Fusarium Photobiology

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Contributor: Javier Pardo-Medina , M. Carmen Limón , Javier Avalos

The genus *Fusarium* comprises a large and heterogeneous group of ascomycetes widely distributed in nature. Many of them have received attention as phytopathogens, with great impacts on crops and as mycotoxin producers, but others are non-pathogenic, endophytic, saprophytic, or parasitic species of other organisms. The global distribution of the genus is attributed both to its metabolic diversity, which broadens its accessibility to very diverse potential substrates, and to its efficient dispersal mechanism, which is based on the production of different types of conidia. The complex taxonomy of *Fusarium* species has been clarified by DNA-based phylogenetic analyses, which revealed a monophyletic lineage consisting of 20 species complexes including almost 300 phylogenetically distinct species. Different species of the *Fusarium* genus are widely used in research, e.g., *Fusarium graminearum*, *Fusarium oxysporum*, and *Fusarium fujikuroi*, which are normally associated with pathogenesis or secondary metabolism. Some features of the biology of these species, especially those related to development and metabolite production, are influenced by light.

light Fusarium RNA

1. Effects of Light on Development

The developmental processes related to asexual reproduction in *Fusarium* are influenced by different factors and environmental cues, including light [1]. Fungi of this species spread asexually through the formation of three types of spores, macroconidia, microconidia, and chlamydospores [2]. The different kinds of spores share common characteristics in different *Fusarium* species, but there is considerable morphological diversity [3][4]. Macroconidia are long, typically sickle-shaped, with transverse septa, usually containing several cells [1]. Microconidia are usually unicellular, although they are not produced by all *Fusarium* species, and a few species can arrange microconidia in chains [2]. Chlamydospores are thick-walled cells, usually formed inside the hyphae, capable of surviving in adverse conditions and for long periods of time [5]. Conidia of either type are usually produced in abundance to promote rapid dispersal and the colonization of new habitats, including other pathogenic hosts. Due to their multinucleated nature, it can be expected that the macroconidia are more resistant than the microconidia to adverse conditions, and it has been reported that they can develop chlamydospores [6].

Visible and near-UV lights have been reported to enhance conidia production in different *Fusarium* species [7]. Thus, in *Fusarium verticillioides*, short-wavelength blue light is particularly effective in stimulating conidia production [8]. Conidiation levels and the presence of macroconidia are very variable among different *F. fujikuroi* strains [9]. Macroconidia are rarely observed in IMI58289, a widely used wild-type strain, but they are frequently found in FKMC1995, which has been used in different works described in this research. Regulatory differences are also observed between both strains. For example, light induces conidiation in IMI58289 [7][9] although it has a negative effect in FKMC1995 [10]. The differential fitness of conidia produced at different wavelengths towards light has also been described [10].

In *F. graminearum*, conidiation under near-UV light requires the *abaA* gene product [11] conserved in other fungi. The induction of conidiation by light in *F. fujikuroi* IMI58289 does not occur in mutants of the GATA factor Csm1 [12]. The latter, and other proteins, such as histone methyltransferase Set1 and demethylase Kdm5, control the expression of the key conidiation regulator gene *abaA* [13]. In this research, conidiation was tested under illumination regimes, but the effect of light was not investigated. The elimination of *Fvve1* in *F. verticillioides* alters the aerial development of the hyphae and reduces their hydrophobicity, and in submerged cultures it activates conidiation. Interestingly, this mutation increases the ratio of macroconidia to microconidia [14]. The relationship of this protein with light regulation provides a possible explanation for the influence of light on conidiation. The possible involvement of photoreceptors in conidiation, investigated through the effect of their gene mutations.

Regulation by light also involves sexual reproduction. In sexually competent species, the formation of perithecia during mating is favored under specific light conditions. This has been investigated in *F. graminearum* [15][16], in which the perithecia are not formed in the dark but under light, with 4 h of daily light being enough for their optimal production. Moreover, reducing UV exposure lowers the number of perithecia. Ascospore release is also stimulated by light in this fungus [17].

2. Effect of Light on Carotenogenesis

Photocarotenogenesis is the most well-characterized light-regulated process in *Fusarium* [18]. The first studies on the effect of light on carotenogenesis were carried out on *Fusarium aquaeductuum*, which showed a gradual accumulation of carotenoids after illumination, reaching a maximum at 12 h [19]. The carotenogenetic reaction to light in this species is independent of temperature in the range of 5 to 25 °C but requires oxygenation and active protein synthesis [20]. The light-inducing effect can be partially replaced by the addition of oxidizing reagents [19][21], suggesting that the oxidation of the -SH groups plays a role in the light sensing system, which disappears when reducing agents are added [22]. However, while brief exposure to light is sufficient for photoinduction, oxidizing agents must be continuously present to maintain their stimulatory effect in addition to that of light [23], indicating different mechanisms of action. Nevertheless, the oxidizing agent *p*-hydroxymercuribenzoate had no effect on other *Fusarium* species [24].

All *Fusarium* carotenoid synthesis genes have been identified [18], and the pathway is well established. Three structural genes, *carRA*, *carB*, and *carX*, required for torulene, β-carotene, and retinal production, are organized in a gene cluster coregulated with a rhodopsin gene, *carO*. The photoinduction of carotenogenesis in *Fusarium* mycelium grown in the dark involves a rapid increase in the transcript levels of most structural genes during the first hour of illumination, followed by an accumulation of carotenoids in the following hours, providing an orange pigmentation to the mycelium. Northern blot and RT-PCR analyses of the four clustered *car* genes of *F. fujikuroi* showed a similar induction kinetics, also found for the *carT* gene, which is required for neurosporaxanthin synthesis. Similar results were obtained in *F. oxysporum* [25] and *F. verticillioides* [26][27]. Recent RNA-seq data have also revealed the significant photoinduction of *ggs1* coding for a prenyl transferase [28], which has been previously underestimated [29]. The *carD* gene exhibited a lower photoresponse in *F. fujikuroi* [30], as corroborated by RNA-seq data [18]. Therefore, in *F. fujikuroi*, all carotenoid metabolism genes are regulated by light. The regulatory proteins responsible for this photoresponse are mentioned in later sections, but other proteins involved in the light signal transduction pathway may also be responsible. *Fusarium* has the predicted components of a Velvet complex, FfLae1, FfVel, and FfVel2 [31], which is connected to light regulation in other fungi [32]. The *carRA* gene is upregulated in *Fflae1* mutants, indicating a repressor function for *lae1* gene [33].

3. Effect of Light on the Production of Other Secondary Metabolites

Light modulates the production of other metabolites in addition to carotenoids. Gibberellin biosynthesis is stimulated by light in some strains of *F. fujikuroi* [7][34], although its effect is minor compared to that caused by nitrogen shortage. The influence of light on the synthesis of enniatins, cyclohexadepsipeptide antibiotics produced by different *Fusarium* species, has also been investigated. Enniatin production is enhanced by light in *Fusarium sambucinum* [35]. In other fungi, such as those of the genera *Aspergillus* or *Neurospora*, light influences the production of secondary metabolites through the Velvet VelB/VeA/LaeA complex [31][36]. In *Aspergillus*, this occurs through light controlling the VeA passage into the nucleus in response to a signal from photoreceptor proteins [37]. In *Neurospora crassa*, light promotes the degradation of the Velvet Ve-1 protein [38]. Disruption of the Velvet complex genes in *F. fujikuroi* almost completely halts the biosynthesis of gibberellins, fumonisin, fusarins, and fusaric acid [32][33], as well as conidiation. *F. graminearum* deletion mutants of the *FgVeA* and *FgVe1* genes show reduced aerial hyphal formation, as well as reduced biosynthesis of deoxynivalenol, aurofusarin, and trichotecene [39][40]. No attention has been paid, for either of the two *Fusarium* species, to the effect of light on these phenotypic changes. However, deleting the Velvet complex genes *veA*, *velB*, and *laeA* drastically reduces beauvericin production in *F. oxysporum* under light and dark conditions, in addition to affecting conidia production and morphology [41]. These mutants exhibited fewer differences in pigmentation and morphology between light and dark growth colonies than those exhibited by the wild type, confirming their connection to light regulation.

4. Fusarium Photoreceptors

The proteins responsible for light detection and signal transmission are known as photoreceptors. They bind to small molecules called chromophores, which can absorb light and cause a conformational or chemical change in the cognate protein. This triggers a direct response or initiates a signal transduction pathway [42]. Depending on the nature of their chromophore, photoreceptors can detect light or radiation within a specific wavelength range. Thus, UV-, blue/UV-, green-, or red-light photoreceptors can be distinguished. Flavin, retinal, and tetrapyrrole chromophores are the typical fungal photoreceptor chromophores [43]. Most light responses studied in fungi are caused by the detection of blue light, although responses at other wavelengths are also known [43][44][45][46]. The main families of photoreceptors in fungi and their presence in *Fusarium* are described below. *Fusarium* genomes contain genes for ten photoreceptors (**Table 1**). Most of them have been studied by targeted deletion in several *Fusarium* species, while others await investigation.

Table 1. Genes for photoreceptor proteins in the genomes of three *Fusarium* species.

Group	Chromophore [1]	Protein [2]		References [3]	*F. fujikuroi* [4]	*F. oxysporum* [5]	*F. graminearum* [6]
Flavoproteins	Flavin (blue)	WCC [7]	WcoA	[15][47][48][49][50]	*FFUJ_13691*	*FOXG_03727*	*FGSG_07941*
			WcoB	[15][49][50]	*FFUJ_00530*	*FOXG_01037*	*FGSG_00710*
		VvdA		[51][52]	*FFUJ_06055*	*FOXG_03254*	*FGSG_08456*
		LovA		-	*FFUJ_11713*	*FOXG_12253*	*FGSG_02972*
		LovB		-	*FFUJ_08848*	*FOXG_09176*	*FGSG_04991*
Cryptochrome photolyase family	MTHF/flavin (blue)	CryD		[34][51][53]	*FFUJ_05732*	*FOXG_03570*	*FGSG_08852*
		CryP		-	*FFUJ_03105*	*FOXG_02060*	*FGSG_06765*
		PhrA		[54]	*FFUJ_00436*	*FOXG_01134*	*FGSG_00797*
Rhodopsins	Retinal (green)	CarO		[55][56]	*FFUJ_11804*	*FOXG_12142*	*FGSG_03064*
		OpsA		[55][57]	*FFUJ_02352*	*FOXG_15406*	*FGSG_07554*
Phytochromes	Biliverdin (red)	FphA		[15]	*FFUJ_05887*	*FOXG_03424*	*FGSG_08608*

[1] Color of absorbed light is indicated in parentheses. [2] Protein denomination in *F. fujikuroi*. [3] References to studies in which the gene or protein was investigated in a *Fusarium* species. [4,5,6] Gene denominations in genome annotations. [4] Strain IMI58289. [5] Strain 4287. Formae specialis *lycopersici*. [6] Strain PH-1. [7] WCC: White Collar complex. WcoA forms a complex with WcoB, in which WcoA is the light-detecting component.

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