



Review

Shedding (far-red) light on phytochrome mechanisms and responses in land plants

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ABSTRACT

In order to monitor ambient light conditions, plants rely on functionally diversified photoreceptors. Among these, phytochromes perceive red (R) and far-red (FR) light. FR light does not constitute a photosynthetic energy source; it however influences adaptive and developmental processes. In seed plants, phytochrome A (phyA) acts as FR receptor and mediates FR high irradiance responses (FR-HIRs). It exerts a dual role by promoting *e.g.* germination and seedling de-etiolation in canopy shade and by antagonising shade avoidance growth. Even though cryptogam plants such as mosses and ferns do not have phyA, they show FR-induced responses. In the present review we discuss the mechanistic basis of phyA-dependent FR-HIRs as well as their dual role in seed plants. We compare FR responses in seed plants and cryptogam plants and conclude on different potential concepts for the detection of canopy shade. Scenarios for the evolution of FR perception and responses are discussed.

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Abbreviations: D, dark; FR, far-red light; P_{fr} , far-red light absorbing form of phytochromes; P_r , red light absorbing form of phytochromes; R, red light.

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1. Introduction

Plants utilise light not only for photosynthesis but also as a source of information, which is critical to survive under natural conditions. In order to perceive different aspects of their light environment, including the light intensity (*i.e.* the fluence rate), the spectral composition and the direction of the light gradient, plants use several classes of photoreceptors. The phototropins (PHOTs), the cryptochromes (CRYs) and the ZEITLUPE (ZTL) family proteins are receptors for blue light, UV RESISTANCE LOCUS 8 (UVR8) is a UV-B receptor and the phytochromes (phys) are red/far-red photoreceptors [1,2]. This review will focus on phytochromes, which originally were discovered in plants. Bacteria and fungi were also found to contain phytochromes, or more precisely, proteins consisting of the light-sensing domain known from plant phytochromes linked to other domains not present or not functional in plant phytochromes [3]. Bacterial phytochromes supplied an important first glimpse of the putative three-dimensional structure of plant phytochromes, but they are not included in this review and we direct readers interested in the highly diverse and colourful world of non-plant phytochromes to a recent review [4].

Phytochromes mainly exist in two different states, the P_r and the P_{fr} forms, which are named after their absorption peaks in red (R, 666 nm) and far-red light (FR, 730 nm), respectively. By absorption of light, the inactive P_r form and the biologically active P_{fr} form reversibly convert into each other. However, as the absorption spectra of the two forms overlap, irradiation with R or FR does not result in a 100% photoconversion to either P_{fr} or P_r . Rather, a dynamic equilibrium between the two forms is established that is characteristic of the light quality (*i.e.* the wavelength) [5]. As discussed in Section 2, this unique feature of phytochromes is of critical importance in detection of canopy shade and anticipation of competition by neighbouring plants [6].

In both seed plants and cryptogam plants (*i.e.* plants that reproduce by spores, such as ferns, mosses and green algae; in the following simply referred to as cryptogams), phytochromes are encoded by small gene families that consist of, for instance, five members in Arabidopsis, three in the fern *Adiantum capillus-veneris*, and seven in the moss *Physcomitrella patens* [7–9]. The phytochrome diversity in seed plants and cryptogams is the result of independent gene duplications that occurred during the course of evolution as determined by phylogenetic analyses [7,8]. Phytochromes from seed plants such as Arabidopsis are therefore more closely related to each other than to *P. patens* or other cryptogam phytochromes and *vice versa*.

Seed plant phytochromes have been grouped into type I and type II phytochromes. Type II phytochromes, such as phyB to phyE from Arabidopsis, are relatively photo-stable and most important in light-grown and adult plants. phyA, the only type I phytochrome, is photo-labile and accumulates to high levels in etiolated seedlings [2,10]. Cryptogam phytochromes have not been sufficiently characterised to assign them to type I or type II.

Phytochromes from seed plants are implicated in a wide range of responses, such as germination, de-etiolation, regulation of flowering, and responses to canopy shade. These responses have been classified into different response types, depending on their characteristics: low fluence responses (LFRs), very low fluence responses (VLFRs) and far-red high irradiance responses (FR-HIRs). LFRs require high P_{fr}/P_{tot} levels and depend on type II phytochromes such as phyB. They are R/FR reversible and follow the law of reciprocity (*i.e.* light pulses of the same total fluence can substitute for continuous irradiation). VLFRs and FR-HIRs are induced by low P_{fr}/P_{tot} levels established by a short light pulse of any wavelength in the case of the VLFRs and by continuous irradiation with high fluence FR in the case of the FR-HIRs. They are not R/FR reversible

and require the type I phytochrome phyA. FR-HIRs do not obey the reciprocity law [10,11].

Many phytochrome-induced responses rely on differential gene expression [10,12]. These responses largely – maybe entirely – depend on the nuclear translocation of light-activated phytochromes, which in their inactive form reside in the cytosol [13–15]. The two main phytochromes in seed plants, phyA and phyB, have different mechanisms for translocation into the nucleus. Light-activated phyA binds to FAR-RED ELONGATED HYPOCOTYL 1 (FHY1) and FHY1-LIKE (FHL), which contain a nuclear localisation signal and transport phyA into the nucleus [15,16]. Although phyA specifically evolved in seed plants, FHY1-like proteins are also present in the fern *Ceratopteris richardii*, the spikemoss *Selaginella moellendorffii*, the moss *P. patens* and the green alga *Closterium* sp. Thus, unlike phyA, FHY1-like proteins appear to be ubiquitous in the plant kingdom [13]. FHY1-dependent nuclear transport of phytochromes has been observed in the moss *P. patens*, suggesting that this mechanism is more ancient than phyA [13]. phyB does not require FHY1/FHL for nuclear translocation, in contrast to phyA and *P. patens* phy1. It has been suggested to contain a nuclear localisation signal that is masked in P_r but becomes surface-exposed upon conversion to P_{fr} [13,15,17]. Alternatively, or in addition, phyB may enter the nucleus bound to transcription factors involved in downstream signalling [18]. Light- and dark-grown plants undergo different developmental programmes controlled by specific sets of light-responsive genes. Photomorphogenesis, the developmental programme in light, is the default programme in seed plants. It is suppressed in dark-grown seedlings by a subgroup of basic helix-loop-helix transcription factors, the PHYTOCHROME INTERACTING FACTORS (PIFs), and an E3 ubiquitin ligase complex consisting of CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1) and SUPPRESSOR OF PHA-105 (SPA1) or SPA1-related proteins [2,10,19–22]. Several positive regulators of photomorphogenesis, including LONG HYPOCOTYL 5 (HY5), LONG HYPOCOTYL IN FAR-RED 1 (HFR1), and LONG AFTER FAR-RED LIGHT 1 (LAF1), are targeted for degradation by the COP1/SPA complex [2,10]. Multiple genes coding for COP1 and SPA homologs have been identified in the *P. patens* genome but it is unknown if these proteins have a similar function in light signalling in *P. patens* as COP1 and SPAs have in seed plants [23]. Basic helix-loop-helix transcription factors, to which the PIFs belong, are also present in *P. patens*, but evidence for the existence of functional PIF proteins in cryptogams is still lacking [24,25]. Research over the past few years extended the role of PIFs beyond light signalling and identified them as central regulators of growth and development. They not only respond to light but also to hormones, temperature and competition by neighbouring plants as reviewed in [24].

It is evident that in seed plants and cryptogams many phytochrome-induced responses depend on nuclear transport and the subsequent regulation of gene expression. It is also clear, however, that there are other responses, which are too fast to involve gene expression or which apparently depend on plasma membrane-associated phytochromes. For detailed discussion of such responses we refer to a recent review on phytochrome cytoplasmic signalling [26].

2. The shade avoidance response and neighbour detection in seed plants

2.1. phyB: a red light activated repressor of the shade avoidance response

Shading of shade-intolerant plants, such as Arabidopsis and many other species growing in habitats without dense vegetation, results in strongly increased elongation growth, changed

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