



## OPEN Effects of light quality on agronomic traits, antioxidant capacity and nutritional composition of *Sarcomyxa Edulis*

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*Sarcomyxa edulis*, a notable edible and medicinal mushroom indigenous to northeast China, is celebrated for its high nutritional value and delightful taste. In this study, white light as a control and examined the effects of red, green, and blue light on the agronomic traits, antioxidant capabilities, and nutritional composition of *S. edulis*. The results showed that different monochromatic light qualities affected the color of *S. edulis* pileus, with blue light demonstrating particular efficacy. Furthermore, blue light also regulated pileus length, whereas red light was instrumental in significantly increasing stalk length. Regarding antioxidant capacity, compared with red and green light, the activities of POD, SOD, and CAT were significantly improved by blue light irradiation, decreased MDA levels, and improved free radical scavenging potential. Additionally, blue light exposure led to an increase in the contents of 15 amino acids. Green light treatment reduced the crude fat content. For the first time, we found that light quality is a key factor in controlling the color of *S. edulis*. Blue light is an effective way to regulate the color and pileus size of *S. edulis*, and improve the antioxidant properties. The photobiological characteristics and the response of nutritional quality to light environment of *S. edulis* were clarified.

*Sarcomyxa edulis*, widely known as “Yuan mo,” “yellow mushroom,” and “frozen mushroom,” predominantly thrives in the cold regions of Northeast China, South Korea, Japan, and Russia’s Far East. *S. edulis* grows on broad-leaved trees such as elm, linden, and birch, particularly on standing deadwood, belonging to the low-temperature edible fungus<sup>1</sup>. *S. edulis* has a variety of colors, mostly yellow, yellow-green, or brown, the fruit body is tender and fragrant, the meat is full, can be eaten fresh, but also can be dried to eat<sup>2</sup>. Nutritionally, it is a rich source of proteins, vitamins, minerals, and other essential nutrients<sup>3</sup>. Previous studies have suggested that the consumption of *S. edulis* is associated with potential benefits, such as preventing arteriosclerosis, improving immunity, and inhibiting tumor growth<sup>4</sup>. In addition, there are many unknown natural products in *S. edulis*. Our laboratory obtained a new highly degraded sterol and a new  $\beta$ -carboline alkaloid from *S. edulis* for the first time, and cell experiments showed that  $\beta$ -carboline alkaloid had good anti-inflammatory activity<sup>5</sup>.

LED is the fourth generation of new lighting sources, offering significant benefits for industrial lighting design, including energy efficiency, environmental friendliness, compact size, and longevity<sup>6</sup>. The emission wavelengths of LEDs are well-suited to plant photoreceptors, optimizing crop yield and quality by influencing crop morphology and metabolism<sup>7</sup>. Light is one of the environmental conditions necessary to induce the differentiation of mushroom primordium and regulate the normal growth of fruiting bodies<sup>8</sup>. Although edible fungi can not perform photosynthesis<sup>9</sup>, they possess a light-sensing system analogous to the blue, red, and green light systems found in plants. This system allows them to detect and respond to environmental light signals<sup>10</sup>. The quality of light is known to have varied effects on plant morphology and development<sup>11</sup>. Among the spectrum of light, blue light is one of the most important environmental signals for various organisms because it regulates their development and physiological processes through photoreceptors<sup>12</sup>. For plants, the blue (425–490 nm) and red light (610–700 nm) spectra are optimally absorbed for photosynthesis, while very small amounts of green light (520–610 nm) are absorbed<sup>13</sup>. Red light is mainly involved in photomorphogenesis and the development of photosynthetic organs, while blue light is crucial for morphogenesis and stomatal opening<sup>14</sup>. In fungi, the effect of blue light on the fruiting body is particularly prominent. Blue light significantly influences the development of *Flammulina filiformis*<sup>15</sup>. Four blue light receptors *FfWC-1*, *FfWC-2*, *FfCpl*, and *FfCry-DASH* were identified in

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the genome of *F. filiformis*, further supporting the importance of blue light on the growth and development of *F. filiformis* from the molecular level<sup>16</sup>. *Coprinosia cinerea* is often used as a model fungus to study the molecular mechanisms of photomorphogenesis<sup>17</sup>. The blue light can stimulate the development of the fruiting body of *C. cinerea*<sup>18</sup>. Moreover, blue light has been shown to enlarge and thicken *Pleurotus ostreatus* pileus and shorten stalk length<sup>19</sup>. Numerous edible mushrooms, including *Lentinula edodes*, *Grifola frondosa*, and *Pleurotus eryngii* exhibit heightened sensitivity to blue light, highlighting its broad significance across fungal species<sup>20</sup>.

The interest in natural antioxidants has significantly increased among consumers and researchers in recent years<sup>21</sup>, with findings indicating that fungi are rich sources of antioxidants and possess antibacterial properties<sup>22</sup>. The quality of light plays a pivotal role in the production of reactive oxygen species and antioxidant capacity<sup>23</sup>. Compared with composite light, monochromatic light has a significant impact on antioxidant activity. Blue light can significantly increase the activity of antioxidant enzymes and enhance the antioxidant defense system in organisms<sup>24</sup>. The ethanol extract from the fruit body and mycelium of *P. ostreatus*, exposed to ultraviolet B light, shows a high content of vitamin D<sub>2</sub>, suggesting that both the fruit body and mycelium could serve as potential antioxidants and be developed into novel dietary supplements<sup>25</sup>. Furthermore, blue light has been found to stimulate the accumulation of non-enzymatic antioxidants, such as carotenoids, flavonoids, and total phenols in plants, effectively enhancing their resilience to extreme environmental conditions<sup>26</sup>.

Light quality elicits varied responses in the biosynthesis of carotenoids, carbohydrates, fatty acids, nucleotide metabolism, and other secondary metabolites within edible fungi<sup>27</sup>. For instance, blue light irradiation has been shown to elevate the ergosterol content in *Hypsizigus marmoreus*<sup>28</sup>. Additionally, the yield of *Ganoderma lucidum* spore powder is influenced by different light qualities, with blue light notably enhancing the polysaccharide levels in *G. lucidum*<sup>29</sup>. The abundance and content of amino acids were also affected under different light quality irradiation. For example, after blue light irradiation, the abundance of amino acids in mycelia changed, significantly increasing phenylalanine while reducing tyrosine levels<sup>30</sup>. In *F. filiformis*, blue light has been found to upregulate the expression of genes within the lysine biosynthesis pathway, thereby fostering lysine production, enriching nutritional value, and improving taste<sup>31</sup>. Furthermore, light is an important cause of pigment production in *Cordyceps militaris*<sup>32</sup>, with blue light inducing carotenoid accumulation, and pink light augmenting cordycepin content in the fruit body<sup>33</sup>.

Currently, the effect of light quality on the cultivation of *S. edulis* has not been studied. This study aims to investigate how different light qualities affect the agronomic characteristics, antioxidant capacity, and nutrient composition of *S. edulis*. Three monochromatic light qualities of red light, green light, and blue light were chosen for the experiment, with white light was used as the control, and three *S. edulis* strains were exposed to light. The ultimate goal of this study was to identify the optimal monochromatic light condition that promotes the growth of *S. edulis*, enhancing its antioxidant properties and nutritional value. This research will provide to theoretical basis for subsequent research on the effects of blue light intensity and photoperiod on the fruiting body of *S. edulis*.

## Materials and methods

### Strains and medium

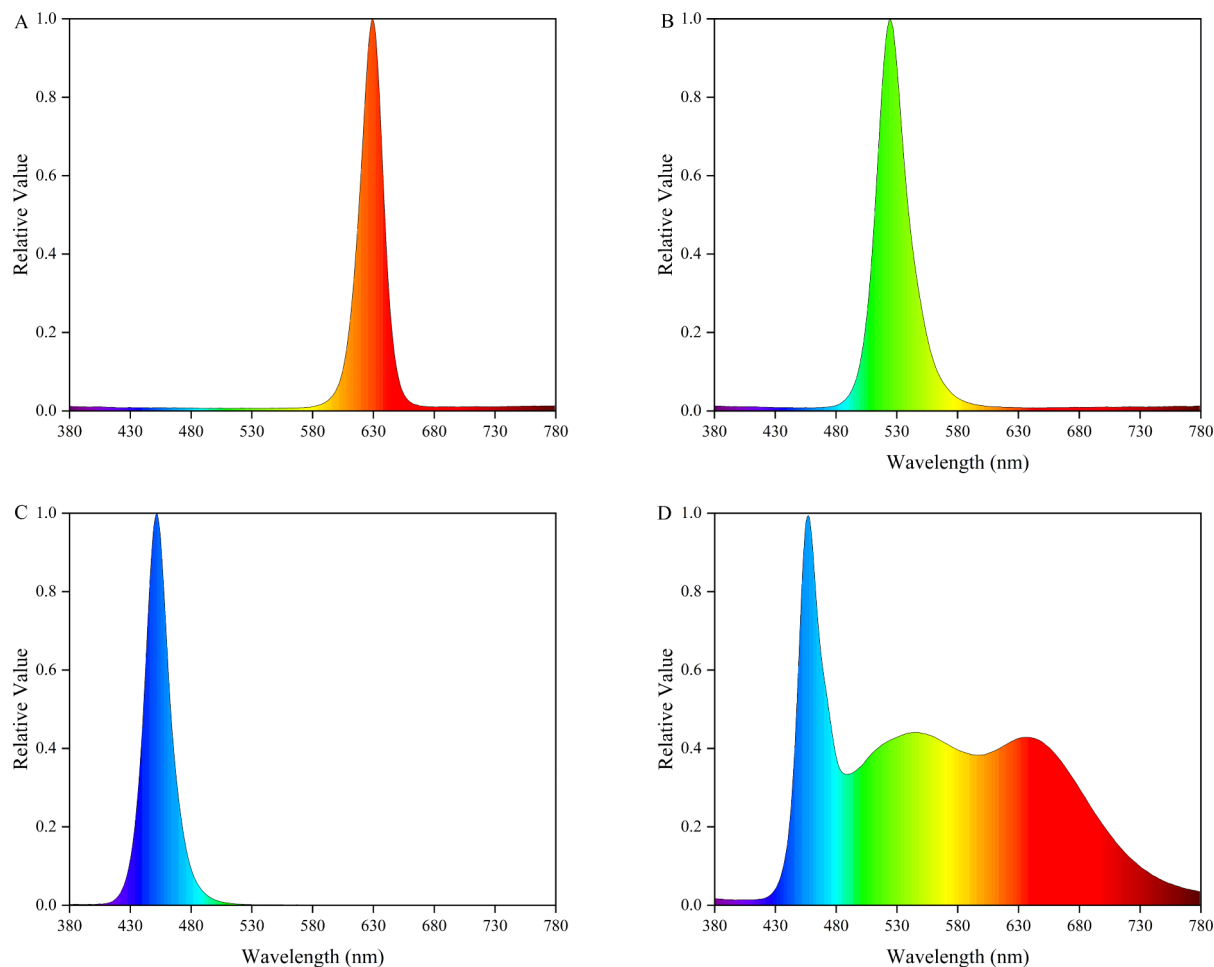
Based on previous laboratory studies, *S. edulis* was divided into 7 colors, including yellow-white, yellow, yellow-green, gray-green, yellow-brown, brown-gray and dark green<sup>34</sup>. Yellow strain H1, yellowish-brown strain H2 and brownish-gray strain H3 were selected as experimental strains. All strains were stored in the Engineering Research Center of Edible and Medicinal Fungi, Ministry of Education, Jilin Agricultural University. The strains were inoculated in potato dextrose agar (PDA) medium, prepared by mixing 200 g of potato, 20 g of glucose, and 20 g of agar in 1 L RO water. PDA medium was placed in a 25 °C incubator for constant temperature culture. The activated strains were inoculated in 1 L conical bottle of 400 mL liquid medium. The liquid culture medium consisted of 200 g of potato, 8 g of glucose, 5 g of yeast extract, 5 g of peptone, 3 g of KH<sub>2</sub>PO<sub>4</sub>, and 1.5 g of MgSO<sub>4</sub> in 1 L RO water. The liquid culture was incubated in a 25 °C shaker (120 rpm) under dark conditions for 12 days.

### Cultivation experiments

*S. edulis* cultivation place was located in the mushroom room No. 22 of the mushroom vegetable base of Jilin Agricultural University. 1 kg of cultivation material was put into polypropylene bag and autoclaved at 121 °C for 90 min. The culture material formula was oak sawdust 78%, wheat bran 20%, lime 1%, light calcium carbonate 1%, pH = 7, and water content 65%. After cooling, 15 mL of liquid strains were inoculated in a bag, placed in a culture chamber, and incubated at 25 °C in the dark for 110 days. Once the mycelium had matured, a sterile knife was used to make a cross-shaped opening on the mushroom bag. Ten mushroom bags were placed under each light treatment. The mushroom bags treated with the same light quality is placed on a mushroom shelf, and the LED light belt (Shenzhen Fangde Lighting Co., LTD.) is installed above each mushroom shelf and surrounded by a blackout cloth. After 30 days of light treatment, mature fruiting bodies were harvested, and agronomic traits were measured. In the light time of 8 h light /16 h dark, at the temperature of 17 ± 1 °C, humidity is 85–90% under the conditions of *S. edulis* management.

### Light quality design

The experiment set up four kinds of light quality treatment, respectively red light (R), green light (G), blue light (B), and white light (CK). Spectral distribution of light quality: R (peak at 629 nm; 5 W), G (peak at 525 nm; 5 W), B (peak at 451 nm; 5 W), and CK (B + R + G), the spectrum was measured in the range of 300–800 nm using the LI-180 plant spectrometer of LI-COR in the United States. Each LED lamp has 105 lamp beads, and the spectral characteristics of different light treatments are shown in Fig. 1.



**Fig. 1.** Relative spectral distribution of different LED strips. (A) red light treatment, (B) green light treatment, (C) blue light treatment, (D) white light treatment.

### Determination of agronomic traits

There was some variability in the growth state of the fruiting bodies. Therefore, in order to more accurately reflect the overall agronomic traits of each strain under each light treatment, samples of each strain under each light quality were randomly selected from 10 mushroom bags to determine 10 fruit bodies. Agronomic parameters including yield, pileus length, pileus width, pileus thickness, stalk length, stalk width, and stalk thickness were recorded. The fresh weight was measured by electronic scale, and the index of pileus and stalk was measured by vernier caliper, and each treatment was measured 10 times. After harvesting, *S. edulis* were dried by a fruit and vegetable dryer at 50 °C for the determination of nutritional content. (Sichuan Changhong Electric Co., Ltd., China).

To quantify the color of *S. edulis* pileus, reference was made to the method determination in the published literature<sup>35</sup>, and some modifications were made. To avoid the influence of different light sources on the color of *S. edulis* pileus, a unified digital camera was used to take pictures in the LED photography lightbox (Canon EOS 700D). The shooting conditions were set as follows ISO value 400, exposure time 1/50 second, aperture value f /5.6, and no flash. By using Adobe Photoshop CS6 software (Adobe Systems, SAN Jose, California, USA), L\*, a\*, and b\* values were extracted from the primary colors of *S. edulis* photos by the L\*a\*b\* model. Where the L\* value represents the lightness value, the a\* value (+ redness /– green), and the b\* value (+ yellow) /– blue). The determination was six replicates to ensure the accuracy of the results and improve the representativeness of the measurement.

### Determination of antioxidant capacity

According to Vatter's method<sup>36</sup>, the free radical scavenging rate (DPPH) was calculated. Weighed about 0.5 g fresh mushroom tissue, added 1 mL sodium acetate buffer, homogenized in an ice bath at 12,000 rpm, centrifuged at 4 °C for 10 min. Took the supernatant and placed it on ice for measurement. Took 20 μL supernatant, added 380 μL DPPH solution. Mixed thoroughly, and allowed it to react at room temperature for 20 min. Took 200 μL

to determine the absorption value of 515 nm. DPPH free radical clearance (%) = [(absorbance of blank solution - sample absorbance)/absorbance of blank solution] × 100%.

Malondialdehyde content (MDA) was slightly modified according to Spitz<sup>37</sup>, weighed about 0.5 g fresh mushroom tissue, added 1 mL phosphate buffer, homogenized at room temperature, and centrifuged at 10,000 rpm for 10 min. Mix 100 µL supernatant with 300 µL 10% trichloroacetic acid containing 0.6% thiobarbituric acid. The mixture was placed in a 92 °C water bath for 30 min, cooled and centrifuged (12000 rpm, 25 °C, 10 min). The light absorption values at 532 nm and 600 nm were measured with supernatant.

According to the determination of superoxide anion (OFR) by Jiao's method<sup>38</sup>, about 0.5 g fresh mushroom tissue was weighed, 1 mL dipotassium hydrogen phosphate and potassium dihydrogen phosphate solution were added and homogenized in an ice bath. Then centrifugation was performed, and the centrifugation condition was 12,000 rpm, 4 °C, 20 min, and the supernatant ice was taken for determination. 200 µL supernatant was added to 160 µL hydroxylamine hydrochloride solution and mixed, a water bath at 37 °C for 20 min. Then, it was mixed with 120 µL p-aminobenzenesulfonic acid solution and 120 µL of alpha-naphthylamine solution, mixed and bathed in 37 °C water for 20 min. Measured the absorption value at 530 nm.

Weighed 0.5 g of fresh fruit bodies and placed them into a centrifuge tube. Added 1 mL of extracted phosphate buffer and centrifuged the mixture at 4 °C at 12,000 rpm for 10 min. Finally, the supernatant was collected to detect the activity of superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD). Determination of SOD, POD, and CAT activity reference reagent test box (Suzhou Michy Biomedical Technology Co., Ltd., Suzhou, China, Catalog nos. M0102A, M0103A, M0105A). SOD activity was measured by assessing the reaction between O<sup>2-</sup> and WST-8, which produced the water-soluble formazan dye that absorbed at 450 nm. SOD scavenged O<sup>2-</sup>, thereby inhibiting formazan formation. A deeper yellow color in the reaction solution indicated lower SOD activity, whereas a lighter color corresponded to higher SOD activity<sup>39</sup>.

POD activity catalyzed the oxidation of guaiacol in the presence of hydrogen peroxide, producing a brownish substance. This substance exhibited maximum absorbance at 470 nm, which was used to measure POD activity<sup>40</sup>.

The determination of CAT activity was based on the ability of CAT to decompose H<sub>2</sub>O<sub>2</sub>, which has a characteristic absorption peak at 240 nm, calculated by measuring the rate of change of absorbance at 240 nm. Each strain was tested three replicates for each enzyme under each light quality<sup>41</sup>.

### Nutrient composition analysis

The dried mushroom was ground with a grinder for 1.5 min and screened with a 200-mesh sieve. The crude fiber content was determined by filter bag technology, and the total sugar content was determined by the phenol-sulfuric acid method. The crude fat content was determined using the "Determination of Fat in Food under National Standards for Food Safety" (GB 5009.6–2016). The total amino acid content was reacted with ninhydrin hydrate using α-amino<sup>42</sup>, and the amino acid content calculated by measuring the absorbance at 570 nm. The reaction of proline and hydroxyproline with ninhydrin has no absorption peak at 570 nm, so the determination results at 570 nm do not contain these two amino acids. For each strain, each nutrient component was three replicates under each light quality.

Determination of 17 free amino acid components: 17 amino acid standards, HPLC-grade acetonitrile (OCEANPAK, purity ≥ 99.9%), hydrochloric acid, n-leucine, triethylamine, n-hexane, anhydrous sodium acetate (Sinopharm Chemical Reagent Co., Ltd., Shanghai, China), phenyl isothiocyanate (sigma, purity ≥ 99.9%). Weighed about 0.1 g of *S. edulis*, added 10 ml 0.1% phenol with 6 mol/L hydrochloric acid, and ground it into pulp. Then, placed it in a 110 °C oven for hydrolysis for 24 h. Removed and cooled, took 1 mL of hydrolysate, and dried it with a nitrogen blower. Added 1 mL 0.1 M hydrochloric acid aqueous solution to dissolve, and obtained the solution to be tested. Agilent 1100 high performance liquid chromatography was used to measure amino acids, UV detector wavelength at 254 nm. The analytical column was a Amethyst C18-H (4.6 mm×250 mm, 5 µm) from Sepax Technologies, Inc. The mobile phases were: A, weighed 7.6 g of anhydrous sodium acetate, added 925 mL of water, dissolved it, and adjusted the pH to 6.5 with glacial acetic acid. Then, 70 mL of acetonitrile was added and mixed thoroughly. Filtered with a 0.45 µm membrane. B, 80% acetonitrile aqueous solution. The elution condition was shown in Table 1. The flow rate was 1 mL/min at 40 °C.

Time(min)	Phase A(%)	Phase A(%)
0	100	0
2	100	0
15	90	10
25	70	30
33	55	45
33.1	0	100
38	0	100
38.1	100	0
45	100	0

**Table 1.** Mobile phase gradient employed for the detect amino acids.



### Statistical analysis

The experimental data were statistically analyzed and plotted using Microsoft Excel 2022, SPSS 24.0, and Origin 2022 software. All data were analyzed by one-way analysis of variance (ANOVA). Duncan's test method was used for multiple comparisons and difference significance analysis. Mean and standard errors were used to draw histograms.

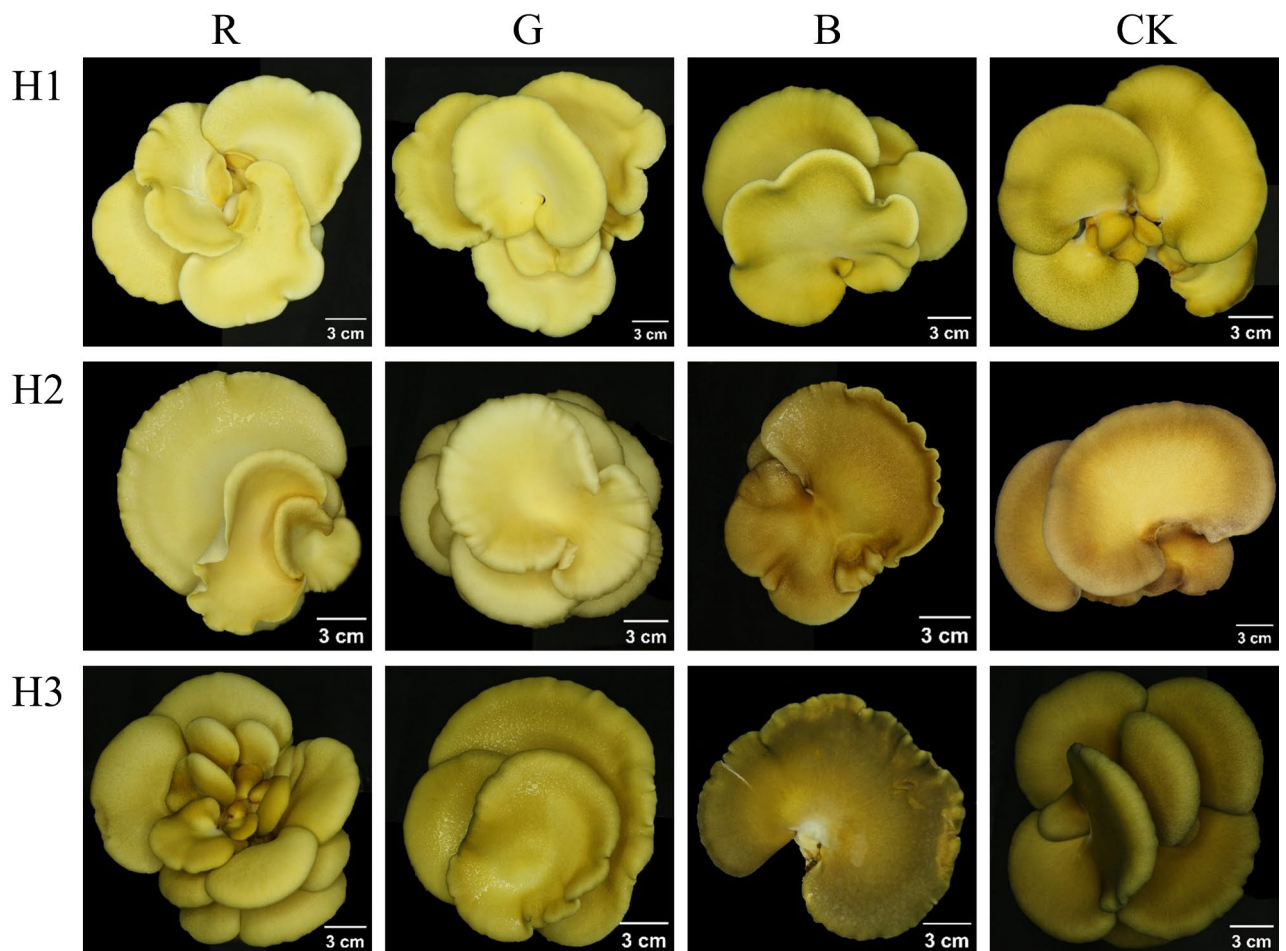
### Results

#### Effect of different light qualities on the color of the pileus of *S. Edulis*

The influence of varying light qualities on the pileus color of *S. edulis* was depicted in Fig. 2, illustrating a noticeable color variation across three strains. The pileus appeared lighter under red and green light, whereas blue light and CK treatment conditions resulted in a darker hue. The color difference results were shown in Table 2. The color difference values of *S. edulis* in different light quality are  $L^*$  (36.67–84.33),  $a^*$  (7.83–7.33) and  $b^*$  (35.67–64.33), respectively. Notably, in the dimension of  $L^*$  value, the lightness value of three *S. edulis* strains was higher under red light and green light, and the difference was significant, which indicated that red light and green light promoted the color brightness of *S. edulis* pileus, and red light was the most significant effect. In the H1 and H3 strains, there was no significant difference between the  $L^*$  value of CK and blue light, and the  $L^*$  value of blue light in H2 was slightly lower than that of CK. On the  $a^*$  value,  $a^*$  of the H2 strain was positive under CK and blue light, and the light quality of other strains was negative. The  $b^*$  values were all positive, reflecting that the pileus of three *S. edulis* strains was yellow, and the  $b^*$  value of H1 was the highest. Through the analysis of the color parameters of the *S. edulis* pileus, compared with red light and green light, blue light deepened the color of *S. edulis* pileus, which was consistent with the appearance of *S. edulis*.

#### Effect of different light qualities on growth characteristics of *S. Edulis*

The agronomic properties of *S. edulis* under different light treatments were shown in Table 3. *S. edulis* showed different growth responses to different light treatments. Strain H3 yielded the highest, while strain H2 showed



**Fig. 2.** Comparison of the coloration of fruiting bodies of *S. edulis* under different light illumination. Light quality treatment from left to right (R-red light, G-green light, B-blue light, CK-white light), the strains were H1, H2, and H3 from top to bottom.

		L*	a*	b*
H1	R	84.33 ± 0.94a	-7.33 ± 0.75c	50.50 ± 2.75c
	G	75.50 ± 2.5b	-5.50 ± 0.76b	59.00 ± 1.73b
	B	70.00 ± 1.29c	-5.83 ± 1.07b	61.17 ± 1.95b
	CK	71.67 ± 2.13c	-2.83 ± 1.07a	64.33 ± 2.29a
H2	R	80.00 ± 1.41a	-5.83 ± 0.37b	46.83 ± 1.57a
	G	74.00 ± 1.15b	-6.83 ± 0.69b	41.50 ± 3.35b
	B	48.33 ± 1.6d	6.17 ± 1.34a	47.83 ± 1.34a
	CK	50.50 ± 2.06c	7.83 ± 2.19a	43.5 ± 4.92ab
H3	R	70.17 ± 2.67a	-6.00 ± 0.58a	53.50 ± 2.87a
	G	51.67 ± 1.8b	-3.17 ± 1.21b	51.33 ± 1.11a
	B	36.67 ± 1.37c	-2.33 ± 0.94ab	35.67 ± 2.69b
	CK	37.33 ± 1.7c	-1.83 ± 0.69a	36.83 ± 1.34b

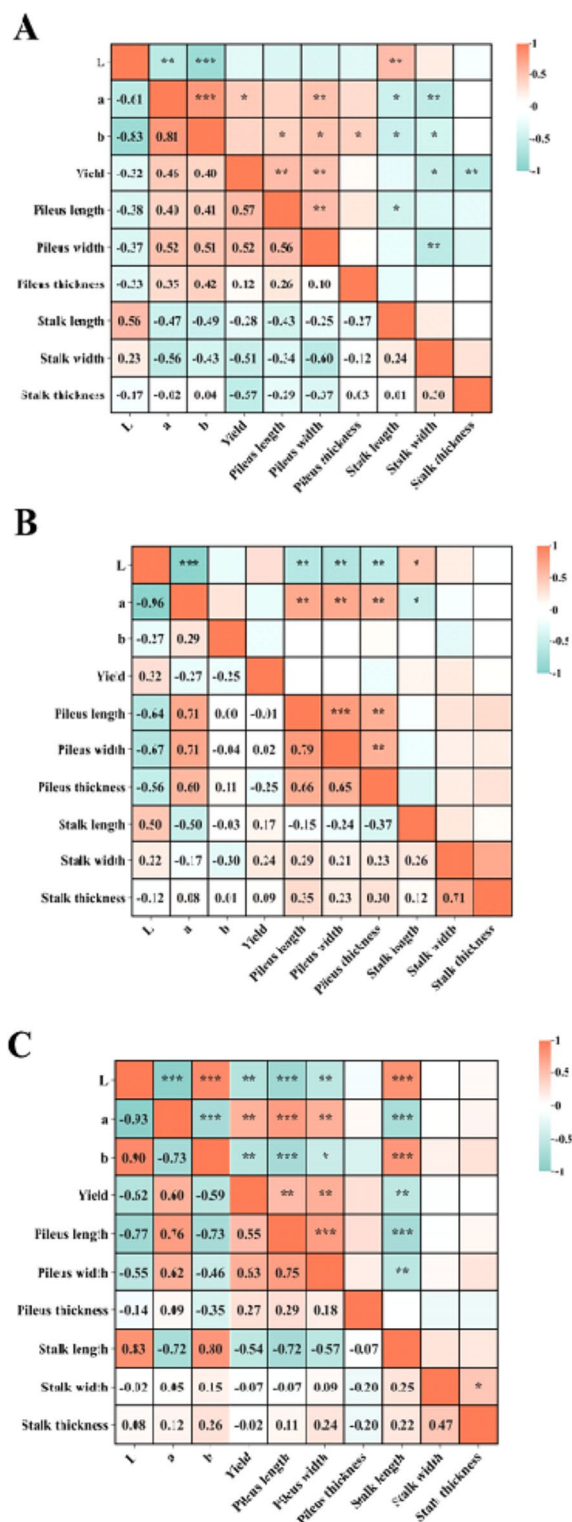
**Table 2.** Color difference value of *S. Edulis pileus* under different light quality. Note: values are means ± SD of six replicate experiments. Different letters indicate significant differences ( $p < 0.05$ ) between treatment groups according to Duncan's test. Different letters indicate that a strain is significant between different light quality treatments.

		Yield	Pileus length	Pileus width	Pileus thickness	Stalk length	Stalk width	Stalk thickness
		(g)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)
H1	R	124.5 ± 20.71b	90.79 ± 5.79b	50.25 ± 4.8c	16.41 ± 2.34bc	35.93 ± 5.72a	18.56 ± 1.14a	14.24 ± 1.45a
	G	127.13 ± 25.16b	85.79 ± 7.89b	54.08 ± 3.5bc	15.64 ± 2.38c	33.46 ± 5.71ab	18.29 ± 1.58a	15.63 ± 1.48a
	B	158.18 ± 38.17a	102.72 ± 9.25a	57.33 ± 6.86b	19.63 ± 2.2a	26.5 ± 3.03c	18.56 ± 1.86a	15.45 ± 2.27a
	CK	160.07 ± 22.2a	111.1 ± 12.93a	66.09 ± 5.48a	18.6 ± 3.84ab	29.02 ± 5.54bc	16.29 ± 1.42b	15.18 ± 1.98a
H2	R	87.17 ± 15.51a	76.35 ± 11.53b	54.98 ± 10.21b	14.33 ± 1.45b	26.4 ± 6.34a	12.77 ± 2.42a	11.53 ± 2.51a
	G	109.37 ± 24.84a	83.31 ± 8.65b	55.61 ± 3.77b	15.34 ± 1.48ab	23.24 ± 3.96ab	14.36 ± 3.27a	12.23 ± 2.96a
	B	89.73 ± 27.81a	92.86 ± 4.01a	61.81 ± 5.54ab	16.94 ± 2.27ab	20.77 ± 3.66b	14.08 ± 1.91a	12.3 ± 3.13a
	CK	93.57 ± 28.17a	98.43 ± 12.32a	64.39 ± 7.44a	17.79 ± 1.98a	19.88 ± 2.93b	13.51 ± 0.9a	11.31 ± 1.15a
H3	R	235.7 ± 40.16a	87.09 ± 5.72c	55.87 ± 10.22b	17.63 ± 8.21b	36.86 ± 2.36a	17.19 ± 2.12a	16.00 ± 1.65a
	G	240.38 ± 32.1a	97.99 ± 9.21b	58.29 ± 6.95b	16.33 ± 2.53b	34.56 ± 2.46b	18.68 ± 1.02a	17.77 ± 1.77a
	B	249.5 ± 43.31a	113.83 ± 11.85a	62.29 ± 6.76ab	22.5 ± 2.28a	27.89 ± 2.56c	17.24 ± 1.28a	16.32 ± 2.53a
	CK	254.35 ± 38.59a	117.82 ± 7.91a	69.66 ± 6.83a	19.34 ± 2.07ab	26.63 ± 1.89c	17.06 ± 2.02a	16.24 ± 3.21a

**Table 3.** Comparison of agronomic traits of *S. edulis* under different light quality. Note: values are means ± SD of ten replicate experiments. Different letters indicate significant differences ( $p < 0.05$ ) between treatment groups according to Duncan's test. Different letters indicate that a strain is significant between different light quality treatments.

the lowest yield. There was no significant difference in yield between blue light and CK treatment in H1 strain. The yield decreased under red and green light in H1 strain. There was no significant difference in yield between H2 and H3 strains under different light quality. Compared to CK, there was no significant difference in pileus length under blue light, while red light and green light reduced pileus length. Similarly, blue light had little effect on pileus width, while either green or red light caused a reduction in pileus width. In H1 and H3 strains, compared with red and green light, the pileus thickness under blue light was the largest, and the difference was significant. Under the red light treatment, the stalk length was the longest. Compared with CK, the stalk width of H1 increased significantly under the three monochromatic lights. There was no significant difference in stalk width between H2 and H3 under each light treatment. There was no significant difference in stalk thickness under different light treatments. In conclusion, after the blue light treatment, the appearance of *S. edulis* is most in line with the higher economic value of the market.

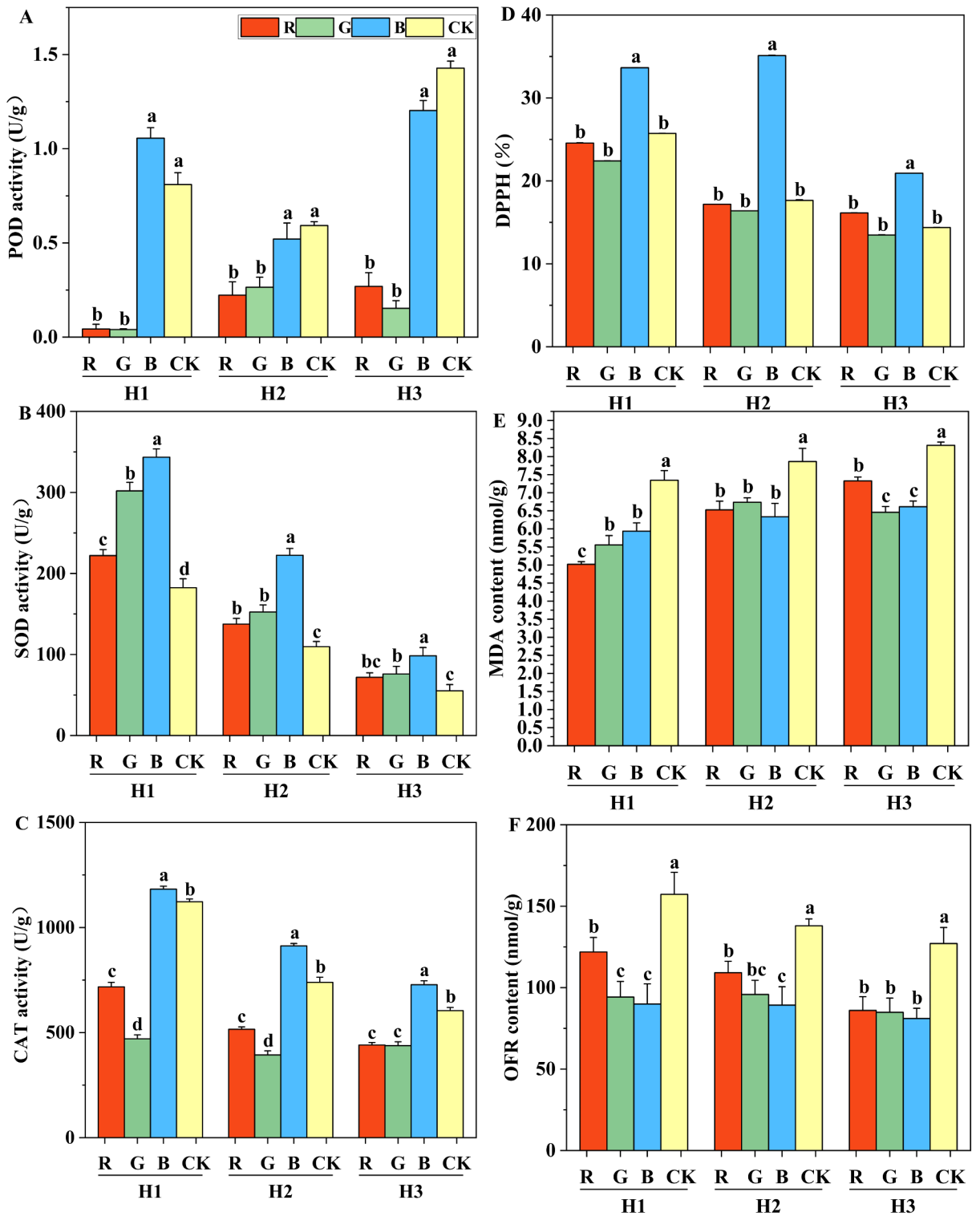
To further explore the effects of different light quality on the agronomic traits of *S. edulis*, the correlation among agronomic and color traits under different light qualities was studied (Fig. 3). The L\* value was positively correlated with stalk length, and the correlation coefficients were as follows: H3 (0.83) > H2 (0.56) > H1 (0.5). The L\* value was negatively correlated with the length and width of the pileus, indicating that the size of the pileus decreased with the increase of the brightness value. In H1 and H2 strains, a\* value was positively correlated with pileus length, pileus width, and pileus thickness.



**Fig. 3.** Correlation of agronomic traits of *S. edulis* under different light quality. (A) represents the H1 strain, (B) represents the H2 strain, (C) represents the H3 strain, correlations were significance. \*\*\*P < 0.001, \*\*P < 0.01, \*P < 0.05).

### Effect of different light qualities on antioxidant enzyme activity, MDA, DPPH and OFR of *S. Edulis*

The antioxidant capacity of *S. edulis* was significantly influenced by light quality (Fig. 4). POD activity in *S. edulis* was higher under blue light and CK treatment. The POD activity in red and green light was significantly different from that in the CK treatment. Red and green light significantly reduced POD activity, while there



**Fig. 4.** Antioxidant capacity of *S. edulis* treated with different light quality. (A) peroxidase (POD) activity, (B) superoxide dismutase (SOD) activity, (C) catalase (CAT) activity, (D) radical scavenging capacity (DPPH), (E) Malondialdehyde (MDA) content, (F) superoxide anion (OFR) content. Different letters indicate significant differences ( $p < 0.05$ ) between treatment groups according to Duncan's test. Different letters indicate that a strain is significant between different light quality treatments.



was no significant difference between blue light and CK treatment. Compared with CK treatment, the use of monochromatic light increased the SOD activity in general, and the SOD activity under blue light was the highest (Fig. 4B). The CAT activity under blue light was the highest. The CAT activity under red and green light was significantly reduced. Under different light quality treatments, blue light treatment had the highest DPPH free radical clearance rate (Fig. 4D). Compared with CK treatment, blue light treatment increased the free radical clearance rate of H1, H2 and H3 strains by 30.78%, 98.98% and 45.55%, respectively. There was no significant difference in free clearance between red light and green light treatment. Compared with the CK treatment, the contents of MDA and OFR were significantly reduced under the three monochromatic light qualities (Fig. 4E and F). In summary, compared with red light and green light, blue light treatment improved the activity of antioxidant enzymes in the fruit bodies of *S. edulis*, monochromatic light was beneficial in reducing the degree of membrane lipid peroxidation and remove a large number of superoxide anion free radicals.

### Effect of different light qualities on the content of various nutrients in *S. Edulis*

The organic nutrients of *S. edulis* were significantly affected by different light treatments Table 4. Under the three light quality treatments, the crude fiber content in green light is the highest. Compared to CK, red and green light increased crude fiber content, while blue light either reduces crude fiber content in H1 strain and H2 strain.

The crude fiber content of H1 strain was significantly different among different light quality treatments. In the H2 strain, there was no significant difference in crude fiber content between CK and blue light. In the H3 strain, there was no significant difference in crude fiber content between CK and red light. Compared with CK, red light significantly increased total sugar content by 60% and 12% in H1 and H2 strains, respectively. The crude fat content of the *S. edulis* was between 0.59 and 1.82 g/100 g. Green light produced the highest reduction, also red light reduced crude fat compared to CK, while blue light did or did not depending on the strain. Compared with CK, there were significant differences in total free amino acid contents under red and blue light treatment, but no significant differences under green light. Compared with CK, total amino acid contents of H1, H2 and H3 under blue light treatment were increased by 6%, 27% and 19%, respectively. In contrast, red light reduced the total amino acid content of H1, H2 and H3 by 7%, 16% and 21%, respectively.

In this study, the composition of free amino acids of *S. edulis* under different light quality was further analyzed. The content of 17 amino acids, including 6 essential amino acids and 9 non-essential amino acids, in the fruit body of *S. edulis* were detected by analysis. The concentration of methionine and cysteine was low, so it was not analyzed. Glu is the most abundant amino acid in *S. edulis*, followed by Asp. In the CK treatment, Glu accounts for 21%, 20% and 20% of the total free acid content of H1, H2 and H3, respectively.

In strain H1, amino acid content changes under different light qualities were shown in Table 5. Blue light had the most significant effect on amino acid content, followed by red light. Blue light significantly increased the content of 15 amino acids. Compared with CK, His content was 8.3 times higher under blue light. There was no significant difference in the content of His between CK and green light. The contents of Ala, Leu, Phe and Lys were not significantly affected under red and green light irradiation.

In H2 and H3 strains, the amino acid content changes under different light quality, as shown in Tables 6 and 7. The content of 15 amino acids under blue light was the highest. Compared with CK, the content of Glu, Ser, Gly, Arg, Ala, Pro, Tyr, Val, Ile, Leu, Phe, Lys and Thr 13 amino acids were decreased under red light, and the content was the lowest. Under green light, Asp and His contents were the lowest.

## Discussion

*S. edulis* is distinguished by its considerable nutritional value, ranking second only to *Hericium erinaceus*. Its cultivation has now started to be systematically developed. According to Traditional Chinese Medicine, *S.*

		Crude fiber	Total sugar	Crude fat	Total amino acids
		(g/100 g)	(g/100 g)	(g/100 g)	(g/100 g)
H1	R	31.46 ± 0.31b	38.61 ± 0.34a	1.46 ± 0.03b	1.5 ± 0.04c
	G	34.54 ± 0.29a	33.86 ± 1.96b	0.97 ± 0.03c	1.57 ± 0.05bc
	B	27.79 ± 0.29d	29.95 ± 0.61c	1.41 ± 0.01b	1.72 ± 0.01a
	CK	29.81 ± 0.17c	24.14 ± 0.52d	1.78 ± 0.02a	1.62 ± 0.04b
H2	R	28.38 ± 0.36b	31.42 ± 0.12a	1.58 ± 0.02b	0.93 ± 0.01c
	G	30.63 ± 0.24a	29.16 ± 1.11b	1.13 ± 0.05c	1.11 ± 0.02b
	B	26.14 ± 0.28c	26.84 ± 0.89d	1.81 ± 0.03a	1.41 ± 0.04a
	CK	26.61 ± 0.13c	28.08 ± 0.46bc	1.82 ± 0.02a	1.11 ± 0.03b
H3	R	32.58 ± 0.21ab	28.6 ± 1.49a	1.22 ± 0.02c	1.5 ± 0.03c
	G	32.84 ± 0.11a	28.75 ± 0.95a	0.59 ± 0.01d	1.94 ± 0.07b
	B	28.25 ± 0.18c	26.77 ± 0.27a	1.33 ± 0.02b	2.27 ± 0.04a
	CK	32.36 ± 0.25b	27.44 ± 0.16a	1.64 ± 0.01a	1.91 ± 0.03b

**Table 4.** Content of organic compounds in *S. edulis* treated with different light quality. Values are means ± SD of three replicate experiments. Different letters indicate significant differences ( $p < 0.05$ ) between treatment groups according to Duncan's test. Different letters indicate that a strain is significant between different light quality treatments.

FAA (g/100 g DW)	H1			
	R	G	B	CK
Asp	1.57 ± 0.025b	0.91 ± 0.016c	1.63 ± 0.012a	0.8 ± 0.011d
Glu	2.32 ± 0.038b	2.42 ± 0.022a	2.43 ± 0.05a	1.8 ± 0.03c
Ser	0.83 ± 0.014b	0.73 ± 0.006c	0.86 ± 0.007a	0.65 ± 0.011d
Gly	0.52 ± 0.009b	0.5 ± 0.009c	0.56 ± 0.007a	0.48 ± 0.01c
His	0.24 ± 0.006b	0.03 ± 0.001c	0.25 ± 0a	0.03 ± 0.001c
Arg	0.61 ± 0.011b	0.55 ± 0.01c	0.66 ± 0.006a	0.5 ± 0.011d
Ala	0.66 ± 0.01b	0.66 ± 0.012b	0.69 ± 0.008a	0.59 ± 0.011c
Pro	0.51 ± 0.008b	0.48 ± 0.01c	0.54 ± 0.008a	0.46 ± 0.01d
Tyr	0.35 ± 0.006b	0.33 ± 0.005c	0.38 ± 0.003a	0.31 ± 0.006d
Val	0.45 ± 0.009b	0.48 ± 0.006a	0.5 ± 0.004a	0.41 ± 0.005c
Ile	0.45 ± 0.009b	0.47 ± 0.003a	0.47 ± 0.003a	0.42 ± 0.004c
Leu	0.78 ± 0.011b	0.77 ± 0.012b	0.82 ± 0.009a	0.69 ± 0.014c
Phe	0.46 ± 0.007b	0.45 ± 0.007b	0.49 ± 0.006a	0.41 ± 0.006c
Lys	0.72 ± 0.012b	0.45 ± 0.007b	0.75 ± 0.005a	0.57 ± 0.012c
Thr	0.64 ± 0.01b	0.61 ± 0.009c	0.69 ± 0.007a	0.52 ± 0.009d

**Table 5.** Effect of different light quality on free amino acids of H1 strain. Values are means ± SD of three replicate experiments. Different letters indicate significant differences between treatments for each FAA ( $p < 0.05$ ) according to Duncan's test.

FAA (g/100 g DW)	H2			
	R	G	B	CK
Asp	1.22 ± 0.008b	0.94 ± 0.003c	1.62 ± 0.016a	1.25 ± 0.016b
Glu	1.64 ± 0.008d	2.01 ± 0.01c	2.27 ± 0.018a	2.06 ± 0.024b
Ser	0.62 ± 0.003d	0.68 ± 0.005c	0.82 ± 0.007a	0.79 ± 0.009b
Gly	0.47 ± 0.001d	0.49 ± 0.001c	0.62 ± 0.002a	0.54 ± 0.007b
His	0.19 ± 0.001b	0.04 ± 0.001d	0.3 ± 0.002a	0.18 ± 0.003c
Arg	0.53 ± 0.002d	0.59 ± 0.004c	0.71 ± 0.005a	0.63 ± 0.006b
Ala	0.58 ± 0.002d	0.69 ± 0.005b	0.76 ± 0.006a	0.63 ± 0.008c
Pro	0.44 ± 0.001d	0.47 ± 0.002c	0.59 ± 0.008a	0.52 ± 0.006b
Tyr	0.29 ± 0b	0.31 ± 0.003b	0.46 ± 0.063a	0.37 ± 0.031b
Val	0.4 ± 0.001d	0.51 ± 0.005b	0.54 ± 0.006a	0.46 ± 0.006c
Ile	0.41 ± 0.004d	0.47 ± 0.001b	0.55 ± 0.006a	0.46 ± 0.004c
Leu	0.67 ± 0.002c	0.77 ± 0.003b	0.88 ± 0.008a	0.76 ± 0.01b
Phe	0.4 ± 0.002c	0.45 ± 0.003b	0.52 ± 0.005a	0.45 ± 0.005b
Lys	0.55 ± 0.004c	0.67 ± 0.017b	0.72 ± 0.008a	0.65 ± 0.009b
Thr	0.53 ± 0.003c	0.62 ± 0.003b	0.71 ± 0.008a	0.61 ± 0.007b

**Table 6.** Effect of different light quality on free amino acids of H2 strain. Values are means ± SD of three replicate experiments. Different letters indicate significant differences between treatments for each FAA ( $p \leq 0.05$ ) according to Duncan's test.

*edulis* possesses properties that promote blood circulation, as well as soothe meridians and alleviate wind<sup>43</sup>. In this study, the light quality experiment was carried out with three representative colors of *S. edulis*. The results indicated that blue light played a pivotal role in the development of the pileus color of *S. edulis*, effectively inducing its color formation. This suggests the presence of a light-responsive substance within *S. edulis*, warranting further investigation to identify this specific compound. This phenomenon aligns with findings from studies on *Morchella sextelata*<sup>44</sup>, and *P. eryngii*<sup>45</sup>, which propose that blue light exerts similar regulatory effects across various edible fungi species. The yields of three *S. edulis* strains differed, with H3 producing the highest yield. Between the H2 and H3 strains, yield did not significantly vary under three distinct monochromatic light conditions. This could be attributed to the fact that, although individual fungi exposed to red and green light weighed less than those exposed to blue light, the overall yield under red and green light matched that under blue light, owing to the higher number of primordia and fruiting bodies.

Light quality not only influences the coloration but also the morphology of *S. edulis*. Specifically, blue light facilitated the regulation of the pileus length and morphology in *S. edulis*, aligning with findings from Wang Huan's research, which suggests blue light might enhance the expansion of the fungus pileus by up regulating

FAA (g/100 g DW)	H3			
	R	G	B	CK
Asp	1.3 ± 0.023c	1.05 ± 0.018d	1.73 ± 0.028a	1.61 ± 0.012b
Glu	2.1 ± 0.034d	2.77 ± 0.042b	2.85 ± 0.022a	2.43 ± 0.017c
Ser	0.7 ± 0.009d	0.79 ± 0.008c	0.94 ± 0.013a	0.86 ± 0.007b
Gly	0.52 ± 0.006d	0.58 ± 0.01c	0.72 ± 0.003a	0.66 ± 0.006b
His	0.25 ± 0.004b	0.04 ± 0.001c	0.35 ± 0.003a	0.25 ± 0.005b
Arg	0.65 ± 0.01d	0.74 ± 0.012c	0.96 ± 0.013a	0.82 ± 0.011b
Ala	0.61 ± 0.008c	0.78 ± 0.011b	0.85 ± 0.007a	0.77 ± 0.005b
Pro	0.49 ± 0.004d	0.55 ± 0.01c	0.69 ± 0.003a	0.64 ± 0.005b
Tyr	0.3 ± 0.002d	0.36 ± 0.005c	0.43 ± 0.003a	0.38 ± 0.004b
Val	0.43 ± 0.006c	0.55 ± 0.035a	0.56 ± 0.035a	0.5 ± 0.004b
Ile	0.44 ± 0.438d	0.54 ± 0.005b	0.59 ± 0.589a	0.51 ± 0.515c
Leu	0.71 ± 0.01c	0.88 ± 0.011b	0.99 ± 0.01a	0.9 ± 0.01b
Phe	0.41 ± 0.006c	0.51 ± 0.008b	0.57 ± 0.005a	0.51 ± 0.005b
Lys	0.65 ± 0.011d	0.87 ± 0.007b	0.95 ± 0.021a	0.8 ± 0.006c
Thr	0.56 ± 0.009c	0.7 ± 0.011b	0.79 ± 0.007a	0.72 ± 0.013b

**Table 7.** Effect of different light quality on free amino acids of H3 strain. Values are means ± SD of three replicate experiments. Different letters indicate significant differences between treatments for each FAA ( $p < 0.05$ ) according to Duncan's test.

genes related to the synthesis of growth regulatory substances<sup>46</sup>. Edible fungi, being extensively cultivated worldwide with high yields throughout the year, demonstrate a critical sensitivity to light quality, which is pivotal in their production. This study reveals that blue light is an effective way to improve the market value of *S. edulis*, which may be related to blue light receptors. Moreover, different light quality has a great influence on plant agronomic traits<sup>47</sup>. Red light can significantly promote the growth of the stalk length of *S. edulis*, potentially due to the wavelength of red light's ability to penetrate deeply into cells and influence stalk cell elongation<sup>48</sup>. The correlation analyses revealed a positive relationship between the L\* value and stalk length, while the a\* value was associated with three characteristics of the pileus. This underscores the significant connection between agronomic traits and light quality, with variations among strains indicating diverse light perception capabilities across different edible fungi. The findings of this study suggest that the morphology of *S. edulis* fruit bodies under blue light aligns with market preferences, avoids interference from other wavelengths, reduces energy consumption, and lowers production costs.

Edible mushrooms are a delicious and economical source of antioxidants in the diet, and in recent years, people have begun to seek functional foods and nutritional supplements with antioxidant properties<sup>49</sup>. This study discovered a distinct specificity in the antioxidant system under varying light qualities. Notably, blue light treatment significantly improved the activities of POD, SOD and CAT in *S. edulis*, compared with red light and green light. These findings align with existing literature that underscores the role of blue light in bolstering the activity of antioxidant enzymes in plants<sup>50</sup>. Furthermore, blue light may stimulate the expression and activation of these enzymes through the activation of specific photoreceptive receptors or signal transduction pathways, thereby augmenting cellular capacity to scavenge reactive oxygen species<sup>51</sup>. Notably, under monochromatic light treatments, MDA content was reduced, particularly with blue and green light, suggesting these treatments effectively shield cell membranes from oxidative harm. DPPH is a stable free radical, and the DPPH scavenging efficiency of plant antioxidant substances can reflect the strength of its antioxidant capacity<sup>52</sup>. *S. edulis* exhibited the highest DPPH free radical scavenging rate under blue light. The blue light was observed to reduce the content of OFR. These findings indicate that the antioxidant molecules in *S. edulis* are significantly influenced by specific light qualities, with blue light potentially enhancing the *S. edulis* overall antioxidant capacity. This enhancement is attributed not only to the activation of the antioxidant enzyme system but also to the increase in non-enzymatic antioxidant components<sup>53</sup>, making blue light an optimal choice for boosting the antioxidant properties of *S. edulis*.

The light quality had an impact on crude fiber content, and studies have shown that the proportion of red light in LED regulated the crude fiber content in lettuce<sup>54</sup>. Consequently, this study further investigated the impact of light quality on the crude fiber content in *S. edulis*. It was observed that green light significantly enhances the crude fiber content of *S. edulis*, suggesting that its metabolic pathways and physiological responses may be particularly responsive to certain wavelengths. This implies that specific wavelengths could modulate metabolic activities via mechanisms yet to be elucidated.

Notably, the crude fiber content in *S. edulis* was all above 20 g/100 g. Food containing at least 6 g of fiber in 100 g could be considered as fiber-rich food<sup>55</sup>. Consequently, *S. edulis* examined in this study qualifies as a high fiber food. Exposure to red light was found to significantly elevate the total sugar content in H1 and H2 strains, indicating that light might influence intracellular signaling molecules responsible for the synthesis of sugars and other metabolites<sup>56</sup>. However, the total sugar content in the H3 strain remained unaffected by light quality, hinting at the possibility of genetic and physiological variances across strains. These disparities could be attributed

to differences in intracellular photoreceptors, cell wall compositions, and metabolic pathway specificity<sup>57</sup>. As a nutrient rich food source, edible fungi offer vitamin D, minerals, dietary fiber and protein, earning the title of “superfood” from both the World Health Organization and the Food and Agriculture Organization of the United Nations<sup>58</sup>. This study found that the crude fat content in *S. edulis* ranged between 0.59 and 1.82 g/100 g, with green light significantly diminishing the crude fat content. Typically, the crude fat content in dried edible mushrooms varies between 2 and 9%. For instance, *P. ostreatus* exhibits a crude fat range from 0.2 to 8 g per 100 g of dried mushrooms<sup>59</sup>. Despite varying light conditions, the crude fat content in the H1, H2, and H3 strains of *S. edulis* remained low, positioning it as an ideal component of a health conscious diet, particularly for individuals seeking low fat options<sup>60</sup>.

Amino acids, crucial compounds influenced by the light environment, were significantly affected in this study<sup>61</sup>. Compared with CK, distinct differences in the content of total free amino acids under various light qualities were observed, with an increase under blue light treatment. This result might be attributed to blue light’s specific regulatory influence on the metabolic pathways of the strain, enhancing amino acid synthesis, an observation that aligns with findings on the impact of light on amino acid content in plants<sup>62</sup>. The response to red light varied among *S. edulis* strains: it positively affected 13 amino acids in H1, whereas it reduced the same in H2 and H3 strains, indicating strain specific amino acid metabolism. Glu and Asp are the two most abundant amino acids in the *S. edulis*, and are known for their unique umami flavor, with Glu being particularly noted for its strong umami taste and high nutritional value<sup>63</sup>. A thorough analysis of amino acid composition provides deeper insight into how light quality influences the synthesis and accumulation of amino acids in *S. edulis*. These insights underscore the potential of utilizing specific light conditions to enhance the nutritional profile of *S. edulis* in cultivation, offering a novel approach to its cultivation and nutritional enhancement.

## Conclusion

In summary, this study demonstrated for the first time that blue light possesses a regulatory effect on the color of *S. edulis*, introducing a novel perspective for selecting light quality in its production. The findings unequivocally establish blue light as the optimal choice for *S. edulis* cultivation, underscoring the necessity for further studies on factors such as blue light intensity in the later stage. Employing blue light in place of white light not only enhances the color depth and increases the size of the *S. edulis* pileus but also boosts its antioxidant capabilities. While green and red lights can also reduce MDA content and OFR content, blue light uniquely fosters the accumulation of total free amino acids, aligning with market demands. This research fills a critical knowledge gap regarding the impact of light quality on the agronomic traits and quality of *S. edulis*, laying the groundwork for the production of high quality *S. edulis* based on scientific evidence.

## Data availability

All data used for this study are contained in this article.

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Tian Tian: Writing – original draft, Writing – review & editing. Huiyue Hu: Data curation. YongSheng Ma: Formal analysis. JiaWen Qin: Software. Changtian Li: Conceptualization, Supervision, Writing – review & editing. Yu Li: Conceptualization.

## Declarations

### Competing interests

The authors declare no competing interests.

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