Photorécepteurs: généralités

Source: Li, J., Li, G., Wang, H. & Wang Deng, X. Phytochrome Signaling Mechanisms. *The Arabidopsis Book / American Society of Plant Biologists 9* (2011).

As sessile organisms, plants have acquired a high degree of developmental plasticity to optimize their growth and reproduction in response to their ambient environment, such as light, temperature, humidity, and salinity. Plants utilize a wide range of sensory systems to perceive and transduce specific incoming environmental signals. Light is one of the key environmental signals that influences plant growth and development. In addition to being the primary energy source for plants, light also controls multiple developmental processes in the plant life cycle, including seed germination, seedling de-etiolation, leaf expansion, stem elongation, phototropism, stomata and chloroplast movement, shade avoidance, circadian rhythms, and flowering time (Deng and Quail, 1999; Wang and Deng, 2003; Jiao et al., 2007).

Plants can monitor almost all facets of light, such as direction, duration, quantity, and wavelength by using at least four major classes of photoreceptors: phytochromes (phys) primarily responsible for absorbing the red (R) and far-red (FR) wavelengths (600-750 nm), and three types of photoreceptors perceiving the blue (B)/ultraviolet-A (UV-A) region of the spectrum (320-500 nm): cryptochromes (crys), phototropins (phots), and three newly recognized LOV/F-box/Kelch-repeat proteins ZEITLUPE (ZTL), FLAVIN-BINDING KELCH REPEAT F-BOX (FKF), and LOV KELCH REPEAT PROTEIN 2 (LKP2). In addition, UV RESISTANCE LOCUS 8 (UVR8) was recently shown to be a UV-B (282-320 nm) photoreceptor (Rizzini et al., 2011). These photoreceptors perceive, interpret, and transduce light signals, via distinct intracellular signaling pathways, to modulate photoresponsive nuclear gene expression, and ultimately leading to adaptive changes at the cell and whole organism levels.

Phytochromes: propriétés et mode d'action (1/2)

Source: Neff, M. M., Fankhauser, C. & Chory, J. Light: an indicator of time and place. *Genes & Development* **14**, 257–271 (2000)

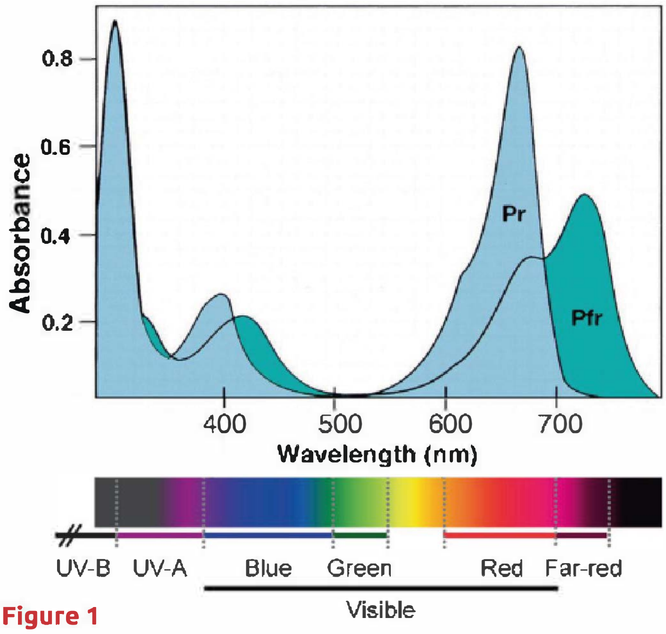

Figure 1

Phytochromes are photochromic proteins composed of a large protein (~125 kD) covalently attached to a linear tetrapyrrole chromophore. Phytochromes are synthesized in a red-light-absorbing form, Pr (λ_{max} = 660 nm) which, upon exposure to red light, can be phototransformed into a far-red-light-absorbing form, Pfr (λ_{max} = 730 nm). Upon exposure to far-red light, Pfr is photoconverted to Pr (Kendrick and Kronenberg 1994). Both Pfr and Pr that has been photocycled have been shown to induce developmental responses (Shinomura et al 2000). Thus, phytochrome acts as a light-controlled developmental switch. Phytochromes have been found in all taxa of lower and higher plants examined (Mathews and Sharrock 1997; Mathews and Donoghue 1999), as well as cyanobacteria (Hughes et al. 1997; Lamparter et al. 1997; Yeh and Lagarias 1997).

Phytochromes: propriétés et mode d'action (2/2)

Source: Neff, M. M., Fankhauser, C. & Chory, J. Light: an indicator of time and place. *Genes & Development* **14**, 257–271 (2000)

Phytochromes are soluble proteins and exist as homodimers. The molecular mass of the apoprotein monomer is approximately 125 kDa. Phytochrome apoproteins are synthesized in the cytosol, where they assemble autocatalytically with a linear tetrapyrrole chromophore, phytochromobillin (PΦB). The synthesis of PΦB is accomplished by a series of enzymatic reactions in the plastid that begins with 5-aminolevulinic acid (Figure 2A). The early steps in the PΦB pathway are shared with chlorophyll and heme biosynthesis. The committed step is the oxidative cleavage of heme by a ferredoxin-dependent heme oxygenase (HO) to form biliverdin IX (BV). BV is subsequently reduced to 3Z-PΦB by the enzyme PΦB synthase. Both 3Z-PΦB and its isomerized form 3E-PΦB can serve as functional precursors of the phytochrome chromophore. PΦB is then exported to the cytosol, where it binds to the newly synthesized apo-PHYs to form holo-PHYs (Terry, 1997; Figure 2A). The chromophore is attached via a thioether linkage to an invariant cysteine in a well-conserved domain among all phytochromes (see below).

The intrinsic photochemical activity of the chromophore prosthetic group allows phytochromes to convert between the two forms. Phytochromes are synthesized in the Pr form in dark-grown seedlings. It has been widely accepted that absorption of R light triggers a "Z" to "E" isomerization in the C15-C16 double bond between the C and D rings of the linear tetrapyrrole, resulting in the FR-absorbing Pfr form (Andel et al., 1996; Figure 2B). However, a recent NMR analysis showed that the A pyrrole ring around C4-C5 double bond rotates during photoconversion (Ulijasz et al., 2010). This discrepancy should be resolved in future studies. In addition, the Pr-to-Pfr transition is associated with rearrangement of the protein backbone (Figure 2B). The active Pfr form can be converted back to the inactive Pr form, either by a slow non-photoinduced reaction (dark reversion) or much faster upon absorption of FR light (Mancinelli, 1994; Quail, 1997a; Fankhauser, 2001; Figure 2B). This property allows phytochrome to function as a R/FR-dependent developmental switch.

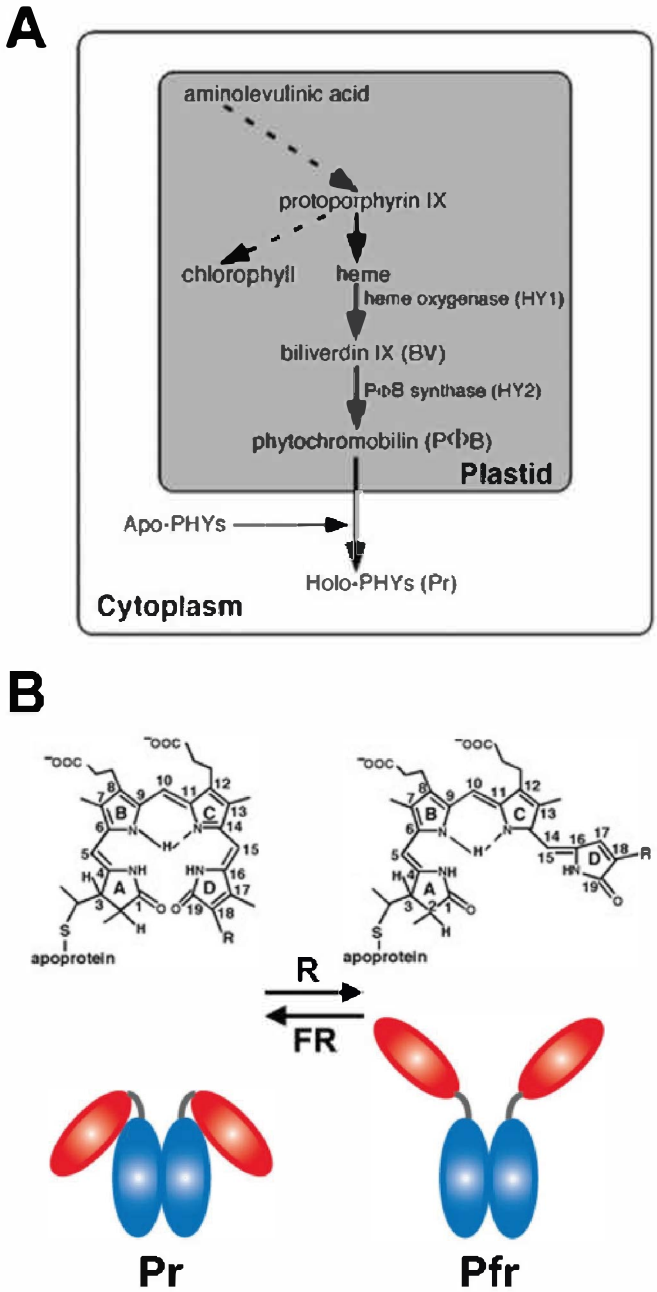

Figure 2

Phytochromes: mode d'action

Source: Li, J., Li, G., Wang, H. & Wang Deng, X. Phytochrome Signaling Mechanisms. *The Arabidopsis Book / American Society of Plant Biologists* 9 (2011).

The term phytochrome, meaning “plant color”, was originally coined to describe the proteinous pigment that controls photoperiod detection and floral induction of certain short-day plants (such as cocklebur and soybean) (Garner and Allard, 1920), and the reversible seed germination of lettuce (c.v. Grand Rapids) by R and FR light (Borthwick et al., 1952). R light promotes seed germination, whereas subsequent FR light treatment abolishes R light induction of seed germination. The germination response of lettuce seeds repeatedly treated with R/FR cycles is determined by the last light treatment. Thus R/FR photoreversibility is a characteristic feature of this response. In addition, the law of reciprocity applies to this response, i.e. the response is dependent on the total amount of photons received irrespective of the duration of light treatment.

Over the years, three action modes for phytochromes have been defined, i.e. low-fluence responses (LFRs), very-low-fluence responses (VLFRs) and high-irradiance responses (HIRs) (Table 1). The above-mentioned F/FR reversible response is characteristic of LFRs.(...)

Photoreversibility occurs because phytochromes exist as two distinct but photoreversible forms in vivo: the R light-absorbing form (Pr) and the FR light-absorbing form (Pfr). The Pr form absorbs maximally at 660 nm, whereas the Pfr form absorbs maximally at 730 nm (Quail, 1997a; Figure 1). The Pfr forms of phytochromes are generally considered to be the biologically active forms. It should be noted that in addition to their maximal absorptions of R and FR wavelengths, phytochromes also weakly absorb B light (Furuya and Song, 1994; Figure 1).

Table 1.
Diagnostic Features of Different Phytochrome Action Modes

Action Mode	Fluence Requirements
VLFR	0.1 µmol/m² - 1 µmol/m²
LFR	1 - 1000 µmol/m²
HIR	> 1000 µmol/m²

VLFR: very-low-fluence response;
LFR: low-fluence response;
HIR: high-irradiance response.

Phytochromes: aspects génétiques

Source: Li, J., Li, G., Wang, H. & Wang Deng, X. Phytochrome Signaling Mechanisms. *The Arabidopsis Book / American Society of Plant Biologists 9* (2011).

In Arabidopsis thaliana, there are five phytochromes, designated phytochrome A (phyA) to phyE. They are encoded by five distinct members of the phytochrome gene family and are classified into two groups according to their stability in light (Sharrock and Quail, 1989). phyA is a type I (light labile) phytochrome, and phyB to phyE are all type II (light stable) phytochromes. phyA is most abundant in dark-grown seedlings, whereas its level drops rapidly upon exposure to R or white (W) light. In light-grown plants, phyB is the most abundant phytochrome, whereas phyC-phyE are less abundant (Clack et al., 1994; Hirschfeld et al., 1998; Sharrock and Clack, 2002).

Sequence analysis suggests that these phytochromes can be clustered into three subfamilies: phyA/phyC, phyB/phyD, and phyE (Figure 3). Analysis of reconstituted recombinant phyA, phyB, phyC and phyE proteins revealed that they have similar but not identical spectral properties (Kunkel et al., 1996; Remberg et al., 1998; Eichenberg et al., 2000). Orthologs of Arabidopsis PHY genes are present in most, if not all, higher plants (Clack et al., 1994; Sharrock and Quail, 1989; Mathews and Sharrock, 1997).

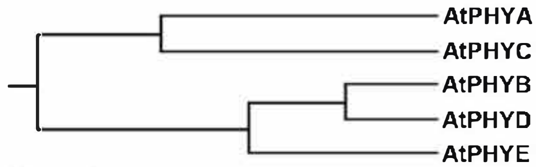

Figure 3

Cryptochromes & Phototropines

Source: Liu, H., Liu, B., Zhao, C., Pepper, M. & Lin, C. The action mechanisms of plant cryptochromes. *Trends in Plant Science* **16**, 684–691 (2011).

Cryptochromes (CRY) are photosensory receptors that regulate growth and development in plants and the circadian clock in plants and animals [1, 2]. Plant cryptochromes are best studied in Arabidopsis (Arabidopsis thaliana). The Arabidopsis genome encodes three cryptochrome genes, CRY1, CRY2, and CRY3. CRY1 and CRY2 act primarily in the nucleus [3, 4], whereas CRY3 probably functions in chloroplasts and mitochondria [5].

Source: Briggs, W. R. et al. The Phototropin Family of Photoreceptors. *The Plant Cell* **13**, 993–997 (2001).

The past decade has seen dramatic advances in our knowledge of plant photoreceptors and in our understanding of the signal transduction pathways that they activate (Briggs and Olney, 2001). A major part of these advances has been the identification and characterization of photoreceptors that respond to signals from the blue region of the electromagnetic spectrum. We now know that there are at least two classes of blue light photoreceptors: the cryptochromes and the phototropins.

Source: Christie, J. M. Phototropin Blue-Light Receptors. *Annual Review of Plant Biology* **58**, 21–45 (2007).

Since the isolation of the Arabidopsis PHOT1 gene in 1997, phototropins have been identified in ferns and mosses where their physiological functions appear to be conserved. Arabidopsis contains two phototropins, phot1 and phot2, that exhibit overlapping functions in addition to having unique physiological roles. Phototropins are light-activated serine/threonine protein kinases. Light sensing by the phototropins is mediated by a repeated motif at the N-terminal region of the protein known as the LOV domain. Photoexcitation of the LOV domain results in receptor autophosphorylation and an initiation of phototropin signaling.