% humidity. Three cultivation conditions, such as (i) 60 d of dark culture and 40-d culture with blue LED (450–460 nm) (4 μmol/m^2/s) (Blue/100), (ii) 60 d of dark culture and 40-d culture with white (usual) light (4 μmol/m^2/s) (White/100), and 60 d of dark culture and 60-d culture with white (usual) light (4 μmol/m^2/s) (White/120), were used. And eight mediums were prepared in each condition. To ensure respiration of shiitake hyphae during dark culture, needle sticking (3 mm in diameter and 50 mm in depth) was performed on the 2nd, 4th, and 6th weeks. After cultivation, fruiting bodies were induced inside a fruiting room maintained with 18 ± 1 °C temperature, 80 ± 5% humidity, and 1000 ppm CO_2.

2.3. Measurement of fruiting bodies

After 2 d of primordium formation, thinning out was performed, leaving 10–12 primordia per medium. Mature fruiting bodies were harvested by cutting them close to the medium. The fruiting body characteristics were assessed according to the Union for the Protection of New Varieties of Plants guidelines [17]. After the first flush, the medium was incubated for 3 weeks under dark conditions in the fruiting room at 18 ± 1 °C and a relative humidity of 60%. The medium was then hydrated by submersion in an immersion tank for 30 h, and the second and third flushes were performed as described above.

2.4. Sample extraction and analysis of ergothioneine content

After harvest, fruiting bodies were sliced and dried at 45 °C in a dry oven (OF-02GW; Jeio Tech. Co., LTD, Daejeon, Republic of Korea) for 3 d. Dried mushrooms were finely ground using a grinder (Hanil, Seoul, Republic of Korea). Subsequent experiments were performed using fine mushroom powder with three biological replicates and three technological replicates. Ergothioneine content was measured as previously described, with some modifications [18]. Fine mushroom powder (0.4 g) was added to 40 mL distilled water and boiled at 80 °C for 30 min. The mixture was centrifuged at 3000 ×*g* for 10 min at 25 °C. The supernatant was passed through a 0.45-μm syringe filter (Whatman, Munich, Germany). Ergothioneine was analyzed using an Ultimate 3000 UHPLC system (Thermo Fisher Scientific, Waltham, MA) equipped with an ACQUITY UPLCVR BEH HILIC column (2.1 × 150 mm, 1.7 μm; Waters, Milford, MA). The mobile phase consisted of solvent A (0.1% formic acid in water) and solvent B (acetonitrile). The flow-rate of the mobile phase was 0.2 mL/min; detection wavelength was 254 nm; the temperature was 35 °C; and injection volume was 2 μL. A calibration curve was generated using commercially available L-ergothioneine (Sigma-Aldrich, St. Louis, MO). Three of biological and technological replicates were used for analysis.

2.5. Measurement of antioxidant activity

Antioxidant activity was measured using the method as previously described [18], with minor modifications. Briefly, 0.4 g shiitake powder was homogenized in 40 mL methanol. The homogenate was filtered through a 0.45-μm syringe filter (Whatman, Brentford, UK), and the flow through was used to measure antioxidant activity. All conditions were analyzed using three biological replicates and three experimental replicates.

A solution of 7 mM of 2, 2′-azino-bis(3-ethylbenzothiazoline-6-sul-fonic acid) (ABTS) in 2.45 mM potassium persulfate was incubated in the dark at 25 °C for 16 h, and then diluted in 70%

ethanol to attain an absorbance of 1.5 ± 0.02 at 734 nm. Mushroom extracts (200 µL) were added to diluted ABTS solution (1 mL) and incubated at 25 °C for 6 min. Absorbance at 734 nm was measured using a spectrophotometer (Epoch; BioTek, Winooski, VT). The ABTS scavenging activity (%) was calculated from the absorbance values.

To measure the 2, 20′-diphenyl-2-picrylhydrazyl (DPPH) scavenging activity, 1 mL flow through and an equal volume of 0.3 mM DPPH were mixed. The absorbance of the mixture at 517 nm was measured using a spectrophotometer (BioTek, Winooski, VT) after incubation at 25 °C for 30 min. The DPPH-scavenging activity (%) was calculated from the absorbance values.

2.6. Statistical analysis

PASW Statistics version 18 (SPSS Inc., Chicago, IL) was used for statistical analysis. Tukey's test was used to determine significant differences, and statistical significance was set at $p < 0.05$.

3. Results and discussion

3.1. Effect of light on shiitake cultivation

Both cultivars were turned deeper browning under blue light than under white light. L808 accelerated primordia formation under blue light (Blue/100) before the end of the light incubation period, whereas Sanbackhyang delayed primordia formation under white light (White/100) (Table 1). This observation is consistent with previous findings that each shiitake strain exhibited different characteristics even under the identical cultivation conditions [19]. Additionally, blue light has been shown to enhance mycelial growth in *L. edodes* by activating photoreceptors linked to growth-related pathways, as demonstrated in *in vitro* [14]. This mechanism may underlie the earlier primordium formation observed in L808 under blue light in our study. Browning occurs during the light cultivation period, and blue light, in particular, forms a pigment [20]. Browning efficiency varies depending on the light source. In a previous study, blue LED has shown the best browning efficiency after processing using blue, white, green, and red LEDs, and a high browning efficiency has been observed at 200 lx, regardless of the type of light source [21].

Table 1. Cultivation characteristics of shiitake cultivars on sawdust medium.

Cultivar	Cultivation condition	Color of browning	Special note
L808	Blue light 100 d L808 (blue/100)	Dark brown	Primordium initiation before the end of light cultivation period
	White light 100 d L808 (white/100)	Light brown	–
	White light 120 d L808 (white/120)	Brown	–
Sanbackhyang	Blue light 100 d Sanbackhyang (blue/100)	Dark brown	–
	White light 100 d Sanbackhyang (white/100)	Light brown	Late primordium initiation
	White light 120 d Sanbackhyang (white/120)	Brown	–

3.2. Fruiting body production and characteristics

Under blue light irradiation, the production was highest for both cultivars at 555 ± 60 g/3 kg media for L808 and 1090 ± 106 g/3 kg media for Sanbackhyang. In Sanbackhyang, production with cultivation period, showing higher yield in Sanbackhyang (White/120) compared to Sanbackhyang (White/100). In contrast, L808 (blue/100) production was different from that of L808 (white/100) but not significantly different from that of L808 (white/120) (Table 2). Blue light strongly stimulates the development of fruiting body [22–24]. Among visible lights, blue light is the most effective monochromatic light for fruiting body development in edible mushrooms [25–29]. Exposure to blue light significantly results in the maximum yield of oyster mushrooms [24].

In terms of morphological characteristics of the fruiting body, the fresh weight was highest in L808 (white/100) at 48 ± 15 (g/ea). The pileus diameter was largest in Sanbackhyang (white/120) at 74 ± 15 mm (mm). In L808(blue/100), the pileus thickness, stipe length, and stipe width were highest in L808 (blue/100) at 17 ± 2, 53 ± 7, and 24 ± 4 mm, respectively (Table 2). In L808, the number of fruiting bodies did not differ by cultivation conditions. however, in Sanbaekhyang, the highest number of fruiting bodies (38 ± 4 per medium) were observed in Sanbaekhyang (Blue/100). Taken together, the production of both cultivars under blue light (100) was similar to or higher than that under white light (120), and the morphological characteristics of the fruiting bodies did not significantly differ depending on cultivation conditions. Blue light treatment affects the cap diameter and color of mushrooms [29]. However, white oyster mushrooms are not sensitive to any light treatment [24]. Our results indicated that shiitake mushrooms were affected by blue light in terms of production; however, morphological characteristics of the fruiting body were not significantly affected. Notably, both cultivars (L808 and Sanbackhyang) exhibited positive responses to blue

Table 2. Fruiting body characteristics of L808 and Sanbackhyang on sawdust media under different cultivation conditions.

Cultivar	Cultivation condition	Production (g/3 kg medium)	Number of fruiting body (ea/ 3 kg medium)	Fresh weight (g/ea)	Pileus diameter (mm)	Pileus thickness (mm)	Stipe length (mm)	Stipe width (mm)
L808	Blue light 100 d L808 (blue/100)	555 ± 60 a	11 ± 3 a	45 ± 14 ab	64 ± 11 ab	17 ± 2 a	53 ± 7 a	24 ± 4 a
	White light 100 d L808 (white/100)	360 ± 69 b	9 ± 3 a	48 ± 15 a	70 ± 10 a	16 ± 3 ab	51 ± 11 a	22 ± 5 a
	White light 120 d L808 (white/120)	482 ± 20 a	12 ± 3 a	39 ± 17 b	64 ± 13 b	15 ± 3 b	51 ± 9 a	18 ± 6 b
Sanbackhyang	Blue light 100 d Sanbackhyang (blue/100)	1090 ± 106 a	38 ± 4 a	43 ± 13 a	67 ± 10 b	16 ± 2 a	51 ± 10 a	18 ± 4 a
	White light 100 d Sanbackhyang (white/100)	611 ± 100 c	17 ± 4 c	43 ± 19 a	69 ± 11 b	14 ± 2 b	50 ± 11 a	15 ± 4 b
	White light 120 d Sanbackhyang (white/120)	727 ± 84 b	25 ± 3 b	46 ± 18 a	74 ± 15 a	14 ± 3 b	48 ± 13 a	15 ± 4 b

The characteristics of fruiting bodies were calculated as the average of the three flushes.
Values are expressed as mean ± standard deviation ($n \geq 8$).
Means with different letters in each strain are significantly different ($p < 0.05$).

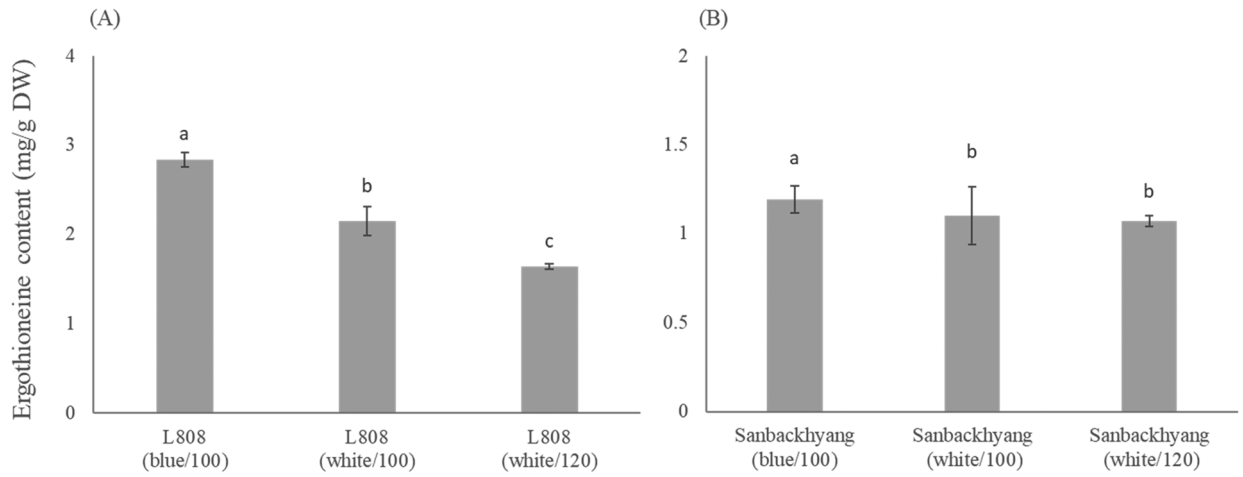

Figure 1. Ergothioneine contents of L808 (A) and Sanbackhyang (B) on sawdust media under different cultivation conditions. Values are presented as mean ± standard deviation ($n = 3$). Means with different letters are significantly different ($p < 0.05$).

light treatment, although the magnitude of these responses differed. This observation suggests that the effects of blue light may vary depending on the cultivar, even under identical treatment conditions.

3.3. Ergothioneine and antioxidant activity

Ergothioneine, an antioxidant representative of mushrooms, is not synthesized in animals or higher plants, but is synthesized by bacteria and fungi [6,30]. In this study, we found that ergothioneine contents of about 2.8 mg/g in L808 and 1.2 mg/g in Sanbackhyang were highest under blue light irradiation conditions, and higher ergothioneine content was noticed in 100-d-cultured fruit bodies than in 120-d-cultured ones (Figure 1(A,B)). Ergothioneine contents of oyster mushrooms significantly increase under irradiation by a mixture of blue and white lights from LEDs compared to those under other mixed light conditions [31]. However, ultraviolet-B (UV-B) radiation do not significantly affect ergothioneine contents in any mushroom types, except shiitake [32]. Therefore, lights of different wavelengths affect ergothioneine accumulation, and blue light increases ergothioneine biosynthesis.

Recently, various spectrophotometric assays have been adopted to measure the antioxidant capacity, and ABTS and DPPH scavenging assays are most widely used [33]. In this study, both ABTS and DPPH scavenging activities of the cultivars increased under blue light irradiation, and fruiting bodies cultured for 100 d showed higher antioxidative activity than did fruiting bodies cultured for 120 d (Figure 2(A–D)). A significant correlation has been observed between the ergothioneine content and radical-scavenging potentials in fungi and plant [34]. In oyster mushrooms, the DPPH radical scavenging potential increases under blue light irradiation at

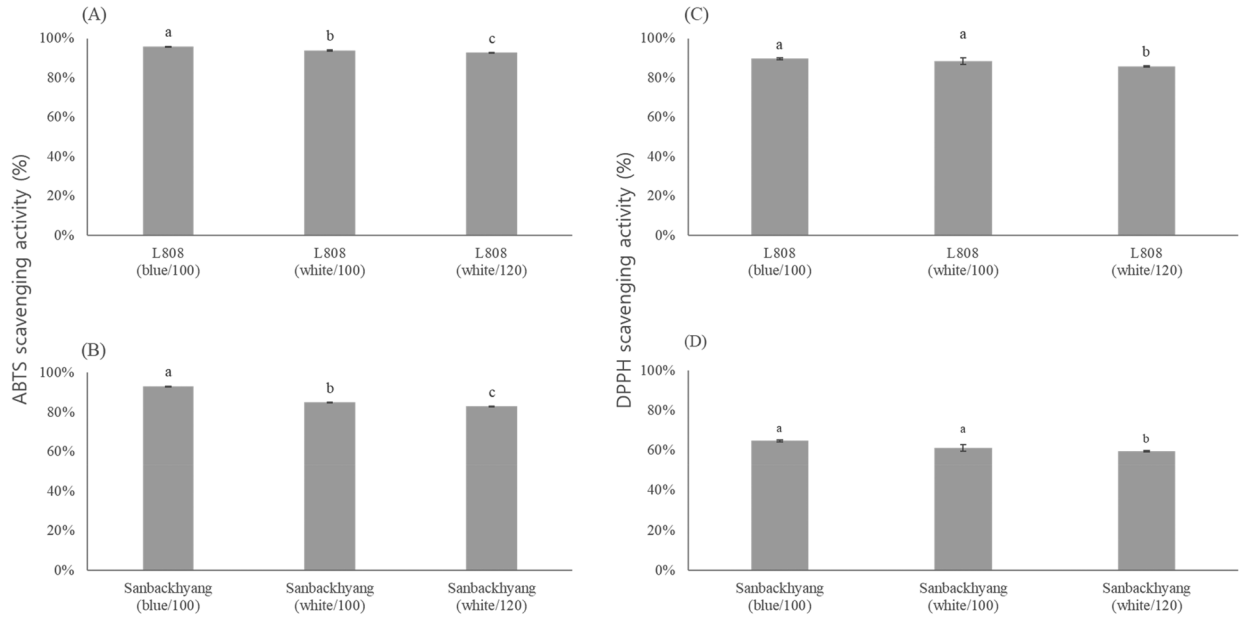

Figure 2. Antioxidative activities of L808 and Sanbackhyang on sawdust media under different cultivation conditions. (A) ABTS scavenging activity of L808. (B) ABTS scavenging activity of Sanbackhyang. (C) DPPH scavenging activity of L808. (B) DPPH scavenging activity of Sanbackhyang. Values are presented as mean ± standard deviation ($n = 3$). Means with different letters are significantly different ($p < 0.05$).

intensities higher than normal light conditions during the development of fruiting bodies [13]. Therefore, blue light may help increase the ergothioneine content and antioxidant activity of shiitake fruiting bodies. Additionally, the long cultivation periods lead to decreased antioxidant activity.

4. Conclusion

Blue light irradiation during light culture period has significant positive effects on shiitake mushroom (*Lentinula edodes*) production, leading to a shortened cultivation period. Moreover, blue light treatment increased the content of ergothioneine, a potent antioxidant compound, and overall antioxidant activity in shiitake fruiting bodies. Our findings have important implications for shiitake mushroom cultivation, indicating that strategic manipulation of light conditions, particularly the use of blue light, can enhance both production efficiency and nutritional quality. This approach could be valuable for commercial mushroom growers seeking to optimize yield and increase the health-promoting properties of their product. Further research is warranted to elucidate the molecular mechanisms underlying the blue light response in shiitake mushrooms and to explore potential synergistic effects with other environmental factors. In conclusion, this study provides valuable insights into the use of blue light as a tool for improving shiitake mushroom cultivation, offering a promising avenue for enhancing both the quantity and quality of this economically important edible fungus.

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Disclosure statement

There are no relevant financial or non-financial competing interests to report.

Author's contribution

Min-Jun Kim, Yeun Sug Jeong, Kang-Hyeon Ka, and Yeongseon Jang conceived and designed the study. Min-Jun Kim and Yeun Sug Jeong conducted the experiments. Min-Jun Kim, Kang-Hyeon Ka, Mi-Jeong Park, and Yeongseon Jang analyzed the data and wrote the manuscript. All authors assisted in interpreting the results.

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ORCID

Min-Jun Kim http://orcid.org/0000-0002-5306-9197
Yeonsug Jeong http://orcid.org/0000-0001-8951-7353
Yeongseon Jang http://orcid.org/0000-0001-7960-4306
Kang-Hyeon Ka http://orcid.org/0000-0002-9364-626X

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