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Light, stress, sex and carbon – The photoreceptor ENVOY as a central checkpoint in the physiology of *Trichoderma reesei*

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ABSTRACT

Trichoderma reesei (syn. *Hypocrea jecorina*) is known as one of the most prolific producers of homologous and heterologous proteins. However, discovery of the photoreceptor ENV1 as a regulator of cellulase gene expression initiated analysis of light response pathways and their physiological relevance for *T. reesei*. The function of ENV1 in regulation of plant cell wall degrading enzymes is conserved in *Neurospora crassa*, albeit the mechanism is not entirely conserved. ENV1 emerged as a central checkpoint for integration of nutrient sensing, light response and development. This photoreceptor exerts its function by influencing transcript abundance and feedback cycles of the alpha subunits of the heterotrimeric G-protein pathway and impacts regulation of the beta and gamma subunits via mutual regulation with the phosphatidylinositol 3-OH kinase PhLP1. The output of regulation by ENV1 is in part mediated by the cAMP pathway and likely aimed at cellulose recognition. Lack of ENV1 causes deregulation of the pheromone system and female sterility in light. A regulatory interconnection with VEL1 and influence on other regulators of secondary metabolism like YPR2 as well as polyketide synthase encoding genes indicates a function in secondary metabolism. The function of ENV1 in integrating light response with signalling of osmotic and oxidative stress is evolutionary conserved in Hypocreales and distinct from other sordariomycetes including *N. crassa*.

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Light response in fungi

Proper response to the changes in environmental conditions in day and night triggered the evolutionary adaptation of organisms to light and darkness. It is of crucial importance for fungi to prepare for the harmful effect of UV light, desiccation and increased abundance of reactive oxygen species (ROS) that coincides with daylight. Similar environmental changes occur on the surface of soil or a substrate compared to under

the surface where it is dark, more humid and lower ROS levels are present (Rodríguez-Romero *et al.* 2010). Thereby, light serves as an important signal and triggers responses in terms of growth, sexual and asexual development, primary and secondary metabolism as well as enzyme production (Fuller *et al.* 2015; Tisch & Schmoll 2010).

Fungi have developed sophisticated mechanisms to anticipate the onset of daylight and to react to light pulses – a photoreception system and circadian rhythmicity (Fischer *et al.*

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2016). The biological machineries for light response are evolutionarily conserved in the fungal kingdom (Dunlap & Loros 2017; Idnurm & Heitman 2005), albeit the components of this machinery differ from species to species (Idnurm et al. 2010). Especially in recent years, investigation of light responses was extended to a broader range of species with analysis of different aspects (Idnurm 2013).

The filamentous ascomycete *Neurospora crassa* has become the most prominent model system for studying mechanisms of photoreception and circadian rhythms. The photoreceptors of *N. crassa* are responsible for transmission of the blue light signal and crucially impact circadian rhythmicity (Dunlap & Loros 2017). The white collar complex (WCC) consisting of white collar 1 (WC-1) and white collar 2 (WC-2) acts as blue light photoreceptor. WC-1 and WC-2 contain PAS domains and exert their function as GATA type transcription factors in a complex. Thereby, DNA binding characteristics and requirements of WC-1 and WC-2 are distinct for light induction and circadian functions (Wang et al. 2015). Both are regulated not only at the level of transcription, but also by phosphorylation at the level of stability and by interaction (Montenegro-Montero et al. 2015). As transcription factors WC-1 and WC-2 impact a flat hierarchical network of regulation by modulating downstream transcription factors with diverse functions (Smith et al. 2010).

The photoreceptor VIVID (VVD) acts by interaction with the WCC (Hunt et al. 2010; Malzahn et al. 2010) to modify light and clock responses and is assumed to serve as a universal brake in light responses (Chen et al. 2009). VVD has a gating function in light response (Heintzen et al. 2001) and is important for photoadaptation to different light intensities, which is crucial for discrimination between day and night despite naturally ambiguous light conditions like moonlight (Malzahn et al. 2010). Homologues to VVD were further characterized in *Fusarium fujikuroi* with functions in hyphal morphology and photoadaptation of carotenogenesis (Castrillo & Avalos 2014, 2015).

The light response machinery in *Trichoderma reesei*

Trichoderma reesei is predominantly known for its high efficiency in production of homologous and heterologous proteins in industry (Bischof et al. 2016; Schmoll et al. 2016). However, it also has served as a model for light responses decades ago (Schmoll et al. 2010a) and in recent years, the investigation of the interconnection of enzyme production and light response in *T. reesei* connected to this history. The *T. reesei* photoreceptors BLR1 and BLR2 are homologues of *Neurospora crassa* WC-1 and WC-2 (Castellanos et al. 2010). BLR1 has a GATA-type zinc finger region as DNA binding domain and three PAS domain, of which the first is a PAS/LOV domain. BLR2 has a similar DNA binding region and only one PAS domain (Schmoll et al. 2010a). The photoreceptor ENV1 shares homology with *N. crassa* VVD, but did not complement loss of VVD in *N. crassa*. Besides the PAS/LOV domain of ENV1 no further functional domain was detected (Schmoll et al. 2005). In the following we specifically discuss functions of ENV1, although in the discussed physiological pathways, also BLR1 and BLR2 were found to be involved. For a more detailed

discussion of these genes, the reader is referred to the respective reviews and original literature (Bazafkan et al. 2017a; He & Liu 2005; Schmoll et al. 2010a; Seibel et al. 2012a; Stappler et al. 2017; Stappler et al. 2016; Tisch & Schmoll 2013).

Identification of ENV1 as a photoreceptor

Despite early studies on light response in *Trichoderma reesei* (Schmoll et al. 2010a), research with this fungus was focused on regulation of enzyme production for decades, due to its high industrial relevance (Bischof et al. 2016; Paloheimo et al. 2016). Surprisingly, a study aimed at identification of novel regulators by comparison of gene expression in a cellulase negative mutant with wild-type, a potential photoreceptor was found to be differentially regulated (Schmoll et al. 2004). This photoreceptor turned out to be the homologue of *Neurospora crassa* VVD and was named ENVOY because of its assumed messenger function that was not limited to light response (Schmoll et al. 2005). In addition to the domain structure of VVD, the gene encoding ENV1 has two DNA sequence motifs, EUM1 and EUM2 in the 5' upstream sequence in common with *vvd* (Schmoll et al. 2005). Illumination causes a strong up-regulation of *env1* (Castellanos et al. 2010; Schmoll et al. 2005), which is independent of the carbon source (Stappler et al. 2017).

In contrast to the mutant phenotypes for deletion strains in homologues of ENV1 in *N. crassa* and *Fusarium fujikuroi* (Castrillo & Avalos 2014; Heintzen et al. 2001), lack of functional ENV1 caused a severe growth defect in light (Schmoll et al. 2005). Besides these first results for deletion of *env1*, the same mutation was later on introduced into the field isolate CBS999.97 and into QM6a and also in a female fertile background derived from QM6a. In all these cases, the growth defect was obvious, which confirmed that lack of ENV1 specifically causes the growth defect in *T. reesei* (Bazafkan et al. 2015; Bazafkan et al. 2017b; Seibel et al. 2012a).

Deletion of the full open reading frame of *env1* showed similar results as deletion of its PAS domain alone (Castellanos et al. 2010; Schmoll et al. 2005). Availability of a truncated mutant for ENV1 that still retained part of the ORF (*env1*^{PAS-}) enabled us to investigate whether there is a feedback mechanism on *env1* transcript levels depending on the presence of the ENV1 PAS domain. Changes in transcript abundance of truncated *env1* were minor in the *env1*^{PAS-} mutant compared to the wild-type, but on glucose, clear differences in expression of the truncated transcript were detected (Schmoll et al. 2005). These results suggested the operation of a carbon source dependent feedback mechanism of ENV1 on the *env1* promoter, albeit the further involved regulators i. e. transcription factors, are still not known.

In the absence of BLR1 or BLR2, transcription of *env1* is not induced and remains at barely detectable darkness levels (Castellanos et al. 2010; Tisch et al. 2014). ENV1 in turn negatively influences transcript levels of *blr1* and *blr2* in darkness and early light response, when *env1* is strongly induced in the wildtype (Tisch et al. 2014). The mutual regulation of ENV1, BLR1 and BLR2 is assumed to lead to a steady state of transcript abundance of the corresponding genes after induction. The strong up-regulation of *env1* in light is diminished in the absence of sulphate and decreased methionine

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