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Review

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

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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.

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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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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

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