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Atypical Fruiting Structure Formation of White Fruitbody-Forming Isolates in *Ganoderma lucidum*

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백색자실체를 형성하는 영지 균주의 非定型 자실체 구조의 형성

서 건 식

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ABSTRACT: Five white fruitbodies of *Ganoderma lucidum* found from two different mushroom farms, and the characteristics of atypical fruiting structure formation of these strains were described. The white fruitbodies were spontaneously generated on *Quercus*-log during the cultivation. They did not differentiate to the normal fruitbodies with pileus, hymenium, stipe and coloration, and fruitbodies remained non-laccateed even after 3 months. Dikaryotic mycelia isolated from the five white fruitbodies differed from wild-type strains in the mycelial growth rate, colony color, and the capacity of atypical fruiting structure (AFS) formation on agar media. These white mutants readily induced brown colored AFSs on the colonies under ventilation and illumination conditions. Both isolates GI-010 and GI-011 that were obtained from a normal and white fruitbody, respectively, did not form AFSs in the dark and/or under black light blue (BLB) light illumination, but induced under the visible light. They required dim light for the AFS formation, and the AFS formation was inhibited up to 0.5 μmol m^{-2} s^{-1} in light intensity. However, the other four isolates induced AFSs even in the dark and BLB illumination, although their parent strain, isolate GI-030, did not form AFSs under any light conditions. The monokaryotic mycelia derived from basidiospores of the AFSs of the white mutants were compatible with the original culture (dikaryon) on a dual culture.

KEYWORDS: Atypical fruiting structure, Compatible mating, Conspecificity, *Ganoderma lucidum*, White fruitbody

Ganoderma lucidum has been well known as a stalked and laccated species. The morphological feature of its fruitbody varies depending on their hosts or habitat (Shin *et al.*, 1986; Ryvarden, 1994). Based on the color of its pileus, it had been called red-, purple-, black-, yellow-, blue- and white-types in Asian countries. In addition, the fruitbodies obtained from artificial cultivation of *G. lucidum* also show polymorphism such as kidney- and antler-type fruitbodies (Hemmi and Tanaka, 1936; Shin and Seo, 1988b). However, no descriptions of the blue, yellow or white fruitbodies of *G. lucidum* had been reported.

To elucidate the taxonomic situation and physiological characteristics of *G. lucidum*, cultural studies have been conducted by fungal taxonomists and mycologists. Some isolates of *G. lucidum* have been reported to form atypical fruiting structure (AFS) bearing the basidiospores and fruitbody primordium (FBP) on some different agar media with the regulated light and ventilation condition (Shin and Seo, 1988a; Seo *et al.*, 1995b). In these AFS, the basidia were formed directly from generative hyphae without formation hymenial layer.

Mutations in the basidiomycetes can occur on each stage of its life cycle. Fruitbodies of mutant strains often generates various morphological abnormalities in such as colorless, no stroma, no primordium, undifferentiated, or sporeless (Komatsu and Kimura, 1968; Arita, 1974; Komatsu, 1977; Ohira, 1979; Hasebe *et al.*, 1991; Ishikawa, 1991).

Cho *et al.* (1993, 1994) reported the formation of white fruitbodies in *G. lucidum* on artificial log cultivation. According to the previous reports (Cho *et al.*, 1993, 1994), the white fruitbodies of *G. lucidum* did not differentiate into a normal fruitbody. Although they did not differentiate stipe, pileus and hymenia in artificial cultivation, the AFSs and non-basidiocarpous basidiospores were formed on the mycelial colony on agar media. However, morphological characteristics of basidiospores of AFSs and wild fruitbodies of *G. lucidum* were almost the same (Seo *et al.*, 1995b). Nevertheless, conspecificity and any physiological difference between these normal and white fruitbody strains have not been elucidate, so far.

The purpose of the present study is to confirm the

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mechanism of AFS formation in the white fruitbody-forming isolates, and whether normal and white fruitbody-forming isolates are conspecific.

Materials and Methods

Isolates The dikaryotic isolates used in this study are listed in Table 1. Isolate Gl-011 (previously G 4142; Cho *et al.*, 1993) was obtained from context tissues of a white fruitbody which was spontaneously generated on a timber log during the cultivation of isolate Gl-010 (previously G 4086; Cho *et al.*, 1993), and the other four isolates (Gl-013, Gl-014, Gl-015 and Gl-016) were obtained from four different white fruitbodies which were generated from isolate Gl-030.

Culture condition All isolates were maintained and cultured on a nutritionally complete agar medium (CM) as reported previously (Seo *et al.*, 1995b). Other culture conditions including the light sources, light illumination and culture process were described in the previous report (Seo *et al.*, 1996).

Selection of monokaryotic strain and mating test To obtain monokaryotic strains, a section of the AFS tissues was attached to the lid of a Petri-dish containing about 20 m*l* of CM. The discharged spores onto the medium were incubated for 2 to 4 days at 27±1°C under dim light. After germination, a colony was aseptically isolated, and transferred onto a fresh medium. All the isolated colonies were confirmed whether monokaryotic or dikaryotic by the presence or absence of clamp connections.

To determine the compatibility among the isolates used in this study, mating tests between the selected monokaryotic strains were conducted. An inoculum from each strain was placed 1 cm apart on CM in a Petri-dish and incubated about 2 weeks. The mycelia of the opposite sides from each inoculum were examined whether they formed clamp connections.

Statistical analysis Four or five replications were made in all cultures. Each value in all data was expressed by the mean with standard deviation.

Table 1. Isolates of *Ganoderma lucidum* and their cultural characteristics

Isolates	Color of		Formation		Mycelial growth[c]
	fruitbody	colony[a]	AFS	FBP	
Gl-010	Reddish brown	Pale yellow	+	-	60.8±5.5
Gl-011	White	White	+	+	73.0±3.2
Gl-013	White	White	+	-	83.0±0.8
Gl-014	White	White	+	-	80.2±0.9
Gl-015	White	White	+	-	81.2±1.1
Gl-016	White	White	+	-	79.2±2.3
Gl-030	Reddish brown	Pale yellow	-	-	64.8±4.2

[a] Isolates were grown for 30 days under continuous illumination with D-L fluorescent lamps.
[b] +, formed: -, not formed; AFS, atypical fruiting structure; FBP, fruitbody primordium.
[c] Colony diameter (mm) obtained at 27±1°C for 10 days incubation in the darkness.

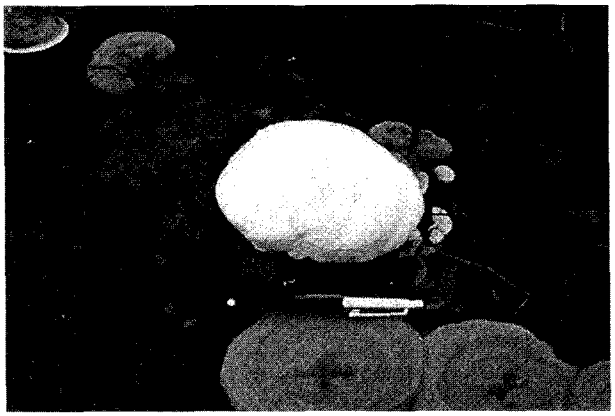


Fig. 1. Fruitbodies of *G. lucidum* Gl-030 and Gl-014 (white colored), generated on timber logs.

Table 2. Effect of irradiation with various fluorescent lamps on the formation of atypical fruiting structures in normal and white fruitbody-forming strains of *G. lucidum*

Light	Area of AFS (mm^2)[a]						
	Gl-010	Gl-011	Gl-013	Gl-014	Gl-015	Gl-016	Gl-030
Dark	0	0	1448.9±233.9	3181.9±626.6	4652.3±303.8	995.9±251.50	0
BLB	0	0	0	1837.2±1039.1	1225.5±48.00	0	0
P-B	216.8±90.3	±[b]	338.7±146.0	4158.1±722.5	1448.9±233.9	2796.6±340.3	0
P-G	495.3±62.6	142.8±32.3	4422.4±435.4	4161.2±143.8	3723.8±79.0	2452.1±133.8	0
P-Y	520.3±73.6	463.3±50.4	4587.8±508.3	5028.7±307.6	5069.3±390.9	2088.3±732.8	0
P-R	460.3±83.6	875.0±76.3	3589.0±673.2	4438.9±659.8	5364.7±61.1	2866.8±120.0	0
D-L	314.0±247.3	778.6±87.3	4184.1±337.6	3015.4±617.1	3669.9±249.8	2107.6±157.4	0

[a] Isolates were incubated for 30 days in the dark or under continuous illumination with black light blue (BLB), pure blue (P-B), pure green (P-G), pure yellow (P-Y), pure red (P-R), and day light (D-L) fluorescent lamps. The spectral energy distributions and transmittance of these colored fluorescent lamps were given as previously (Seo *et al.*, 1995a). The light intensity of each lamps were adjusted to about 0.3 to 0.5 μmol m^{-2} s^{-1}. Area of AFSs was measured 30 days after inoculation. Each value represents a mean value of five replication with standard deviation.
[b] AFS formation was confirmed by the observation with light microscopy, but could not measured as area.

Results

Macro- and microscopic characteristics of white fruitbodies

White fruitbodies were spontaneously generated on *Quercus* logs during the cultivation of *G. lucidum* (Fig. 1). One and four white fruitbodies were collected from two different cultivation farms, respectively. Although white and normal fruitbodies were initiated synchronously, the former did not differentiate to a fruitbody with normal pileus, hymenium, stipe and coloration, and remained non-laccate even after three months from generation. The context was pure white and woody. The size of white fruitbodies was 10 to 15 cm in diam., and 6 to 9 cm in height. All specimens collected had a trimitic hyphal system that consisted of generative, skeletal and binding hyphae. There were no significant differences on hyphal system between white and normal fruitbodies.

Cultural characteristics and AFS formation of white fruitbody-forming isolates

The isolates used in this study varied in mycelial growth rate, colony color, and AFS- or FBP-forming capacity on agar media (Table 1). White fruitbody-forming isolates grew faster than their original culture on CM. Two normal fruiting isolates formed pale yellow colonies under the light illumination and ventilation conditions, while white fruitbody-forming isolates formed pure white colonies until AFS formation. However, brown colored AFS in the white fruitbody-forming isolates was more readily induced than in the normal fruiting isolates under the ventilation and light illumination. Whereas isolate Gl-010 did not form FBP, isolate Gl-011 formed both AFS and FBP. Similarly, although isolate Gl-030 did not form any fruiting structure on CM, four isolates obtained from context tissues of its white fruitbodies formed AFSs on most mycelial mats (Table 2, Fig. 2). AFSs of isolates Gl-010 and Gl-011 formed coralloid-type bodies, but those of Gl-013, Gl-014, Gl-015 and Gl-016 formed incomplete poroid-type bodies. AFSs were densely organized with vegetative and skeletal hyphae and cuticular cells. The development of AFS significantly differed from the hymenial development in the normal fruitbody. The AFS differentiated basidia directly from the generative hyphae on the surface of the AFSs.

Basidiospores formed on AFSs were brown and ellipsoid, and had one or two large vacuoles and a double wall. They were truncated to narrowly rounded at the apex with an eccentric hilar appendix on a rounded spore base. Basidiospores formed on AFSs of the white fruitbody-forming isolates were very similar in size, $7.7\pm2.4\times4.3\pm1.5$ μm to those of isolate Gl-010. The other morphological characteristics such as surface structures, color and shape were also indistinguishable from each other.

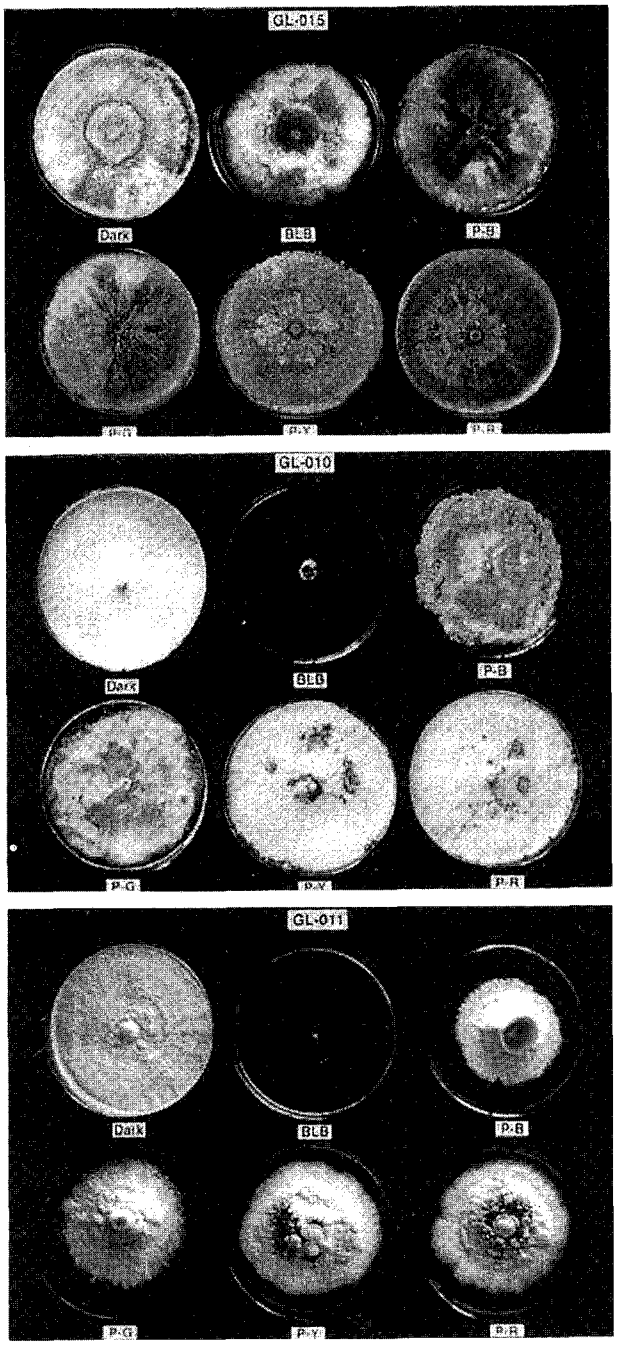


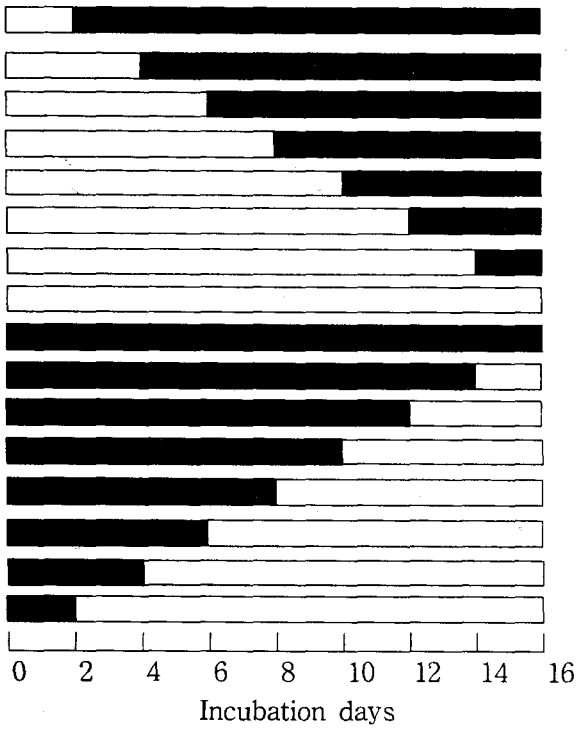
Fig. 2. Formation of AFSs in *Ganoderma lucidum* isolate Gl-010, Gl-011, and Gl-015 under different colored fluorescent lights. The fungus was grown at 27 ± 1°C for 30 days in continuous light.

Effect of light on AFS formation

All isolates were grown on CM for 30 days under the colored fluorescent lamp illuminations with different wavelength fluorescences or in the dark (Table 2). Isolates Gl-010 and Gl-011 did not form AFSs in the dark and under BLB (black light blue fluorescent lamp) illumination, but

Table 3. Influence of light illumination and duration on the formation of atypical fruiting structures (AFSs) by *G. lucidum* strains

Light treatment[a]	Gl-010		Gl-011	
	IDA[b]	Area[c]	IDA[b]	Area[c]
	-	0	-	0
	-	0	-	0
	-	0	-	0
	-	0	-	0
	-	0	10	±[d]
	-	0	12	±[d]
	-	0	12	86.5±19.7
	-	0	12	941.7±144.8
	-	0	-	0
	16	30.6±4.9	-	0
	16	35.3±9.5	-	0
	15	45.0±18.7	-	0
	11	575.0±163.3	14	11.3±3.3
	12	208.3±31.2	12	116.0±12.7
	-	0	8	370.8±199.0
	-	0	10	650.0±163.3



[a]Day light (D-L) fluorescent lamps (light intensity: 3.5 μmol m^{-2} s^{-1}) were used as light sources; ■: Dark, □: Light.
[b]IDA: The initial day of AFS appearence after inoculation.
[c]The area (mm^2) of AFSs was measured 16 days after inoculation. Each value represents a mean value of five replication with standard deviation.
[d]AFSs were formed in the light conditions, but reversed to vegetative growth when transmittance to dark conditions.

formed AFS under the visible light illumination. The other four white fruitbody-forming isolates formed AFS even in the dark and BLB illumination, although the original isolate Gl-030 did not form AFS under any light irradiation conditions.

Duration of the light illumination for the AFS induction was required differently between isolates Gl-010 and Gl-011 (Table 3). The AFSs of isolate Gl-010 were induced by pre-incubation in the dark for 6 to 14 days, then subsequent incubation in the light for 10 to 2 days, respectively, but not induced on the light illumination after inoculation. Thus, pre-incubation in the dark before light illumination promoted the AFS formation in isolate Gl-010. On the other hand, isolate Gl-011 did not induce AFSs by the incubation of more than 8 days in the darkness regardless of pre- or post-light illumination. Although the AFSs were formed in the light illumination for 10 or 12 days, they were covered with aerial mycelia by the transferring to the dark conditions.

The optimum light intensity for the AFS formation of isolate Gl-011 was same as that of the original culture isolate Gl-010 (Data not shown). Both isolates were inhibited up to 0.5 μmol m^{-2} s^{-1} in light intensity. Furthermore, AFSs were not formed by irradiation of up to 10 μmol m^{-2} s^{-1}. The areas of AFS in isolate Gl-011 were broader than those in isolate Gl-010.

Basidiospore germination and mating test

Monokaryotic strains from dikaryotic isolate Gl-010, Gl-011, Gl-014 and Gl-015 were obtained from germinating basidiospores. The spores germinated on CM after about 4 days, and the germination rate of the basidiospores was as

Table 4. Mating tests among the monokaryon strains derived from normal fruiting and white fruiting isolates of *G. lucidum*

	Gl-010M[a]	Gl-011M	Gl-014M	Gl-015M	Gl-030[b]
Gl-010M[1]	-[c]	+	+	+	+
Gl-011M	-	-	+	+	+
Gl-014M			-	+	+
Gl-015M				-	+
Gl-030[2]					-

[a]"M" indicates monokaryon derived form each isolate.
[b]Dikaryotization of monokaryotic mycelia was confirm as compatible mating between dikaryotic mycelia of isolate Gl-030 and monokaryotic mycelia.
[c]+; compatible matings, -; incompatible matings.

low as 0.3%. The monokaryotic strains were used to determine the conspecificity by a dual culture. Among the monokaryotic strains that were selected from each dikaryotic isolates, the conspecificity or mating compatibility was recognized by clamp connection formation (Table 4).

Discussion

As a result of reproductive growth in the basidiomycetes, fruiting occurs. Fruiting in the basidiomycetes has been well known as affected by genetic background and environmental factors such as light, aeration, humidity and temperature conditions (Schwalb, 1978). Genetic background is considered as a primary factor, and environmental factors as a secondary factor for fruiting (Arita, 1974; Tokimoto, 1974). Some previous reports (Takemaru and Kamada, 1971, 1972; Bromberg and Schwalb, 1977; Ohira, 1979) showed that fruiting ability, morphology of fruitbody and basidiospore formation are regulated by genetic factors.

In nature, *G. lucidum* complex required a long time for the fruitbody formation. Therefore, the morphological features such as size, color and shape of the fruitbodies are considered to be affectable by environmental factors during the fruitbody development. According to the cultivation conditions such as light and ventilation, *G. lucidum* forms kidney- and antler-type fruitbodies. Non-coloration and abnormal fruitbodies also generate by intercepting light (Hemmi and Tanaka, 1936; Shin and Seo, 1988b). However, *G. lucidum* fruitbodies that were cultivated under the same environmental conditions were divided into kidney-, antler-types and dimorphic according to the isolates (Shin and Seo, 1988b). It is supposed that kidney- and antler-type fruitbodies are regulated by different genetic factors for fruitbody differentiation. Although fruitbodies of *G. lucidum* show polymorphism by the cultivation condition and isolates, the white fruitbody seems to be a pileus and stipe differentiation-deficient and non-coloration mutant. Although the mutant did not differentiate pileus or hymenia, they produced AFSs bearing basidiospores on various agar media. Therefore, the white fruitbody-forming strains were supposed to be a non-differentiation and white fruiting mutant, but not non-sporulation. However, due to the brown basidiospores formed on the AFS, those of *G. lucidum* are not an albino mutant.

On the other hand, although the formations of white fruitbodies were reported on *Lentinus edodes* (Komatsu and Kimura, 1968), *Pleurotus ostreatus* (Arita, 1968) and *Auricularia polytricha* (Komatsu, 1977), their fruitbodies occurred almost normally except for a coloration. Because they differentiated to a fruitbody with normal stipe, pileus and hymenium, the white fruitbody-forming strains are supposed to be an albino-type, but not a differentiation-deficient mutant. The formation of white fruitbody by *A. polytricha* is genetically controlled by a single recessive gene (Komatsu, 1977).

The colonies of *G. lucidum* develop various features which are affected by the incubation conditions. Isolates could be divided into three groups according to the *in vitro* morphogenetic responses under light and ventilation conditions. The first group is those which produce well-developed AFSs under the light and ventilation condition. The second one is those which form FBP under the light condition. The third one is those which develop only a vegetative mycelial growth even in light condition (Seo *et al.*, 1995b). Although the white fruitbody-forming isolate Gl-011 formed FBP on agar media, this isolate belongs to the first group that is AFS-forming isolate group. The FBP of isolate Gl-011 readily changed to AFS in a successive culture under light and ventilation. However, the wild type *G. lucidum* strains that were tested for the formation of AFS and FBP on CM form either AFSs or FBPs (Seo *et al.*, 1995b). Although the light wavelength and intensity for the induction of AFS formation were similar in isolate Gl-010 and Gl-011, the light illumination process for AFS induction was different (Table 3) (Cho *et al.*, 1994). Furthermore, the morphology of AFSs and color of colonies formed on CM were significantly different in the two isolates. On the other hand, Seo *et al.* (1995b) reported that light and ventilation were absolutely required for the AFS formation of *G. lucidum*. However, although isolate Gl-030 did not form AFSs on CM, the four white fruiting isolates derived from isolate Gl-030 well developed AFSs even in dark and/or BLB illumination condition. This fact suggests that the white fruiting isolates were mutated on the sites of photo-receptor that relate to AFS formation as well as fruitbody differentiation.

The white fruitbody of *G. lucidum* is considered to be a mutant that pileus differentiation mechanism is mutated. Thus, the fruitbody primordia could not differentiate to the reddish brown stipe, pileus and hymenium. However, the fact that AFS could form on agar media might suggest that the capacity of basidiospore formation remained. Another interesting characteristic of the white mutant isolates is that they show a different photo-response in AFS formation. The white mutant isolates may be useful to clarify the transition mechanisms from vegetative to reproductive growth in *G. lucidum*.

적 요

영지버섯 원목재배시 발생한 백색자실체에서 2핵 균사체 5균주를 분리하였다. 이들 균주의 자실체는 정상적인 갓, 자실층, 대로 분화되지 않았고, 발생해서 3개월 후에도

착색되지 않았다. 이들 백색자실체 형성균주와 재배용 균주는 배지상에서의 생장률, 균총의 색 그리고 비정형자실체(atypical fruiting structure; AFS)의 형성에 차이를 보였다. 백색자실체 형성균주는 환기와 광 조건하에서 갈색의 AFS를 쉽게 형성하였다. GI-010과 GI-011 균주는 암상태와 BLB 광을 조사하였을 때에는 AFS를 형성하지 않았지만, 가시광선하에서는 AFS를 형성하였다. 이들 균주의 AFS형성은 0.5 μmol m^{-2} s^{-1} 이하의 약한 광에서 잘 형성되었고, 그 이상의 광도에서는 억제를 받았다. 한편, GI-010과 GI-011 균주 이외의 4 균주는 암상태와 BLB에서도 AFS를 잘 형성하였으나, 이들의 모균주인 GI-030은 어떠한 광조건하에서도 AFS를 형성하지 못하였다. AFS에서 형성된 담자포자를 발아시켜 얻은 단핵 균사체는 모균주와 화합성이었다.

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