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Invited review

The impact of the phytochromes on photosynthetic processes

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ABSTRACT

This review describes the phytochrome system in higher plants and cyanobacteria and its role in regulation of photosynthetic processes and stress protection of the photosynthetic apparatus. A relationship between the content of the different phytochromes, the changes in the ratios of the physiologically active forms of phytochromes to their total pool and the resulting influence on photosynthetic processes is reviewed. The role of the phytochromes in the regulation of the expression of genes encoding key photosynthetic proteins, antioxidant enzymes and other components involved in stress signaling is elucidated.

1. General information on phytochromes in higher plants and cyanobacteria

1.1. Phytochromes in higher plants

It is known that a system of regulatory photoreceptors plays a key role in the perception of light. These photoreceptors include phytochromes (or phytochrome-like structures), cryptochromes, phototropins, protochlorophyllide, and UV-B photoreceptors (UVR8) [1–3].

The phytochrome (Phy) system regulates a wide range of physiological processes from seed germination to flowering and fruiting [2,4,5]. The response of the plant metabolism to the action of various damaging factors, such as unfavorable temperatures, salinity, drought, UV radiation, is also under control of the phytochrome system [5–14]. It is assumed that the regulatory effects of phytochromes are primarily related to their effects on the activity of enzymes that regulate the metabolic processes, in particular the biosynthesis of low- molecular weight antioxidants and photosynthetic pigments, and the level of expression of phytochrome-regulated genes involved primarily in cellular signaling [11,12,15,16].

Phytochrome is a protein dimer (molecular weight above 240 kDa), consisting of two monomeric forms with a covalently bound chromophore consisting of four unfolded pyrrole rings that form an open tetrapyrrole (Fig. 1). In higher plants, the chromophore molecule – phytochromobilin - is initially synthesized as a closed tetrapyrrole ring structure, which opens up and binds to the protein via sulfur to cysteine. Detailed information on the structure of phytochromes in both prokaryotes and plants is presented in a number of reviews [17–20]. The family of phytochrome-like photoreceptors is well described [21,22]. Three from the four rings of the tetrapyrrole, rings A, B and C are fixed by the local protein environment. The phytochromobilin undergoes photoisomerization after absorption of red light (RL, λ_m – 660 nm) which leads to a rotation of 4th ring D resulting in cis-trans isomerization in the tetrapyrrole chain and subsequent formation of the Lumi-R state. This state can thermally relax into the Meta-R state that finally relaxes into the physiologically active form (Pfr) with red shifted absorption (Fig. 2). Associated proton translocation leads to a change in the secondary structure of the protein stabilizing the Pfr for a characteristic time (Fig. 3) [23,24]. The reversed transition occurs by absorption of far-red light (FRL, λ_m – 730 nm) converting phytochrome from the physiologically active form back into the physiologically inactive form (Pr).

Abbreviations: Phy or P, phytochrome; Pfr, physiologically active form of phytochrome; Pr, initial inactive form of phytochrome; Ptotal, total phytochrome pool; PhyA, phytochrome A; PhyB, phytochrome B; PA, photosynthetic apparatus; *PSII*, photosystem II; RL, red light; FRL, far-red light; WT, wild type

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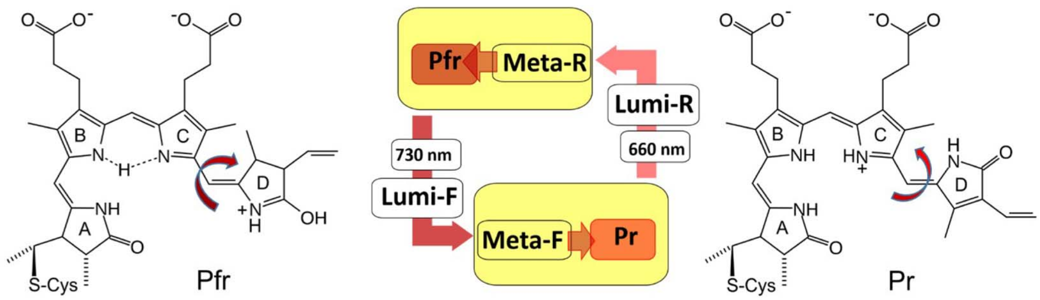

Fig. 1. Middle: Light induced general photocycle of phytochromes. Meta-R, Meta-F, Lumi-R and Lumi-F – are the intermediates of photocycle. Right side: molecular configuration of the Pr state of the phytochromobiline. Left side: structure of the Pfr state.

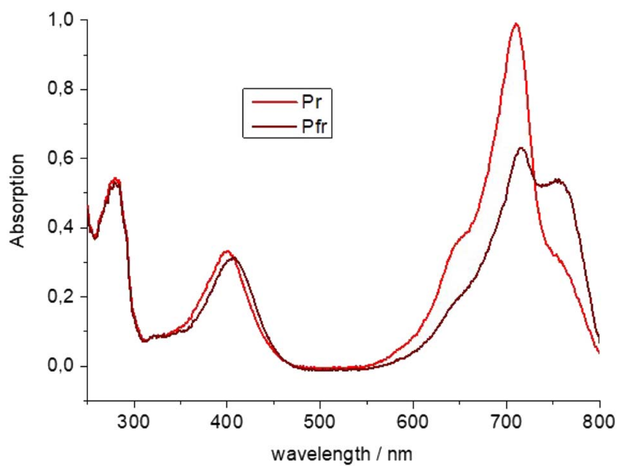

Fig. 2. Absorption spectra of phytochrome from bacteriophytochrome Bph4 from *Rhodopseudomonas palustris* strain CGA009 in the Pr state (red curve), and a mixture of both Pr and Pfr state after photoactivation (brown curve).

Both isomers form the stable forms of the phytochrome – Pfr with a maximum absorption in the region of 705–740 nm and Pr with an absorption maximum in the region of 650–670 nm. The Lumi-R, Meta-R and possible other unstable short-lived forms can be detected during the photocycle by time resolved spectroscopy [19,24]. Phytochrome is synthesized in the form of Pr (P_{660}). Dark reversion of Pfr to Pr and degradation especially of the Pfr is also possible (Fig. 3). The reversibility of the phototransformation is inherent in phytochrome B (PhyB), and probably also phytochromes C, D and E [25].

Fig. 1 presents a simplified scheme for the Phy photocycle, as it refers to a single type of phytochrome. PhyB is the most prominent and possibly important light-regulated switch for the light induced regulation by phytochromes. However, other phytochrome species are

Table 1
Types of phytochrome-controlled reactions (B): very low fluence response (VLFR), low fluence response (LFR) and high irradiance response (HIR). HIR are divided into reactions, which are controlled with RL (660 nm) and FRL (710–720 nm) [25].

Type of response	Light intensity, μmol (quantum) $м^{-2}$ s^{-1}	Phytochrome	Reversibility	Light
VLFR	10^{-4}–10^{-1}	PhyA, PhyB	absent	RL, FRL
LFR	1–1000	PhyB (PhyA?)	present	RL
HIR	> 1000	PhyA	absent	FRL
HIR	-.-	PhyB	-.-	RL

involved into the response of photosynthetic organisms to the external light conditions. In rice plants, for example, phytochromes C and A take part in photomorphogenetic responses, and in plants like *A. thaliana* there are also the phytochromes A, C, D, E [26]. The range of intensities in low and high-energy reactions inducible in phytochromes is very broad (Table 1). For example, on quadrupole *Arabidopsis* mutants containing only PhyA, it was shown that the involvement of PhyA in certain responses is observed only at high light intensity of at least 160 μmol quanta $m^{-2}s^{-1}$ [27]. Therefore, it cannot be ruled out that PhyA is inactive in many photomorphogenetic experiments, where light of an intensity < 50 μmol quanta $m^{-2}s^{-1}$ was used.

1.2. Phytochromes and phytochrome-like systems in prokaryotes

There are many phototrophic photosynthetic organisms that perceive light signals from different photoreceptors, including cryptochromes, carotenoids, orange carotenoid proteins and phytochrome-like photoreceptors [28–31]. Among these organisms, some of the most ancient and common are cyanobacteria [32] which are part of this review together with phytochromes in higher plants.

Histidine kinases with the properties of plant phytochromes [33,34] acting as light sensors in prokaryotic cyanobacteria are called

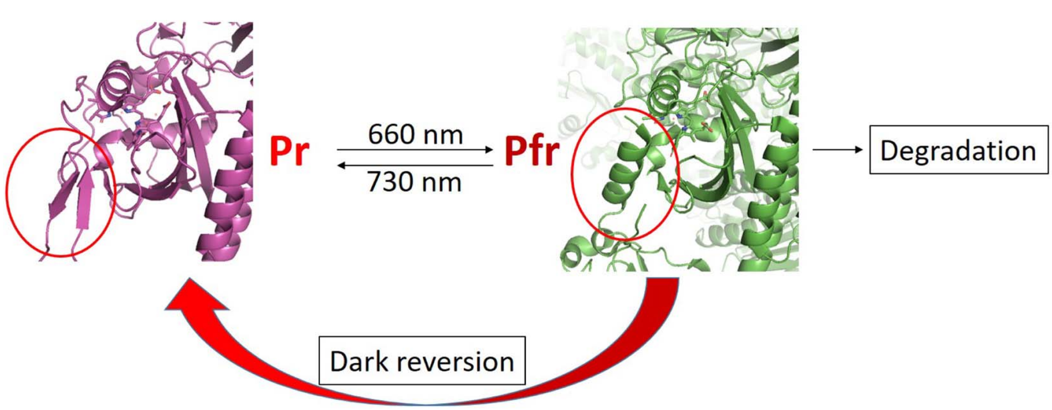

Fig. 3. Transitions in the protein structure associated with the light-induced cis-trans isomerization in the biliverdine. The activation of the Pfr state is associated with a proton translocation that leads to a change in the secondary structure of the protein from two beta-sheets (Pr-state) to an alpha-helix (Pfr-state) (marked by red circles).