



Influences of Light Regimes on Reproduction, Germination, Pigmentation, Pathogenesis and Overall development of a Variety of Filamentous Fungi – A Review

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Authors' contributions

This work was carried out in collaboration among all authors. Authors FWN and LOA designed the study, performed the statistical analysis, wrote the protocol and wrote the first draft of the manuscript. Authors FWN and LOA managed the analyses of the study. Authors FWN, LOA and NNN managed the literature searches and sponsorship. All authors read and approved the final manuscript.

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ABSTRACT

Light influences important physiological and morphological responses in fungi, hence they can sense near UV, blue, green, red and far-red lights using up to eleven (11) photoreceptors and signaling cascades to control a larger proportion of the genomes and adapt to environmental factors. Though light is an environmental signal regulating myriad of biological processes, fungi do not utilize it as a source of energy for synthesis of food but for information and other developmental processes. Two genes WC-1 and WC-2 have been identified to function as photoreceptor for blue light proteins or orthologs and transcription factor for other light induced phenomenon. Additionally,

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conserved WCC photoreceptor orthologs (FaWC1 and FaWC2) may also perform divergent roles in some fungal species such as light signals to regulate UV resistance, secondary metabolism and sexual reproduction as well as for virulent expression. Response to white light irradiation has also elicited different morphological and physiological changes in various species of fungi such as asexual reproduction and induction or inhibition of several developmental processes. Mushrooms also requires light for developmental processes such as the asexual stage for completion of its life cycle whereas it is unnecessary at the vegetative stage. This review provides some recent crucial impact of light irradiation on the developmental processes of fungi such as sporogenesis, germination/conidiation, reproductive development, pathogenesis, mycotoxin and mushroom development even though they are generally known to be achlorophyllous and non-photosynthetic. Thus, identifying conditions of light regime that will favour fungal development with reduced mycotoxin production will be beneficial to animals and human health. Additionally, developing new techniques to control fungal species may lead to the development of faster and more effective food-processing methods.

Keywords: Fungi; photoresponses; sporogenesis -blue light; WC-1; orthologs and Achlorophyllous.

1. INTRODUCTION

It is difficult to generalise the effect of light on fungal development. This is because, while many fungi grow faster when exposed to light, many others may grow better when left in dark. It is reported earlier that low light intensity favours more mycelial growth [1]. Apart from *Neurospora crassa*, the molecular components for blue light sensing appeared to be widely conserved in the fungal genomes of Ascomycetes, Mucoromycetes, and Basidiomycetes. Moreover, genes under the control of the white collar complex (WCC) can be either light responsive or not and WC-1 and WC-2 can also have individual functions besides acting cooperatively as the WCC [2,3]. Many Mucoraceae seem to be unaffected by moderate light illumination; while strains of the common mould, *Rhizopus stolonifer* grow appreciably faster in diffuse light than in the dark [4]. Fungi are achlorophyllous and do not require light for nutritional synthesis hence it inhibits photophosphorylation as the environment needs to be humid and dark to facilitate their growth, although, some measure of light are not detrimental to growth and development [5,6]. The most significant role light plays for fungi are in phototropic responses of reproductive structures and their formation [7].

Study with *Rhizoctonia solani* in different light intensities of 120, 20, 5 lux and darkness showed that a low light intensity was best for its growth and neither darkness nor high light intensities were preferred [8]. Although, it has been reported earlier that low light intensity favours more mycelial growth [1]. In *Aspergillus nidulans* illumination promotes sexuality whereas asexual structures were induced when exposed to dark

[9]. Light is an environmental signal that regulates numerous biological processes of various organisms and most known responses of light in fungi are mediated by blue light, though other wavelengths may as well have effect, indicating that photoreceptor system occurs in the fungal photoresponses [10]. Fungi, like other organisms are actively sensitive to their environmental light conditions in order to drive adaptive responses including protective mechanisms against the light-associated stresses and regulate development. However, unlike other organisms such as plants, fungi do not use light to produce energy but use it solely as a source of information [11]. Light irradiation affects not only primary metabolism but also secondary metabolism.

Many photoreceptors have been characterised and identified in fungi as well as white collar (WC), phytochrome and rhodopsin. The white collar photoreceptor proteins are encoded by WC-1 and WC-2 genes which interact with each other to form the heterodimeric WCC; a key element in light signal transduction pathway initially characterized and identified in *Neurospora crassa* [10,11]. The commonly observed effect of light regimes on fungi ranges from the induction or inhibition of sexual development and condition to the resetting of the circadian clock and suppression of spore release [12]. It has been reported that some fungi such as *N. crassa*, *Phycomyces* and *Pilobulos* are phototropic. The effect of light on fungi have been investigated in model fungal species such as *N. crassa* and *Phycomyces* species. While spectral analyses and morphology have been well characterized in *Coprinus* and *Phycomyces* at the molecular level, *N. crassa* is the best understood based on the functions of the WC-1

and WC-2 genes in the light sensing [13,14,15,16].

In *N. crassa*, light regulates induction of carotenoid pigment production, protothecia and phototropism of perithecial beaks and circadian rhythm, all of which are inhibited by the mutations in WC-1 or WC-2 genes. These two genes encode proteins with several conserved domains, including a zinc finger DNA binding domains in both proteins [10,11]. The two proteins interact through PAS (conserved in per Arut, sim proteins) domains [11,17]. Fungi respond to light irradiation by changing physiologically and several workers have demonstrated that blue-light irradiation influences conidiation in *Neurospora crassa*, *Bipolaris oryzae*, and *Trichoderma atroviride* [18,19,20,21] and circadian rhythms of *N. crassa* [22]. *B. oryzae* has blue-light receptors named BLR1 and BLR2, and *N. crassa* has homologous receptors named WC-1 and WC-2. Such receptors are also conserved in *Aspergillus nidulans*, *Aspergillus fumigatus* and *Aspergillus oryzae* [23,24,25,26]. In addition, species with red-light receptors have been reported [24]. Therefore, it is highly possible that the blue-light response system was conserved among various fungal strains. This system activates conidial formation and its receptors act as transcription factors [25] but also inhibits mycelial growth. *A. oryzae* forms conidia in response to white-light irradiation and inhibited by red-light irradiation [25]. However, [27] reported that blue-light irradiation inhibits the conidial formation of some *Aspergillus* strains. Additionally, blue-light irradiation inhibits the

mycelial growth of *Aspergillus carbonarius* and *Aspergillus westerdijkiae* [28]. Thus, light irradiation influences fungal metabolism but the effects are complex.

The WC-1 proteins function as the blue light receptor through a specialized PAS domain responsible for sensing light, oxygen and voltage (LOV) domain in other proteins and together with WC-2, act as transcription factor. The WC-1 protein interacts with a flavin chromophore (flavin Adenine Dinucleotide-FAD) to act as the blue light through a LOV domain and modulates *N. crassa* sensitivity to light [19]. *Neurospora crassa* also have an additional four candidates proactive protein homologue which functions in photoreception that remains elusive [29,30]. Fischer et al. [31] also reported the protein complex in fungi that function as light perception centre translating different colour information and identifying their colours either as blue, green, red or far-red. Phytochromes and flavin proteins have been reported in *Aspergillus nidulans*, the mould light regulating complex that can react to different light regimes wave length. When the complex captures light, it interacts with the nuclear DNA of the fungi and controls the transcription rate of different genes hence this possibly has an effect on the physiology and development of the fungi [32]. This review gives an update on fungal responses to light regimes and how it influences their developmental processes such as reproduction, spore formation/germination, mushroom growth, pathogenesis, mycotoxin and pigmentation Fig. 1.

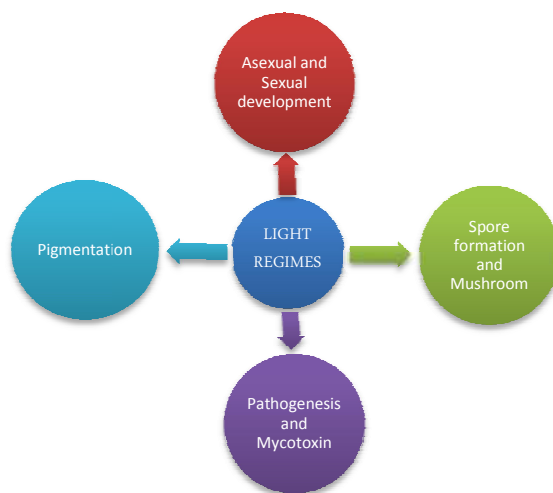


Fig. 1. Fungal developmental processes as influenced by light regimes

2. INFLUENCE OF LIGHT REGIMES ON ASEXUAL AND SEXUAL DEVELOPMENT OF FUNGI

2.1 Asexual Reproductive Structures

Cycles of light and darkness can influence the patterns of reproduction in fungi. This effect appears as alternating concentric rings of sporulating and vegetative mycelium across a colony. This can at times be seen on the surface of infected fruits. As the infection grows on the fruits, mycelium extends across and through the substance; but in the light, the extension is inhibited. Submerged hyphae receive less light as such continue to extend, eventually emerging from the underneath surface mycelium. The resulting hyphal zones would have different capacities for reproduction and alternating rings of sporulation and vegetative mycelia are formed [33]. Some reproductive structures grow towards light source (Phototropic).

Recent reports had shown that the activity of about 5% of cell genes in *Aspergillus* are influenced by light [7]. In several fungi, (e.g., *N. crassa*) light regulates conidiation in a circadian fashion. During vegetative growth on an *Aspergillus* surface the clock initiates macroconidiation in mid-subjective night, building and giving rise to conidiophore. Sometime later during the subjective day, this developmental cycle is turned off and fungal growth continues as undifferentiated vegetative hyphae. The cycle persists 22-hours periodicity in constant dark at 24°C. *Aspergillus nudilans* is reported to produce asexual spores when exposed to light; while the asexual spores are adapted for survival, the production of sexual spores in the dark are adapted for survival in times of unfavourable conditions and mix the genetic materials of two individuals [34]. When light falls unevenly on developing structures, unequal growth results, which is the effect of orienting that structure symmetrically to the light source. Sporangiothecia of phycomycetes are particularly responsive and grow vigorously towards light [23]. *Aspergillus ornatus* was also reported to produce abundant conidia when exposed to continuous light and virtually none when in the dark. Alternatively, Cleistothecia were produced in the light, and none in the dark [35].

Sanchez-Murillo et al. [36], also reported that conidiation in *Paecilomyces fumosoroseus* (a microbial alternative to chemical insecticide) is highly dependent on light. Light is required for

the induction of its (*P. fumosoroseus*) conidiophores, but light does not suppress the development of the conidia. This implies that in *P. fumosoroseus*, induction of conidiophores required light while the development of the conidia occurs in the dark or less light intensities. In addition, to the fact that light regulates conidiation in many fungi in circadian fashion; the period of a circadian rhythm remains unchanged over a broad physiologically appropriate temperature range. As earlier reported; during vegetative growth observed on an agar surface, the circadian clock initiates macroconidiation in a mid-subjective night; budding, resulting to formation of conidiophore takes place. This is not therefore a surprise that exposure to light is a signaling exit of fungi from the soil and entry into the air induces asexual development [7,36].

2.2 Sexual Reproductive Structures

Commonly observed effect of light on fungi reproductive development ranges from the induction or inhibition of sexual development and conidiation to circadian clock resetting and suppression of spore release [12]. For a coordinated sexual development of a fungus, it is useful to get a correct temporal or spatial distribution of signaling molecules in its cell or generate mutants of such fungus that was unable to form KIN3 enzyme. This is because KIN3 plays a vital role in the sexual development of a fungus hence any mutant that lacked the enzyme remains sterile. The importance of KIN3 enzyme in the sexual life cycle of a fungus was reported by [6]. In contrast to plants, fungi use light as a source of information rather than a source of energy. The effects of light on sexual reproduction of some mould fungal species have been investigated in this regard. Sexual development is another light-dependent process for the induction of sexual development in a homothallic fungus; *Fusarium graminearum*, a pathogen of economically important crops such as corn, barley and wheat. Despite the fact that it requires light for sexual development, not much is known about the mechanism with which it occurs. But considering the importance of FGWC-1 and FGWC-2 for light-dependent processes, it is expected that deletions of FGWC-1 and FGWC-2 would have effects on the sexual development such as abolishment of peritheca or ascospore formation. Contrary to that, it was reported that instead of abolishment; it only led to the delay of maturity of the spores in the FGWC-1 and FGWC-2 mutants and not their formation. This led to the suggestion that other

light responsive regulatory proteins and photoreceptors may be involved in the sexual development of *F. graminearum* and further reported that some fungi such as *Phycomyces blakesleans* and *Pilobus* species are phototropic [37,4]. They added that light stimulates production of spores and fruiting bodies. It was also reported that some Ascomycetes and fungi imperfecti, on exposure to light, commenced sexual sporulation. *Aspergillus flavus* and *Trichoderma viride* were also reported to produce spores after being exposed to light and very few of them when incubated in the dark. In *Aspergillus nidulans* illumination promotes sexuality whereas asexual structures were induced when exposed to darkness [8,9]. *Aspergillus ornatus* produced abundant conidia when grown in continuous light and almost none while in the dark; alternatively, cleistothecia and ascospores were produced in the dark and none when exposed to light [6,38]. Blue light regulates induction of carotenoid pigment production, protoperithecia or sexual fruiting body formation and phototropism of perithecial beaks and circadian rhythm, all of these are abolished by mutations of *wc-1* or *wc-2* [10].

3. EFFECT OF LIGHT REGIMES ON FUNGAL SPORE GERMINATION AND MUSHROOM DEVELOPMENT

3.1 Spore Germination

The relationship between light irradiation and fungi has been investigated, and the most obvious phenotypical change is in conidial formation [25,27]. The light-response mechanism related to conidial formation has become clear [26,39], and may be distributed throughout fungi. However, different responses to the same colour of light radiation have been reported in different fungal strains [28]. Therefore, knowing the phenotypic characteristics of test strains should be a preliminary requirement for light-irradiation studies. Light-irradiation tests have demonstrated that blue-light conditions of 401 nm and 470 nm irradiation stimulated conidial formation whereas white-light resulted in its formation [40]. Light influences many aspects of fungi growth and development. In majority of cases, the most effective wavelengths on light controlling photoresponses in fungi lie in the blue and UV regions of the spectrum [41]. The action spectra for these responses suggest that the photoreceptor is either a carotenoid or flavin protein [42,43]. The evaluation on the effect of light on fungal spore germination of *Puccinia*

psidii inter in continuous light and darkness showed that highest germination occurred under continuous light.

Naruzawa et al. [44] also evaluated the effect of light and darkness regimes on the spore germination of *P. envitiae ono* and reported that absence of light produced the greatest germination and appressorium formation and development in *P. pachyrhizzi* between one and two hours after inoculation of plant in the light in a moist chamber of 20 in the dark. Light induces hyphal branching in *Rhizoctonia solani* but at a specific intensity [8]. Inhibition of Uredospore demonstrates that they are relatively transparent in red and far-red regions of the spectra [45]. This obviously, showed that germination of *Puccinia graminis* is inhibited by continuous irradiation but a detailed study also revealed that pre-hydration of spores enhances germination in both dark and light. Photoinhibition simultaneous irradiation with ineffective red (653nm) and inhibitory far-red light (720nm) results in partial nullification of the inhibition brought about by far-red light alone. It was suggested that this would be consistent with the involvement of a photoreversible pigment system similar to photochrome, operating via the high irradiance reaction [46].

3.2 Mushroom Growth and Development

It is difficult to generalize the effect of light on fungal growth and development. This is because many fungal species seem to grow well either in the light or dark. Mushroom do not contain chlorophyll, as such they do not require extreme photosynthesis to grow; while the environment needs to be as dark as possible to spawn, some form of light do not harm their growth [5]. The most significant role light plays for mushroom is in the phototropic response of reproduction structures and their formation. Mycelial growth of mushrooms do not require light; although cultivation of mushroom (oysters) in the dark gives better result than in the light. The positioning of the stipe and pileus have been shown to be controlled by phototropic responses. The primordia initiation and formation of fruiting bodies also require light to trigger off the process [47]. It had been reported that the length of stipe and size of pileus were greatest when exposed to light than in the dark, for *Pleurotus ostreatus*. A blue-light photoreceptor has also been identified as a resident protein containing a photo-reactive domain responding to stimuli essential for fruiting development of mushrooms

[48]. Okwujiako [49,50] also reported that light was important in the production of mushrooms fruiting bodies as light acts as trigger or shock in fructification for most mushrooms. Generally, the mushroom cycle is divided into vegetative and sexual reproductive phases; while the vegetative phase (spawning or spawn running) does not require light, the sexual reproductive phase (fructification) require light as a shock to trigger the process [48,51]. This implies that light and darkness do not play any strict role in primordial formation but light is required at a later stage of a mushroom. Though response to light is not generalized it works according to species of mushroom.

4. INFLUENCE OF LIGHT REGIMES ON FUNGAL MYCOTOXIN PRODUCTION AND PATHOGENESIS

4.1 Mycotoxin Production

Light irradiation enhances the detection of aflatoxin (AF) production. For instance, blue light irradiation influences conidiation and perhaps AF synthesis. This was demonstrated using laboratory fungal cultures with light irradiation increased, the observational efficiency for AF-derived fluorescence from *A. bombysis* MAFF111712 and *A. nomius* MAFF111739 under 401 nm irradiation conditions compared with dark conditions [40]. However, for *A. nomius* MAFF111739, 720 nm red-light irradiation increased the AF fluorescence despite the low level of conidial formation. Conversely, *A. flavus* IFM55891 and *A. parasiticus* NRRL2999, at 401 nm blue-light irradiation increased conidial formation, although AF-derived fluorescence intensity levels were not increased. These different phenotypic changes among fungal strains suggest that the regulation of AF synthesis and conidial formation are separately influenced by light irradiation, although there was a commonality in that the DNA methyltransferase protein contributes to both [39]. A different result was also obtained after 3d incubation periods from those of *A. carbonarius*, in which ochratoxin A (OTA) was increased by red-light irradiation [28]. But AF synthesis in *A. parasiticus* BFE96p and OTA synthesis in *A. westerdijkiae* are repressed by both blue- and red-light irradiation [27,28]. This suggests that the light intensity, like the wavelength, was important. Based on the four strains studied the low-intensity condition was more suitable for AF synthesis. Thus, blue-green low intensity irradiation may increase AF synthesis in fungi.

4.2 Fungal Pathogenesis

Effect of light or its absence represents an environmental signal that is known to regulate many properties of a microbial cell which may directly or indirectly influence the development of disease. Light regulates the filamentous mating process of fungi through the white collar homologs BWC-1 and BWC-2. Mutations of these genes causes a reduction in resistance to UV light and also renders the strain less virulent in a mouse inhalation model of the disease [52,53] and differential behaviour of pathogens under different light intensity [8].

Recently, light became recognized as an important modular of fungal pathogenesis on plants, syndicated as a relevant variable with the potential to affect the outcome of the plant-pathogen interaction by modulating either plant defence responses, adaptation to environment and virulence of the pathogen. Such virulent expression especially by *Fusarium asiaticum* have been proved to happen in a light-independent fashion [54,55]. Besides fungal development and metabolism, the involvement of light receptors in fungal pathogenesis is increasingly arousing interests of researchers. The orthologs of white collar complex (WCC) have been recognized in fungal pathogenesis. White collar complex (WCC) or orthologs are involved in affecting the infection activities of *Botrytis cinerea*, *C. zeaemaydis* and *M. oryzae* in a light-development manner [37,54,55]. However, in contrast WCC are required for full virulence of *C. neoformans* and *F. oxysporium* in mammals, in a light sensitive way. The involvement of WC-1 orthologs in virulence have also been reported in *Magnaporthe oryzae*; the pathogen of rice blast disease, responsible for suppression in constant light mediated by MGWC-1 as well as WC-1 which was required for stomatal tropism, appressorium and lesions formation in maize [56]. Interestingly, previous report by Ruiz-Rolden et al. [57] indicated that *Fusarium oxysporium* required WC-1 to cause vascular wilt in plant. *Borytis cinerea*, a necrotrophic plants pathogen that cause infections through the air; forms sclerotia, a surviving infectious structure awaiting favourable condition, has a strain that responds to light for infection. *Botrytis cinerea* was sensitive to white light especially during infection, resulting in increased disease expression levels of photoreceptor encoding gene and WCC was required for coping with excessive light, oxidative stress and also to achieve full virulence

[58,59,60,61]. Light has an outstanding relevance in fungal pathogenesis, as they use light as energy for the process; hence the complex photo receptor, phytochromes and blue light sensing phototropins are present in plants, thereby making light relevant in fungal pathogenesis, even as blue light receptor are known to be required for microbial virulence [52].

5. EFFECT OF LIGHT REGIMES ON FUNGAL PIGMENTATION

Light has crucial influence on many organisms due to its capacity of inducing morphological and behavioural changes. Light induces varied responses in nearly all forms of life [62]. Several types of photoreceptors (i.e., molecules that receive and transduce the photo energy to produce a cell response) have been developed in fungi [47]. Fungal pigment are secondary metabolites produced due to scarcity in nutritional quality. They are classified as carotenoid and polyketides. The polyketides are made up of tetraketides and octaketides. Melanin pigment helps fungi to survive in severe environmental stress; and cope with UV light. Pigments produced by *Monascus* species are believed to be sensitive to heat and light hence the condition makes it unstable at low pH and low water solubility [63]. Light actually may or not influence pigment formation in fungi, however it has been reported that incubation of *Monascus* species in the dark results in effective production of red pigment while illumination results in loss of pigment. Experimental results of such investigations have demonstrated that pigment forming *Monascus* species may not need light to form pigments since the presence of light has the ability to impact on pigmentation, even red and blue lights affect the yield of pigments in *Monascus purpureus* which were more stable in dark light [64,65]. Conversely, growing the fungus in direct illumination could result in total suppression of pigment yield. All these are indications of photoreceptor response of fungi which is controlled or mediated by the WC-1 gene or blue light.

6. CONCLUSION

The review reveals that fungi are not photosynthetic but requires light as a source of information to controls important physiological and morphological responses as they are sensitive to a wide spectra of light using up to eleven (11) photoreceptors and signaling cascades to control larger proportion of their

genome, thereby adapting to environmental conditions.

Cycles of light and darkness influences fungi patterns of reproduction as alternating concentric rings of spore formation and vegetative mycelium across a colony. The commonly observed effect of light on fungal reproduction ranges from induction or inhibition of sexual development to the resetting of circadian clock and suppression of spore release. Light influences early spore germination and can also inhibit the process. Sexual development is a light dependent process as reported for *Fusarium graminearum* and possibly other light responsive regulatory proteins and photoreceptors may be involved in the sexual developmental process which may not be inhibitory to the development of perithecia in *Neurospora* but rather delayed the maturity only. Mushroom respond phototropically to light during development and the formation of reproductive structures,

Positioning of stipe, pileus and fruiting bodies. Light stimulates production of spores and fruiting body formation as well as fungal mycotoxin and pathogenesis because the strains that infect plant leaves and enter through the stomata requires WC-1 for stomata tropism, appressorium and lesions formation. Light regimes also influences fungal pathogenesis as it affects pathogen motility, infectivity and virulence in *Monascus purpureus* and blue light receptor as well is required for microbial virulence. Pigments are sensitive to heat and light because they become unstable. However, several types of photoreceptors are domicile in fungi and the most effective wavelengths of light controlling photoresponses are mediated in the blue and UV regions of the spectra. The blue light photoreceptor or the WC-1 orthologs is the fundamental of all and this explains why fungi use light as a source of information, rather than source of energy.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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