Mycoscience 36: 227–233, 1995

Effect of light on the formation of atypical fruiting structures in *Ganoderma lucidum*

Geon Sik Seo, Hiroshi Otani and Keisuke Kohmoto

Faculty of Agriculture, Tottori University, Tottori, Tottori 680, Japan

Accepted for publication 10 May 1995

Ganoderma lucidum **develops atypical fruiting structures (AFSs) with non-basidiocarpous basidiospores during the incubation under light on nutrient agar media. To examine the light quality effective in inducing AFSs, 17 isolates of *G. lucidum* were incubated on agar media under light from different colored fluorescent lamps. Of the 17 isolates, 13 isolates produced AFSs and basidiospores under fluorescent lamps. Nine isolates formed AFSs in a broad light region from P-B (pure blue) to P-R (pure red) lamps. The remaining 4 isolates produced AFSs under different colored fluorescent lamps. No isolates formed AFSs in the dark or under BLB (black light blue) illumination. The mycelial growth was inhibited by light illumination, especially BLB light. Although the AFSs were induced at a very low light intensity such as 0.5 μmol $m^{-2}s^{-1}$, the optimum light intensity for the AFS formation varied depending on the kind of fluorescent lamp and the isolate. The AFS formation in *G. lucidum* isolates was also tested under monochromatic light produced by the combination of interference filters and colored glass filters. *G. lucidum* isolates were separable into various types in the responses of AFS formation to monochromatic light, indicating that *G. lucidum* is heterogeneous in its photo-response with regard to AFS formation.**

Key Words——atypical fruiting structure; colored fluorescent lamp; *Ganoderma lucidum*; monochromatic light.

A stalked mushroom with porous hymenium, *Ganoderma lucidum* (Fr.) Karst. causes white rot of wood, decomposing lignin as well as cellulose and related polysaccharides, as the fungus decays hard wood such as oak, maple sycamore and ash (Hepting, 1971; Blanchette, 1984). The fruit bodies produced on the infested wood have long been used as a traditional medicine in China, Japan and Korea.

Several reports have dealt with morphological and cultural characteristics of mycelium of *G. lucidum*, aiming at its classification. Some have reported that *G. lucidum* forms aberrant fruit bodies in in vitro culture (Bose, 1929; Banerjee and Sarkar, 1956; Adaskaveg and Gilbertson, 1986). Adaskaveg and Gilbertson (1986) found that this fungus formed occasional basidiospores on red laccate coral-like fruit bodies. Shin and Seo (1988) also reported that *G. lucidum* produces atypical fruiting structures (AFSs) on nutrient agar media without basidiocarp formation. Due to the lack of detailed descriptions of fruit bodies by Adaskaveg and Gilbertson, it was almost impossible to determine whether their fruit bodies corresponded to our AFSs, but circumstantial evidence suggests that they were probably the same. The AFSs were induced by light illumination and ventilation (Shin and Seo, 1988; Seo et al., 1995). Although the mycelial growth was inhibited by light illumination and ventilation, the AFSs appeared on the white mycelial colony, and basidia with basidiospores were produced on the AFSs.

The effects of light on morphogenesis and induction of fruit body primordium in many basidiomycetes have been demonstrated by many researchers (Kitamoto et al., 1968; Perkins and Gordon, 1969; Morimoto and Oda, 1973; Schwalb and Shanler, 1974; Eger-Hummel, 1980; Manachère, 1980; Raudaskoski and Viitanen, 1982; Yli-Mattila, 1985). However, the photomorphogenesis of *G. lucidum* has not been examined.

The purpose of the present study was to determine the light quality effective for AFS induction in *G. lucidum*, using colored fluorescent lamps and monochromatic light.

Materials and Methods

Isolates The dikaryon isolates of *G. lucidum* used in this study are listed in Table 1. Nine isolates were obtained from the context tissue of wild-type fruit bodies collected in Korea (seven isolates) and in Papua New Guinea (two isolates). Two isolates were obtained from artificial log-cultivation of the mushroom in Korea. Other isolates were presented by Agriculture Science Institute, Korea (two isolates obtained from wild-type fruit bodies in Korea and Japan, respectively), Tottori Mycological Institute, Japan (two isolates) and Mushroom Research Institute, University of Pennsylvania, U.S.A. (two isolates).

Culture condition All isolates were cultured and maintained on a nutritionally complete agar medium (CM) as reported previously (Seo et al., 1995). Mycelial disks (6 mm in diam) from plate cultures were placed in 90-mm plastic Petri dishes containing about 30 ml of CM, and were incubated at 27±1°C for 30 days in the dark or under light and with ventilation. Thereafter, the appear-

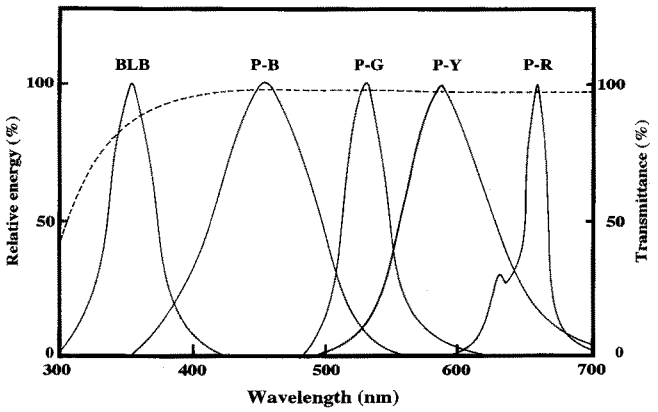


Fig. 1. Energy spectra of colored fluorescent lamps (——) and transmission spectrum (·····) of the plastic Petri dish. BLB: black light blue lamp (FL20S BLB, 352 nm in peak wavelength); P-B: pure blue lamp (FL20S B-F, 452 nm in peak wavelength); P-G: pure green lamp (FL20S G-F, 530 nm in peak wavelength); P-Y: pure yellow lamp (FL20S Y-F, 585 nm in peak wavelength); P-R: pure red lamp (FL20S R-F, 656 nm in peak wavelength). Energy and transmission spectra of lamps were reproduced from the data of Matsushita Electric Industrial Co., Ltd.

ance of basidiospores on the AFS was confirmed using a light microscope (Optiphoto, Nikon). The AFS areas on the colony were measured using an image analyzer (SAC 40-10, Shimadzu).

To examine the effect of light on mycelial growth, diameter of colony was measured after 10 days of incubation and the inhibition rate of mycelial growth was calculated according to the following formula:

$$\text{Inhibition rate (\%)} = \left(1 - \frac{\text{Mycelial growth under light condition}}{\text{Mycelial growth under dark condition}}\right) \times 100$$

Light illumination As light sources, various colored fluorescent lamps (FL 20 SD, Matsushita) and a 250 W halogen lamp were employed. The spectral energy distributions and transmittance of the colored fluorescent lamps are shown in Fig 1. The light intensity of colored fluorescent lamps was adjusted to about 0.3 to 0.5 μmol $m^{-2}s^{-1}$ by controlling the distance between lamps and the Petri dishes. Light intensity was determined with an LI-189 Quantum-meter (LI-COR, Inc.). Monochromatic light was obtained from the halogen lamp, using combinations of nine interference filters (KL-40, KL-45, KL-50, KL-55, KL-60, KL-65, KL-70, KL-75 and KL-80, Toshiba Machine Co., Ltd.) and seven colored glass filters (Y-43, Y-48, O-53, O-57, R-63, R-68 and R-69, Toshiba Machine Co., Ltd.). The spectral energy distributions and transmittance of interference filters are showed in Fig. 2A. An example of the wavelength distribution and transmittance for the combination of the interference filter (KL-55) and the colored glass filter (O-53) is shown in Fig. 2B. The intensity of the monochromatic radiation was adjusted to 0.3 μmol $m^{-2}s^{-1}$ by controlling the distance between the lamp and the filter.

All experiments were replicated four or five times and each value was expressed by the mean with standard deviation.

Results

Effect of irradiation with colored fluorescent lamps on AFS formation The 17 isolates of *G. lucidum* were grown on CM for 30 days under the different colored fluorescent lamps or in the dark. Thirteen isolates were induced to produce AFSs and basidiospores under the light, while the other 4 isolates continued only vegetative mycelial growth under the light of all lamps (Table 1). Of the 13 isolates, GI-019 (Fig. 3) and GI-023 produced AFSs only under the P-B (pure blue) and P-R (pure red) fluorescent lamps, respectively (Table 1). Isolates GI-004 and GI-020 produced AFSs under P-B and P-G (pure green), and P-B, P-G and P-Y (pure yellow) fluorescent lamps, respectively. The other isolates produced AFSs in a broad light region (Table 1, Fig. 4). No isolates formed AFSs in the dark or under the BLB (black light blue) illumination.

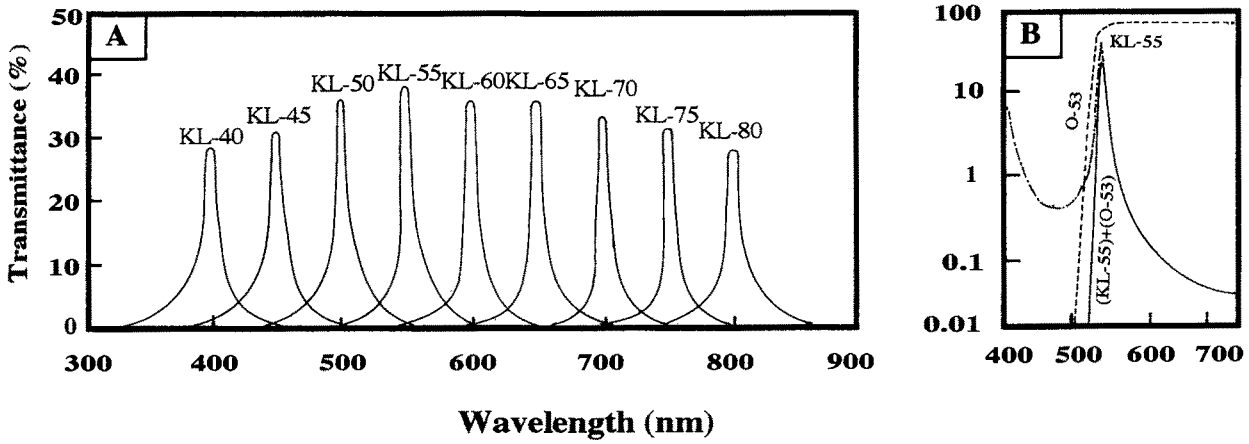


Fig. 2. Energy spectra and transmittance of interference filters (A) and transmitted light region for the combination of an interference filter (KL-55) and colored glass filter (O-53) (B). Energy spectra and transmittance of filters were reproduced from the data of Toshiba Machine Co., Ltd.

Table 1. Effect of irradiation with various fluorescent lamps on formation of atypical fruiting structures in *G. lucidum* isolates.

Isolate no.	Source of isolates (Collected country)[1]	AFS formation[2]					
		Dark	BLB	P-B	P-G	P-Y	P-R
GI-004	Wild fruit body (Korea)	−	−	+	+	−	−
GI-005	Wild fruit body (Korea)	−	−	+	+	+	+
GI-006	Wild fruit body (Korea)	−	−	+	+	+	+
GI-007	Wild fruit body (Korea)	−	−	+	+	+	+
GI-008	Wild fruit body (Korea)	−	−	+	+	+	+
GI-010	Cultivated fruit body (Korea)	−	−	+	+	+	+
GI-019	TMI-50040 (Japan)	−	−	+	−	−	−
GI-020	TMI-50087 (Japan)	−	−	+	+	+	−
GI-021	Wild fruit body (Korea)	−	−	+	+	+	+
GI-022	ASI-7005 (Korea)	−	−	+	+	+	+
GI-023	ASI-7011 (Japan)	−	−	−	−	−	+
GI-025	Wild fruit body (Papua New Guinea)	−	−	−	−	−	−
GI-026	Wild fruit body (Papua New Guinea)	−	−	+	+	+	+
GI-027	MRI-5006 (U.S.A.)	−	−	−	−	−	−
GI-029	MRI-5005 (U.S.A.)	−	−	−	−	−	−
GI-030	Cultivated fruit body (Korea)	−	−	−	−	−	−
GI-031	Wild fruit body (Korea)	−	−	+	+	+	+

[1] TMI: Tottori Mycological Institute, Japan; ASI: Agriculture Science Institute, Korea; MRI: Mycological Research Institute, University of Pennsylvania, U.S.A.

[2] Isolates were incubated for 30 days under continuous irradiation with BLB, P-B, P-G, P-Y, and P-R lamps, or in the dark. The light intensity was adjusted to about 0.3 to 0.5 μmol $m^{-2}s^{-1}$. All cultures were replicated five times; −: only vegetative growth; +: formation of AFSs.

Representative isolates showing different characteristic responses to light in AFS formation were cultured, and their AFS areas were measured (Table 2). The area markedly varied depending upon the isolate. Isolates GI-004, GI-019 and GI-023, which formed AFSs in narrow light regions had smaller AFS area than isolates which formed AFSs in a broad light region (Table 2).

Mycelial growth of *G. lucidum* isolates was affected by light illumination during the incubation (Table 3). BLB light gave a marked reduction in the mycelial growth of all isolates. Visible light from P-B, P-G, P-Y and P-R lamps also inhibited mycelial growth in many isolates, but it did not affect the growth of isolate GI-029, which did not produce AFSs. However, no clear correlation was observed between the capacity of AFS formation and the inhibition rate of mycelial growth.

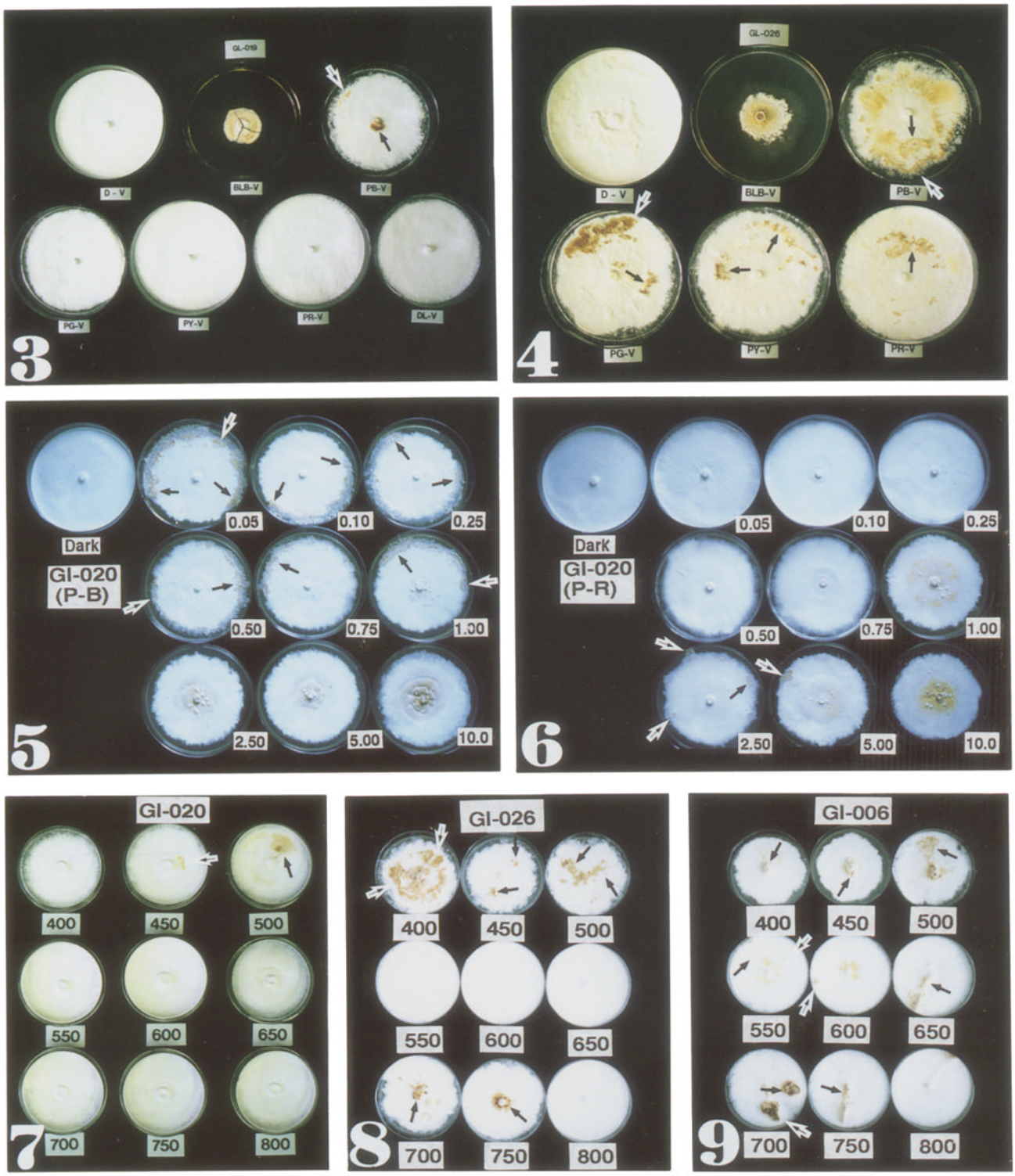
Relationship between light intensity and AFS formation

To elucidate the influence of light intensity on the AFS formation of *G. lucidum*, light intensity was adjusted to nine levels from 0.05 to 10.0 μmol $m^{-2}s^{-1}$ under P-B and P-R fluorescent lamps. Isolates GI-004, GI-006, GI-020 and GI-023 were selected, based on their different responses to light (Tables 1, 2), and incubated under light for 30 days. Isolate GI-004 produced AFSs at light intensity above 0.1 μmol $m^{-2}s^{-1}$ under the P-B lamp, and began to form AFSs at high light intensity above 5 μmol $m^{-2}s^{-1}$ under the P-R lamp (Table 4). Isolate GI-020 showed a similar response to GI-004, except that AFS formation was inhibited at high light intensity under both lamps (Table 4, Figs. 5, 6). On the other hand, isolate GI-006 produced

Table 2. Area of atypical fruiting structures produced by *G. lucidum* isolates under light from various colored fluorescent lamps.

Light source	AFS area (mm^2)[1]						
	GI-004	GI-006	GI-019	GI-020	GI-022	GI-023	GI-031
Dark	0	0	0	0	0	0	0
BLB	0	0	0	0	0	0	0
P-B	63±20.0	28± 5.4	51±44.0	281±68.8	217± 86.8	0	550±74.4
P-G	63± 0.0	229±109.1	0	143± 4.1	171± 50.4	0	192±65.6
P-Y	0	825±181.4	0	45±10.9	260±100.9	0	405±49.7
P-R	0	717±473.2	0	0	275± 73.6	53±6.2	383±71.7

[1] Culture conditions were the same as in Table 1. Area of AFSs was measured 30 days after inoculation. All cultures were replicated five times and each value shows the mean with standard deviation.



Figs. 3–9. Formation of AFSs in *G. lucidum* isolates under different colored fluorescent lamps and monochromatic lights. All cultures were grown at 27±1°C for 30 days in continuous light.

Fig. 3. Cultures of the GI-019 isolate under different colored fluorescent lamps. AFSs (arrowheads) were formed on the culture under PB-V (pure blue and ventilation).

Fig. 4. Cultures of the GI-026 isolate under different colored fluorescent lamps. AFSs (arrowheads) were formed on the culture under PB-V, PG-V (pure green and ventilation), PY-V (pure yellow and ventilation) and PR-V (pure red and ventilation).

Fig. 5. Cultures of the GI-020 isolate under various intensities of P-B fluorescent lamps. AFSs (arrowheads) were formed on the culture under light intensities of 0.05, 0.10, 0.25, 0.50, 0.75 and 1.0 μmol $m^{-2}s^{-1}$.

Fig. 6. Cultures of the GI-020 isolate under various intensities of P-R fluorescent lamps. AFSs (arrowheads) were formed on the culture under light intensities of 2.50 and 5.0 μmol $m^{-2}s^{-1}$.

Table 3. Inhibitory effect of light illumination on mycelial growth of *G. lucidum* isolates.

Light source	Inhibition rate (%)[1]					
	GI-004	GI-010	GI-022	GI-023	GI-029	GI-031
BLB	79.6± 2.0	99.1±1.9	73.9±3.4	52.4±5.4	41.9±14.8	93.9± 3.8
P-B	34.4± 1.5	76.6±1.4	29.5±5.8	27.6±0.7	6.4±2.1	24.5± 3.8
P-G	23.7± 3.3	57.9±2.4	8.1±2.6	24.3±1.1	5.5±1.6	23.9±12.5
P-Y	7.7± 5.9	61.2±1.4	10.7±1.2	25.7±1.1	0.4±2.2	−0.1± 1.5
P-R	18.8±10.1	60.5±0.9	9.0±3.8	28.1±0.7	0.0±1.1	1.8± 2.2

[1] Culture conditions were the same as in Table 1. Mycelial growth under the various colored fluorescent lamps or dark control was measured 10 days after inoculation, and inhibition rate was calculated by the formula given in Material and Methods. All cultures were replicated five times and each value shows the mean with standard deviation.

Table 4. Effect of light intensity on formation of atypical fruiting structures in *G. lucidum* isolates.

Intensity (μmol $m^{-2}s^{-1}$)	Area of AFS (mm^2)[1]							
	GI-004		GI-006		GI-020		GI-023	
	P-B	P-R	P-B	P-R	P-B	P-R	P-B	P-R
Dark	0	0	0	0	0	0	0	0
0.05	0	0	338± 29.7	10± 1.7	1451±415.5	0	0	0
0.10	120±20.0	0	118± 60.2	287± 23.1	1326±219.8	0	0	0
0.25	140±20.0	0	157±117.8	269± 14.6	1688±862.0	0	0	0
0.50	103± 7.0	0	10± 0.0	243±151.3	1382±696.2	0	0	±[2]
0.75	98±15.9	0	10± 0.0	407±100.7	1418±205.1	0	0	0
1.00	135±35.0	0	0	480±184.7	1536±261.5	0	0	0
2.50	217±38.6	0	0	229±122.2	0	620±139.4	0	0
5.00	223±44.9	54±23.8	0	0	0	334± 56.5	0	0
10.0	180± 0.0	161±63.4	0	0	0	0	0	0

[1] Culture conditions were the same as in Table 1. Area of AFSs was measured 30 days after inoculation.
[2] Although AFS formation was initiated, it was impossible to measure the area.

AFSs in the range of light intensity as low as 0.05 to 0.75 μmol $m^{-2}s^{-1}$ under the P-B lamp, and 0.05 to 2.5 μmol $m^{-2}s^{-1}$ under the P-R lamp (Table 4). Isolate GI-023, which formed AFSs specifically under P-R lamp (Table 1), showed AFS formation only at a light intensity of 0.5 μmol $m^{-2}s^{-1}$ under the P-R lamp, although it was hard to measure AFS area (Table 4).

Effect of monochromatic light irradiation on AFS formation To determine more precisely the wavelength of light effective for AFS formation in *G. lucidum*, 11 isolates were incubated under continuous irradiation of monochromatic lights with different wavelengths for 30 days (Table 5).

Most isolates produced AFSs in the blue region of wavelength from 400 to 500 nm. Isolates GI-004 and GI-020, which formed AFSs under the P-B and P-G lamps, produced AFSs at ranges of 500 to 600 nm and of 450 to 500 nm, respectively (Fig. 7). Among the isolates that formed AFSs under almost all fluorescent lamps, GI-006, GI-007 and GI-008 produced AFSs in broad ranges of wavelength from 400 to 700 or 750 nm. On the other hand, isolates GI-010 and GI-026 had two effective regions for AFS formation which consisted of short (400 to 500 nm) and long (650 to 700 or 750 nm) wavelength bands (Fig. 8), while isolates GI-005 and GI-022 produced AFSs at short (400 to 500 nm) wavelength. Isolates GI-019 and GI-023, which specifically produced AFSs under P-B and P-R fluorescent lamps, respectively, did not form AFSs under monochromatic irradiation.

Discussion

The initiation of fruit bodies and sporulation in many basidiomycetes are affected by various environmental factors such as light, aeration, temperature, humidity and

Fig. 7. Cultures of the GI-020 isolate under monochromatic light. AFSs (arrowheads) were formed on the culture irradiated with 450 and 500 nm lights.

Fig. 8. Cultures of the GI-026 isolate under monochromatic light. AFSs (arrowheads) were formed on the culture irradiated with 400, 450, 500, 700 and 750 nm lights.

Fig. 9. Cultures of the GI-006 isolate under monochromatic light. AFSs (arrowheads) were formed on the culture irradiated with 400, 450, 500, 550, 600, 650, 700 and 750 nm lights.

nutritional conditions (Suzuki, 1979; Manachère, 1980; Yli-Mattila, 1990). Of these environmental factors, light is essential for the fruiting of many basidiomycetes (Perkins and Gordon, 1969; Morimoto and Oda, 1973; Eger-Hummel, 1980; Raudaskoski and Yli-Mattila, 1985; Yli-Mattila, 1985). Based on the effect of light on fruiting, Eger-Hummel (1980) divided basidiomycetes into four groups: i) light is not required for fruiting, ii) light is not necessary for initiation of primordia but indispensable for further development and maturation of fruit bodies, iii) light is necessary for primordium initiation and further development of fruit bodies, and iv) the fourth group differs from the third group in requiring a dark period between primordia and fruit body formation. *G. lucidum* belongs to the third group, because light is essential for normal fruit body initiation and further development in artificial cultivation (Hemmi, 1936), and for fruit body primordium initiation on agar media (Shin and Seo, 1988; Seo et al., 1995). In addition to fruit bodies, this fungus produces AFSs with non-basidiocarpous basidiospores on agar media, and light also absolutely affects AFS initiation and basidiospore formation (Shin and Seo, 1988; Seo et al., 1995).

The effect of light on AFS formation in *G. lucidum* isolates was investigated by using colored fluorescent lamps and monochromatic light. Light was necessary for AFS formation, but the effective light quality differed among isolates. Of 13 isolates which formed AFSs, 9 produced AFSs in a broad light region from P-B to P-R lamps. Under monochromatic light, however, these isolates divided into three types, which formed AFSs at 400-500 nm, 400-500 nm and 650-750 nm, and 400-700 nm, respectively, in which the response to blue light of 400-500 nm was common to all. On the other hand, the remaining 4 isolates (GI-004, GI-019, G1-020 and GI-023) showed different responses to light. Isolates GI-019 and GI-023 produced AFSs under P-B and P-R lamps, respectively, but not under monochromatic light. Isolates GI-004 and GI-019, which formed AFSs under P-B and P-G lamps, produced AFSs at 500-600 nm and 450-500 nm under monochromatic light, respectively. These results indicate that *G. lucidum* is heterogeneous in its photo-response with regard to AFS formation.

Optimum light intensity for the initiation and development of fruit bodies in basidiomycetes varies according to isolate, species and light quality (Suzuki, 1979). In most basidiomycetes, the formation of fruit body primordium is promoted by higher irradiation of light, though extremely strong irradiation inhibits and delays the formation of fruit body primordia (Kitamoto et al., 1968; Kitamoto et al., 1972; Yli-Mattila, 1985). On the other hand, the initiation of fruit body primordia in *Coprinus congregatus* increases under higher irradiation, but subsequent developmental stages such as sporulation are inhibited by the same light intensity as induction of fruit body primordia (Durand and Furuya, 1985). In *G. lucidum*, AFS formation of isolate GI-004 under the P-B lamp did not show any significant change on increasing of light intensity. However, AFS formation of isolates GI-006 and GI-020 was inhibited by high light intensity under the P-B lamp. Under the P-R lamp, AFS formation of isolate GI-006 was severely inhibited by high intensity, but isolates GI-004 and GI-020 formed AFSs at high intensity. Thus, the optimum light intensity for AFS formation in *G. lucidum* varies depending on light quality and isolate.

The action spectra for fruiting in most basidiomycetes have peaks in both UV-A (315-400 nm) and blue light (400-520 nm) (Perkins and Gordon, 1969; Kitamoto et al., 1972, 1974; Badham, 1980; Durand and Furuya, 1985; Richartz and MacLellan, 1987). Flavins have been speculated as UV-A and blue light photoreceptors in fungi (Briggs, 1976). In addition to flavins, the pigment pterin (containing the pteridine ring) has been proposed as a photoreceptor candidate for UV-A light in the fruiting of *Schizophyllum commune* (Yli-Mattila, 1985). Although the optimum action spectra for AFS formation in isolates of *G. lucidum* showed diversity, the effect of blue light was detected in almost all isolates.

Table 5. Effect of monochromatic irradiation on formation of atypical fruiting structures in *G. lucidum* isolates.

Wavelength[1)]	AFS Formation[2)]										
	GI-004	GI-005	GI-006	GI-007	GI-008	GI-010	GI-019	GI-020	GI-022	GI-023	GI-026
Dark	−	−	−	−	−	−	−	−	−	−	−
400	−	+	+	+	+	+	−	−	+	−	+
450 (430)	−	+	+	+	+	+	−	+	+	−	+
500 (480)	+	+	+	+	+	+	−	+	+	−	+
550 (530)	+	−	+	+	+	−	−	−	−	−	−
600 (570)	+	−	+	+	+	−	−	−	−	−	−
650 (630)	−	−	+	+	+	+	−	−	−	−	−
700 (680)	−	−	+	+	+	+	−	−	−	−	+
750 (690)	−	−	+	−	−	+	−	−	−	−	+
800 (690)	−	−	−	−	−	−	−	−	−	−	−

[1)] Numbers indicate the peak wavelength (nm) of each interference filter and the lower cut wavelength (nm) is given in parenthesis, respectively.

[2)] All cultures were grown under light in combination with interference and colored glass filters for 30 days. Intensity of the monochromatic radiation was equivalent at 0.3 μmol $m^{-2}s^{-1}$. −: Only vegetative growth, +: Formation of AFSs.

However, AFSs were not induced under BLB light (300-400 nm) illumination. Therefore, whether flavins are associated with AFS formation in *G. lucidum* is unclear. On the other hand, yellow and/or red lights have an effect on fruit body development in some basidiomycetes (Ingold and Nawaz, 1967; Tan, 1977; Leatham and Stahmann, 1987). Some isolates of *G. lucidum* also formed AFSs in yellow and/or red lights in addition to blue light. However, photoreceptors for these lights have not yet been reported in basidiomycetes.

Studies on the effect of light in basidiomycetes have mainly focused on induction and development of fruit bodies. Light quality for AFS formation in *G. lucidum* seems to be different from that for fruit body formation in basidiomycetes reported so far. AFSs are organized with vegetative hyphae, skeletal hyphae and cuticular cells, while basidia with basidiospores differentiate directly from generative hyphae on the outside of the AFSs (Seo et al., 1995). Therefore, the photo-response of AFS formation may reflect that of basidiospore formation on the hymenium in fruit bodies of *G. lucidum*.

Acknowledgements——We wish to thank Dr. N. Hiratsuka (Tottori Mycological Institute, Japan) and Dr. S. J. Go (Agricultural Science Institute , Office of Rural Development, Korea) for the gift of cultures used in this study. We also thank Prof. Y. Kitamoto (Tottori Univ., Japan), Dr. K. Tokimoto and Mr. N. Maekawa (Tottori Mycological Institute, Japan) for helpful suggestions on the study.

Literature cited

Adaskaveg, J. E. and Gilbertson, R. L. 1986. Cultural studies and genetics of sexuality of *Ganoderma lucidum* and *Ganoderma tsugae* in relation to the taxonomy of the *Ganoderma lucidum* complex. Mycologia **78**: 694-705.

Badham, E. R. 1980. The effect of light upon basidiocarp initiation in *Psilocybe cubensis*. Mycologia **72**: 136-142.

Banerjee, S. and Sarkar, A. 1956. Formation of sporophores of *Ganoderma lucidum* (Leyss.) Karst. and *Ganoderma applanatum* (Pers.) Pat. in culture. Indian J. Mycol. Res. **2**: 80-82.

Blanchette, R. A. 1984. Screening wood decayed by white rot fungi for preferential lignin degradation. Appl. Environ. Microbiol. **48**: 647-653.

Bose, S. R. 1929. Artificial culture of *Ganoderma lucidus* Leyss from spore to spore. Bot. Gazett **87**: 665-667.

Briggs, W. R. 1976. The nature of the blue light photoreceptor in higher plants and fungi. In: "Light and plant development," (ed. by Smith, H.), pp. 7-18. Butterworth, London.

Durand, R. and Furuya, M. 1985. Action spectra for stimulatory and inhibitory effects of UV and blue light on fruit body formation in *Coprinus congregatus*. Plant and Cell Physiol. **26**: 1175-1183.

Eger-Hummel, G. 1980. Blue light photomorphogenesis in mushrooms (Basidiomycetes). In: "The blue light syndrome," (ed. by Senger, H.), pp. 555-562. Springer-Verlag, Berlin.

Hemmi, T. and Tanaka, I. 1936. Experiments for developing sporophores of *Ganoderma japonicum*. Botany and Zoology **4**: 13-23.

Hepting, G. H. 1971. Diseases of forest and shade trees of the United States. U. S. Dept. Agric., Agric. Handb. **386**: 1-658.

Ingold, C. T. and Nawaz, M. 1967. Sporophore development in *Sphaerobolus*: effect of blue and red light. Ann. Bot. N. S. **31**: 469-477.

Kitamoto, Y., Horikoshi, T. and Suzuki, A. 1974. An action spectrum for photoinduction of pileus formation in a basidiomycete, *Favolus arcularius*. Planta **119**: 81-84.

Kitamoto, Y., Suzuki, A. and Furukawa, S. 1972. An action spectrum for light induced primordium formation in a basidiomycete, *Favolus arcularius* (Fr.) Ames. Plant Physiol. **49**: 338-340.

Kitamoto, Y., Takahashi, M. and Kasai, Z. 1968. Light induced formation of fruit bodies in a basidiomycete, *Favolus arcularius* (Fr.) Ames. Plant and Cell Physiol. **9**: 797-805.

Leatham, G. F. and Stahmann, M. A. 1987. Effect of light and aeration on fruiting of *Lentinula edodes*. Trans. Br. Mycol. Soc. **88**: 9-20.

Manachère, G. 1980. Conditions essential for controlled fruiting of macromycetes. A review. Trans. Br. Mycol. Soc. **75**: 255-270.

Morimoto, N. and Oda, Y. 1973. Effect of light on fruit body formation in a basidiomycete, *Coprinus macrorhizus*. Plant and Cell Physiol. **14**: 217-225.

Perkins, J. H. and Gordon, S. A. 1969. Morphogenesis in *Schizophyllum commune*. II. Effects of monochromatic light. Plant Physiol. **44**: 1712-1716.

Raudaskoski, M. and Viitanen, H. 1982. Effect of aeration and light on fruit body induction in *Schizophyllum commune*. Trans. Br. Mycol. Soc. **78**: 89-96.

Raudaskoski, M. and Yli-Mattila, T. 1985. Capacity for photoinduced fruiting in a dikaryon of *Schizophyllum commune*. Trans. Br. Mycol. Soc. **85**: 145-151.

Richartz, G. and MacLellan, A. J. 1987. Action spectra for hyphal aggregation, the first stage of fruiting, in the basidiomycete *Pleurotus ostreatus*. Photochem. Photobiol. **45**: 815-820.

Schwalb, M. N. and Shanler, A. 1974. Phototropic and geotropic responses during the development of normal and mutant fruit bodies of the basidiomycete *Schizophyllum commune*. J. Gen. Microbiol. **82**: 209-212.

Seo, G. S., the late Shin, G. C., Otani, H., Kodama, M. and Kohmoto, K. 1995. Formation of atypical fruiting structures in *Ganoderma lucidum* isolates on a nutrition agar medium. Mycoscience **36**: 1-7.

Shin, G. C. and Seo, G. S. 1988. Formation of the non-basidiocarpous basidiospore of *Ganoderma lucidum*. Kor. J. Mycol. **16**: 230-234. (In Korean.)

Suzuki, A. 1979. General review on environmental factors affecting primordium formation in Homobasidiae. Trans. Mycol. Soc. Japan **20**: 253-265. (In Japanese.)

Tan, K. K. 1977. Light-induced fungal development. In: "The filamentous fungi III," (ed. by Smith J. E. and Barry, D. R.), pp. 334-357. John Wiley, New York.

Yli-Mattila, T. 1985. Action spectrum for fruiting in the basidiomycete *Schizophyllum commune*. Physiol. Plant. **65**: 287-293.

Yli-Mattila, T. 1990. Photobiology of fruit body formation in the basidiomycete *Schizophyllum commune*. Reports from the Department of Biology, University of Turku. No. 27, Turku. 67p.