

Effect of Photoblastism on Rice Morphogenesis and Seedling Development

M. N. Hoque^{1*}, M. A. Islam¹, M. Z. islam², M. Rahman¹ and B. Biswas¹

¹Department of Agriculture, Bangabandhu Sheikh Mujibur Rahman Science and Technology
University, Gopalganj-8100

²Bangladesh Rice Research Institute, Regional Station Gopalganj-8100

*Corresponding email: shikshatoroo@gmail.com

Abstract

The effect of continuous light and complete dark period on seed germination to first leaf emergence was examined in BRRIdhan71 and BRRIdhan81 in controlled environment at 22 ± 2 °C and 82 ± 2 % of relative humidity, with or without supplemental LED white light. In the dark, BRRIdhan71 had a germination rate of 97 percent and BRRIdhan81 had a germination rate of 57 percent. Germination was 92 percent in BRRIdhan81 and 77 percent in BRRIdhan71 under photoblastic conditions (Light). The dark and light treatments had a noticeable impact on the percentage of seeds that germinated. Coleoptile was longer in dark than light in BRRIdhan71. In both rice varieties, the light and dark treatments had little effect on the first leaf length, although the first leaf breadth increased noticeably in BRRIdhan81. The growth condition had an impact on root length, seedling fresh weight, and dry weight. Germination percent, coleoptile length, prophyll length, first leaf length, and root length all decreased in BRRIdhan71, whereas germination percent, first leaf length, first leaf breadth, seedling freash, and dry weight all increased significantly in BRRIdhan81. The findings imply that BRRIdhan71 and BRRIdhan81, in particular, responded to photoblastic treatment and predominantly possess photoblastic biocomponents in seed, which affect germination and subsequent growth phases. Rice seed during germinate in the field will light stress if photoblastism is not considered during the development and release of rice varieties for different seasons, such as Aman and Boro, because light affects seeding photomorphogenesis differently in different growth environments.

Key words: Growth, Morphogenesis, Photoblastism, Rice

Introduction

All organisms must sense and interpret information from both their biotic and abiotic environments in order to grow and develop efficiently. Light is a very essential environmental signal, to which organisms respond in a variety of ways (Neff *et al.*, 2000). Light is the primary source of energy for photosynthesis in plants, as well as an environmental signal that causes them to develop and differentiate structurally. The morphogenesis, growth, and differentiation of plant cells, tissues, and organ cultures are influenced by light quality, amount, and photoperiod (Chen *et al.*, 2014).

Photoblastism, or light-induced seed germination, is a biologically significant process. Rice (*Oryza sativa* L.) seed germination is known to be unaffected by light or darkness, however a photoblastic rice (PBR) with light-favored germination was observed in weedy rice (Chung and Nam, 2003). Even in ideal growing conditions, photoblastism causes the buried seeds to remain dormant until they are unearthed.

Photoblastism has long been recognized as a common feature of small-seeded plant species and a broad range of weeds (Simpson, 1990; *Milberg et al.*, 2000). Large seeded cereal crop plants germinate equally effectively in darkness or under any wavelength of light under ideal seedling growth conditions, and are thus classified as nonphotoblastic seeds (Gardner *et al.*, 1985).

Nonphotoblastic seeds, on the other hand, may be encouraged to germinate independently of light by pre-existing Pfr in dormant seeds or fast conversion to Pfr during rehydration (Mancinelli *et al.*, 1967; Simpson, 1990). Seed germination becomes less light-dependent as seed mass increases, implying that light responsiveness and seed mass coevolved together (Milberg *et al.*, 2000).

Light inducible germination happens in a certain set of environmental conditions in many photoblastic plant species. Because light-inducible mechanisms have evolved differently for adaptation to local environmental conditions, phytochrome species differ in their role in germination. Other environmental factors, such as the dark imbibition period, influence photoblastism in many species (Simpson, 1990; Toole, 1973; Duke, 1978).

The commencement of seed germination is controlled by the photoconversion of phytochromes by R and FR light. R light-absorbing phytochrome (Pr) is changed into FR light-absorbing phytochrome (Pfr) by R light, and FR light changes Pfr back into Pr form. PhyA that is light-labile is produced from scratch during dark imbibition, while phyB that is light-stable is found in all plant tissues (Dehesh *et al.*, 1991; Shinomura *et al.*, 1994, 1996; Quail *et al.*, 1995). Over a broad spectrum, phyA-mediated germination occurs irreversibly through a very low-fluence response. The absolute Pfr content in photoblastic seeds affects photoreversible phyB-

mediated germination as well as the low-fluence response (Reed *et al.*, 1994; Botto *et al.*, 1996; Shinomura *et al.*, 1998).

Germination frequency drops to practically zero at temperatures above 30°C, and the promoting effect of R light fades away as well. Other environmental factors that affect photoblastism in many species include dark imbibition period, diurnal temperature fluctuations, and soil burial depth (Kristie and Fielding, 1994; Duke, 1978; Ekstam and Forseby, 1999; Scopel *et al.*, 1991; Benvenuti *et al.*, 2001).

Temperature affects the Pfr level of total phytochrome and the conversion of Pfr to Pr in dry or imbibed seeds in the majority of situations (Thompson *et al.*, 1979; Kristie *et al.*, 1981). Phytochromes quickly hydrated or synthesized, but at high temperatures, Pfr to Pr conversion was equally swift (Toole, 1973; Kristie and Fielding, 1994).

Rice, a model monocotyledonous plant, has three phytochromes (phyA, phyB, and phyC) and three cryptochromes (OsCRY1a, OsCRY1b, and OsCRY2) (Mathews S, Sharrock RA. 1996). (Matsumoto *et al.*, 2003, Zhang *et al.*, 2006). The presence or absence of light has a significant impact on the root shoot growth ratio and dry matter production in rice seedlings (Zhang *et al.*, 2016).

During germination and seedling establishment, the presence or absence of light is very important (Gommers CMM, Monte E. 2018). Seed reserves feed early seedling growth and development, and this heterotrophic lifestyle can last for a few days in the dark. In rice, skotomorphogenic development is characterized by long coleoptiles, lengthy initial leaves, and

elongation of the second internode in seedlings grown in darkness. Coleoptile, first leaf, and internode elongation is blocked by light illumination, and seedlings move to a photomorphogenesis pattern of growth with the establishment of fully functional chloroplasts and shift to autotrophy (Takano M *et al.*, 2005). The root shoot growth ratio and dry matter production in rice seedling is greatly affected by presence or absence of light (Zhang *et al.*, 2016).

There is a dearth of study on the influence of supplemental light sources on seed germination and seedling growth in BRRI developed rice cultivars. Rice growth phases are affected by light quality, illuminance, and illumination time, according to the previous research findings. As a result, a study was carried out to investigate the effects of continuous dark and light on different growth stages: S0 (Dry, unimbibed seed); S1 (Emergence of coleoptile); S2 (Emergence of radicle); S3 (Emergence of prophyll from coleoptile); and VI (Collar formation on first complete leaf [Leaf 1] on main stem) and changes in morphological condition of different organ of rice seedlings.

Materials and Methods

Seed material and germination tests

Rice seeds of BRRIdhan71 and BRRIdhan81 (Table 1) were collected from the Bangladesh Rice Research Institute, Regional station Gopalganj. The laboratory studies were conducted in the laboratory of Department of Agriculture, Bangabandhu Sheikh Mujibur Rahman Science and Technology University and Laboratory of Bangladesh Rice Research Institute, regional station Gopalganj.

Table 1. Description of the two rice variety used in the present study

| Rice variety | Growing season | Special phenotypic feature | Year of Release, Institution |
|--------------|----------------|----------------------------|------------------------------------|
| BRRIdhan71 | Aman | Drought tolerant | 2014, BRRI |
| BRRIdhan 81 | Boro | Premium quality | 2017, BRRI |

Light source and treatments

For the dark treatment of rice seeds, the petriplates were covered with two layer black cloth with zero light illuminance. Photoblastic treatment of the rice seed with petriplates were kept under 24 h illumination using a cool, white light emitting diode source. Seeds were incubated at 22 ± 2 °C and relative humidity of 82 ± 2 % during the incubation period. The germination test was conducted using the petridish method with three replicates of 100 seeds. Seeds were soaked in distilled water for 72 h at room temperature and placed on whatman filter paper no.1. The petridishes were observed every day and the numbers of germinated seeds were recorded at 24 h interval up to 14 days from

set up of the test. Within 4-5 days after seed setting in petridishes.

Data collection

Germination

Germination was recorded daily and was considered complete once the radicle protruded about 2 mm in length. The experiments were continued for 14 days (Ellis and Roberts, 1981).

Germination percent

A seed was considered to be germinated as seed coat ruptured, plumule and radicle came out and were >2mm long. Germination count was expressed in percentage. The germination percentage was calculated using the following formula (International Seed Testing Association, 2006).

Germination (%) = (Number of seed germinated/Total number of seed for test) \times 100

Measurement of root and shoot length

Randomly selected five seedlings were taken from each petridish to measure root and shoot length. It was measured with a measuring scale and expressed in centimeters. Root and shoot length of the seedlings were measured after 17 days of seed setting (Kouio, 2003).

Measurement of fresh weight and dry weight of the seedling

After 17 days of seed setting 15 seedlings of each petisdish were wrapped with brown paper and weighed the fresh weight first and then they were died in oven at 70° C for 48 hours and weighed the dry weight. These were measured by four digit balance and expressed in gram.

Germination percentage and growth parameter reduction calculation

It was calculated as, [(parameter value at dark condition – parameter value at light condition)/ parameter value at dark condition] × 100

Data analysis

All measurements were evaluated for significance using analysis of variance (ANOVA) followed by the least significant difference (LSD) test at the P < 0.05 level. All statistical analyses were conducted using MSTAT-C (Statistical analysis software) computer package program (Gomez and Gomez, 1984).

Results and Discussion

All the studied parameters, viz. germination percent, coleoptile length, prophyll length, first leaf length, first leaf breadth, root length, seedling fresh weight, seedling dry weight of two rice varieties BRRIdhan71 and BRRIdhan81 are presented in Table 2.

Photoblastic effect

The seeds were placed in petri plates and incubated under white light or in darkness at 22±2°C, controlled temperature of germination in rice seeds (Table -2). In dark and under white light, BRRIdhan71 began to germinate after 24 h and BRRIdhan81 after 48 h. In dark condition germination percent of BRRIdhan71 was 97% and 57% in BRRIdhan81. Under white LED light, germination percent of BRRIdhan71 was 77% and 92% BRRIdhan81. Dark condition enhance the germination percent and photoblastic condition reduce germination percent in BRRIdhan71, whereas in BRRIdhan81 the phenomenon was just reverse. Therefore germination frequency is dependent on light and dark condition in this two rice varieties, which is evident from the statement of Simpson (1990) that light inducible germination happens in a certain set of environmental conditions in many photoblastic plant species. Early seedling growth and development are fueled by seed reserves, and this heterotrophic lifestyle can endure for several days in the dark (Takano et al., 2005).

Effect on vegetative growth

Coleoptile, prophyll and first leaf

Rice coleoptile emerges from the seed first and in other cases the radicle emerges first. In dark coleoptile length of BRRIdhan71 was 1.37 cm and 0.93 cm in BRRIdhan81. Under light condition coleoptile length of BRRIdhan71 was 0.57 cm and 0.87 cm in BRRIdhan81 (Table 2).

The prophyll is the first leaf to emerge, but it lacks a blade and a collar and consist only leaf sheath. In dark the prophyll length of BRRIdhan71 was 1.67 cm and 1.77 cm in BRRIdhan81. Under light condition prophyll length of BRRIdhan71 was 1.43 cm and 1.70 cm in BRRIdhan81 (Table 2).

Emergence of the first leaf (one with a blade and sheath) is one of the stage of seedling development. In dark the first leaf length and leaf blade breadth of BRRIdhan71 was 3.63 cm, 1.17 cm and 3.57 cm, 0.80 cm in BRRIdhan81. Under light condition first leaf length and leaf blade breadth of BRRIdhan71 was 3.30 cm, 1.43cm and 3.93, 1.73 cm in BRRIdhan81 (Table 2).

Table 2. Growth parameters of rice seedlings of BRRIdhan71 and BRRIdhan81 with or without light

| Characters | Dark | | Light | |
|--------------------------|---------------------|--------------------|----------------------|----------------------|
| | BRRIdhan71 | BRRIdhan81 | BRRIdhan71 | BRRIdhan81 |
| Germination (%) | 97±1.2* | 57±2.6* | 77±1.5*** | 92±3.1*** |
| Coleoptile length (cm) | $1.37\pm0.09^*$ | $0.93\pm0.22^*$ | 0.57±0.07*** | $0.87\pm0.07^{***}$ |
| Prophyll length (cm) | $1.67\pm0.07^*$ | 1.77±0.15* | 1.43±0.07ns | 1.70 ± 0.10^{ns} |
| First leaf length (cm) | 3.63±0.29* | $3.57\pm0.23^*$ | 3.30±0.12* | $3.93\pm0.19^*$ |
| First leaf breadth (cm) | 1.17 ± 0.09^{ns} | 0.80 ± 0.06^{ns} | 1.43±0.03* | $1.73\pm0.07^*$ |
| Root length (cm) | $7.80\pm0.76^{***}$ | 6.17±0.33*** | 7.27 ± 0.54^{ns} | 5.70 ± 0.25^{ns} |
| Seedling fresh weight(g) | 0.133±0.015** | 0.103±0.009** | $0.210\pm0.017^{**}$ | $0.127\pm0.012^{**}$ |
| Seedling dry weight(g) | $0.0154\pm0.0017^*$ | $0.0119\pm0.001^*$ | $0.0242\pm0.002^*$ | $0.0146\pm0.0014^*$ |

Values show Mean \pm SE (n=15). *, **, *** Indicate significant differences between dark and light treatment at 0.1,1 and 5 % level, respectively. Ns: Not significant difference at 0.1,1 and 5 % level.

The presence or absence of light during germination and seedling establishment is critical (Gommers CMM, Monte 2018). According to Takano *et al.*, (2005), in rice, skotomorphogenic development is characterized by long coleoptiles, lengthy initial leaves, and elongation of the second internode in seedlings grown in darkness. Coleoptile, first leaf, and internode elongation is suppressed by light illumination, and seedlings move to a photomorphogenesis pattern of growth with the establishment of fully functional chloroplasts and shift to autotrophy, as reported in the present study.

Root and root biomass

In dark the root length of BRRIdhan71 was 7.80 cm and 6.17 cm in BRRIdhan81. Under light condition the root length of BRRIdhan71 was 7.27 cm and 5.70 cm in

BRRIdhan81. Root length of the two rice variety differ with little difference (Table 2).

Seedling fresh and dry weight of BRRIdhan71 was 0.133 g, 0.0154 g and 0.13 g, 0.0119 in BRRIdhan81 in dark condition. Under white light seedling fresh and dry weight of BRRIdhan71 was 0.210 g, 0.0242 g and 0.127 g, 0.0146 in BRRIdhan81 (Table 2).

The root shoot growth ratio and dry matter production in rice seedling is greatly affected by presence or absence of light (Zhang *et al.*, 2016). Moreover, root growth of rice seedling enhanced by the addition of basic light spectra. The response of different organ system depend on the intensity of different light. The low percentage of a specific light in the light source could not only promote the stem elongation, shoot dry weight accumulation and the root respiration activity but also could change the root morphology, while the high percentage of specific light only change the root morphology and increase the root respiration activity.

Table 3. Differences in growth parameters of BRRIdhan71 and BRRIdhan81 with or without light

| Characters | Differences | | |
|---------------------------|-------------|------------|--|
| | BRRIdhan71 | BRRIdhan81 | |
| Germination (%) | 25.97 | -38.04 | |
| Coleoptile length (cm) | 141.18 | 7.69 | |
| Prophyll length (cm) | 16.28 | 3.92 | |
| First leaf length (cm) | 10.10 | -9.32 | |
| First leaf breadth (cm) | -18.60 | -53.85 | |
| Root length (cm) | 7.34 | 8.19 | |
| Seedling fresh weight (g) | -36.51 | -18.42 | |
| Seedling dry weight (g) | -36.51 | -18.42 | |

Growth increase or reduction

Significant differences were observed germination and growth parameters of the studied to rice varieties (Table-3). For better comparison and actual increase or reduction in parameters were also observed. Germination percent (25.97%), coleoptile length (141.18%), prophyll length (16.28%), first leaf length (10.10%), root length (7.34%) remarkably increased, whereas leaf blade breadth (-53.85%), seedling fresh weight (-36.51%) and seedling dry weight (- 36.51%)

were decreased in BRRIdhan71 when compared between dark and light condition. In BRRIdhan81, germination percent (-38.04 %), first leaf length (-9.32%), leaf blade breadth (-53.85%), seedling fresh weight (-18.42%) and seedling dry weight (-18.42%) were decreased and coleoptile length (7.69%), prophyll length (3.92%) and root length (8.19%) were increased as compared between dark and light condition. This findings revealed the importance of photoblastism and darkness in relation to growth stage S0 to SVI in rice seedlings (Plate 1).

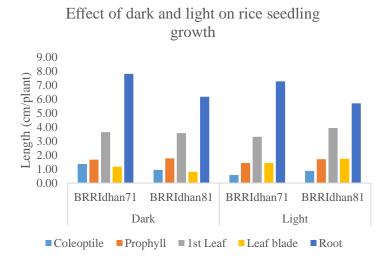


Fig. 1. Differences in growth parameters of rice seedlings of BRRIdhan71 and BRRIdhan81 in dark and light condition.





Plate 1. Effect of light (Left) and dark (Right) on seedling morphology of BRRIdhan71 and BRRIdhan81.

Rice seedling morphogenesis and development depends on the growth condition and growing environments. Rice is short day plant. Photosensitivity is one of the crucial factor. Edaphic factor are also important. Plant's growth and exterior quality are influenced by the light environment, which influences a variety of life activities such as photosynthesis, photomorphogenesis, and photoperiod control. Rice growth status and quality are affected differently by different rice varieties, rice growth stages, and light environment. photosynthesis, photomorphogenesis, metabolism, and gene expression are all influenced by light quality, either directly or indirectly. Different plant species or growth phases of the same species, as well as different organs, respond to the same light quality in different ways, demonstrating the complexity and diversity of light quality in biological processes. This necessitates a more in-depth investigation of the changes in the demand for light quality of various rice varieties at various growth stages, as well as the appropriate proportion of combined light, in order to provide a theoretical reference for the more efficient and

energy-saving artificial light source application in rice seedling growth. Further study is needed to elucidate the influence of different spectra of light in rice seedling morphogenesis and finally its contribution to yield.

References

Benvenuti, S., M. Macchia, and S. Miele. 2001. Light, temperature and burial depth effects on *Rumex obtusifolius* seed germination and emergence. *Weed Res.* 41:177–186.

Botto, J.F., A.L. Scopel, C.L. Ballare, and R.A. Sanchez. 1998. The effect of light during and after cultivation with different tillage implements on weed seedling emergence. *Weed Sci.* 46:351–357.

C. Chen.2014. The effects of light quality on the growth, development, and metabolism of rice seedlings (*Oryza sativa* L.). *Research Journal of Biotechnology*. 9. 15-24.

- Chung, Nam-Jin & Paek, Nam-Chon. (2003).

 Photoblastism and Ecophysiology of Seed
 Germination in Weedy Rice. Agronomy Journal AGRON J. 95. 10.2134/agronj2003.0184.
- Dehesh, K., J. Tepperman, A.H. Christensen, and P.H. Quail. 1991. PhyB is evolutionarily conserved and constitutively expressed in rice seedling shoots. *Mol. Gen. Genet.* 225:305–313.
- Duan L, Ruiz-Sola MÁ, Couso A, Veciana N, Monte E. 2020. Red and blue light differentially impact retrograde signalling and photoprotection in rice. Phil. Trans. R. Soc. B 375: 20190402. http://dx.doi.org/10.1098/rstb.2019.0402
- Duke, S.O. 1978. Interactions of seed water content with phytochrome-initiated germination of *Rumex crispus* (L.) seeds. Plant Cell Physiol. 19:1043–1049.
- Ekstam, B., and A. Forseby. 1999. Germination response of *Phragmites australis* and *Typha latifolia* to diurnal fluctuations in temperature. Seed Sci. Res. 9:157–163.
- Ellis, R.H., Roberts, E.H., 1981. The quantification of ageing and survival in orthodox seeds. Seed Science and Technology 9, 373–409.
- Gardner, F.P., R.B. Pearce, and R.L. Mitchell. 1985. Physiology of crop plants. 1st ed. Iowa State Univ. Press, Ames.
- Gomez AK., Gomez AA. 1984. Statistical Procedures for Agricultural Research 2nd ed. International Rice Research Institute, Los Banos, Philippines, pp 207-215.
- Gommers CMM, Monte E. 2018. Seedling establishment: a dimmer switch-regulated process between dark and light signaling. Plant Physiol. 176, 1061–1074. (doi:10.1104/pp.17.01460)
- International Seed Testing Association, 2006. ISTA Handbook on Seedling Evaluation, second ed. International Seed Testing Association, Zurich, Switzerland.
- Kouio, A.G. 2003. Chemical and biological changes in seed treatment of rice varieties. Journal of rice Science. International Rice Research Institute, Los Banos, Philippines, pp 207-215.
- Kristie, D.N., and A. Fielding. 1994. Influence of temperature on the Pfr level required for germination in lettuce cv. Grand Rapids. Seed Sci. Res. 4:19–25.
- Kristie, D.N., P.K. Bassi, and M.S. Spencer. 1981. Factors affecting the induction of secondary dormancy in lettuce. Plant Physiol. 67: 1224–1229.
- Mancinelli, A.L., H.A. Borthwick, and S.B. Hendricks. 1966. Phytochrome action in tomato-seed germination. Bot. Gaz. 127:1–5.
- Mathews S, Sharrock RA. 1996 The phytochrome gene family in grasses (Poaceae): a phylogeny and evidence that grasses have a subset of the loci found in dicot angiosperms. Mol. Biol. Evol. 13,

- 1141–1150. (doi:10.1093/oxfordjournals.molbev. a025677)
- Mathews S, Sharrock RA. 1996. The phytochrome gene family in grasses (Poaceae): a phylogeny and evidence that grasses have a subset of the loci found in dicot angiosperms. Mol. Biol. Evol. 13, 1141–1150.
 - (10.1093/oxfordjournals.molbev.a025677)
- Matsumoto N, Hirano T, Iwasaki T, Yamamoto N. 2003 Functional analysis and intracellular localization of rice cryptochromes. Plant Physiol. 133, 1494– 1503. (doi:10.1104/pp.103.025759)
- Matsumoto N, Hirano T, Iwasaki T, Yamamoto N. 2003. Functional analysis and intracellular localization of rice cryptochromes. Plant Physiol. 133, 1494–1503. (10.1104/pp.103.025759)
- Milberg, P., L. Andersson, and K. Thompson. 2000. Large-seeded species are less dependent on light for germination than small seeded ones. Seed Sci. Res. 10:99–104.
- Neff MM, Fankhauser C, Chory J. Light: an indicator of time and place. Genes Dev. 2000 Feb 1;14(3):257-71. PMID: 10673498.
- Quail, P.H., M.T. Boylan, B.M. Parks, T.W. Short, Y. Xu, and D. Wagner. 1995. Phytochromes, photosensory perception and signal transduction. Science 268:675–680.
- Reed, J.W., A. Nagatani, T.D. Elich, M. Fagan, and J. Chory. 1994. Phytochrome A and phytochrome B have overlapping but distinct functions in Arabidopsis development. Plant Physiol. 104:1039–1049.
- Scopel, A.L., C.L. Ballare, and R.A. Sanchez. 1991. Dormancy patterns in buried seeds of *Datura ferox* L. Can. J. Bot. 69:173–179.
- Shinomura, T., A. Nagatani, H. Hanzawa, M. Kubota, M. Watanabe, and M. Furuya. 1996. Action spectra for phytochrome A- and B-specific photoinduction of seed germination in Arabidopsis thali- ana. Proc. Natl. Acad. Sci. USA 93:8129–8133.
- Shinomura, T., A. Nagatani, J. Chory, and M. Furuya. 1994. The induction of seed germination in *Arabidopsis thaliana* is regulated principally by phytochrome B and secondarily by phytochrome A. Plant Physiol. 104:363–371.
- Shinomura, T., H. Hanzawa, E. Schafer, and M. Furuya. 1998. Mode of phytochrome B action in the photoregulation of seed germina tion in *Arabidopsis thaliana*. Plant J. 13:583–590.
- Simpson, G.M. 1990. Seed dormancy in grasses. 1st ed. University Press, Cambridge, UK.
- Takano M 2005 Distinct and cooperative functions of phytochromes A, B, and C in the control of deetiolation and flowering in rice. Plant Cell 17, 3311–3325. (doi:10.1105/tpc.105.035899)
- Takano M, Inagaki N, Xie X, Kiyota S, Baba-Kasai A, Tanabata T, Shinomura T. 2009 Phytochromes are the sole photoreceptors for perceiving red/far-red

- light in rice. Proc. Natl Acad. Sci. USA 106, 14 705–14 710. (doi:10.1073/pnas.0907378106).
- Thompson, D.A., S.A. Cox, and R.H. Sanderson. 1979. Characteriza tion of germination response to temperature of lettuce (*Lactuca sativa* L.) achenes. Ann. Bot. 43:319–334.
- Toole, E.H., V.K. Toole, H.A. Borthwick, and S.B. Hendricks. 1955. Photocontrol of Lepidium seed germination. Plant Physiol. 30:15–21.
- Zhang S.X., Huang D.D., Yi X.Y., Zhang S., Yao R., Li C.G., Liang A., Zhang X.P. (2016): Rice yield

- corresponding to the seedling growth under supplemental green light in mixed light-emitting diodes. Plant Soil Environ., 62: 222-229.
- Zhang YC, Gong SF, Li QH, Sang Y, Yang HQ. 2006 Functional and signaling mechanism analysis of rice CRYPTOCHROME 1. Plant J. 46, 971–983. (doi:10.1111/j.1365-313X.2006.02753.x)
- Zhang YC, Gong SF, Li QH, Sang Y, Yang HQ. 2006. Functional and signaling mechanism analysis of rice CRYPTOCHROME 1. Plant J. 46, 971–983. (10.1111/j.1365-313X.2006.02753.x)