International Journal of Basic and Applied Biology (IJBAB)
Print ISSN: 2349 – 5820; Online ISSN: 2349 – 5839 ; Volume 2, Number 1; October, 2014 pp. 113 – 120

http://www.krishisanskriti.org/ijbab.html

Phytochrome mediated growth and development in rice: A review

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Abstract : **Phytochromes are photoreceptors that sense red and far-red light to regulate a range of developmental processes throughout the life cycle of plants. In rice three species of Phytochromes (PHY), namely PHYA, PHYB and PHYC are present. It has been reported that individual Phytochromes perform both unique and overlapping roles in rice Photo-morphogenesis by characterization of all rice Phytochrome mutants including single mutants, all combinations of double mutants as well as triple mutants. Significant functions performed by Phytochromes in rice are regulation of seedling de-etiolation, regulation of angle between leaf blade and sheath, regulation of root gravitrophic response, inhibition of seminal root elongation, suppression of internode elongation, regulation of stomatal number and regulation of fertility. Phytochromes are also involved in the regulation of genes encoding the smaller subunit of ribulose-1,5 bisphosphate carboxylase and chlorophyll a/b binding (CAB) protein of the light harvesting chlorophyll-protein complex. Rice grown in Kharif season (June to December) received reduced light due to overcast of sky. Studies related to Phytochrome shall be helpful for improvement of rice breeding program specially grown in the monsoon season and low light conditions.**

1. INTRODUCTION

Light source is essential for regulating the growth, development, and metabolic activities of many plants [1], although light is not the only source of energy for photosynthesis [2]. Higher plants use Phytochrome and related photoreceptor molecules including Cryptochromes [3] to receive light source required for photosynthesis [4]. Most commonly studied photoreceptors include Phytochromes (PHY), Cryptochromes, Phototropins, etc [2].

Phytochromes belong to class of soluble chromoproteins available in both homodimer and heterodimer forms in vivo. Both of these forms have the molecular weight of about 125KDa that are covalently linked with other molecules such as phytochromobilin as well as tetrapyrrole chromophore [2]. Irrespective of the plant source, all phytochromes have two major domains known as N-terminal and C-terminal domain. N-terminal domain consists of four sub-domains such as P1, P2, P3 and P4. P3 is commonly referred to as GAF while P4 is commonly referred to as PHY. The C-terminal domain is further divided into three different domains such as PAS-A, PAS-B, and HKRD [5]. Different domains perform various functions. N terminal domains are necessary for perceiving light as well as for light induced signal transduction events. The C terminal domains are necessary for dimer formation, as well as inducing protein-protein interaction in light induced signal transduction [6][7].

These Phytochromes highly influence various photo-morphogenic events [4] [8][9][10] by controlling the expression of light responsive genes [11]. Especially in the case of Phytochromes that perceive and respond greatly to two red (R) and far-red (FR) regions of light. This process, thereby, regulates various events in plant growth and development [5]. However, recent studies have showed that Phytochrome mediated light responses can be three different modes which include the following: low fluence response (LFR) related to the reversible conversion of red(R) to far red (FR); very low fluence response (VLFR) and High irradiance response (HIR) respectively [12][13]. The response of plants in LFR and VLFR is 1 to 1000μmolm^{-2} and 0.1 to 1μmolm^{-2} towards Red (R) light respectively. The third mode HIR needs long time exposure of plants to light with high proton flux and thereby, depending on the Fluence rate [1].

Phytochromes are majorly seen in cytoplasm which are produced in an inactive form R-absorbing form (Pr form) in dark. When these phytochromes are exposed to red light, conformational change in their shapes happens to convert the inactive form (Pr) of Phytochromes into an active form called FR-absorbing form (Pfr). When exposed to a particular FR wavelength, photo-conversion of Pfr to Pr results. Continuous conversion of Pr to Pfr results in the translocation of Phytochromes into the nucleus where they are involved in

triggering light induced signal transduction pathways. As a result, the task of regulating light responsive genes with the interaction of proteins happens. Among various proteins, basic helix-loop-helix group (bHLH) proteins especially Phytochrome interacting factors (PIFs) are involved in regulating photo-morphogenesis by directly interacting with its active form (Pfr). Interaction of phytochromes in its active form (Pfr) with PIFs phosphorylates PIFs which results in subsequent degradation of PIFs by 26S proteasome mediated by ubiquitin ligase. The study results in freeing the elements involved in light responses along the promoter region of light regulated genes, thereby inducing their expression and regulating photo-morphogenesis [2]. Different processes that are regulated by Phytochromes include germination of seed, de-etiolation of seed, shade avoidance response, alteration in flowering time, and changes in fertility levels [14][15].

Small gene families in higher plants are responsible for the production of Phytochromes [16][17]. For instance, the plant *Arabidopsis thaliana* has five different Phytochrome genes encoded by a small gene family that includes PhyA, PhyB, PhyC, PhyD and PhyE respectively [18]. The apoproteins of these Phytochrome molecules in *Arabidopsis thaliana* have been sequenced and characterized [16]. However, in rice plants only three Phytochrome genes such as PhyA, PhyB and PhyC have been identified. Map cloning analysis revealed the exact location of these gene products that PhyA and PhyC gene products are situated on the long arm side of chromosome number 3 while PhyB is situated on the shorter arm side of chromosome number 3. Additionally, restriction digestion analysis of rice phytochrome genes revealed that these phytochromes genes PhyA, PhyB and PhyC are appearing only one in the entire rice genome [19][20][21]. Spectral analysis of VLFR, LFR and HIR with the help of phytochrome lacking mutants of model organism Arabidopsis Thaliana inferred that among all available phytochrome molecules, PhyA is important phytochrome molecule involved in VLFR mode of light response including seed germination [22], expression of CAB gene [23]. Induction of HIR by FR light inhibits elongation of hypocotyl [24][25]. Additionally, PhyB regulates LFR in R/FR reversion process [1]. Exclusive molecular properties as well as its physiological function, PhyA has been studied extensively among all Phytochromes [26]. Several studies have been conducted to study the importance of PhyA Phytochrome molecule in regulating the growth and development of plants. Mutant studies showed PhyA is involved in regulation of various metabolic processes in plants including shortening of internodes, thickening of stems, and delay in flowering time as well as senescence, prolonged peduncles and enhanced seed yield [27]. However when comparing the mutant variety of Arabidopsis PhyA with its corresponding wild type plants, there is no morphological differences observed [28][29].

The rice plant is found to be the right model organism for exploring complex genetic, as well as, physiological characteristics due to the knowledge about its genomic structure and functions [30]. Different tools are available for understanding the structure and function of the rice genome including a genetic linkage map and sequence analysis. In addition to this, recent tools include gene knockout study of a rice retrotransposon called Tos17 [31]. This enables further researchers to isolate desirable phytochrome mutants [1]. Hy3 mutant is the first reported mutant product of PhyB [32]. When this mutant gene containing plant is grown in continuous red light it results in the loss of inhibition action of hypocotyl elongation [33]. Mutant studies may further facilitate the understanding of the role of phytochrome in regulating plant growth and development. Screening of Tos17 retrotransposon enabled Takano et al (2011) to successfully isolate alleles of PhyA mutant alleles as well as one allele of PhyC[1][11]. Between isolation of various PhyB mutant alleles from gamma ray mutagenized seeds have occurred [11]. These mutant studies of single, double, and triple mutation inferred that phytochromes are found essential in processes such as photo-morphogenesis, de-etiolation of seed, architecture and development of reproductive organs in seeds, etc [2].

2. PHYTOCHROME INFLUENCE RICE SEEDLING

2.1 Phytochromes induce de-etiolation

Skotomorphogenic phenotype contains the traits associated with the elongation of coleoptiles along with the absence of chlorophyll when rice seedlings are grown in the dark. Exposure to light induces de-etiolation responses including: coleoptile inhibition, elongation of internode, induced light-regulated genes, as well as chlorophyll synthesis in promoting the survival of photoautotrophs. When plants are exposed to continuous red light, de-etiolated responses happen which include the inhibited elongation of coleoptiles along with the chlorophyll synthesis that resembled the wild type. The mutant study with PhyB and PhyBPhyC plants confirmed that the Phytochrome gene PhyB is necessary for red light induction of inhibited coleoptile growth [2].

When plants are exposed to continuous far red light, elongation of coleoptile was totally inhibited in plants including wild type and other mutants such as PhyA, PhyB, PhyC and PhyBPhyC mutants when compared to those which are grown in the dark. Elongated coleoptile in PhyA seedlings suggested that PhyA is necessary for coleoptile inhibition with continuous far red light. Double mutation of PhyAPhyC in plants showed long coleoptiles when compared with the etiolated rice seeds. This study revealed the fact that both phytochrome genes PhyA and PhyC are necessary for perceiving far red light, and inhibiting the length of coleoptiles. This result was not observed when single mutation of PhyC was done which confirmed that PhyC has no effect in inhibiting coleoptile elongation. Therefore, it is very promising that PhyA is the only molecule in the rice variety which is necessary for inhibiting coleoptile elongation.

Takano et al (2009) conducted the study where the response of red and far red light pulse irradiation towards both LFR and VLFR regarding the growth of coleoptile in both wild type rice seedlings as well as mutant seedlings that lack the gene osphyA-1. Rice seedlings that are etiolated with coleoptile length of about more than 10mm were then exposed to red light under LFR, far red or red light under VLFR, which are then kept in the dark. The length of coleoptiles was recorded for forty-eight hours. When these plants are exposed to LF-Red light showed that the inhibition of coleoptiles happens in both wild type as well as mutant type osphyA-1 plant variety. When these plants are subsequently exposed to far red light, the condition was reversed which was not observed in the mutant variety. This study inferred that the phytochrome gene PhyA is not responsible for the reversal of R to FR state in inhibiting the growth of rice coleoptiles [1].

In the wild type rice seedlings, Takano et al (2011) could observe the gene Lhcb which was induced by the single red light. When these seedlings are subsequently exposed to far red light with reduced total induction to up to seventy percent, then exposure of the rice seedlings to FR would reverse the condition. This reversal was seen in mutant plant varieties that lacked phytochrome genes including PhyA, PhyC, PhyAPhyC and PhyBPhyC which thereby confirms that both phytochrome genes PhyA as well as PhyB are found to be responsible in the reversible response between R/FR. Additionally, when PhyB is involved in inhibition of coleoptile elongation which indicated that PhyA could not provide such a reversible response [34]. Another study conferred the presence of two varieties of PhyA molecules that had different photoperception abilities. The ratio of these two varieties of PhyA molecules differ from different physiological responses [11].

When plants are exposed to a pulse of red light (R), chlorophyll contents were found to fall down in mutants lacking phytochrome genes including PhyA, PhyB and PhyC when compared with the wild variety of plants. The decreasing level of chlorophyll content in the PhyB mutant is found to be at a maximum when compared with the PhyA and PhyC mutants. This study confirmed that PhyA, PhyB and PhyC perceive red light in chlorophyll synthesis [2]. To conclude, PhyC Phytochrome gene could perceive red light and far red light in regulating photo-morphogenic responses while the PhyB protein is indispensable towards light perception of phytochrome gene, PhyC [2].

2.2 Phytochromes induce change in angle between leaf blade and leaf sheath

When wild type and phytochrome mutant plants are exposed continuously to blue light, there is a change in the declining angle of a second leaf blade. While comparing wild type varieties and PhyA mutants for such a declining angle of the second leaf blade, there is no difference at all. However while comparing it with PhyC and PhyAPhyC, it showed a greater reduction in angle of second leaf blade but lower than PhyB and PhyBPhyC mutant varieties. The reduction was found to be at a maximum, which is almost at a right angle to the shoot in case of a double mutation (PhyAPhyB) and triple mutation (PhyAPhyBPhyC). This confirms that exposing plants to blue light induces lead declination which is induced by PhyB and PhyC greatly. Comparison results between mutant varieties of PhyA and PhyAPhyB plants confirmed that PhyA has its own significant role in reduction of second leaf when PhyB is absent. The study concluded that PhyB antagonistically regulates reduction of leaf blades when plants are exposed to blue light [11].

2.3 Gravitropic response of root and seminal roots elongation

Gravity is the driving force for the continuous directional growth of plants. This ensures the right growth of roots towards the deep soil where sufficient level of water and nutrients are available, and the right growth of shoots towards the direction of the sunlight. When both wild types as well as PhyA mutant seedlings are grown in the dark, they all grew horizontally. When these plants are exposed to red light the observation was very similar to seedlings grown in the dark. The growth of crown roots grew downward at 50° to 80°. This showed that all phytochromes especially PhyB could perceive red light in inducing root gravitropism. Results showed that PhyA could perceive far red light in inducing crown root gravitropic response in rice [1]. A recent study showed that both PhyA and PhyB receives red and far red light in inhibiting seminal roots elongation while PhyC has almost no effect in inhibiting seminal root elongation [2]. Prolonged exposure of wild type plants to far red light pulse induces gravitropic growth [1].

3. PHYTOCHROME ALTER MATURE PLANT SHAPE

Comparing phenotypic similarities in mature plants of wild type as well as the PhyA mutant have found to have no difference in their plant shapes [1]. Comparison starts with mature plants whose ages are sixty-six days in the field. The comparison is based on their corresponding wild type as well as Phytochrome mutant varieties on the basis of their plant shape. The shape of these plants looks similar except for the double mutant PhyAPhyB and triple mutant PhyAPhyBPhyC. The triple mutant, PhyAPhyBPhyC plants were seem to be dwarf like in their plant shapes when compared to their respective wild type plants [15]. Many differences were observed while comparing other plants shapes with triple mutants and wild type plants. In triple mutant plants, the leaf blades were found to be shorter than normal plants. A decline of 90° between the leaf sheath as well as the leaf blade was observed. When considering the wild type plants, they all had four stretched and measurable internodes with the first internode being the longest in the case of wild type plants. Contrastingly, there were seven stretched internodes found in this triple mutant with a uniform internode length. In these triple mutants, there were seven leaves used for photosynthesis in comparison to the five leaves used for wild type plants. The lengths of the leaf slowly declined with lower leaf position in

case of wild type plants whereas these triple mutants were all found to be uniform in size. The results of this study clearly indicate that Phytochromes are necessary in suppressing the elongation of the internode, especially in the vegetative growth of wild type plants. This attribute is highly useful in producing more beneficial rice varieties during its vegetative growth. Another study confirmed that ethylene is another important molecule that potentially stimulates intermodal growth in rice plants which were grown under deepwater [35][36]. Microarray studies with ACC oxidase I (ACO1) gene revealed the fact that the expression of this gene is found elevated in light induced growth of triple mutant, PhyAPhyBPhyC when compared to the wild type [2].

4. PHYTOCHROMES INFLUENCE RICE REPRODUCTIVE GROWTH

4.1 Altering flowering time

During the long day (LD) scenario, there was no difference found in flowering of PhyA mutants when compared with its respective wild type. However, this is not the scenario for PhyB, PhyC as well as the double mutant PhyBPhyC where they flowered twelve days before the wild type. This study reveals the fact that PhyA has no effect on flowering time when PhyB and PhyC are present. However, in the absence of these Phytochromes, PhyB and PhyC, PhyA induces earlier flowering time than the wild type [2].

During the short day (SD) scenario, PhyA mutants were found to have flowered later when compared to wild type plants. However, PhyB mutants have flowered earlier than wild type plants just as the LD scenario. There is no difference in the flowering time observed in case of PhyC mutants when compared to its wild type plants. These results confirmed that PhyC has no remarkable role in initiating flowering under short day scenario. Therefore, in both scenarios PhyB mutants have found to have been flowering earlier than wild type plants while PhyB was found to have suppressed floral initiation in both scenarios. Other results also showed that in rice plants, Phytochrome mediated light signals have found to promote floral initiation in short day and delayed flowering in case of the long day scenario [2].

While considering the genes that are responsible for flowering regulation, only two were studied in rice plants including Heading date 1(Hd1) and Heading date 3α(Hd3α). Hd3α is found to be the ortholog of the Flowering Locus T(FT) gene of Arabidopsis thaliana. When this gene is over expressed, it induces early flowering; however on suppressing the expression of this gene using RNAi technology induces delayed flowering [37][38].

4.2 Influencing fertility

Double mutants PhyAPhyB and triple mutant PhyAPhyBPhyC were found to have shown low fertility when compared to wild type plants. These results were not identified in mutations in other phytochrome molecules where they all show similar results with that of wild type plants. In wild type plants, self pollination happens only when dehisced anther releases mature pollen grains, but in triple mutant PhyAPhyBPhyC opening of spikelets happens without release of mature pollens from respective anthers post flowering also. Though there is no release of mature pollens from anthers in triple mutant PhyAPhyBPhyC, these pollens have the ability to germinate through a reciprocal cross with wild type plants. This ensures the restoration of fertility [15]. The reduced level of fertility in this triple mutant PhyAPhyBPhyC is due to the repaired anther wall dehiscence. In *Arabidopsis thaliana*, Jasmonates (JAs) in anther dehiscence have been reported earlier [39][40]. JA-lacking rice variety called Hebiba showed male sterility [41]. PhyA and PhyB induced red light biosynthesis of JA in rice have been reported earlier [42]. Reduction in fertility levels in double mutant PhyAPhyB as well as triple mutant PhyAPhyBPhyC has found to show effect in JA synthetic pathway.

Table 1 - Functions of Phytochromes in rice

Function / Response	Phytochromes	References
Hy3 mutant of PhyB	PhyB	Koornneef et al, 1980
Inhibited coleoptile growth	PhyB PhyBPhyC mutant	Xin & Wei et al, 2011
Right angle decline in angle between leaf blade and leaf sheath	PhyAPhyB mutant PhyAPhyBPhyC mutant	Takano et al, 2005
Inducing Crown root gravitropic response in rice	PhyA	Takano et al, 2001
Induced dwarfness in rice plants	PhyAPhyBPhyC mutant	Takano et al, 2009

Ethylene induced internodal growth in rice plants		Mekhedov & Kende, 1996 Vriezen et al, 2003
Low fertility	PhyAPhyB mutant PhyAPhyBPhyC mutant	Takano et al, 2009
Jasmonates (JAs) in anther dehiscence		Xie et al, 1989 Ishiguro et al, 2001
Reduced fertility levels through defective JA synthetic pathway	PhyAPhyB mutant PhyAPhyBPhyC mutant	Haga & Lino, 2004

5. ROLE OF PHYTOCHROME IN PHOTOSYNTHESIS GENE EXPRESSION

Phytochromes are also involved in the regulation of genes encoding the smaller subunit of ribulose-1, 5 bisphosphate carboxylase or oxygenase and chlorophyll a/b binding (CAB) protein of the light harvesting chlorophyll protein complex [43]. Following this, exploitation of transcription assays revealed the fact that action of Phytochrome on genes of Ribulose 1,5 bisphosphate carboxylase or oxygenase and chlorophyll a/b binding (CAB) during transcription itself [44][45][46]. Phytochrome also mediates the expression of photophilic gene [47]. Study detected the single gene etiolation of Phytochrome in rice [47].

A Study conducted by Kay et al (1988a) included the isolation and characterization of cDNA and genomic clones that code for the apoprotein belonging to rice phytochrome. In etiolated leaves, the expression of mRNA was found to be low. When they are exposed to red light, the level of mRNA drastically reduced in first 15 minutes and after 2 hours, it vanished completely. However, when they are exposed to far red light, the condition reversed positively which confirmed that the auto regulation of Phytochrome mRNA is dependent on far red light. Nuclear run-on experiments revealed that the size of Phytochrome mRNA present in leaves is two times higher than those found in roots. The condition is upside down when it comes to Greenish plants. The presence of single gene for single Phytochrome gene study is done through DNA blotting technique and library screening methods. The nuclear factor GT-1 was found to bind with conserved sequence of rice genes [47].

The study was successfully comparing the 5' flanking sequence of rice gene Phy18 with Oat Phy3 to understand the *cis* and *trans* elements related to Phytochrome response [47a].

6. FUTURE PERSPECTIVES

Presently Phytochrome research deals only with *Arabidopsis* the most due to their advantageous features. Gradually, the research on Phytochrome induced growth and development in rice has gained its popularity. Recently, by isolating and characterizing the photomorphogenesis process of Phytochrome mutants in rice has made us acquire clear knowledge. However, there are still more things to be understood. The major attention should be given for the availability of Phytochrome Interacting proteins observed in rice which is quite less. We need to identify more Phytochrome interacting proteins and understand its pathways. The information on the deal between Phytochrome genes and hormones in rice is very limited which are found very necessary in better understanding of biosynthetic pathway of photomorphogenesis in rice and plant hormone signalling pathway respectively.

Rice grown in Kharif season (between June and December) received reduced light due to overcast of sky. Studies related to Phytochrome shall be helpful for improvement of rice breeding program specially grown in the monsoon season and low light conditions. Among all these studies, the down regulation study with Phytochrome mRNA gene is found intriguing. There are needs for future studies to determine the potential role of the nuclear factor called GT-1 or any other elements involved in Phytochrome regulation in both through photophillic and photophobic regulatory pathways.

7. CONCLUSION

Currently, dicot plant *Arabidopsis thaliana* served to be the right model for conducting Phytochrome related experiments because of their molecular traits and functions in inducing light mediated signal transduction [48][49][50]. Different Phytochrome molecules perceive light more differently that were observed in *Arabidopsis thaliana* [22] with different functions [51][52][53]. Several studies using Phytochromes have elevated our knowledge about the actual roles of these Phytochromes in various different plants apart from *Arabidopsis.* Different types of phytochromes are isolated and expressed as different family gene products in various plants including: tomato, wheat, alfalfa, potato, and rice. As we have great knowledge about molecular traits of Phytochromes in different plant sources, still the potential aspects of Phytochromes are not yet realized. Research data

has proven the potential importance of phytochromes in improving various traits of particular plant types. Traits that can be developed and improved as of today include contents of pigments, flowering time, and Phytochrome gene expression. The role of these Phytochromes in altering different aspects of crop traits including contents of pigments, flowering time, and expression status of Phytochrome genes [54][55]. Studying the complete cycle of Phytochrome-mediated light induced signal transduction processes is necessary. Knowing how exactly these Phytochromes alter different processes, it would be helpful when modifying particular characteristics of plants through genetic modification of related molecules in the pathway.

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