Journal of Photochemistry and Photobiology C: Photochemistry Reviews 10 (2009) 63–80

Contents lists available at ScienceDirect

Journal of Photochemistry and Photobiology C: Photochemistry Reviews

journal homepage: www.elsevier.com/locate/jphotochemrev

Review

Transduction mechanisms of photoreceptor signals in plant cells

Vladimir D. Kreslavski[a], Robert Carpentier[b], Vyacheslav V. Klimov[a], Suleyman I. Allakhverdiev[a,*]

[a] Institute of Basic Biological Problems, Russian Academy of Sciences, Pushchino, Moscow Region 142290, Russia
[b] Groupe de Recherche en Biologie Végétale, Université du Québec à Trois-Rivières, C.P. 500, Québec, Canada G9A 5H7

ARTICLE INFO

Article history:
Received 13 January 2009
Received in revised form 28 April 2009
Accepted 30 April 2009
Available online 12 May 2009

Keywords:
Ion exchange
Phytochrome
Plant
Photoreceptors
Signal transduction
Transcriptional factors

ABSTRACT

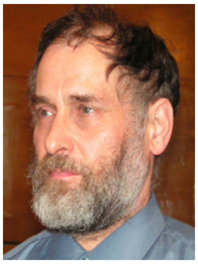
During a plant life, light is necessary not only as a source of energy, but also as a regulatory factor of plant metabolism with information signal function. In this review we consider basic links of primary stages of light signal transduction in higher plants. The transformation circuits and possible pathways of photoreceptor light signal transduction, as well as possible roles of photoreceptor-interacting proteins, secondary messengers and some transcriptional factors are discussed. The review is also focused on examination of rapid signaling events such as activation of ion exchange systems as well as interaction of photoreceptors in signaling pathways.

Contents

Abbreviations: cAMP, adenosine-3′,5′-cyclophosphate or 3′,5′-cyclo-AMP; AMP, adenosine-5′-monophosphate; GMP, guanosine monophosphate; GTP, guanosine triphosphate; GC, guanylyl cyclase; IP_3, inositol-1,4,5-triphosphate; PIP2, phosphatidylinositol-4,5-diphosphate; phy, phytochrome; PDE, phosphodiesterase; RL, red light; FRL, far-red light.

* Corresponding author. Tel.: +7 496 77 31 837; fax: +7 496 73 30 532.
E-mail addresses: vkreslav@mail.ru (V.D. Kreslavski), Robert.Carpentier@uqtr.ca (R. Carpentier), klimov@issp.serpukhov.su (V.V. Klimov), suleyman@issp.serpukhov.su (S.I. Allakhverdiev).

1389-5567/$20.00
doi:10.1016/j.jphotochemrev.2009.04.001



Vladimir D. Kreslavski is a senior researcher. He is the head of group in Laboratory of Ecology and Physiology of phototrophic organisms at Institute of Basic Biological Problems, RAS, Pushchino, Moscow Region, Russia. The field of interests: photoreceptor signaling, molecular mechanisms of plant stress resistance and acclimation of photosynthetic apparatus as well as the pathways of photosynthetic improvement.

Robert Carpentier is professor at Université du Québec à Trois- Rivières, Québec, Canada. He obtained his Ph.D. in Biochemistry from Laval University (1983, Québec). He is editor of *Journal of Photochemistry and Photobiology B: Biology*, associate editor of the journal *Photosynthesis Research* and was the chair of the XIIIth International Congress on Photosynthesis (Montréal, 2004). His research interests concern the influence of environmental stresses on electron transport pathways in photosystems I and II and energy dissipation in photosynthesis.

Suleyman I. Allakhverdiev is the Chief Research Scientist at the Institute of Basic Biological Problems, RAS, Pushchino, Russia. He received Dr.Sci. degree in Photochemistry, Photobiology, and Plant Physiology (in 2002, Moscow); and Ph.D. in Physics and Mathematics, (in 1984, Pushchino). He graduated from Azerbaijan State University, Department of Physics (Baku). He has been guest-editor and is a member of the Editorial Board of several international journals. His research interests include the structure and function of photosystem II, water oxidizing complex, artificial photosynthesis, hydrogen photoproduction, catalytic conversion of solar energy, plant under environmental stresses, photoreceptor signaling. He has been cited ca. 3000.

1. Introduction

Light is known to regulate almost all physiological and biochemical processes in plants. Together with photosynthesis, photomorphogenesis, phototaxis, phototropism, etc. play an important role in vital activity of different plant species. These processes are triggered by light and transformed into a cell response via a system of transduction of the light signal [1–13]. The mechanisms and components of these processes have not been adequately studied in plant cells. This is primarily true for the rather fast first stages of the light signal transduction chain, when light-induced proteins have no time to be synthesized. The term “signal transduction” became popular in the early 1980s, therefore the problem of light signal transduction in plant cells belongs to a fairly new area of biochemistry designated as “cell signaling”. In biology, signal transduction refers to any process by which a cell converts one kind of signal or stimulus into another. Most often, this involves ordered sequences of biochemical reactions inside the cell that are carried out by enzymes and linked through second messengers resulting in what is thought of as a “second messenger pathway”. The concept of “cell signaling” implies not only the signals' transduction, but the entire set of events connected to it, including signal multiplication, depression, and suppression (or switching off) [4,8,11]. Such processes are usually rapid, lasting on the order of milliseconds in the case of ion flux, to minutes for the activation of protein and lipid mediated kinase cascades. Thus, sensing both external and internal environments at the cellular level relies on signal transduction.

Signal transduction usually involves the binding of small extracellular signaling molecules to receptors that face outwards from the plasma membrane and trigger events inside the cell. Between them, steroids represent an example of extracellular signalling molecules that may cross the plasma membrane due to their lipophilic or hydrophobic nature [14].

Environmental stimuli may be both molecular in nature (as above) or more physical, such as light absorbed by plant photoreceptors. In this case light may affect photoreceptor molecules localized in the whole cell. In that case, inner membranes are most likely to be involved in the signal transduction chain, whereas the receptors of the hormones are mainly located on the plasma membrane.

Various effector proteins (the effectors), for example adenylate cyclase (ADC) and GTP-binding proteins (G-proteins) are involved in the transduction chain from receptors to subsequent compartments of the cell. Activation of the effectors may be initiated by the detachment of the α-subunit of the heterotrimeric G-proteins. The activated G protein subunits can initiate the signaling for many downstream effector proteins, including phosphodiesterases and adenylyl cyclases, phospholipases, and ion channels that permit the release of second messenger molecules such as cyclic nucleotides (cyclic guanosine 3′,5′-monophosphate—cGMP and cyclic adenosine-3′,5′-monophosphate—cAMP), the components of the phosphatidylinositol signaling system (inositol 1,4,5-triphosphate–IP_3 and 1,2-diacylglycerol—DAG), as well as Ca^{2+} [10,15–20]. The central position in the system of intracellular signalling is occupied by these three important messengers: Ca^{2+}, IP_3 and DAG. The origin of the two last compounds merits special notice. They are formed from the plasma membrane component phosphatidyl-4,5-bisphosphate (PIP_2) with the participation of phosphoinositide-specific phospholipase C. Several reactive oxygen species such as H_2O_2, O_2^-, as well as NO, cADP-ribose and nicotinamide adenine dinucleotide phosphate also belong to the important family of secondary messengers.

The increasing concentration of free cytosolic Ca^{2+} is the most widespread mechanism of transduction signaling chain independently from the nature of various signals. In this case Ca^{2+}-sensitive proteins, in particular calmodulin (CaM) can be the targets of free cytosolic calcium. A certain amount of evidence of the participation of Ca^{2+}, cAMP, cGMP, CaM, as well as G-proteins and the components of the phosphatidylinositol signaling system in the transduction of the phytochrome signal has been obtained [7,10,11,19–25].

The activated receptors located in the plasma membrane transmit the signal to the intracellular targets. If a target, or the effector protein, is an enzyme, then the signal modulates its catalytic activity. If an ion channel serves as effector protein, then the conductivity and lifetime of this channel is modulated. Nevertheless, it is important to note that a small quantity of hormonal molecules or light quanta, affecting the corresponding receptors, can produce a great number of messenger molecules activating synthesis of several proteins. The adenylate kinase system, catalyzing the formation of cellular cAMP, functions in such manner [19,26]. In that case a significant amplification of the signal is observed as a result of the interaction of an external signal with a receptor. Another mechanism of signal amplification involves regulation of the expression of light-controlled genes.

A cell receptor involved in light signal transduction can interact with different cell components. Hence, several signal transduction pathways are possible. Second messengers such as Ca^{2+} and cyclic nucleotides are involved in the most widespread pathways of signal transduction (Fig. 1). Some receptors can also activate directly (without involvement of second messengers) protein kinases, for example the enzyme tyrosine kinase, which phosphorylates the residues of tyrosine in the proteins [27]. In this case a cascade of cytosolic protein kinases is triggered. They phosphorylate various proteins that cause subsequent physiological effects.

Regulation of gene expression can result from the transduction of signals of various natures. The signal can be transduced into the cell nucleus by translocation of cytosolic protein kinases or activating transcription factors. Transcription factors produced