



Review

Recent advances in understanding the molecular mechanism of chloroplast photorelocation movement[☆]Sam-Geun Kong, Masamitsu Wada^{*}

Department of Biology, Faculty of Sciences, Kyushu University, Fukuoka 812-8581, Japan

ARTICLE INFO

Article history:

Received 21 August 2013

Received in revised form 25 November 2013

Accepted 4 December 2013

Available online 12 December 2013

Keywords:

Actin filament

Blue light

Chloroplast movement

Cytoskeleton dynamics

Photoreceptor

Phototropin

ABSTRACT

Plants are photosynthetic organisms that have evolved unique systems to adapt fluctuating environmental light conditions. In addition to well-known movement responses such as phototropism, stomatal opening, and nastic leaf movements, chloroplast photorelocation movement is one of the essential cellular responses to optimize photosynthetic ability and avoid photodamage. For these adaptations, chloroplasts accumulate at the areas of cells illuminated with low light (called accumulation response), while they scatter from the area illuminated with strong light (called avoidance response). Plant-specific photoreceptors (phototropin, phytochrome, and/or neochrome) mediate these dynamic directional movements in response to incident light position and intensity. Several factors involved in the mechanisms underlying the processes from light perception to actin-based movements have also been identified through molecular genetic approach. This review aims to discuss recent findings in the field relating to how chloroplasts move at molecular levels. This article is part of a Special Issue entitled: Dynamic and ultrastructure of bioenergetic membranes and their components.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Plants play a role as the major agent of inorganic carbon fixation into biomass. The photoautotrophic process converts light energy into chemical energy, which occurs in chloroplasts that serve as the photosynthetic factory equipped with photosystems. However, excess light energy is harmful, because it can lead to an overproduction of highly reactive intermediates and by-products that cause photo-oxidative damage and inhibit photosynthesis [1,2]. To protect themselves from the adverse effects of high light intensity, plants have evolved two distinct mechanisms for sensing and responding to light. It involves chloroplast photorelocation to avoid strong light and non-photochemical quenching relying on the conversion and dissipation of the excess excitation energy into heat [3].

The ability of chloroplasts to change their intracellular position in response to light fluctuations was discovered over a century ago [4]. The chloroplast movement is a phenomenon commonly observed in all plant groups from algae to land plants [4–6]. Depending on the plant groups, however, chloroplasts exhibit various positioning in the cells

under different light conditions [7–9] (Fig. 1). Chloroplasts dynamically change their positions by monitoring incident light position and intensity [8]: they accumulate to the area illuminated with low-intensity light (accumulation response), while they move away from the area illuminated with high-intensity light within a few tens of minutes (avoidance response). These phenomena were clearly observed when cells were irradiated partially. Blue light is the most effective wavelength to induce these two responses in most plants tested including angiosperms (*Arabidopsis*, spinach, tobacco, etc.) [10,11] and cryptogams (ferns, mosses, liverworts, algae, etc.) [12]. However, red light is also effective for the induction of chloroplast photorelocation movement in some cryptogam plants such as the alga *Mougeotia scalaris*, the fern *Adiantum capillus-veneris*, and the moss *Physcomitrella patens* [5,12,13].

Chloroplast photorelocation responses are strongly correlated with the function of chloroplast: The accumulation response helps to optimize photosynthetic ability [10,14] and the avoidance response aids to reduce photodamage by excess light [15–17]. Plants that carry mutations impairing the chloroplast avoidance are more susceptible to oxidative stress under excess light [11,18,19]. Thus, chloroplast photorelocation movement is essential for plant survival under fluctuating light conditions.

Genetic studies of chloroplast photorelocation movement contributed to the identification of several components involved in signal transduction as well as actin-based movement [20]. The regulation mechanisms of chloroplast photorelocation movement have been progressively elucidated through recent progress in imaging techniques for the visualization of chloroplasts and cytoskeletal components [21–23]. In this review, we

Abbreviations: BDM, 2,3-butanedione monoxime; BFA, Brefeldin A; cp-actin, chloroplast actin; GFP, green fluorescent protein; FMN, flavin mononucleotide; LOV, light, oxygen or voltage; P2C, C-terminal 534–915 amino acid fragment of *Arabidopsis* phototropin 2; P2N, N-terminal 1–533 amino acid fragment of *Arabidopsis* phototropin 2; phot1, phototropin 1; phot2, phototropin 2; TIRF, total internal reflection fluorescence

[☆] This article is part of a Special Issue entitled: Dynamic and ultrastructure of bioenergetic membranes and their components.

^{*} Corresponding author. Tel.: +81 92 642 7252; fax: +81 92 642 7258.

E-mail address: wadascb@kyushu-u.org (M. Wada).



Fig. 1. A visible pattern of chloroplast movements drawn by blue light on a young leaf of *Solanum americanum*. Chloroplasts in pale green areas take the high light-induced avoidance position, while those in darker green areas do the low light-induced accumulation position.

summarized recent advances on chloroplast photorelocation responses covering from light perception to actin-based movement.

2. Photoperception for chloroplast photorelocation movement

Plants as sessile organisms have evolved unique systems for sensing and responding to environmental light. Members of both the phototropin and phytochrome families of photoreceptors regulate the sophisticated blue-light- and/or red-light-induced chloroplast relocation movements.

2.1. Blue light receptors: phototropins

Light-driven chloroplast relocation responses are well described in *Arabidopsis thaliana* using photometric and microscopic analyses, or observed by the naked eye (named white and green band assay) [10,23,24]. The blue light-dependent chloroplast movements are mediated by plant specific photoreceptors, phototropins. Phototropins are found in various organisms from unicellular algae to higher plants

[7,25]. *Arabidopsis* has two phototropins (phot1 and phot2). phot1 (originally named NPH1) was discovered as a blue light receptor kinase that regulates phototropic response in *Arabidopsis* [26,27]. Later, phot2 as a homolog of phot1 (formerly NPL1) was identified from a mutant defective in high light-induced avoidance response in *Arabidopsis* [28,29].

Phototropins have well-conserved structural properties with two LOV (light, oxygen or voltage) domains (LOV1 and LOV2) in their N-terminus and a serine/threonine kinase domain in their C-terminus [25] (Fig. 2). The two phototropins in *Arabidopsis* have highly overlapping functions not only in chloroplast accumulation response but also in phototropism, stomatal opening, and leaf flattening [27–31]. However, phot2 plays specific roles on chloroplast avoidance response [28,29] and leaf morphogenesis [32]. phot1 also induces the avoidance response transiently, but the response is not significant compared to that of phot2 [33]. These distinct functional properties of phototropins are not simply explained because phot1 and phot2 possess intrinsically different properties in many aspects including gene expressions, photochemical properties, and cellular and subcellular localizations (see below).

2.2. Photochemical properties of LOV domain

The LOV domains are widely found not only in plants but also in bacteria, archaea, and fungi, and play a role as the chromophore-binding site to perceive a broad range of UVA to blue light (350–500 nm) via a flavin mononucleotide (FMN) cofactor [34]. The LOV domains undergo a photocycle upon blue light stimulation including transient adduct formation between the chromophore and a conserved cysteine. Of those, two LOV domains (LOV1 and LOV2) of phototropins have been well characterized on their structure and photochemical properties. Core structures and the photochemical reactions of the LOV1 and LOV2 domains are very similar to each other [35]. However, the LOV domains of phot1 differ from those of phot2 in their reaction kinetic properties and relative quantum efficiencies [36].

The LOV domains of phototropins have also important roles in multimer formation [37–39]. The LOV1 domain exists as a dimer in the dark [37,38]. Photochemical analysis using the time-resolved transient grating method further suggested that the dimer of phot1 LOV1 domain associates to form a tetramer upon photoexcitation and the homo-tetramer dissociates into the dimer via the dark recovery process of the chromophore [40]. However, transgenic analysis with the deletion mutant of phot1 LOV1 domain suggested that phot1 LOV1 domain is dispensable to mediate phot1 responses in *Arabidopsis* [41]. By contrast, the activity of phot2 LOV1 domain on the phototropic response

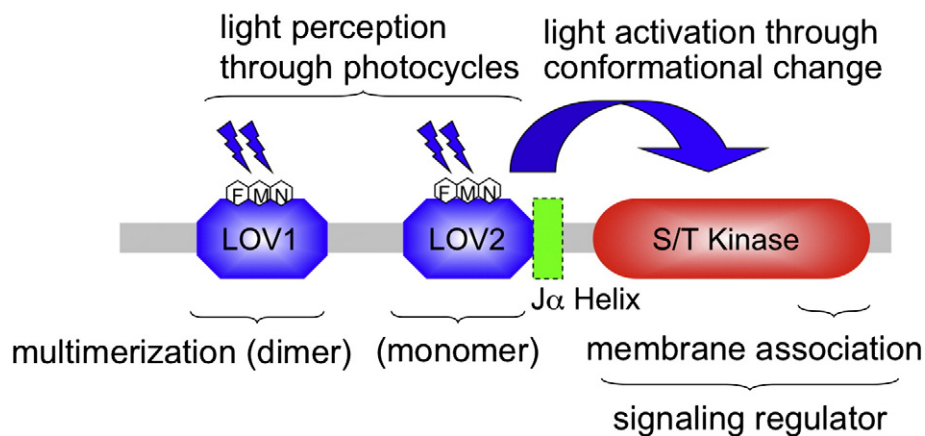


Fig. 2. Schematic illustration of the molecular structure, functional role, and regulation mechanism of phototropins. Phototropins consist of LOV1 and LOV2 as the photosensory domains in their N-terminus and an S/T kinase domain in their C-terminus. The kinase is regulated through the photocycles of LOV domains and conformational changes in LOV2 domain and J α helix in response to blue light and consequently activates downstream signaling by phosphorylating not-yet-known downstream signaling factor(s). The C-terminus also plays an essential role for the membrane association of phototropin. The details are shown in the text.

Download English Version:

<https://daneshyari.com/en/article/10795496>

Download Persian Version:

<https://daneshyari.com/article/10795496>

[Daneshyari.com](https://daneshyari.com)