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Review

Trichoderma in the light of day – Physiology and development

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ABSTRACT

In recent years, considerable progress has been made in the elucidation of photoresponses and the mechanisms responsible for their induction in species of the genus *Trichoderma*. Although an influence of light on these fungi had already been reported five decades ago, their response is not limited to photoconidiation. While early studies on the molecular level concentrated on signaling via the secondary messenger cAMP, a more comprehensive scheme is available today. The photoreceptor-orthologs BLR1 and BLR2 are known to mediate almost all known light responses in these fungi and another light-regulatory protein, ENVOY, is suggested to establish the connection between light response and nutrient signaling. As a central regulatory mechanism, this light signaling machinery impacts diverse downstream pathways including vegetative growth, reproduction, carbon and sulfur metabolism, response to oxidative stress and biosynthesis of peptaibols. These responses involve several signaling cascades, for example the heterotrimeric G-protein and MAP-kinase cascades, resulting in an integrated response to environmental conditions.

Contents

1. Introduction

During evolution nearly all forms of life have been exposed to the electromagnetic radiation emitted by the sun, which for our purpose we will call light. Given the optic properties of light, it may be considered that it is non-randomly structured in time

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and space (low entropy), and such properties have to important consequences for living organisms: it can be used to produce thermodynamic work and carries information. In order to survive and compete in their natural habitat all forms of life are continuously obtaining and decoding information from their environment (including that contained in light), which they use for their own benefit.

Our sun emits light in a wide wavelength range, of which the radiation of longer wavelength is called infrared, and is mostly transformed in molecular movement (heat). Radiation of shorter wavelength, corresponds to the ultraviolet (UV), and can initiate photochemical reactions. Among the molecules that can be affected by UV, DNA must be highlighted, since the result of one of such reactions can be transmitted as a mutation to the next generation. UV radiation can also damage molecules through its capacity to initiate uncontrolled free radical reactions, in most cases involving reactive oxygen species (ROS). Additionally, visible light can indirectly act in photosensitive reactions in which ROS may be produced through energy transfer from a molecule that can be activated by light such as flavin or porphyrin. In this way, blue light is potentially harmful (Lledias and Hansberg, 2000). In this context, it is understandable that sunlight is a significant element for life, and that besides the utilization of its energy and information, during evolution many mechanisms to resist its negative effects have been selected for. Thus, light has contrasting roles in relation to life, on one side all organisms depend on its energy and information, and on the other it is potentially harmful, and even deadly. For fungi life in light requires significant adjustments in numerous regulatory processes, a fact reflected in the widespread effects on their behavior (Herrera-Estrella and Horwitz, 2007; Tisch and Schmoll, 2009).

2. The discovery of light responses and the initial experiments

Even though *Phycomyces* was probably the first fungus in which the effect of light was analyzed, the study of the "informational" use of light by plants started much earlier. Darwin became interested in plant movements such as orientation towards the sun or the escape from the excess of light provoked or influenced by blue-light, and dedicated a complete volume to them, in which he described the use of a yellow-orange solution of potassium dichromate as a filter to eliminate phototropism (Darwin, 1880). This phenomenon was considered as key to solve the identity of the blue-light photoreceptor. The similarity of the action spectra for various biological responses to blue light in organisms as diverse as plants, bacteria, ferns and fungi, was intriguing. This led to the proposal that all such responses should be controlled by the same type of photoreceptor of ancestral origin (Bergman et al., 1969), which was named simply the "near UV/blue" receptor or "Blue Light-Receptor" (BLR). Other authors adopted the nickname "cryptochrome"; a term coined by Jonathan Gressel, while studying in detail the effects of blue light in *Trichoderma* to highlight its hidden absorption (cryptic), and its preponderance in lower plants (cryptogams) and fungi (Gressel, 1979).

In several species of the genus *Trichoderma* a brief pulse of light triggers conidiation. In contrast to the organisms mentioned above this was the only obvious response of *Trichoderma* to light and hence the reason, which led to the use of this fungus as a simple photomorphogenic model.

Two action spectra of photoconidiation, which depict the relative effectiveness of different wavelengths of light in eliciting the physiological response, were determined (Gressel and Galun, 1967; Kumagai and Oda, 1969). Both action spectra show the characteristic shape attributed to the "cryptochrome", including a sharp peak in the near UV 350–380 nm, and a wider peak in the blue with a maximum at 440–450 nm. Accordingly, experiments with the riboflavin structural analog roseoflavin indicated the participation of a flavin as the photoreceptive pigment (Horwitz et al., 1984a).

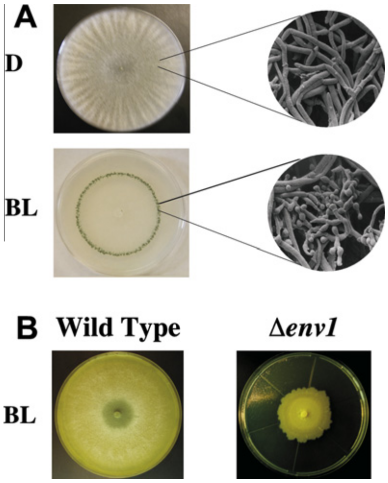

Fig. 1. Effect of blue light on *Trichoderma*. (A) The pictures show the effect of a short (5 min) pulse of blue light (BL) on *T. atroviride*. The upper photographs show a colony of *Trichoderma* growing in the dark (D). The lower photograph shows a colony of *Trichoderma* 36 h after exposure to light, with the characteristic ring of green conidia at the what was the colony perimeter at the time of exposure. Photographs at the right correspond to scanning electron micrographs of the indicated area (fine lines), hyphae (top), and hyphae and conidiophores (bottom). (B) The pictures show the dramatic effect of light on colony growth in the Denv1 mutant of *T. reesei* (left), as compared to the wild type strain (right). *T. reesei* was grown under continuous exposure to blue light (BL) for 72 h.

3. The early studies of *Trichoderma* photoresponses

The first description of the effect of light on conidiation of *Trichoderma* was made in 1957 (Gressel and Galun, 1967; Gutter, 1957). In the dark *Trichoderma* grows indefinitely as mycelium, and a brief pulse of light applied to the actively growing zone of the mycelium leads to the formation of dark green mature conidia, forming a ring at what was the edge of the colony when light was applied (Fig. 1A). The first event induced by light is a fast, first-order, photochemical reaction that does not require the presence of molecular oxygen and is independent of temperature. The fungus appears to be responsive to light (competent) only after 16 h of growth (Gressel and Galun, 1967). Three to seven hours after the induction abundant branching of aerial hyphae with an increased number of septa can be observed, as well as the formation of new aerial hyphae, leading to conidiophore development (Galun, 1971).

This developmental program can be suppressed using RNA synthesis inhibitors, such as 5-fluorouracil, once it was triggered by light, but only in a time-window of approximately 7 h after illumination (Galun and Gressel, 1966; Gressel and Galun, 1967). *T. atroviride* photoconidiation obeys the Bunsen–Roscoe law of reciprocity for pulses of blue light lasting from nanoseconds to minutes. Based on these data, it would appear that in *Trichoderma* photoconidiation is triggered by a single receptor system that is neither recycled to the photoreceptive form nor counted by enzymatic processes during or immediately following irradiation (Horwitz et al., 1990). This conclusion is supported by the observation that photoinduction is "remembered" while the culture is maintained in conditions that do not allow cellular growth (cold or absence of oxygen), as soon as growth is resumed, under optimal conditions, the colony conidiates (Gressel et al., 1975; Horwitz et al., 1990).