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Review

Influences of environmental factors on fruiting body induction, development and maturation in mushroom-forming fungi

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ARTICLE INFO

Article history:
Received 18 July 2017
Received in revised form
7 February 2018
Accepted 22 February 2018

Keywords:
Fruiting body
Gravity
Light
Nutrient
Senescence
Temperature

ABSTRACT

Mushroom-forming fungi (restricted to basidiomycetous fungi in this review) differentiate by sensing several environmental factors for fruiting body formation. For fruiting body induction, nutrient, temperature and light conditions are critical environmental factors. Higher nitrogen and carbon sources in the media will suppress fruiting body induction in many mushroom-forming fungi, with induction being triggered by lower nitrogen and carbon concentrations. Low temperature or temperature downshift is another critical influencing factor for fruiting body induction in many cultivated mushrooms, such as *Flammulina velutipes*, *Lentinula edodes*, and *Volvariella volvacea*. Fungal response toward starvation and cold involves the production of sexual spores as the next generation. Species like *F. velutipes* and *Coprinopsis cinerea* can form fruiting bodies in the dark; however, light accelerates fruiting body induction in some mushroom-forming fungi. Remarkably, fruiting bodies formed in the dark have tiny or no pileus on heads (called dark stipe, pinhead fruiting body, or etiolated stipe). Light is essential for pileus differentiation in many, but not all mushroom species; one exception is *Agaricus bisporus*. Mushrooms have positive phototropism and negative gravitropism for effective dispersal of spores. Carbon dioxide concentrations also affect fruiting body development; pileus differentiation is suppressed at a high concentration of carbon dioxide. Thus, the pileus differentiation system of mushrooms may allow the most effective diffusion of spores. Full expansion of the pileus is followed by pileus autolysis or senescence. In *C. cinerea*, pileus autolysis occurs during spore diffusion. Fruiting body senescence, browning of gill, and softening occur after harvesting in several mushroom species. Fruiting body induction, development, and maturation in mushroom-forming fungi are discussed in this review.

1. Introduction

Mushrooms are large fruiting bodies that comprise basidiomycetes and some ascomycetes. Mushrooms are consumed as fresh or dried food, or as a medicinal nutrient. Thousands of species of mushroom-forming fungi have been identified, but limited species are commercially cultivated. The latter include *Agaricus bisporus* (white button mushroom), *Lentinula*

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https://doi.org/10.1016/j.fbr.2018.02.003
1749-4613/

edodes (Shiitake), *Pleurotus ostreatus* (oyster mushroom), and *Flammulina velutipes* (Enokitake) and so on. Many edible mushrooms are not commercially cultivated, but instead are collected in the wild. Some, including *Tricholoma matsutake* (Matsutake) and *Boletus* species (Porcini), are mycorrhizal fungi that cannot be cultivated artificially.

Understanding the molecular basis of fruiting body development is important as a research issue. This knowledge will also benefit the commercial production of mushrooms. Fungal development, mainly in basidiomycetous mushroom-forming fungi, has been studied for decades (Kües, 2000; Kües and Liu, 2000; Wessels, 1993; Whiteford and Thurston, 2000). More recently, fungal genome sequences have been deduced and are publicly available for model mushroom species including *C. cinerea* (Stajich *et al.*, 2010) and *Schizophyllum commune* (Ohm *et al.*, 2010); cultivated mushrooms including *L. edodes* (Chen *et al.*, 2016; Sakamoto *et al.*, 2017), *F. velutipes* (Park *et al.*, 2014), *Ganoderma lucidum* (Liu *et al.*, 2012), *Agaricus bisporus* (Morin *et al.*, 2012), and *Volvariella volvacea* (Bao *et al.*, 2013); and for the mycorrhizal species *Laccaria bicolor* (Martin *et al.*, 2008). Gene expression for fruiting body development has been explored using transcriptome analyses in many species, including *S. commune* (Ohm *et al.*, 2010), *A. bisporus* (Morin *et al.*, 2012), *G. lucidum* (Yu *et al.*, 2012), *C. cinerea* (Muraguchi *et al.*, 2015), *F. velutipes* (Park *et al.*, 2014), *V. volvacea* (Tao *et al.*, 2014), and *L. edodes* (Chen *et al.*, 2016; Sakamoto *et al.*, 2017). However, the molecular basis of fruiting body development in basidiomycetous fungi has not been well characterised compared with ascomycetes (Busch and Braus, 2007; Engh et al., 2010; Steffens *et al.*, 2016; Voigt *et al.*, 2013). There are three reasons for this. First, it takes longer to form a fruiting body in basidiomycetes, especially in commercially cultivated fungi, than in ascomycetes. Second, gene manipulation technology is limited in basidiomycetes. Third, multiple environmental factors are involved in fruiting body induction and development.

Mushroom-forming fungi sense multiple environmental conditions in order to decide on the proper location and timing of sexual reproduction, as well as to form fruiting bodies with a shape that is suitable for effective spore dispersal. In this review, environmental factors for fruiting body induction (light, temperature, and nutrients as three examples), development (light, gravity, and carbon dioxide concentration as three examples), and maturation or senescence (during/after sporulation and after artificial harvesting) of mushroom-forming basidiomycetes are summarized. Future perspectives to understand molecular basis of fruiting body formation in basidiomycetes are described.

2. Environmental factors for fruiting body induction

Environmental factors that individually or in combination influence fruiting body induction in basidiomycetes comprise physical and physiological factors. Physical factors include light, temperature, and injury. Physiological factors include nutrients, gaseous components, and hormones. The precise details of the effect of the individual environmental factors on fruiting body induction in basidiomycetes remain unclear. Efforts to clarify these details have included the use of model organisms like *C. cinerea* and *S. commune*. These fungi can form fruiting bodies when exposed to a constant temperature with/without light during growth on agar. In these conditions, *C. cinerea* forms the initial fruiting body (stage I primordia, Kües 2000). In contrast, temperature is critical for fruiting body induction in many cultivated mushrooms (Stamets, 2000). In several species, fruiting body-inducing molecules, such as cerebrosides (Kawai and Ikeda, 1982) and saponins (Magae, 1999), have been identified. In some cultivated mushrooms, mechanical injury or scratching of the mycelia on the surface of a cultivating medium ("kinkaki" in Japanese) is effective for fruiting body induction (Kitakamoto *et al.* 1992; Yoshimura *et al.*, 1995). In this section, environmental factors that influence the induction of fruiting bodies are discussed.

Light

Light is crucial for morphogenesis in plants and fungi for photosynthesis or morphogenesis. Its influence has been well characterized in ascomycetes (Fuller *et al.*, 2015). It is considered that mushroom forming fungi sense light for spatial recognition for sexual reproduction, but the relationship between light and fruiting body induction in basidiomycetes has been unclear. The presence of light may not always be essential for fruiting body induction; fruiting body production can be induced under complete darkness in some basidiomycetes (Kamada *et al.*, 2010; Kinugawa, 1977; Sakamoto *et al.*, 2004, 2002; Tsusué, 1969). However, light can induce fruiting body or promote fruiting body production; such as *L. edodes* (Leatham and Stahmann, 1987), *Polyporus* (*Favolus*) *arcularius* (Kitamoto *et al.*, 1968), and *C. cinerea* (Tsusué, 1969). The effective wavelength for fruiting body induction includes ultraviolet wavelength (280 nm) and blue light (520 nm) (Durand and Furuya, 1985; Kitamoto *et al.*, 1972). Similar wavelengths are effective for the induction of pileus development in *P. arcularius* (Kitamoto *et al.*, 1974). More recently, it was revealed that light can induce hyphal knot formation on circle in *C. cinerea* cultured on limited glucose media (Muraguchi *et al.*, 2015). These observations suggest that light can affect fruiting body induction in some basidiomycetous fungal species but is not necessarily required in some species. Light receptors that have been identified in ascomycetes include blue light receptors WC1/WC2 complex and cryA, or red light receptor phyA (Dunlap, 2006; Fuller *et al.*, 2015; Linden *et al.*, 1997). Several blue light reception mutants have been identified in basidiomycetes. In *C. cinerea*, *dst-1* encodes WC1 (Terashima *et al.*, 2005) and *dst-2* encodes photolyase (Kuratani *et al.*, 2010). The WC2 homologue gene was identified in *C. cinerea*, and the gene was disrupted (Nakazawa *et al.*, 2011). Knockout mutants of *dst-1*, *dst-2*, and *Ccwc2* can form fruiting bodies that have an abnormal shape (see section 3 for a further discussion), suggesting that these blue light receptors do not affect, or only have a limited effect, on fruiting body induction in *C. cinerea* (Kuratani *et al.*, 2010; Nakazawa *et al.*, 2011; Terashima *et al.*, 2005). There might be other, yet unknown, blue light receptor(s) that affect fruiting body induction in *C. cinerea*. In contrast, Δwc1/Δwc1 andΔwc2/Δwc2 in *S. commune* prevent fruiting body induction (Ohm *et al.*, 2013). This suggests that

the roles of blue light receptors for fruiting body induction vary among mushroom species.

Temperature

Low temperature threatens life of fungal mycelia, therefore, low temperature is one of important trigger for sexual reproduction. Temperature downshift is used for fruiting body induction in many mushroom species (Stamets 2000), such as *L. edodes* (Nakazawa *et al.*, 2008), *A. bisporus* (Morin *et al.*, 2012), *F. velutipes* (Sakamoto *et al.*, 2002), and *Pleurotus eryngii* subsp. *tuoliensis* (Bailinggu) (Fu *et al.*, 2016), and *Armillaria mella* (Ford *et al.*, 2015). Yet, fruiting body primordia can be induced without any temperature shift in model mushroom species like *C. cinerea* and *S. commune* (Muraguchi *et al.*, 2015; Ohm *et al.*, 2010). Thus, there is still a limited understanding of the molecular basis for fruiting body induction affected by temperature. Transcriptome analyses of fruiting body induction have been carried out in several cultivated mushroom species like *F. velutipes* (Park *et al.*, 2014) and *A. bisporus* (Morin *et al.*, 2012). However, in these studies, several environmental factors including light and aeration were active simultaneously, which made it difficult to distinguish the individual effect of temperature.

In *F. velutipes*, also termed the winter mushroom, the temperature conditions for fruiting body induction are known (Aschan, 1954). Fruiting body formation is induced in *F. velutipes* in the dark upon temperature downshift (Kinugawa, 1977; Sakamoto *et al.*, 2002). Therefore, *F. velutipes* is a good species to use to investigate the relationship between fruiting body induction and temperature. Protein expression studies in *F. velutipes* during fruiting body induction revealed that most of the proteins that are specifically expressed during fruiting body induction are induced by temperature downshift (23 °C → 16 °C) in the dark (Sakamoto et al., 2002). In constrast, light without temperature downshift cannot induce protein expressions specifically expressed during fruiting body induction (Sakamoto *et al.*, 2002). A gene, *FDS* is identified as a fruiting body specific gene in *F. velutipes* (Azuma *et al.* 1996a, b) and it is revealed that the FDS protein expressed by temperature downshift without light exposure (Sakamoto *et al.*, 2002). The *FDS* gene is conserved only in a few basidiomycetous species, such as *L. bicolor* and *Piloderma croceum*. More recently, a comprehensive proteomics analysis in *F. velutipes* cultivated under cold stress revealed the cold-shock upregulation of energy metabolism and amino acid metabolism-related proteins and Class V chitinase ChiB1 (Liu *et al.*, 2017). In *Pleurotus eryngii* subsp. *tuoliensis* (Bailinggu), a much lower temperature (25 °C → −3 °C) is used for fruiting body induction. The analysis of gene expressions after cold shock in Bailinggu suggested the upregulation of genes involved in cell wall and membrane stabilisation (hydrophobin, fatty acid desaturases, phospholipase), calcium signalling and osmotic regulation, production of soluble sugars and protein biosynthesis and metabolism, and transcription regulation (Fu *et al.*, 2016).

Although these results are helpful for a better understanding of the role of temperature in fruiting body induction, more comparative analyses are needed to fully understand the effect of temperature on fruiting body induction. A cold temperature sensing system has been identified in ascomycetes. One example is *Mga2* in *Saccharomyces cerevisiae* (Hoppe *et al.*, 2000; Nakagawa *et al.*, 2002; Shcherbik *et al.*, 2003). In contrast, there is little knowledge on temperature sensing systems for fruiting body induction in basidiomycetes. In *S. commune* and *C. cinerea*, fruiting body formation can be optionally induced by temperature downshift (Sen *et al.*, 2016; Tsusué, 1969). These species should be ideal to investigate the mechanism of fruiting body induction by temperature downshift.

Nutrient factors and chemical compounds for fruiting body induction

Starvation is also critical signal of environmental deterioration, therefore, nutrients are also critical signal for sexual reproduction in mushroom-forming fungi (Aschan-Aberg, 1958; Aschan, 1954; Plunkett, 1953). Nitrogen starvation is one of the most important factor for fruiting body induction in mushroom-forming fungi (Plunkett, 1953). Nitrogen starvation is a trigger for sporulation in *S. cerevisiae* and autophagy is involved in sporulation triggered by starvation (Abeliovich and Klionsky, 2001). Autophagy is also involved in conidia formation in filamentous fungi (Kikuma *et al.*, 2006a, 2006b). In several species, increased proteinase activity is correlated to fruiting body induction (Burton *et al.*, 1997; Terashita *et al.*, 1998, 1997), and the autophagy-related gene is upregulated during fruiting body formation in *Moniliophthora perniciosa* (Gomes *et al.*, 2016). However, there is no clear evidence that autophagy is involved in fruiting body induction triggered by nitrogen starvation in mushroom-forming basidiomycetes.

Carbon concentration (mainly glucose concentration) also affects fruiting body induction in several species (Kitamoto and Gruen, 1976; Madelin, 1956; Moore and Jirjis, 1976). For example, in presence of low glucose (0.2 %), light exposure induces fruiting body formation in *C. cinerea* (Muraguchi *et al.*, 2015). Low concentration of carbon and nitrogen induces expression of galectin, *cgl1* and *cgl2* in *C. cinerea* (Boulianne *et al.*, 2000).

In *S. commune*, it is reported that cAMP affects fruiting body induction (Schwalb, 1974); the amount of cAMP is increased by the addition of indole and caffeine under several conditions in *S. commune* (Kinoshita *et al.*, 2002). It has been suggested that caffeine represses phosphodiesterase activity, resulting in the accumulation of cAMP (Kinoshita *et al.*, 2002). Furthermore, a TRP (tryptophan requiring) *S. commune* mutant (*trp*-) displays delayed fruiting body induction, and the expression of indole-3-glycerol phosphate synthase (IGPS) in this mutant increases fruiting body formation (Sen *et al.*, 2016). These observations suggest that tryptophan and indole metabolism would affect fruiting body induction via cAMP signalling. Remarkably, the tryptophan metabolites anthranilic acid, benzoic acid, and nicotinic acid can induce fruiting body formation in *P. arcularius* and *F. velutipes* (Murao *et al.*, 1984). Further studies are needed to fully reveal the relationships between environmental factors, cAMP, and tryptophan metabolism for fruiting body induction in basidiomycetes.

Penicillium funiculosum affects fruiting body formation in *S. commune* when the two organisms are co-cultivated (Kawai *et al.*, 1985). Cerebrosides were isolated from *P. funiculosum* as a fruiting body inducing factor in *S. commune* (Kawai *et al.*, 1985), and similar compounds were also identified from *S. commune* (Kawai, 1989; Kawai and Ikeda, 1983, 1982).

Cerebrosides in *S. commune* can induce fruiting body formation, but do not function without *P. funiculosum* co-cultivation. This suggests that *P. funiculosum* affects a cerebroside-sensing system in *S. commune*. Saponins induce fruiting body formation in *P. ostreatus* (Magae, 1999; Magae *et al.*, 2005; Magae and Ohara, 2006). Saponins and cerebrosides are membrane-interactive compounds. The gene encoding cyclopropane fatty acyl phospholipid synthase, *cfs1*, is essential for fruiting body induction in *C. cinerea* (Liu *et al.*, 2006). It is suggested that CFS1 produces membrane-interacting compound stimulating fruiting body induction in *C. cinerea* (Liu *et al.*, 2006). Membrane interactive compounds and sensing system would be key factors for fruiting body induction in mushroom-forming basidiomycetous fungi.

Gene expression during fruiting body induction

Several transcriptome studies have compared vegetative mycelia and primordia in mushroom-forming fungi. Transcription factor genes have been identified in *C. cinerea* (Muraguchi *et al.*, 2015) and *S. commune* (Ohm *et al.*, 2011). During fruiting body initiation, genes with phospholipid biosynthesis process are also upregulated in *C. cinerea* (Muraguchi *et al.*, 2015). In *C. cinerea*, several chromosome remodelling genes are essential for fruiting body induction (Ando *et al.*, 2013; Nakazawa *et al.*, 2016a). Upregulation of protein synthesis, energy production, and hydrophobins have been described in the fruiting body initiation stage in *S. commune* (Ohm *et al.*, 2010). Stress response genes are upregulated in mycelia during fruiting body formation in several cultivated mushrooms. These observations suggest that global gene expression changes occur during fruiting body induction. However, how environmental factors, light, temperature, or nutrients stimulate these global gene expression changes for fruiting body induction remains to be investigated.

3. Environmental factors for fruiting body development

Aggregation of hyphae occurs in the early stage of fruiting body development, and fruiting body shape can be immediately affected by environmental factors including nutrients, humidity, temperature, carbon dioxide concentration, gravity and especially light. These environmental factors affect one another to form appropriate shape of fruiting body for effective spore dispersal. In general, light affects pileus formation and stipe elongation, and fruiting bodies that form in the dark have an abnormal shape that is characterised by a long stipe with tiny or no pileus (called dark stipe: *C. cinerea* (Terashima *et al.*, 2005), etiolated stipe: *C. cinerea* (Kües, 2000), or pinhead fruiting body: *F. velutipes* (Sakamoto *et al.*, 2007)). Light also affects the direction of stipe elongation, which results in positive phototropism. Many mushrooms also display gravitropism, and carbon dioxide can affect fruiting body shape. For example, pileus formation is suppressed and stipe elongation is promoted in an environment with a high concentration of carbon dioxide. Thus, mushrooms sense light, gravity, and carbon dioxidide concentration to develop proper pileus to enable effective diffusion of spores.

Carbon dioxidide concentration affects fruiting body shapes

The influence of the gaseous condition on fruiting body shape is relevant in commercial mushroom production. Respiration and the concentration of carbon dioxide during fruiting body formation have been investigated (Kinugawa and Tanesaka, 1990, 1994). Respiration activity increases during primordia formation in the development of fruiting bodies, and a high concentration of carbon dioxide affects fruiting body morphology. Sensitivity to carbon dioxide has been investigated in the commercially cultivated mushroom varieties of *F. velutipes*, *P. ostreatus*, *Pholiota nameko* (*microspora*), *L. edodes*; of these, *P. ostreatus* is most sensitive to carbon dioxide (Kinugawa *et al.*, 1994). In many mushroom species, pileus is not fully developed and stipe is spindly elongated at a high carbon dioxide concentrations (Kinugawa *et al.*, 1994; Kinugawa and Tanesaka, 1990). The morphology is similar to that produced in the absence of light (see section 3.3). In the early stage of fruiting body development, sensitivity to carbon dioxide is more pronounced (Kinugawa *et al.*, 1994). Elevated carbon dioxide affects the synthesis of the cell wall component, R-glucan (Sietsma *et al.*, 1977) and fruiting body cell morphology (Raudaskoski and Salonen 1984).

Tropism toward gravity and light

Many mushrooms possess tropism toward gravity and light, termed gravitropism and phototropism, respectively, because the angle of the gill toward the ground is critical for spore diffusion (Kern, 1999). Both have been observed in many mushroom species (Buller, 1909; Moore, 1991; Moore *et al.*, 1996). Fruiting bodies of Agaricales that are exposed to light from one side often grow toward the light (positive phototropism), and an exception is *Agaricus bisporus* (Eger-Hummel, 1980). Many mushrooms possess negative gravitropism. It is suggested that the lifestyle of each mushroom (e.g. wood rotting or epigeous) affects the gravitropism or phototropism (Buller, 1909). Basically, lignicolous agaric fruiting bodies tend to develop upward under the influence of light, whereas the gills develop downward under the influence of gravity (Kaneko and Sagara, 2001a, 2001b). Remarkably, when exposed to light from below, the fruiting bodies grow downward through all stages of development (Kaneko and Sagara, 2001a, 2001b). Gravitropic bending involves growth inhibition at the upper side of a horizontally oriented transition zone, termed the graviperceptive region of the stipe. Pileus differentiation affects stipe elongation in mushroom-forming fungi (Kamada and Tsuji, 1979; Sakamoto *et al.*, 2004). The pileus itself may not be needed for gravitropism (Kern, 1999). However, stipe bending occurs at the upper region closest to the pileus (Kern, 1999), and it is suggested that stipe requires a signal that meiosis has been sufficiently advanced (Moore, 1996; Moore *et al.*, 1996). Monoterpentriols may be involved in this process; those isolated from stipe segments showed growth-promoting activities on excised stipes (Hirai *et al.*, 1998). Furthermore, calcium-mediated signal transduction may be involved in directing growth differential (Haindl and Monzer, 1994; Kern, 1999; Moore, 1996). The fastest ultrastructural response to the altered direction of the acceleration force is the accumulation of cytosolic vesicles at the lower part of

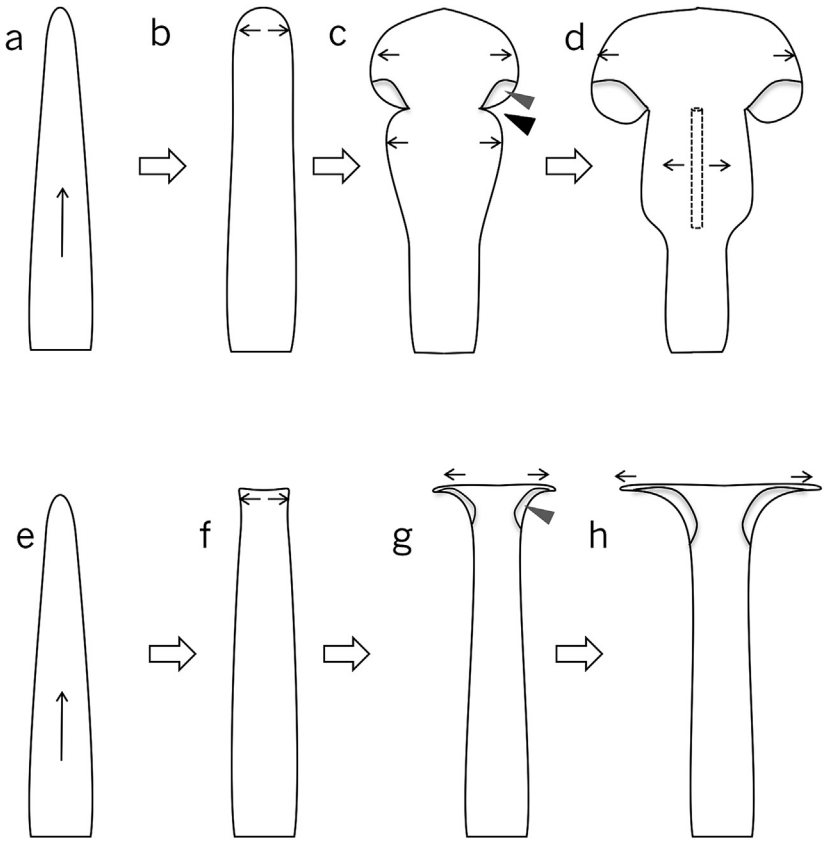

Fig. 1 – Pileus differentiation of *Flammulina velutipes* (a–b) and *Polyporus (Favorus) arcularius* (e–h) after harvest. Arrows indicate the direction of expansion of the pileus and elongation of stipes. The black triangle indicates the fracture between pileus and stipes formed after light exposure. The grey triangle indicates the developing hymenium.

this region (Kern, 1999; Moore *et al.*, 1996). They contribute to the expansion of the central vacuole and therefore, to the differential enlargement of the lower side of the stipe (Kern, 1999; Kern and Hock, 1995). Genes expressed in fruiting bodies developed under normal condition and three-dimensional clinostat-simulated microgravity condition were compared in *P. ostreatus* (Miyazaki *et al.*, 2010). The comparison revealed the downregulation of aegerolysin and ostreolysin, which are homologues of haemolysins, under simulated microgravity. Furthermore, a vacuole-specific protease was upregulated under simulated microgravity (Miyazaki *et al.*, 2010).

Induction of pileus development by light

Light is crucial for pileus differentiation in basidiomycetous mushroom-forming fungi, with a few exceptions like *A. bisporus*. Notably, some species can form fruiting bodies in dark. These fruiting bodies have long and tiny pileus or no pileus on long stipes. *C. cinerea* fruiting bodies formed in complete darkness have tiny pileus (Tsusué, 1969). This suggests that the very early stage of pileus development can occur in complete darkness (Terashima *et al.*, 2005; Tsusué, 1969), whereas further development cannot (Kües, 2000). Light induce pileus formation, but darkness is necessary for further maturation in *C. cinerea* (Kamada and Tsuji, 1979). In *F. velutipes*, fruiting body formation can be induced in complete darkness by temperature downshift, but the pileus cannot develop in the dark (Sakamoto *et al.*, 2007, 2004, 2002). Pileus differentiation can be observed at the very early stage of fruiting body development in *F. velutipes* (Sakamoto *et al.*, 2007, 2004) and the fruiting body of *P. arcularius* induced by light and grown in dark displays a long stipe without differentiated pileus on its apex, which is called the epileate stipe (Kitamoto *et al.*, 1974). After light exposure, the pileus differentiates immediately on the apical region of the pinhead fruiting body in *F. velutipes* (Sakamoto *et al.* 2004, 2007) and the epileate stipe in *P. arcularius*, and pileus primordia is formed 24 h after light exposure in *P. arcularius* (Kitamoto *et al.*, 1974). This suggests that only apical cells have the capability of pileus development in these species. However, differentiation steps for pileus differ between *F. velutipes* and *P. arcularius* (Fig. 1). In *F. velutipes*, separation of pileus and stipe tissue is observed and hymenium cells start to develop inside of the fruiting body (Sakamoto *et al.*, 2007, 2004; Fig. 1c). In contrast, separation of pileus and stipe tissue is not observed in *P. arcularius*, and hymenium cells start to develop outside of the fruiting body (Fukutomi *et al.*, 1982; Horikoshi *et al.*, 1974; Fig. 1g). Light also affects the length and thickness of the stipe in *F. velutipes*. The stipe elongates faster in darkness than in light. When a light-exposed fruiting body forms under light, stipe elongation is immediately suppressed and the stipe thickens (Sakamoto *et al.*, 2004). Interestingly, the latter study found that stipe

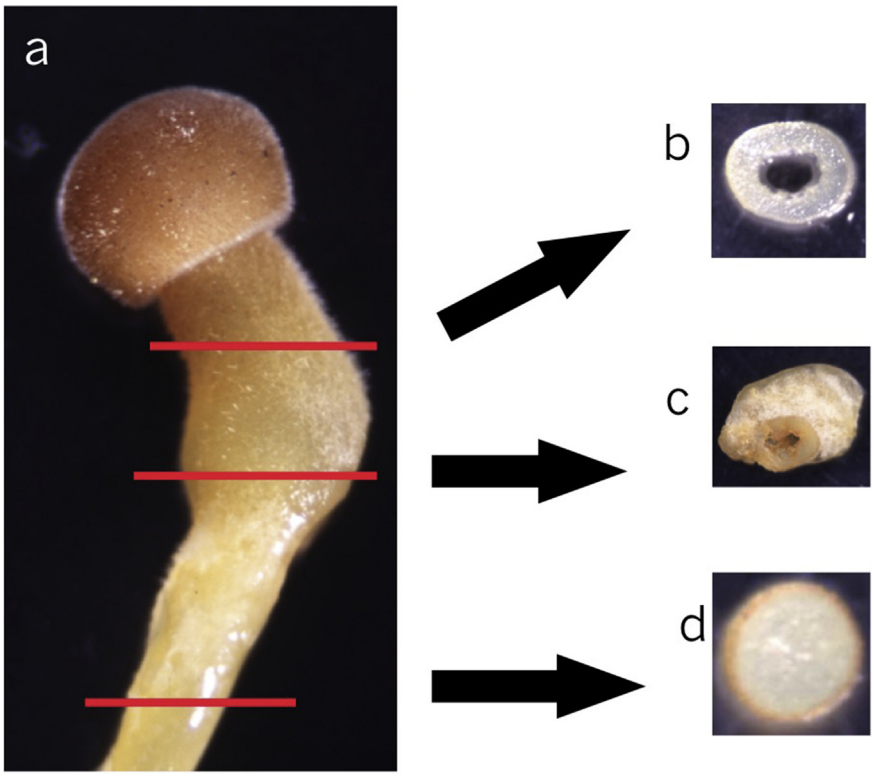

Fig. 2 – Stipe thickening after light treatment of *F. velutipes*. Appearance of the fruiting body 6 d after light exposure of the pinhead fruiting body formed in the dark (a). Horizontal sections of thickened stipe (c-d).

thickening stopped at 8 d after light exposure and stipe elongation restarted. *F. velutipes* stipe formed under light is like a hollow cylinder (Figs 1d and 2b); however, stipe formed in the dark is packed, not hollow (Fig. 2d). It was observed that after light exposure, the stipe expanded outward and became hollow, and the cells on the surface of the stipe also divided (Sakamoto *et al.* 2004, Fig. 2c). Thickening did not occur on the basal side of the stipe (Fig. 2).

Light also induces coloration of the fruiting body in mushrooms. The pinhead fruiting body of *F. velutipes* that forms in darkness is whiter compared with the normal fruiting body that forms in light conditions. The pinhead fruiting body browns immediately after light exposure, and reaches a brown colour that is similar to that of the fruiting body under light within 2 d after light exposure (Sakamoto *et al.*, 2007). A similar phenomenon is observed for *L. edodes*; the fruiting body formed in darkness is whiter than fruiting body formed in light, and immediately becomes brown after light exposure (Fig. 3).

Regulation of gene expression by light in basidiomycetous mushrooms

Several transcriptome analyses have explored gene expression during fruiting body development in basidiomycetous mushrooms. The species involved include *A. bisporus* (Morin *et al.*, 2012), *S. commune* (Ohm *et al.*, 2010), *F. velutipes* (Park *et al.*, 2014), and *C. cinerea* (Muraguchi *et al.*, 2015). In contrast, fewer transcriptome studies have been carried out for pileus development after light exposure. The *psh* gene in *F. velutipes*

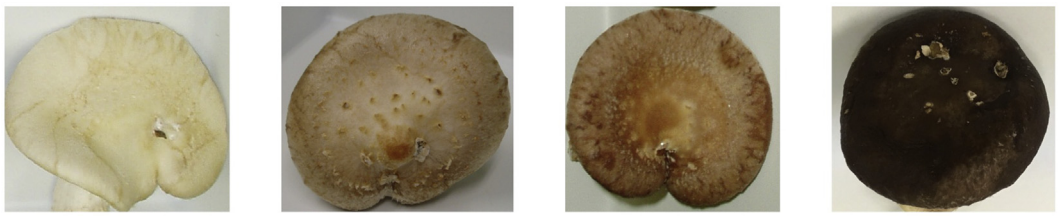

Fig. 3 – Coloration of cap in *Lentinula edodes* after light exposure. Light-exposed fruiting body formed in dark (0 h: just before light exposure, 8 h, 16 h, and 24 h).

is specifically expressed in the pileus, and not in the pinhead fruiting body formed in darkness, and expression begins immediately after exposure of the pinhead fruiting body to light (Sakamoto *et al.*, 2007). Pileus-specific hydrophobin-like protein (PSH) is isolated as cell wall-associated protein from *F. velutipes* pileus. PSH is not a typical hydrophobin, but has a similar motif to hydrophobin at the C-terminus. The molecular weight of PSH (63 kDa) is far larger than that of a typical hydrophobin (~10 kDa). PSH has threonine- and serine-rich domains, but no further functional domain has been found. Furthermore, *psh* is a unique gene in *F. velutipes*; no similar gene has been identified in other basidiomycetous genomes. Transcriptome analysis of fruiting bodies formed in the dark following exposure to light should be addressed.

Several light receptors exist in basidiomycetous mushrooms. Homologues of white-collar blue light receptors, WC1 and WC2, have been identified. WC1 was identified from *C. cinerea* mutant dst-1 that forms a dark stipe like the fruiting body under light (Terashima *et al.*, 2005). A homologous gene has been identified in *L. edodes*, PHRA (Sano *et al.*, 2007). The WC2 homologue, PHRB, was identified in *L. edodes* (Sano *et al.*, 2009), and the homologous gene in *C. cinerea* was disrupted (Nakazawa *et al.*, 2011). Interaction of PHRA (WC1) and PHRB (WC2) was confirmed in *L. edodes* (Sano *et al.*, 2009). This suggests that the WC1/WC2 complex is necessary for blue light reception in basidiomycetous mushrooms, like blue light reception in ascomycetes (Dunlap, 2006). Expression of genes for fruiting body development was analysed in a Δwc2/Δwc2 strain of *S. commune* (Ohm *et al.*, 2013). The results suggest that WC2 regulates a transcription factor gene, *c2h2*, for primordia formation, several hydrophobins, laccase, and other putative blue light receptors (Ohm *et al.*, 2013). Further transcriptome analyses and gene manipulations (gene silencing, gene disruption, or genome editing) will provide further insight of mushroom development in the presence of light.

4. Maturation and senescence of fruiting bodies

After the pileus fully develops, the fruiting bodies will mature and senesce. In the maturation stage, fruiting body colour intensifies in many mushroom species and spores become coloured in some mushroom species. *C. cinerea* spores turn black, pileus autolysis occurs after spore maturation (Kües, 2000). And some spores are diffused with droplets of the lysed pileus. Similar maturation and senescence steps occur in many cultivated mushroom species, and the quality of fruiting bodies decreases after the pileus fully expands. In cultivated mushrooms, postharvest maturation and senescence is a quality-control concern from the commercial viewpoint. Colouration (melanin synthesis) and softening (cell wall degradation) are observed in many cultivated mushroom species after harvest (Sakamoto *et al.*, 2012). In this section, the molecular aspects of maturation and senescence (postharvest quality loss) are discussed.

Maturation of fruiting body and autolysis of pileus

Stipe elongation, pileus expansion, and pileus autolysis are strictly controlled by the progression of karyogamy and spore formation in *C. cinerea* (Kües, 2000). For example, the light and darkness cycle is necessary for karyogamy induction in *C. cinerea*, and diffusible factor(s) affecting basidiocarp maturation are induced by the darkness in phase 3 (Kamada and Tsuji, 1979). Pileus autolysis will occur at the karyogamy stage, and spores are diffused with droplets of lysed pileus *in C. cinerea* (Kües, 2000). It is suggested that cell wall-degrading enzymes are involved in cap expansion and autolysis. Several cell wall-degrading enzymes have been isolated from lysing pileus. 1,3-β-Glucan hydrolases (Zhou *et al.*, 2015) and chitinase have been purified from *C. cinerea* (Niu *et al.*, 2016; Zhou *et al.*, 2016). Lysed cell walls will be substrates for cell wall of new spores and be a nutrient for spore germination. Previously, a pileus expansionless mutant was identified in *C. cinerea* and shown to be defective for pileus expansion and autolysis (Muraguchi *et al.*, 2008). The defects are due to recessive mutations in a single gene, *exp1*. This gene is predicted to encode an HMG (high mobility group) 1/2-like protein with two HMG domains that regulate global gene expression. The *exp1* gene is upregulated in the pileus 3 h before pileus expansion. Although genes that are regulated by *exp1* remain to be identified, a homologous gene in *L. edodes* is upregulated in the fruiting body after harvest. It has been suggested that *exp1* in *C. cinerea* for cap autolysis and *exp1* in *L. edodes* postharvest regulates the same cell wall degrading enzymes (Sakamoto *et al.*, 2012). This suggests that pileus autolysis and postharvest senescence of the fruiting body (discussed below) would share a common mechanism.

Postharvest problems in mushrooms

Harvesting is a critical environmental change for mushrooms, because harvesting means a sudden discontinuation of the nutrient supply. Under these conditions mushrooms may retrieve nutrients from the fruiting body itself in order to proceed with spore formation. This triggers senescence of the fruiting body, including gill browning, softening, and odour production (Sakamoto *et al.*, 2012), which poses post-harvest problems for the mushroom industry. Molecular aspects of postharvest changes have been well characterized in *A. bisporus* and *L. edodes*. Postharvest gill browning by melanin synthesis is common (Jolivet *et al.*, 1998). Enzymes for *de novo* melanin synthesis after harvest in *A. bisporus* and *L. edodes* include tyrosinase (Mauracher *et al.*, 2014; Nerya *et al.*, 2006; Sakamoto *et al.*, 2017; Sato *et al.*, 2009; Weijn *et al.*, 2013; Wichers *et al.*, 2003) and laccases (Nagai *et al.*, 2003; Sakamoto *et al.*, 2017, 2015). Tyrosinase- and laccase-encoding genes are upregulated after harvest. Multiple tyrosinase and laccase encoding genes exist in the genome of *L. edodes*, and specific genes for postharvest melanin synthesis are upregulated. In *L. edodes*, postharvest cell wall degradation is a concern because of fruiting body softening and lentinan degradation (Sakamoto *et al.*, 2012). Lentinan is a β-1,3-1,6-glucan that has anti-tumour activity. β-1,3-Glucanase activity

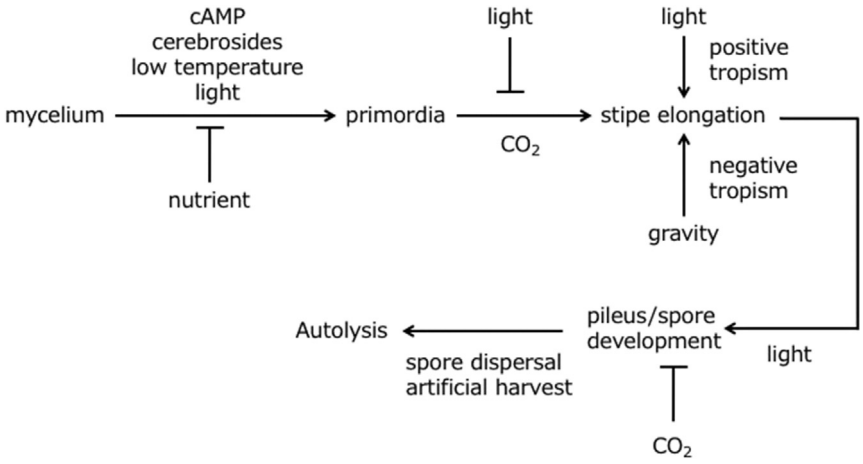

Fig. 4 – Summary of developmental pathway (including exceptions) of mushroom-forming baisidiomycetes influenced by environmental factors.

increases after harvest, with multiple enzymes for β-1,3-1,6-glucan degradation being upregulated. Exo-β-1,3-glucanase 2 (EXG2) is a member of glycoside hydrolase (GH) family 55 (Konno *et al.*, 2014; Sakamoto *et al.*, 2005), TLG1 is an endo-β-1,3-glucanase that is similar to the thaumatin-like protein (Sakamoto *et al.*, 2006), and GLU1 is a endo-β-1,3-glucanase that belongs to the GH128 family. These three have been identified as enzymes that catalyse the degradation of lentinan (Sakamoto *et al.*, 2011). Furthermore, the β-1,6-glucanase, PSU30, that cleaves the β-1,6-side chain of lentinan has been identified in *L. edodes* (Konno and Sakamoto, 2011). Genes encoding these enzymes (*exg2, tlg1, glu1*, and *pus30*) are upregulated after harvest. More recently, MLG1, which belongs to GH16 family, was demonstrated to degrade β-1,3-1,6-oligo saccharides and was shown to be upregulated after harvest (Sakamoto *et al.*, 2017). This suggests that multiple enzymes are involved in β-1,3-1,6-glucan degradation synergistically.

Chitinase is also involved in postharvest quality loss of mushrooms. Compared to β-1,3-1,6-glucan, little is known about the involvement of chitinases in postharvest cell wall degradation. In *L. edodes*, a hexosaminidase, Hex20A belonging to the GH20 family was purified from postharvest fruiting bodies, and was shown to participate in the degradation of chitin oligosaccharides (Konno *et al.*, 2012). Hex20A preferentially degrades chitin oligosaccharides but can exogenously degrade crystallised chitin. The *hex20A* gene is upregulated after harvest. Transcriptome analysis revealed that several genes encoding typical endo-chitinase belonging to the GH18 family are also upregulated after harvest. Interestingly, the gene encoding a putative chitosanase belonging to GH75 (*cho1*) is also upregulated after harvest (Sakamoto *et al.*, 2017, 2009). These results suggest that *L. edodes* has an effective chitin and chitosan degrading system due to the activities of multiple enzymes for postharvest cell wall degradation as well as β-1,3-1,6-glucan degradation. The transcription factor gene *exp1* is upregulated following harvest in *L. edodes*, as are several putative transcription factor genes (Sakamoto *et al.*, 2017, 2009). These observations indicate that multiple transcription factors regulate multiple enzyme encoding genes for postharvest fruiting body senescence in *L. edodes*.

Increased expression of argininosuccinate synthetase (*ass*) and argininosuccinate lyase (*asl*) have been described in *A. bisporus* fruiting bodies after harvest (Eastwood *et al.*, 2001; Wagemaker *et al.*, 2007). The genes encode two ornithine cycle enzymes that catalyse the last two steps in the arginine biosynthetic pathway (Wagemaker *et al.*, 2007, 2006). Arginine is the main precursor for urea formation. Urea accumulation is observed in postharvest fruiting bodies in *A. bisporus* (Wagemaker *et al.*, 2005). Gene silencing of the *asl* by RNA interference was shown to reduce yield and cap expansion during postharvest fruiting body development, but did not affect the concentration of urea (Eastwood *et al.*, 2008). Thus, downregulation of *asl* could reduce postharvest maturation by disrupting amino acid metabolism.

5. Conclusion

Advancements in the -omics analysis technology, such as genome, transcriptome, and proteome studies have broadened the knowledge on mushroom-forming fungi. For example, transcriptome studies have focused on fruiting body induction and development (Morin *et al.*, 2012; Muraguchi *et al.*, 2015; Ohm *et al.*, 2010). Although -omics research on mushroom-forming fungi has blossomed, many questions posed in this review remain unsolved. Answers should be forthcoming as -omics approaches focus on the relationship between environmental factors and fruiting body induction and development summarized in Fig. 4. Gene manipulation technologies have advanced in research on mushroom-forming fungi. Gene silencing (Costa *et al.*, 2008; Eastwood *et al.*, 2008; Nakade *et al.*, 2011) and disruption technology (Nakazawa *et al.*, 2011) has been established for many mushroom-forming fungi. For multi-gene disruption, marker recycling systems have been established (Nakazawa *et al.*, 2016b; Nakazawa and Honda, 2015). More recently, genome

editing by the clustered regularly interspaced short palindromic repeats (CRISPR)/Cas9 technology has become available in C. *cinerea* (Sugano *et al.*, 2017). These gene manipulation technologies will be helpful for the identification of key genes involved in fruiting body induction and development as influenced by environmental factors. Many important genes for fruiting body induction and development have been identified by mutant screens (Ando *et al.*, 2013; Nakazawa *et al.*, 2016a; Terashima *et al.*, 2005). Genome sequence data have made it easier to identify responsible genes in mutants. Mutant screen analysis has become more important to identify genes involved in fruiting body induction and development under the influence of environmental factors. More knowledge of environmental factors that influence fruiting body induction and development is critical from the commercial viewpoint. Analysis of genes involved in fruiting body induction and development under differing environmental conditions will be helpful for commercial cultivation of mushrooms.

Conflict of interest

The author has declared no conflict of interest.

Acknowledgement

The author thanks László Nagy and Robin Ohm for the invitation to write this manuscript.

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