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FULL PAPER

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Influence of light on the morphological changes that take place during the development of the *Flammulina velutipes* fruit body

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Abstract We show that fruit bodies of *Flammulina velutipes* can be induced in complete darkness after a sharp temperature reduction (23° to 16°C). However, the fruit bodies that form in complete darkness have a long stipe with an undeveloped pileus on the top (pinhead fruit bodies) and are thinner and whiter than the normal fruit bodies which are formed in the light. This finding suggests that *F. velutipes* fruit bodies cannot mature in complete darkness. However, when we irradiated the fruit bodies that had formed in complete darkness, a pileus developed immediately, and 4 days later the separation between the stipe and the pileus could be observed. Immediately after light exposure, the stipe also thickened and became increasingly pigmented. The stipe elongation was inhibited until 8 days after light exposure, although stipe elongation progressed very quickly thereafter. Basidospores were also visible in the gills 8 days after light exposure. We consider that the basidiospore development is involved in this rapid stipe elongation, which aids the effective dispersal of basidiospores.

Key words *Flammulina velutipes* · Light · Pileus formation · Pinhead fruit body · Stipe elongation

Introduction

Environmental factors such as light and temperature are believed to stimulate the morphological changes that take place during the fruit body formation of many basidiomycetous mushrooms. For example, light is known to stimulate the formation of the fruit body primordia of *Favolus arcularius* (Kitamoto et al. 1968), *Schizophyllum commune* (Perkins and Gorden 1969), *Coprinus cinereus* (Tusué 1969), and *Lentinula edodes* (Mohamed et al. 1992a,b). It is also known to stimulate the formation of the pileus of *F. arcularius* (Kitamoto et al. 1974), *C. cinereus* (Kamada et al. 1978; Kamada and Tuji 1979), and *L. edodes* (Mohamed et al. 1992a,b). Furthermore, light induces several other morphological changes that occur during the life cycle of basidiomycetous mushrooms, such as those take place during asexual sporulation (Kües et al. 1998; Kertesz-Chaloupkova et al. 1998). With regard to the molecular mechanisms involved in these light-regulated events, the formation of the fruit body of *S. commune* is known to involve the expression of several genes (Wessels et al. 1987; Ruiters et al. 1988). In addition, the levels of cyclic adenosine monophosphate (cAMP), which is known as a fruiting stimulating factor (Uno and Ishikawa 1973; Swamy et al. 1985), increase after light irradiation (Yli-Mattila 1987). Thus, light is one of the most important factors that regulate fruit body formation in basidiomycetous mushrooms.

Flammulina velutipes can survive at low temperatures (Ingold 1978, 1980), and sometimes it requires low-temperature treatments to form a fruit body (Aschan 1954; Aschan-Åberg 1958; Plunkett 1953, 1956). Indeed, *F. velutipes* can form fruit bodies when it is briefly exposed (minimal duration, 12 h) once to low temperature, 15°C (Kinugawa and Furukawa 1965). Furthermore, it has been reported that *F. velutipes* can form fruit bodies in total darkness (Plunkett 1953, 1956; Aschan 1954; Kinugawa 1977), although these fruit bodies lack mature pilei (Plunkett 1953, 1956; Kinugawa 1977; Sakamoto et al. 2002). It was shown that the diameter of the pileus increases in proportion to the light intensity (up to 100 lx; Inatomi et al. 2001), and thus it is believed that the formation of the pileus of *F. velutipes* is stimulated by light. Fruiting in the darkness has also been reported for several other basidiomycetous mushrooms. For example, when *C. cinereus* is grown in complete darkness, it forms fruit bodies with a long stipe and a very tiny, undeveloped pileus on top that is

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denoted as a dark stipe (Tusué 1969). In addition, when the light-induced fruit body primordia of *F. arcularius* are transferred into darkness, their pilei do not develop, resulting in fruit bodies with a long stipe and an undeveloped pileus (Fukutomi et al. 1982; Kitamoto et al. 1997) that is denoted as an epilete stipe (Kitamoto et al. 1968). However, when the dark stipe of *C. cinereus* and the epilete stipe of *F. acularius* are exposed to light, both can form a pileus on the apical region of the stipe (Tusué 1969; Fukutomi et al. 1982). To date, however, it is not clear whether *F. velutipes* fruit bodies that have formed in complete darkness can also form a pileus in response to light stimulation. To investigate this question, we conducted the experiments reported here.

Materials and methods

Strains and culture conditions

The dikaryon Fv-4 (*Flammulina velutipes*: obtained from the Hokkaido Forest Products Research Institute, Asahikawa, Japan) was used in this study. Mycelia grown on potato dextrose agar (PDA) plates for 5 days at 23°C in the dark were punched out to create disks 5 mm in diameter. These were then inoculated on sawdust medium, which contained beech (*Fagus crenata*) sawdust and wheat bran (sawdust : wheat bran, 4 : 1 v/v) and had a water content of 65%. The cultures were incubated at 23°C in the dark for 1 month.

Investigation of the influence of light to the morphology of the *F. velutipes* fruit body

To induce normal fruit body formation, the 1-month-old cultures were transferred into a 16°C room that was continually illuminated with fluorescent lights at 500 lx (fruiting treatment; Sakamoto et al. 2002). For the light irradiation experiments (light treatment; Sakamoto et al. 2002), the 1-month-old cultures were transferred into a 23°C room that was continually illuminated with fluorescent lights at 500 lx. To induce the fruit body in complete darkness, the 1-month-old cultures were transferred into a 16°C room that was continually dark (low-temperature treatment). To investigate the morphological changes that occur after fruit bodies formed in complete darkness are stimulated with light, the fruit bodies were allowed to form under the same conditions as those for the low-temperature treatment in complete darkness, as described above. After 21 days of the low-temperature treatment (approximately 1 week after pinhead fruit bodies were formed), the fruit bodies were transferred into a room that was under the same conditions as the fruiting treatment (secondary light stimulation). These experiments are summarized in Fig. 1.

Investigation of stipe elongation

To investigate the influence of light on stipe elongation, the stipe lengths of fruit bodies that continued to develop in continuous darkness were compared to the stipe lengths of fruit bodies that were subjected to secondary light stimulation. For this, we used the fruit bodies that had formed 21 days after low-temperature treatment and divided them into two groups. One group continued to be cultured in complete darkness (the low-temperature treatment conditions) while the other group cultured under light (the secondary light stimulation conditions). We then measured the stipe lengths and the thicknesses of 20 samples from each group. The samples from each group were measured 0, 4, 8, 12, and 16 days after the secondary light treatment (the day just before the secondary light stimulation was defined as day 0). We measured the stipe thickness at two points, namely, 15 mm down from the bottom of the pileus (upper thickness; in the case of fruit bodies that continued to be cultured in complete darkness, the measurement was taken from the top of the pinhead fruit bodies) and 15 mm above the base of the stipe (lower thickness).

Results and discussion

Morphological features of *F. velutipes* fruit bodies that develop in complete darkness

When dikaryotic mycelia are grown under fruiting conditions (lowered temperature and continual light illumination), young fruit bodies form 14 days later, while by 21 days, the pilei have expanded widely. These are referred to as normal fruit bodies (Sakamoto et al. 2002). On the other hand, no fruit body was observed after the light treatment. We found that when mycelia grown in sawdust medium for 1 month were subjected to the low-temperature treatment, namely, complete darkness at 16°C, young fruit bodies were observed 14 days later (Fig. 2a). However, the tops of these young fruit bodies looked spiky (Fig. 2a). These fruit bodies are referred to as pinhead fruit bodies. Pileus tissue was not observed when apical sections of the 14-day pinhead fruit bodies were examined by light microscopy (Fig. 3a). These observations support the previous accounts of the fruiting of *F. velutipes* in complete darkness (Aschan 1954; Aschan-Åberg 1958; Plunkett 1953, 1956; Kinugawa 1977). It has been reported that the young fruit bodies of *F. velutipes* that are smaller than 0.2 mm and which have formed under light also have a spiky appearance, and that as the primordia increase in size the rudimentary pileus differentiates (Williams et al. 1985). Our observations support the finding by Williams et al. (1985), namely, that during the early stages of the primordia development of *F. velutipes*, the pileus is not differentiated. However, unlike the normal fruit bodies, the fruit bodies that formed 21 days after low-temperature treatment in complete darkness had a long thin stipe and no pileus (Fig. 2b). This fruit body is similar in shape to that of *C. cinereus* after its cultivation in complete darkness; such *C. cinereus* stipes have been denoted as dark stipes (Tusué 1969). This finding suggests that in complete darkness, the primordia of *F. velutipes* can be induced and stipe elongation does occur. However, pileus formation does not occur in the dark.

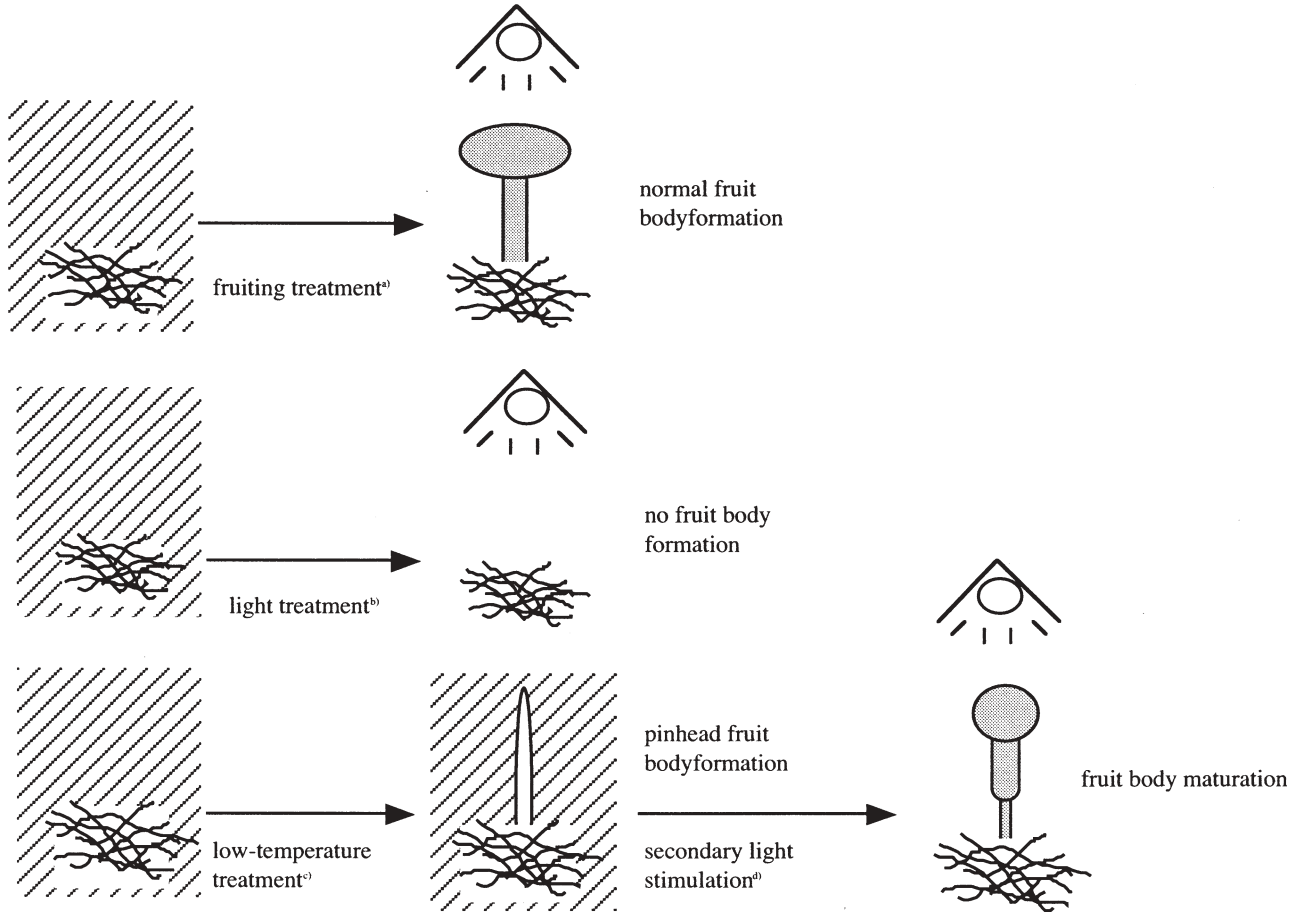

Fig. 1. Experimental scheme used to investigate the effect of temperature and light on the morphology of the *Flammulina velutipes* fruit body. **a–c** One month-old cultures grown in complete darkness at 23°C were then subjected to fruiting treatment (continuous illumination at 16°C) (**a**), light treatment (continuous illumination at 23°C) (**b**), and low-temperature treatment (continuous darkness at 16°C) (**c**). **d** One month-old cultures grown in complete darkness at 23°C were then subjected to the low-temperature treatment for 21 days, at which point pinhead fruit bodies had formed, and were then subjected to secondary light stimulation (continuous illumination at 16°C)

The fruit bodies that formed in complete darkness were found to be thinner than the normal fruit bodies that formed during fruiting treatment (see Fig. 2b) (Sakamoto et al. 2002). Furthermore, the fruit bodies that formed in complete darkness were not pigmented, which supports the current understanding that the fruit body color of commercially cultivated *F. velutipes* is correlated to the degree of light exposure (Shiratori et al. 1982; Inatomi et al. 2001). These findings suggest that although low temperature is a critical factor for the fruit body induction of *F. velutipes*, the fruit bodies cannot mature in complete darkness. In the experiments described next, we subjected the fruit bodies that had formed 21 days in complete darkness to light exposure (secondary light stimulation) and compared them to the fruit bodies that continued to be cultivated in the dark. This analysis revealed that light induced marked morphological changes in the pinhead fruit bodies, as described next.

Morphological changes induced in pinhead fruit bodies by secondary light stimulation

We irradiated the pinhead fruit bodies that formed after 21 days of the low-temperature treatment in complete darkness, and found that the pileus immediately began to develop on top of the pinhead fruit body (Fig. 2c). This suggests that light can stimulate the formation of the pileus of *F. velutipes*. Microscopic examination revealed that 4 days after the secondary light treatment commenced, the pileus and stipe separated (Fig. 3b). Moreover, 8 days after secondary light treatment commenced, basidiospores were observed, and after 14 days the pileus was widely expanded (Fig. 2d). In contrast, the fruit bodies that continued to be cultivated in the dark did not exhibit any of these developments. These findings suggest that the *F. velutipes* fruit bodies that form under complete darkness have the potential to form a pileus. This result is similar to what has been observed for other species whose fruit bodies can form in the dark, including *C. cinereus* (Tusué 1969) and *F. arcularius* (Fukutomi et al. 1982). That we could not observe pileus

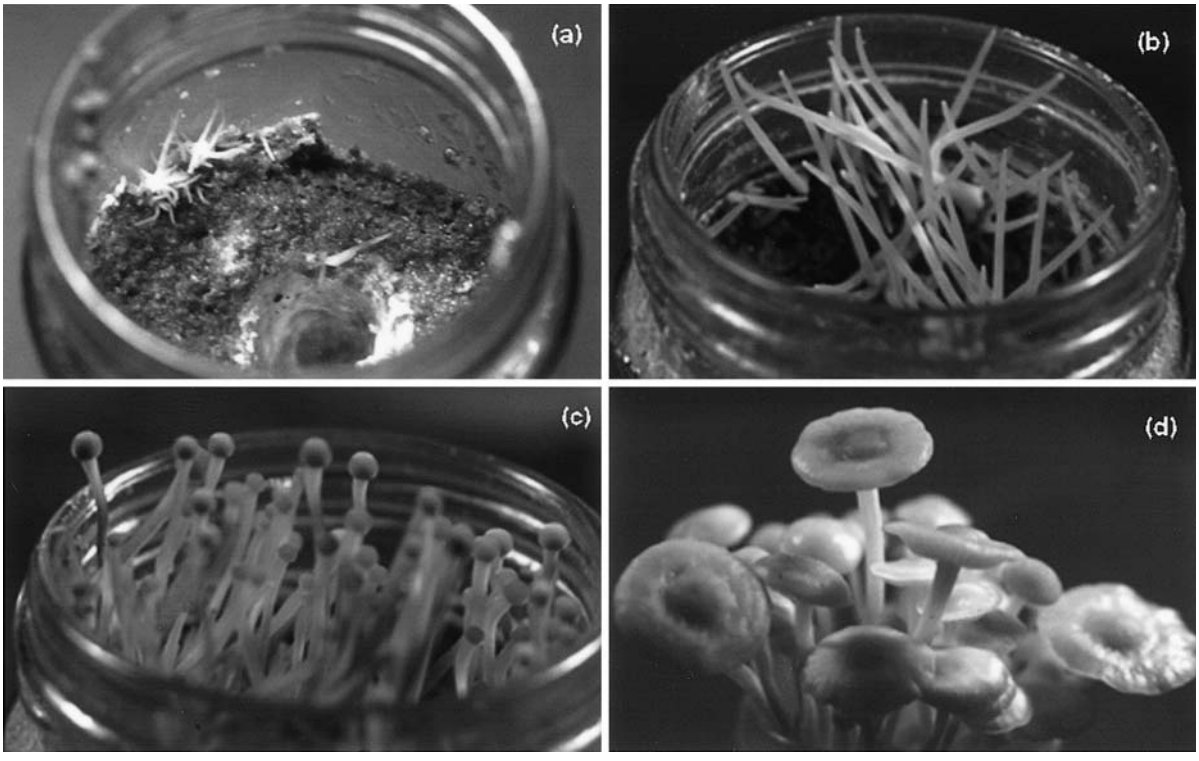

Fig. 2. Pinhead fruit body and pileus of *F. velutipes* after being grown under varying light conditions. **a** The pinhead fruit bodies that form after 14 days of the low-temperature treatment. **b** The pinhead fruit bodies that form 21 days after the low-temperature treatment. **c** The pileus that forms on the apical region of the pinhead fruit body 7 days after secondary light stimulation. **d** The pileus that forms on the apical region of the pinhead fruit body 14 days after secondary light stimulation

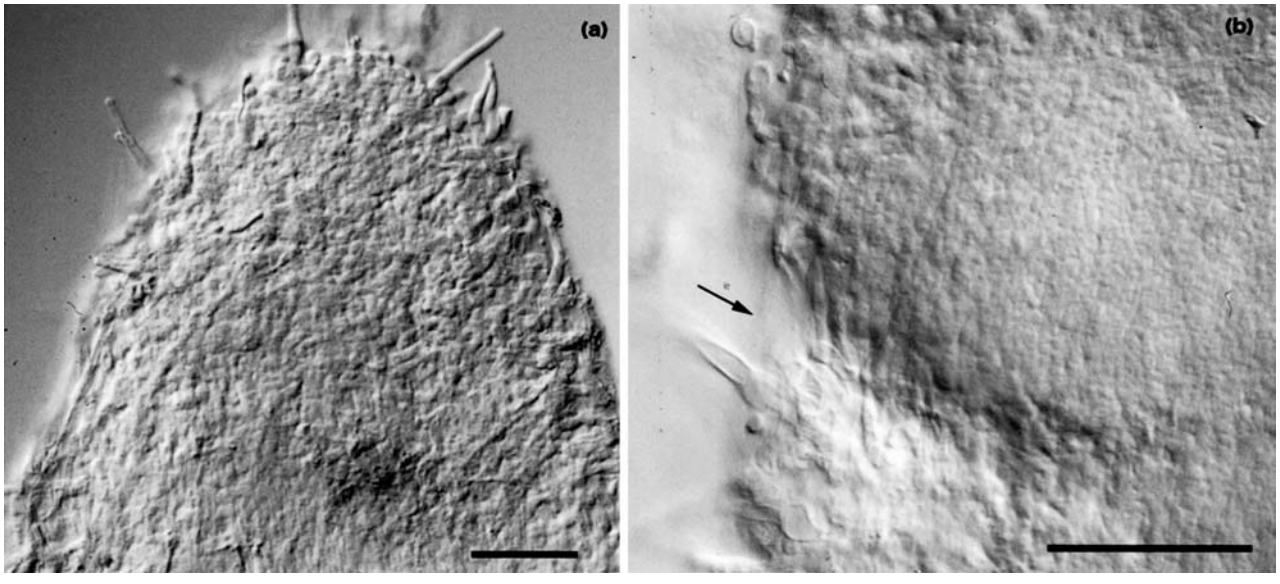

Fig. 3. Differential interference (Nomarski) micrographs. **a** The apical region of the fruit body that formed after 14 days growth in the dark at 16°C. **b** The junction (*arrow*) between the pileus and the stipe of the fruit body that first developed in the dark at 16°C for 21 days and was then grown for 4 days in the light. *Bar* 50 μm

tissue in the apical region of the pinhead fruit bodies that had formed in the dark, and that the secondary light stimulation induced pilei only at the apical regions, suggests that only the apical regions of the pinhead fruit bodies have the potential to develop into pilei. It seems that the cells that can be differentiated into the pileus have already been established during the differentiation of the fruit body primordium. As a result, these cells should be defined as pileus

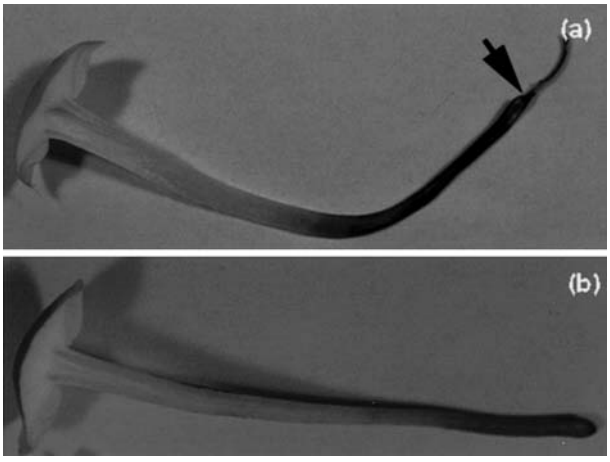

Fig. 4. Vertical sections of a normal fruit body and the fruit body that forms after secondary light treatment of the pinhead fruit body. **a** Fruit body that was grown for 21 days in complete darkness and then for 14 days under light. The beginning of the fruit body thickening is indicated by an *arrowhead*. **b** The normal fruit body that forms after 21 days of the fruiting treatment

primordium, which is the term used in describing the pileus formation of *F. arcularius* (Fukutomi et al. 1982).

We found that the pinhead fruit bodies became pigmented after secondary light stimulation (Figs. 2c,d, 4a). During normal fruit body formation, the brown fruit body gradually darkens to the base of the stipe (Fig. 4b). We found that the browning of the fruit bodies after secondary light stimulation occurred in a similar graduated manner (Fig. 4a). In Japan, the white strains of *F. velutipes* are of commercial importance (Kitamoto et al. 1993) and as a result the fruit body color of *F. velutipes* has been repeatedly studied. It has been found that the activity rates of two enzymes, phenol oxidase and superoxide dismutase, correlate with the color of the *F. velutipes* fruit body (Kitamoto et al. 1997). It was also shown that the color of the fruit body is influenced by the quality and quantity of light (Shiratori et al. 1982). However, the relationship between light exposure and the activities of the enzymes associated with the pigmentation is not well understood. The experimental system that we have described in this report, namely, fruiting of *F. velutipes* in low temperatures in the dark followed by secondary light stimulation, should be useful in investigating the roles that enzymes play in fruit body pigmentation.

The stipes of the pinhead fruit bodies thickened immediately after secondary light stimulation (Figs. 4a, 5a), although thickening did not occur on the basal side of the stipe (Figs. 4a, 5a). In contrast, stipe elongation was inhibited until 8 days after secondary light treatment commenced (Fig. 5b), although the stipe length of the fruit bodies that continued to form in the dark were longer at this time point (Fig. 5b). However, after this time point, the stipes of the secondary light-exposed fruit bodies elongated very rapidly (Fig. 5b). Indeed, 12 days after the secondary light stimulation, the stipes were longer than the stipes of the fruit bodies that continued to be cultured in the dark for the same period (Fig. 5b). In previous studies, it was observed that

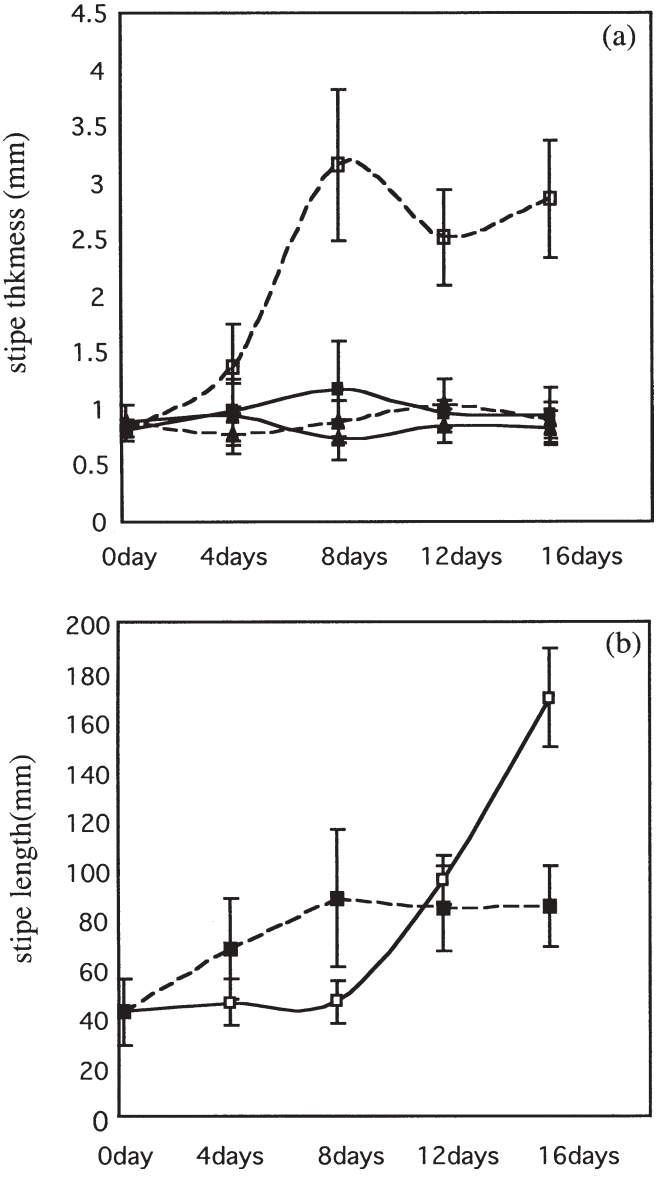

Fig. 5. Comparison of the stipe thickness and stipe length of the pinhead fruit bodies that continued to develop in the dark or that were subjected to secondary light stimulation. The values are shown as mean ± SD. **a** ■, upper stipe thickness of fruit bodies that continued to be incubated in the dark; ▲, lower stipe thickness of fruit bodies that continued to be incubated in the dark; □, upper stipe thickness of fruit bodies after secondary light stimulation; △, upper stipe thickness of fruit bodies after secondary light stimulation. **b** ■, stipe length of fruit bodies that continued to be incubated in complete darkness; □, stipe length of fruit bodies after secondary light stimulation

F. velutipes fruit bodies that form in the dark have long and narrow stipes (Kinugawa 1977), whereas fruit bodies that form in the strong light (200lx) have short stipes (Inatomi et al. 2001). Consequently, it is believed that light inhibits stipe elongation in *F. velutipes*. Notably, Gruen (1969) has demonstrated that the molecule(s) that induces stipe elongation may be located in the pileus lamellae, which suggests that the pileus of *F. velutipes* may promote the elongation of the stipe (Gruen 1976). However, that light on the one hand stimulates pileus formation (our observation) yet on the

other hand appears to inhibit stipe elongation contradicts the hypothesis that pileus formation stimulates stipe elongation in *F. velutipes*. This discrepancy may be reconciled by our observations that stipe elongation was inhibited temporally until 8 days of secondary light stimulation, and that the stipe elongated rapidly after the time point. We consider that this rapid elongation may occur in response to the molecule(s) from the pileus. Light microscopy did revealed that basidiospore were not visible at 4 days after the secondary light stimulation commenced, but basidiospores were visible on the surface of the gill at 8 days. Kamada and Tuji (1979) have reported that the phase 3 pileus (meiosis progress in the basidia) promotes fruit body maturation including stipe elongation. Thus, we consider that the time point that switches to rapid stipe elongation is influenced by the stage of basidiospore development in *F. velutipes*. This stipe elongation system may ensure the effective dispersal of basidiospores. However, we also noted rapid elongation of the stipe at the early stage of development in the dark, after which the elongation rate decreased (Fig. 5b). This observation suggests that there must be another stipe elongation system that operates in the dark which does not involve the pileus-derived stipe elongation molecule(s).

F. velutipes fruit bodies have been used to investigate the mechanisms underlying stipe elongation (Gruen 1969, 1974) and used for a model of gravitropism in mushrooms (Kern et al. 1997). It is believed that stipe gravitropism is caused by a combination of longitudinal and horizontal axis growth. Stipe growth in *C. cinereus* has been studied at the histological level (Moore 1996), and it was found that *C. cinereus* fruit body stipes elongate by cell elongation without cell division (Kamada and Takemaru 1977). In contrast, the stipe of *F. velutipes* appears to elongate by both cell division and cell elongation (Wong and Gruen 1977). However, *F. velutipes* stipe thickening and gravitropism have not been analyzed at the histological level as yet. Therefore, the relationships between pileus formation, stipe thickening, and stipe elongation in *F. velutipes* remain unclear. Careful studies on the direction of cell division and elongation during the stipe elongation and thickening that take place in certain conditions are needed to answer these questions.

Although stipe length, pileus size, and fruit body pigmentation of *F. velutipes* are very important from a commercial point of view, the mechanisms behind the stipe elongation, pileus formation, and fruit body pigmentation of *F. velutipes* are not well understood. In this article, we observed that *F. velutipes* fruit bodies develop in complete darkness, and that these fruit bodies have a long stipe and an undeveloped pileus on the top. Furthermore, we found that we could induce pileus formation and stipe thickening, elongation, and pigmentation in fruit bodies formed in the dark by secondary light stimulation. This finding suggests that light is the critical factor in the morphological changes that take place during the development of the *F. velutipes* fruit body. These observations will aid further histological and molecular biological investigations into the mechanisms behind fruit body induction, stipe elongation and thickening, fruit body pigmentation, and pileus formation in *F. velutipes*.

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