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Functions of Phytochrome in Rice Growth and Development

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Abstract: Phytochrome family mainly senses red and far-red light to regulate a range of developmental processes throughout the life cycle of plants. Rice phytochrome gene family is composed of three members known as *PHYA*, *PHYB* and *PHYC*. It has been elucidated that individual phytochromes display both unique and overlapping roles in rice photomorphogenesis by characterization of all rice phytochrome mutants including single mutants, all combinations of double mutants as well as triple mutants. Based on the published data and authors' ongoing studies, current knowledge of rice phytochrome functions in regulating seedling de-etiolation, root gravitropic response and elongation, plant architecture, flowering time and fertility is summarized. Additionally, the important issues in the field of rice phytochromes are proposed.
Key words: rice; phytochrome gene; photomorphogenesis; growth and development; function

For higher plants, light is not only a source of energy for photosynthesis, but also a key environmental factor that regulates plant growth and development. Plant monitors external light conditions including presence or absence of light as well as the duration, wavelength and intensity of incident light, and makes light-specific adjustments in physiological and developmental processes to adapt the changing environment (Suetsugu and Wada, 2007; Bae and Choi, 2008). To accomplish this vital task, plants use an array of photoreceptors that includes phytochromes (phy), cryptochromes, phototropins and several others. The phy family mainly perceives and responds to the red (R) and far-red (FR) light regions, and is involved in controlling multiple responses in the plant life cycle (Takano et al, 2005; Bae and Choi, 2008).

Plant phytochromes are soluble chromoproteins present as homodimers and heterodimers *in vivo*, and each subunit typically consists of an apoprotein with a molecular mass of about 125 kDa covalently linked with phytochromobilin, and a linear tetrapyrrole chromophore. All plant phytochromes contain two domains: N-terminal domain and C-terminal domain. The N-terminal domain can be artificially divided into four subdomains P1, P2, P3 (also known as GAF) and P4 (also known as PHY); and the C-terminal domain can be divided into PAS-A, PAS-B and HKRD subdomains (Bae and Choi, 2008). N-terminal subdomains are involved in light perception and light signaling transduction, whereas C-terminal subdomains are mainly involved in dimerization and interaction with proteins downstream of light signaling transduction (Quail, 1997; Matsushita et al, 2003). Phytochromes, located in cytoplasm, are synthesized in the dark in a biologically inactive R-absorbing (Pr) form. Red light induces the Pr form to a biologically active FR-absorbing (Pfr) form with a conformational shift. The photoconversion of Pfr form back to Pr form is optimized at FR wavelengths. Flowing conversion to the Pfr form, phytochromes translocate to the nucleus. In the nucleus, phytochromes trigger a transcription cascade that leads to regulation of light-responsive genes by interacting with proteins. Among phytochrome associated proteins, members of the basic helix-loop-helix (bHLH) transcription factor superfamily called phytochrome interacting factors (PIFs) play a diverse array of regulatory functions in controlling photomorphogenesis by direct interaction with the Pfr form of phytochromes. Physical interaction between phytochromes and PIFs results in phosphory-lation of PIFs. The phosphorylated forms of PIFs are recognized by an ubiquitin ligase and are subsequently degraded by the 26S proteasome. Thus, the degradation of PIFs relieves light-responsive elements in the promoter of light-

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regulated genes from binding of PIFs, which promotes the expression of light-regulated genes and regulates photomorphogenesis, including seed germination, seedling de-etiolation, shade avoidance, photoperiodic flowering time and fertility (Quail, 2002; Nagatani, 2004; Takano et al, 2005; Rockwell et al, 2006; Khanna et al, 2007; Takano et al, 2009).

Phytochromes in higher plants are encoded by a small gene family. In the model species *Arabidopsis thaliana*, five genes (*PHYA* to *PHYE*) encoding phytochrome apoproteins have been sequenced and characterized (Sharrock and Quail, 1989; Clack et al, 1994), but only three genes, *PHYA*, *PHYB*, and *PHYC* in rice have conducted. Analysis based on map cloning combined with rice genome database revealed that *PHYA* and *PHYC* genes were located on the long arm of chromosome 3 and *PHYB* gene on the short arm of chromosome 3. Restriction-enzyme-digested rice genomic DNA was probed with gene-specific probes representing the 3′UTR regions of rice *PHYA*, *PHYB* and *PHYC*, and verified that *PHYA*, *PHYB* and *PHYC* are single- copy genes in the rice genome (Kay et al, 1989; Dehesh et al, 1991; Basu et al, 2000). Rice *PHYA*, *PHYB* and *PHYC* respectively encode 1128, 1171 and 1137 amino acid polypeptides. Amino acid sequence alignments of the three phytochrome proteins were carried out using ClustalW2 (http://www.ebi.ac.uk/ Tools/msa/clustalw2/). The identity of the amino acid sequence of PHYA was 52% to PHYC, and 48% to PHYB. Amino acid identities in different subdomains were further analyzed among the three rice phytochrome proteins. The subdomains P2 and P3 are similar in PHYA and PHYC, but rather variable between PHYA and PHYB. However, with regards to the C-terminal subdomains, the identity of the amino acid sequence of PHYC was 45% to PHYB, and 40% to PHYA, which could explain that the physical interaction exists between PHYB and PHYC, rather than PHYA and PHYC (unpublished data).

The identification of phytochrome mutants has enabled the roles of individual phytochromes to be elucidated in rice. Takano et al (2001 and 2005) isolated several alleles of *phyA* mutants and one allele of *phyC* mutant by screening the Tos17 retrotransposon mutant panels. Meanwhile, several alleles of *phyB* mutants were isolated from γ-ray-mutagenized seeds (Takano et al, 2005). Based on the single mutants, double mutant combination of phytochrome and triple mutants were obtained by crossing single mutant with each other (Takano et al, 2005 and 2009). Through characterizing every single, double and triple phytochrome mutants in terms of photomorphogenesis, individual phytochromes display both unique and overlapping roles in regulating rice de-etiolation, rice architecture and reproductive development.

Roles of phytochromes in rice seedling

De-etiolation

Dark-grown rice seedlings display a 'skotomorphogenic' phenotype, which is characterized by elongated coleoptiles and the absence of chlorophyll. Light signals initiate a variety of de-etiolation responses, including inhibition of coleoptile and internode elongation, induction of light-regulated genes and synthesis of chlorophyll, to promote photoautotrophic survival.

Under continuous red light (Rc), de-etiolated responses in terms of inhibition of coleoptile elongation and synthesis of chlorophyll were similar in wild type, *phyA*, *phyC* and *phyAphyC* mutants. *phyB* and *phyBphyC* mutants similarly exhibited longer coleoptile than the wild type under Rc, suggesting that phyB plays a major role in Rc-induced inhibition of coleoptile growth.

Under continuous far-red light (FRc), the coleoptile elongation was clearly inhibited in wild type, *phyA*, *phyB*, *phyC* and *phyBphyC* mutants compared with those in the dark condition. *phyA* seedlings displayed elongated coleoptile compared with the wild type, which suggests that phyA plays an important role in coleoptile inhibition by FRc. *phyAphyC* double mutants had coleoptiles as long as those of etiolated seedlings. Therefore, both phyA and phyC can perceive FR to inhibit coleoptile length. However, the phyC single mutation did not affect the coleoptile inhibition. It was deduced that when phyA is functional, phyC function is dispensable.

Takano et al (2005) observed that the *Lhcb* gene was highly induced by a single red-light pulse (Rp) treatment in wild-type seedlings, whereas a subsequent

far-red-light pulse (FRp) diminished 70% of the total induction, and the left level was comparable with the level observed in seedlings exposed to a single FRp. Therefore, the expression of *Lhcb* genes induced by Rp was reversed by FRp in rice. This reversible response was observed in *phyA*, *phyC, phyAphyC* and *phyBphyC* mutants, indicating that both phyA and phyB are responsible for R/FR reversible response. In addition, inhibitory response of coleoptile elongation mediated by phyB is also reversible; by contrast, this response mediated by phyA is not reversible (Xie et al, 2007). Thus, it was postulated that there are two types of phyA molecules with different photoperception properties and the ratio of these two types varies depending on the physiological responses (Takano et al, 2005).

Under Rc, the contents of chlorophyll were decreased in *phyA*, *phyB* and *phyC* mutants, compared to that in the wild type. The decrease was the greatest in the *phyB* mutant, then in the *phyA* and *phyC* mutants in turn. These observations indicate that phyA, phyB and phyC perceive R to participate in the synthesis of chlorophyll (Takano, personal communication).

Under either R or FR, both *phyAphyB* and *phyAphyBphyC* mutants had the same phenotype as the etiolated seedlings. Moreover, *phyB* single mutants always exhibited the phenotypes completely the same as the *phyBphyC* double mutants. Thus, it was deduced that phyC is dysfunctional in the absence of functional phyB protein probably because the residue content of phyC protein in *phyB* mutants was too low to trigger the R- or FR-induced photo- responses. The other hypothesis is that phyC in *phyB* mutants can neither perceive light nor participate in signaling transduction. To access this hypothesis, the mutated *PHYB* with the chromophore attachment site (cysteine) changed into alanine, was introduced into the *phyAphyB* mutant. As the result, transgenic lines showed obvious de-etiolated phenotypes under Rc or FRc (unpublished data). We concluded that phyC can perceive R and FR to regulate the photomorphogenic responses, and the PHYB protein is indispensable for light perception of phyC.

Angles between leaf blade and leaf sheath

Under continuous blue light (Bc), wild type and phytochrome mutants exhibited the declination angles of the second leaf blades to different extend. Wild type and *phyA* mutants had the same declination angles. *phyC* and *phyAphyC* mutants showed a slightly greater declination than the wild type, but smaller than *phyB* and *phyBphyC* mutants. The declination angles were the greatest in *phyAphyB* and *phyAphyBphyC* mutants (almost at a right angle). These observations suggested that blue light induced leaf declination by blue light receptors, and phyB and phyC were involved in different ways in the second leaf declination upon perceiving Bc. Comparison of the declination angles between *phyA* and *phyAphyB* mutants indicates that phyA also makes a significant contribution to the second leaf declination in the absence of phyB. Under continuous white light (Wc), *phyB*, *phyBphyC*, and *phyAphyB* seedlings showed the same declination angles as under Bc, but wild-type and *phyA*, *phyC* and *phyAphyC* mutants did not. These observations suggest that phyB seems to function antagonistically to blue light receptors in the term of declination of leaf blades (Takano et al, 2005).

Root gravitropic response and elongation of seminal roots

Gravity provides a continuous directional signal to plants, ensuring that roots grow downwards towards water and nutrients in the soil and shoots grow upwards towards sunlight. When grown in the dark, crown roots of both wild-type and *phyA* seedlings grew mostly horizontally with a peak frequency distribution at about 10° relative to the surface. Under Rc, both wild-type and *phyA* seedlings displayed the same gravitropic responses with most of crown roots grew downwardly at +50° to +80°. It is suggested that other phytochromes (probably phyB) perceive R to induce root gravitropism. Under FRc, wild-type seedlings showed a similar gravitropic response as grown under Rc, but crown roots of *phyA* were insensitive to FRc, which indicates that phyA perceives FR to induce the gravitropic response of rice crown roots (Takano et al, 2001). Recently, Shimizu et al (2009) reported that phyA and phyB perceive R and FR to inhibit the elongation of seminal roots, and phyC has little or no effect on the inhibition of seminal root elongation.

Influence of phytochromes on mature plant shape

Mature plants grown in the field for 66 d were compared among the wild-type and phytochrome mutants. Plant shapes of all other phytochrome mutants except for *phyAphyB* and *phyAphyBphyC* were similar to that of wild type. Because *phyAphyB* and *phyAphyBphyC* mutants exhibited the essentially same phenotypes, we only describe the phenotypes of *phyAphyBphyC* mutants in this review. The *phyAphyBphyC* triple mutants were dwarf with shapes quite distinguished from that of wild-type plants (Takano et al, 2009). 1) Leaf blades were short and declined at a right angle between leaf sheath and leaf blade as mentioned above. 2) After heading, wild-type plants have four elongated and measurable internodes, with the topmost being the longest in the wild type. By contrast, seven elongated internodes were observed in the *phyAphyBphyC* triple mutants, and the elongated internodes all had relatively uniform lengths. 3) After heading, seven living leaves with photosynthetic activity were left in the *phyAphyBphyC* triple mutants, whereas about five leaves were left in the wild-type plants. 4) The leaf lengths gradually decreased along with lower leaf position in the wild-type plants, whereas all leaves in the triple mutants were almost uniformly-sized. 5) In the wild-type plants, when the first young panicle primordium was initiated, the first internode elongation began. In contrast, no correlation was observed between the phase transition and the internode elongation in the triple mutants. These results indicate that phytochromes suppress internode elongation during the vegetative growth in the wild type. Such regulation is important for the life cycle of rice because it is advantageous for plants to devote most of their resources to maximize photosynthesis during vegetative growth. It has been reported that partial submergence greatly stimulated internodal growth in deepwater rice, which was, at least in part, mediated by ethylene (Mekhedov and Kende, 1996; Vriezen et al, 2003). Microarray experiments have revealed that the expression of *ACC Oxidase 1* (*ACO1*) gene, a key enzyme gene in ethylene biosynthesis pathway, was greatly enhanced in the light-grown *phyAphyBphyhC* triple mutants compared to that in the wild type. It was thus speculated that the ectopic internodal growth in the triple mutants might be mediated by ethylene.

We compared the number and size of stomata in different leaves of wild-type, *phyA* and *phyB* mutants at the six-leaf stage. It was observed that the stomatal density (average number of stomata per mm^2 of leaf) in the *phyB* mutant was less than those in the wild-type and *phyA* mutant at the third, fourth and fifth leaves, and the average stomatal length of the fourth leaf in the wild-type plants was statistically larger than that in the *phyB* mutant. These results suggest that phyB regulates the stomatal density and stomatal length in rice (unpublished data).

Roles of phytochrome in rice reproductive growth

Flowering time

Under long-day conditions (LD), *phyA* mutants flowered the same as the wild type, whereas *phyB*, *phyC* and *phyBphyC* mutants were about 12 d earlier than the wild type. These observations clearly indicate that phyB and phyC exert the same effect on delaying floral determination under LD. Interestingly, *phyAphyB* and *phyAphyC* double mutants flowered dramatically earlier than any single mutants under LD. It is suggested that phyA mutation alone does not affect the flowering time much, but in the *phyB* or *phyC* mutant background, phyA mutation makes a big contribution in determining the flowering time under LD.

Under short-day conditions (SD), wild type flowered obviously earlier, compared with under LD. The *phyA* mutants flowered slightly later than the wild type, and the *phyB* mutants flowered earlier than the wild type as it did under LD. The *phyC* mutant flowered approximately the same time as the wild type. In addition, double mutants of *phyAphyC* and *phyBphyC* flowered the same time as *phyA* or *phyB* single mutants, respectively. These results suggest that phyC have no significant effect on the floral initiation under SD. Under both LD and SD, *phyB* mutants flowered earlier than wild type, indicating that phyB represses the floral initiation under both LD and SD.

The *phyAphyB* and *phyAphyBphyC* mutants

flowered earlier than the wild type under LD, but significantly later than the wild type under SD (Takano et al, 2005). It is postulated that in rice, the light signals mediated by the phytochromes (except phyB) promote flowering in response to SD conditions, whereas delay flowering under LD.

In rice, *heading date 1* (*Hd1*) and *heading date 3α* (*Hd3α*) genes play important roles in regulating flowering. *Hd3a* encodes an ortholog of *Arabidopsis FLOWRING LOCUS T* (*FT*). Overexpression of *Hd3a* causes an early-flowering phenotype, whereas suppression of *Hd3a* with RNA interference (RNAi) delays flowering. Rice is a short-day plant. *Hd1* activates the expression of *Hd3α* in inductive short-day conditions, and represses the expression of *Hd3α* in non-inductive long-day conditions. Moreover, Hd1 protein level is also regulated by circadian clock. Therefore, it is speculated that phytochrome-mediated light signals serve double purpose in photoperiodic flowering. Firstly, phytochrome-mediated light signal sets the phase of the circadian rhythm, which, in turn, affects Hd1 protein level. Secondly, phytochrome-mediated signals directly regulate the expression of *Hd3α*. In night-break (NB) experiment, NB down-regulates the *Hd3α* expression in wild type, but not in *phyB* mutants, suggesting that phyB is necessary for the suppression of *Hd3α* (Ishikawa et al, 2005 and 2009).

Fertility

Fertility of *phyAphyB* and *phyAphyBphyC* mutants is quite low, as indicated by small panicles and low seed setting rate. However, other phytochrome single mutants and double mutants have similar fertility as the wild type. During flowering in wild-type rice, the mature pollen is released form the dehisced anther, and self-pollination occurs. However, in the *phyAphyBphyC* mutants, the spikelets opened normally but the anthers rarely dehisced and the pollen was still within the anther even after flowering. In addition, pollen from the *phyAphyBphyC* mutants was able to germinate and a reciprocal cross with wild-type pollen restored fertility in the triple mutants (Takano et al, 2009). Therefore, the reduced fertility of the triple mutants seems to be caused by impaired dehiscence of the anther wall. The involvement of jasmonates (JAs) in dehiscence has been reported in *Arabidopsis* mutants (Xie et al, 1998; Ishiguro et al, 2001). In addition, JA-deficient rice mutant, *hebiba*, also shows male sterility (Riemann et al, 2003). It has been reported that the JA biosynthesis is induced by phyA- and phyB-mediated red light signal in rice (Haga and Iino, 2004). Therefore, the reduced fertility of *phyAphyB* and *phyAphyBphyC* mutants is possibly attributed to JA pathway.

In summary, individual phytochromes display both unique and overlapping roles in rice growth and development by characterization of all rice phytochrome mutants and the wild type (Table 1).

Future perspectives

At present, research on phytochrome mainly focus on dicotyledonous model plant *Arabidopsis*, such as the molecular characteristics and functions of phytochrome-mediated light signal transduction components in China (Kang et al, 2009; Wang et al, 2009; Wang et al, 2010). Recently, Professor YANG Hongquan's group in Shanghai Jiaotong University, found that phytochromes were involved in the regulation of stomatal development and aperture in *Arabidopsis* (Kang et al, 2009; Wang et al, 2010). This observation links the phytochrome-mediated light

Table 1. Functions of phytochromes in rice development.

Function	Phytochrome	Reference
Regulation of seedling de-etiolation	phyA, phyB, phyC	Takano et al, 2001 and 2005; Xie et al, 2007
Regulation of angle between leaf blade and sheath	phyB, phyC, phyA	Takano et al, 2005
Regulation of root gravitropic curvature	phyA, phyB	Takano et al, 2001
Inhibition of seminal root elongation	phyA, phyB	Shimizu et al, 2009
Suppression of internode elongation	phyA, phyB	Takano et al, 2009
Regulation of stomatal density	phyB	Liu Jing et al, unpublished data
Repression of flowering under long-day conditions	phyB, phyC, phyA	Takano et al, 2005 and 2009; Ishikawa et al, 2005 and 2009
Repression of flowering under short-day conditions	phyB	Takano et al, 2005
Regulation of fertility	phyA, phyB	Takano et al, 2009

signals with water metabolism in *Arabidopsis*. Furthermore, isolation and expression of phytochrome family genes in other plants, such as tomato, alfalfa, potato and wheat, have been reported. These studies have greatly enriched our knowledge about the molecular characteristics of phytochromes in diverse plants, although the roles of phytochromes are not comprehensively studied in these plants. Based on the reports that phytochrome-mediated light signals can affect many important agronomic traits, some domestic researchers have tried to modify certain crop traits, such as pigment content and flowering time, by overexpression or repression of phytochrome genes (Hong et al, 2009; Wu et al, 2009). However, phytochrome-mediated light signal transduction pathway is a complex genetic network. Artificial alteration of the expression level of phytochromes can improve target traits, but probably affect other outstanding traits at the same time. Therefore, we should explore the key components in phytochrome-mediated light signal transduction pathway. Then it would be possibly more meaningful to modify the specific traits by the genetic modification of certain components.

Relative to a wealth of research reports about *Arabidopsis* phytochromes, the reports about rice phytochromes throughout the world are limited. In recent years, with the isolation and characteristics of photomorphogenesis of rice phytochrome mutants, roles of phytochromes in rice growth and development have become increasingly clear. However, there are still many unanswered questions about rice phytochromes. In our opinion, the following aspects should get more attention: Firstly, research on phytochrome interacting proteins in rice is quite limited. Nakamura et al (2007) identified six PIFs transcription factors (OsPIL11 to OsPIL16) in rice by homology analysis. The over-expressing of OsPIL11 to OsPIL15 in *Arabidopsis* showed that these transcription factors play important roles in regulating R signal transduction (Nakamura et al, 2007). However, how these PIFs transcription factors interact with rice phytochromes as well as their roles in rice growth and development remain elusive. Secondly, phytochromes may act in photomorphogenesis by changing the biosynthesis and signaling of plant hormones. However, only few observations about the relationship between rice phytochromes and plant hormones have been reported. Answering these questions will enable us to get a comprehensive understanding about rice phytochrome signal pathway, the interaction between light signals and other signals.

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