Review

Low-light and its effects on crop yield: Genetic and genomic implications

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Shade indicates decreased sunlight. The agricultural importance of shade imparts to its deteriorative effect of crop yield. Rice is not only the most widely used food crop by a third of the population of the world, but it has also been established as the model monocot plant for study. This article describes several important aspects of shade on rice yield with appropriate examples in other plants such as *Arabidopsis*. To start with, how different environmental or growth conditions create shade is explained. The morphological, physiological and biochemical characteristics due to different kinds of shade are selectively explained. The molecular characteristics of rice under shade from genetic, genomic and epigenetic studied are discussed. Signalling components for the manifestation of shade tolerance responses and their interconnection with other signalling networks and hormone pathway components are from recent reports. A list of genes, micro-RNAs and metabolites that are involved in shade responses is presented. Lastly, implications for sustainable yield under shade is discussed. This review will be useful not only for cutting-edge information on shade tolerance but will also build framework for upcoming new rice varieties with sustainable yield under shade.

Keywords. Low red/far-red; low-light; rice; shade avoidance; tolerance; yield

1. Introduction

Phytochromes (P) are interconvertible photoreceptors that exist as biologically inactive far-red (FR) light-absorbing Pfr form and active red (R) light-absorbing Pr form. These photoreceptors respond to ambient light environments by their dynamic equilibrium between the Pr and the Pfr form according to light quality (Kevei *et al.* 2007). The visible spectrum ranges from 400 nm to 700 nm. The light quality in the natural environments is explained by the photon irradiance in the red region to that in the FR region of the spectrum.

1.1 *Definition of shade*

The ratio of R:FR fluctuates daily at the dawn and dusk, which is known as twilight. During this period there is significant enhancement in the longer wavelengths causing a significant drop in the R:FR ratio (Kendrick and Kronenberg 1994). In addition to this, daylight transmitted through living vegetation also results in enrichment of FR wavebands, reducing R:FR ratio. Hence, a dramatic decrease in the R:FR ratio for plants in vegetation implies a threat of shade from neighbouring plants and initiation of adaptation responses due to shade. Actual shading, however, includes the decreased photosynthetically active radiation (PAR) in the visible range of the spectrum, which is associated with increased synthesis of ethylene (Das *et al.* 2016).

Thus, shade light causes severe reduction in blue and red wavelengths and the least reduction in the FR wavelengths (figure 1), which is caused due to stronger absorption of red and blue wavebands by the vegetation (Casal 2012). The reduction in R:FR ratio is

perceived by the phytochromes, whereas the reduction in blue and UV-A light irradiance is perceived by the cryptochromes.

1.2   *Natural environmental or growth conditions that create shade*

Under experimental conditions, shade can, therefore, be attained by multiple methods. In field conditions for study in crops, shade is achieved by growing them under a quantified cut-off shade net (Panigrahy *et al.* 2018), which can restrict the incident sunlight to variable percentages such as 25%, 50% and 75%. These nets could be covered under specific growth stages of the plant which is under study (Panigrahy *et al.* 2019). Shade is also applied by simply decreasing the intensity of incident white light in experimental growth chambers (Pierik *et al.* 2005). Simulated white light mimicking the twilight has been used some reports by employing white light enriched with specific FR lights of 730 nm (Sessa *et al.* 2005). Monochromatic lights containing simultaneous irradiations red (660 nm) and FR (730 nm) so as to obtain a low ratio of R:FR intensities can also be used in principle to study the effect of shade in experimental plants grown in plant growth chambers (Panigrahy *et al.* 2019). Shade treatments for plants growing in day/night cycles can be induced by a pulse of FR light at the end of the photoperiod, also called as end-of-day-FR (EOD-FR) effect (Casal 2012). The perception of strong FR pulse changes the status of the photoreceptor through severe reduction in R:FR ratio and effects during the subsequent night. Another approach of reducing R:FR in the incident light is to use neutral colour filters of selected wavebands (Sessa *et al.* 2005). It is known that yellow and orange filters cut blue light and copper-sulphate filte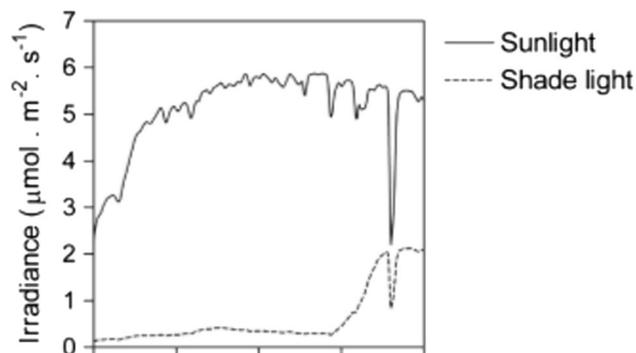rs reduce far-red light (Casal 2012). To create artificial shade, these filters can be selectively placed above the plants or surrounding the stem.

1.3   *Shade avoidance and shade tolerance*

Primarily the phytochrome photoreceptors sense the reduction in the R:FR ratio, which may occur either due to the neighbouring vegetation, actual shade, future shade or reduced PAR, and induce a suite of traits to grow towards the light. Collectively this is known as shade avoidance response (SAS), including apical dominance, elongation of stems and petioles, upward movement of leaves (hyponasty), branches and accelerated flowering (Bardhan *et al.* 2019). All major crops show SAS when grown at high densities (Franklin 2008). SAS in crops leads to the allocation of carbon towards, root, leaf and stem elongation at the expense of harvestable organs that contribute to yield (Carriedo *et al.* 2016). SAS is also exhibited in vegetation where plants are of approximately similar heights such as grasslands.

Among the two strategies to deal with shade, shade tolerance is exhibited by species from forest understories that cannot outgrow the surrounding trees and adopt tolerance responses (Gommers *et al.* 2012). This includes various physiological and morphological characteristics such as reduced specific leaf area, leaf longevity, root–shoot ratio, relative growth rate, rate of dark respiration and elongation responses to shade (Gommers *et al.* 2012). In contrast to SAS, shade-tolerant species suppress SAS, direct the harvested light and assimilated resources towards other pathways such as optimization of photosynthesis and physical defence responses.

Phytochrome (*Phy*) *B* suppresses shade avoidance responses. *PhyD* and *PhyE* act redundantly along with *PhyB* in mediating shade avoidance (table 1). However, *PhyC* was shown to have no functional roles in controlling SAS. *PhyA* also functions to antagonize shade avoidance albeit through FR-high irradiance response mode (Salter *et al.* 2003). Hypocotyl elongation under shade was earlier shown to be regulated by (*HY5 HOMOLOG*) *HYH* (Ciolfi *et al.* 2013). *HYH* was late induced by low R/FR and its upregulation depends on transcription factor *HY5*.

2.   **Morphological adaptions under shade**

2.1   *Stem and petiole elongation*

Stem elongation followed by irradiation to low R:FR is not a fast response and is initiated after a lag of 45 min

Figure 1.   Spectral difference at the top (sunlight) and at the base of a dense canopy (shade light) (Casal 2012).

Table 1. Summary of genes and their functions involved in response to shade in *Arabidopsis* and Rice

Gene	Functions	References
PHYB	Sensor of R:FR ratio and of red irradiance	Franklin (2008)
	Perceive low R:FR and induce flowering at an earlier developmental stage	Devlin *et al.* (2003)
	Exert part of its action on branching by altering strigolactone signalling and polar auxin transport	Domagalska and Leyser (2011)
	Promote petiole growth in response to low R:FR or EODFR	Nagatani *et al.* (1991), Devlin *et al.* (2003), Pierik *et al.* (2009) and Kozuka *et al.* (2010)
	Promote height of inflorescence stem by low R:FR	Finlayson *et al.* (2010)
	Promote leaf hyponasty during low R:FR	Ballaré and Scopel (1997)
PHYD	Acts redundantly with *PHYB* in mediating the suppression of shade avoidance	Aukerman *et al.* (1997), Devlin *et al.* (1999)
PHYE	Acts redundantly with *PHYB* and *PHYD* in the suppression of shade avoidance	Devlin *et al.* (2003)
	It has an additional regulatory role	Devlin *et al.* (2003)
	Acts redundantly with *PHYB* to suppress *ATHB2* expression	Franklin (2008)
PHYA	FR sensor in high irradiance response (HIR) mode	Hennig *et al.* (2000)
	Antagonizing shade avoidance	Johnson *et al.* (1994) and Salter *et al.* (2003)
	Perceives reduced red plus far red irradiance	Sellaro *et al.* (2010)
	Reduce extent of *PHYB*-mediated inhibition of hypocotyl growth	Cerdán *et al.* (1999)
CRYs	Involved in control of stomata development	Kang *et al.* (2009)
	Indirectly regulate leaf conductance by reducing the levels of ABA	Boccalandro *et al.* (2011)
	Involved in repressing a low blue-mediated SAS by regulating *PIF* abundance and activity	de Wit *et al.* (2013) and Pedmale *et al.* (2016)
CRY1	Inhibition of hypocotyl growth predominantly at higher photon irradiances of blue light	Lin *et al.* (1998)
	Promote leaf hyponasty during low R:FR	Keller *et al.* (2011)
	Perceive reduced blue/green ratio	Sellaro *et al.* (2010)
CRY2	Enhance blue light sensitivity in light limited conditions	Lin *et al.* (1998)
	Redundant role in suppressing hypocotyl growth	Mazzella *et al.* (2001)
PHOT1, PHOT2	Mediate plant growth and development in conditions of low-light quantity	Takemiya *et al.* (2005)
	Perceive horizontal gradients created by canopies	Briggs and Christie (2002)
ATHB2	Elevated abundances of *ATHB2* displayed reduced apical dominance and early flowering, phenotypes	Schena *et al.* (1993)
	Reminiscent of shade avoidance syndrome	
PIL1, PIL2	Regulate shade avoidance responses by connecting with circadian clock	Khanna *et al.* (2006)
PIL1	Positive or negative regulator of shade avoidance responses, depending on the kinetics of the shade light signal	Salter *et al.* (2003)
TOC1	Interact physically with *PIL1*	Makino *et al.* (2002)
	Regulate circadian gating of hypocotyl shade avoidance responses	Salter *et al.* (2003)
PIFs	Promote shade avoidance independently of phytochrome interaction	Lorrain *et al.* (2008)
	Promote expression of genes mediating elongation growth in low R:FR	Lorrain *et al.* (2008)
PIF7	Regulate the expression of *YUCCA* genes	Hornitschek *et al.* (2012)
HFR1	Mediate negative feedback loop controlling magnitude of shade avoidance responses	Sessa *et al.* (2005)
	Forms non-binding heterodimers with *PIF4* and *PIF5*, preventing their binding to DNA and biological activity	Hornitschek *et al.* (2009)
DELLA	Mediate shade avoidance responses	Djakovic-Petrovic *et al.* (2007)
	Bind to PIF proteins and prevent them from binding DNA and thus negatively regulate the expression of genes involved in cell elongation	De Lucas *et al.* (2008) and Feng *et al.* (2008)

Table 1 (continued)

Gene	Functions	References
	Negatively regulate BR signalling by binding *BZR1* and reducing the expression of BR-responsive genes	Bai *et al.* (2012) and Gallego-Bartolomé *et al.* (2012) and Li *et al.* (2012)
	Positively regulate JA signalling by interacting with JAZs, and this interaction weakens the ability of *JAZ*s to repress *MYC2*	
GA	Interact with light signalling	López-Juez *et al.* (1995); Reed *et al.* (1996); Pierik *et al.* (2004)
	Target *DELLA*s for degradation thereby relieving the inhibition of *PIF* activity and promoting elongation growth	De Lucas *et al.* (2008) and Feng *et al.* (2008)
GA20ox1, GA20ox2, GA3ox	Shade-induced GA biosynthetic enzymes that account for the increase in active GA	Hisamatsu *et al.* (2005) and Yu *et al.* (2015)
GA20OX3	Its expression increases in low R:FR. Encodes an enzyme involved in the synthesis of gibberellins	Devlin *et al.* (2003)
GA20OX2	Promote petiole elongation in response to EODFR	Hisamatsu *et al.* (2005)
FT	Operates light quality pathway mediating acceleration of flowering in low R:FR	Cerdán and Chory (2003)and Halliday *et al.* (2003)
SPA/COPI	Enhance *PIF* activity by degrading *HFR1* and *HY5* to augment shade responses	Sheerin *et al.* (2015) and Pacín *et al.* (2016)
AUX/IAAs	Modulate shade avoidance syndrome	Steindler *et al.* (1999) and Procko *et al.* (2016)
SAV3	Auxin synthesis gene required for promotion of hypocotyl growth by low R:FR	Tao *et al.* (2008)
SAV	Required for petiole elongation in response to low blue light	Keller *et al.* (2011)
PIN3	Auxin efflux transmembrane transporter required for promotion of hypocotyl growth by low R:FR	Keuskamp *et al.* (2011)
	Promote petiole extension in growing canopies	Keuskamp *et al.* (2011)
PIN7	Required for promotion of hypocotyl growth by low R:FR	Keuskamp *et al.* (2011)
AXR1	It controls stability of auxin efflux carriers and is required for hypocotyl growth promotion by low R:FR	Keuskamp *et al.* (2011)
TIR1	Auxin receptor required for hypocotyl growth promotion during low R:FR	Keuskamp *et al.* (2011)
SAV3/TAA1	Mediate auxin synthesis in the leaves during low R:FR	Tao *et al.* (2008)
BBX	Involved in hypocotyl growth responses to shade light	Crocco *et al.* (2010)
BBX21, BBX25	Regulate shade response through the function in the *COP1* signalling pathway	
Ethylene	Induce responses similar to shade avoidance responses	Pierik *et al.* (2003)
	Functions, in part, through altering GA responsiveness	Pierik *et al.* (2003)
	Regulate *DELLA* stability in *Arabidopsis*	Achard *et al.* (2003)
	Promote petiole growth at low R:FR	Schaller and Kieber (2002)
	Positive regulator of shade-induced petiole elongation, suggested from *ein2-1* and *ein3-1eil1-3* mutation in which shade-induced petiole elongation was absent	Pierik *et al.* (2009)
BRs	Required for promotion of stem growth by shade light as BR biosynthesis mutant dwarf1 and rot3 are unable to show the hypocotyl elongation under shade	Luccioni *et al.* (2002) and Kim *et al.* (1998)
	Required for petiole growth under low R/FR	Kozuka *et al.* (2010)
BEE, BIM	Positive regulators of SAS hypocotyl responses	Cifuentes-Esquivel *et al.* (2013)
Strigolactones	Repress bud activity	Domagalska and Leyser (2011)
COR genes	Upregulated by low R:FR treatments at low temperature	Franklin and Whitelam (2007)
XTH15	Xyloglucan endotransglycosylase is significantly upregulated following simulated shade treatment	Sessa *et al.* (2005)
XTH5, XTH17	Helps in growth promotion induced by low R:FR	Sasidharan *et al.* (2010)
UVR8	Perceive reduction in UVB irradiance	Rizzini *et al.* (2011)
COP1	Required for the accumulation of *PIF3* in the dark	Bauer *et al.* (2004) and Leivar *et al.* (2008)

Table 1 (continued)

Gene	Functions	References
ELF3	Required for hypocotyl growth response to low R:FR or EODFR	McNellis *et al.* (1994)
	Acts as an adapter protein facilitating *COP1* activity	Yu *et al.* (2008)
	Acts by forming an evening complex required for the correct diurnal expression of *PIF4* and *PIF5*	Nusinow *et al.* (2011)
	Regulate the flowering time response to shade	Jiménez-Gómez *et al.* (2010)
PAR1, PAR2	Negative regulators of shade avoidance responses	Roig-Villanova *et al.* (2007)
HY5	Highly expressed under sun fleck conditions	Sellaro *et al.* (2011)
	Reduce expression of auxin related genes and *PKS4* causing reduced hypocotyl growth	Sellaro *et al.* (2011)
	Form non-functional complexes with *PIF*s	Chen *et al.* (2013) and Toledo-Ortiz *et al.* (2014)
DOC1/BIG	Promote petiole growth by shade light signals	Gil *et al.* (2001)
ROT3	Promote petiole growth by shade light signals	Kozuka *et al.* (2010)
BRI1	Promote petiole elongation in response to low blue light	Keller *et al.* (2011)
AHK3	CK receptor that has been reported to mediate the root-to-hypocotyl ratio response under shade avoidance	Novák *et al.* (2015)
CKX6	Trigger a rapid arrest of leaf-primordia growth by the breakdown of auxin-induced CK during shade	Carabelli *et al.* (2007)
JAZ10	Required for the inhibitory effect of shade on JA responses	Leone *et al.* (2014)
COI1	Central component of JA signalling and important for FR light induced expression of several genes	Robson *et al.* (2010)
PFT1	Required for both JA-dependent defence gene expression and shade-induced early flowering	Cerdán and Chory (2003), Çevik *et al.* (2012) and Iñigo *et al.* (2012)
NCED3, NCED5	ABA biosynthesis genes that are upregulated particularly in hypocotyls during shade	Kohnen *et al.* (2016)
BRC1, BRC2	Required for shade-mediated branch suppression	Aguilar-Martínez *et al.* (2007), González-Grandío *et al.* (2013) and Finlayson *et al.* (2010)
Karrikins	Enhance the sensitivity of seedlings to light	Waters and Smith (2013)
CO	Low R:FR increase the expression and activity of *CO* at dawn and dusk, thereby enhancing photoperiodic pathway of flowering induction	Wollenberg *et al.* (2008)
PTF1	Promote flowering through *CO*-dependent and independent mechanisms	Iñigo *et al.* (2011)
LP2 (Rice)	Gene promoter in rice that is highly responsive to light	Liu *et al.* (2014)
Chlorophyll	In rice chlorophyll content increased under low irradiance, hence plays a role in shade avoidance response	Restrepo and Garcés (2013)
SPIKE (Rice)	Indirectly affect panicle spikelet numbers	Fabre *et al.* (2016) and Adriani *et al.* (2016)
miR156	SPL-mediated increase of levels of PIFs for a portion of low R:FR responses and EOD-FR responses	Xie *et al.* (2017)
HYPONASTIC LEAVES (HYL1)	Activation and deactivation of miRNA biogenesis	Achkar *et al.* (2018)

in *Arabidopsis* seedlings. The first phase of growth promotion occurs between 45 and 150 min, while the second phase of hypocotyl growth occurs beyond 230 min (Cole *et al.* 2011). Under free-running condition, hypocotyl growth elongation was recorded 24 h after 2 h exposure to low R:FR (Salter *et al.* 2003). The attenuated promotion of hypocotyl elongation and phase shift in the *timing of cab expression 1* (*toc1*) mutant was evidenced for the circadian gating of this response under shade.

PhyB acts in suppressing leaf elongation, mesocotyl elongation and apical dominance. Cryptochromes (*CRY*) also play roles in suppressing hypocotyl growth under low-light. Phototropins play a major role in

mediating plant growth and development under low-light conditions. Elongated hypocotyl under low R:FR requires normal levels of Phytochrome Interacting Factor (*PIF*) *4* and *PIF5*. Accumulation of PIF4 and PIF5 after transfer to low R:FR is an immediate response that occurs after 15 min of exposure and continues during the subsequent 2 h (Cole *et al.* 2011). Moreover, long-term promotion of hypocotyl growth occurs due to low levels of *PhyB* Pfr due to low R wavebands, which is also reciprocally regulated by levels of *PIF3*, *PIF5* and *PIF7* (Leivar *et al.* 2008). Despite the knowledge of the requirement of *CONSTITUTIVE PHOTOMORPHOGENIC 1* (*COP1*) for the accumulation of *PIF3* in dark and *EARLY FLOWERING 3* (*ELF3)* for facilitating *COP1* activity, the role of *COP1* and *ELF3* in controlling low R:FR stem elongation is not known. However, controls of the circadian clock on shade avoidance through direct binding of Pseudo-response Regulators (PRR) with the PIFs to repress their transcriptional activity and subsequent activation of their direct target genes was recently sown (Zhang *et al.* 2020)

Low R:FR promotes free auxin levels in a *PIN FORMED 3* (*PIN-3*)-dependent manner. Low R:FR mediates *SHADE AVOIDANCE3/TRYPTOPHAN AMINOTRANSFERASE* (*SAV3/TAA1*)-mediated auxin synthesis in leaves and *PIN-3*-mediated lateral auxin redistribution in the epidermal and cortical cells of hypocotyl for promoting cell elongation (Morelli and Ruberti 2000). Hypocotyl elongation in *Arabidopsis* under low R:FR is regulated also by the rapid and reversible expression of *ARABIDOPSIS THALIANA HOMEOBOX 2* (*ATHB2*), *HOMEOBOX ARABIDOPSIS THALIANA 2* (*HAT2*) transcription factors, which is partially dependent upon *PIF4* and *PIF5*.

The involvement of Gibberellins in promoting hypocotyl elongation under low R:FR was indicated by the expression of gibberellin biosynthesis *GIBBERELLIN 20-OXIDASE 3* (*GA20OX3*) gene (Hisamatsu *et al.* 2005). Further, shade promotes the expression of B-Box transcription factors (*BBX*)*21*, *BBX19*, *BBX22* and reduces the expression of *BBX18* and *BBX24*. Low-light-induced elongated petioles are mediated by the degradation of *DELLA* proteins (Crocco *et al.* 2015), which is controlled by auxin (Keuskamp *et al.* 2011). Hence, petiole elongation requires coordination of auxin and brassinosteroid signalling and ethylene signalling through *ETHYLENE INSENSITIVE2* (*EIN2*) and *ETHYLENE INSENSTIVE3-LIKE1* (*EIL1*), required for petiole growth (Pierik *et al.* 2009). Enhanced xyloglucan degrading activity and enhanced expression of *XYLO-GLUCAN ENDOTRANS-GLUCOSYLASE/HYDROLASE* (*XTH*)*5* and *XTH17* was shown associated with petiole growth promotion in low R:FR.

2.2   *Increase in leaf area*

PhyD has specific roles in leaf expansion redundant to *PhyB*. *LONG HYPOCOTYL IN FAR-RED LIGHT 1* (*HFR1)* negatively regulated leaf area expansion (Sessa *et al.* 2005). Leaf lamina growth rapid increase in expression of auxin and brassinosteroid responsive genes and degradation if cytokinin via promotion of *CYTOKININ OXIDASE 6* (*CKX6*) (Carabelli *et al.* 2007).

2.3   *Reduced branching*

Under normal light conditions, high R:FR perceived by *PhyB* promotes branching. *PhyB* under low-light acts to produce fewer branches by controlling bud activity (Finlayson *et al.* 2010). This control on branching under low-light requires intact *AUXIN RESISTANT 1* (*AXR1*) of auxin and *MORE AXILLARY BRANCHES 2* (*MAX*)*2*, *MAX4* of strigolactones signalling (Domagalska and Leyser 2011). The control of branching is regulated by TCP-domain transcription factor *BRANCHED 1* (*BRC*)*1* and *BRC2*, which are expressed in the buds and suppress the bud growth under low R:FR (Aguilar-Martínez *et al.* 2007; Finlayson *et al*. 2010).

2.4   *Leaf hyponasty*

More erect position of leaves to capture more light is known as hyponasty which is observed in plants growing in canopies. This plant shape adaptation is observed 2 h after exposure to low-light and reaches a maximum after 16 h. *PhyB* and *CRY1* are known to control leaf hyponasty (Keller *et al.* 2011). *SAV3* (Tao *et al.* 2008; Moreno *et al.* 2009) and *PIN3* (Keuskamp *et al.* 2011) positively regulate hyponasty. Moreover, polar auxin transport is required for this response.

2.5   *Accelerated flowering*

FLOWERING LOCUS T (*FT*) protein is produced in leaves and transported to the apex to regulate the transition of the vegetative stage to the reproductive stage. *PhyB* along with *PhyD* and *PhyE* control accelerated flowering under low R:FR (Cerdán and Chory 2003; Halliday *et al.* 2003) and this action

requires increased *FT* levels. Increased *FT* expression requires reduced *FLOWERING LOCUS C* (*FLC*) expression in long days (Silva *et al.* 2020). Under shade, constitutive *FLC* expression accelerates flowering bypassing the vernalization (Wollenberg *et al.* 2008). Shade signals accelerate flowering by enhancing photoperiodic pathways by increased expression of *CONSTANS* (*CO*). However, photoperiod-independent control of early flowering by *PhyB* operates through *PHYTOCHROME AND FLOWERING TIME 1* (*PFT1*) (Iñigo *et al.* 2012). Additionally, *ELF3* and *HFR1* are also involved in controlling the early flowering under low-light.

2.6   *Changes in mature plant phenotype*

Reduced spikelet number and number of filled grains along with increased root dry weight were observed in rice due to low light along with an increase in culm dry weight under low-light (Yamamoto *et al.* 1995). In the shade-tolerant genotype, increased panicle length rather than the susceptible genotype was seen to be associated when Swarnaprabha was grown under low-light (Panigrahy *et al.* 2019). Low-light in the reproductive phase results in a decrease in panicle dry weight, as most of the dry matter is attributed to sustaining the growth of vegetative organs such as leaves, culm and sheaths (Sun *et al.* 2012). This decrease was shown due to decreased photoassimilates and dry matter translocation under low-light (Zhu *et al.* 2008).

Stem mechanical strength is decreased in rice due to shading. This is a result of a decrease in non-structural carbohydrate, sucrose, lignin and cellulose in the culms, and is due to a decrease in carbon source under low-light conditions (Wu *et al.* 2017). Expression of genes involved in lignin and cellulose biosynthesis such as (*Oryza sativa CELLULOSE SYNTHASE*) *OsCesA1*, *OsCesA3* and *OsCesA8* were downregulated, resulting defective cell wall development and poor lodging resistance (Wu *et al.* 2017).

Yield in rice is severely affected by low-light, the extent of which has been shown to vary from 14% to 55% depending on the type and duration of shade, the genotype used for study and the growth season (dry or rain). However, it reconfirms that low-light during reproductive stages starting from booting till grain maturation impose greater negative impact on grain yield (Sun *et al.* 2012; Liu *et al.* 2014; Panigrahy *et al.* 2019). This happens due to the decreased photosynthesis rate in the source organs such as leaves, culm and seaths, as the diffused light under shade is enriched

with blue-purple proportions and lower red proportions. This is supplemented with the decreased translocation of photosynthates from the source to the sink organ (seed). However, reports have shown that shade-tolerant varieties are able to minimize yield loss and maintain a sustainable yield by the presence of higher chlorophyll content and higher antioxidant activity, and thereby restricted membrane damage and maintained photosynthesis rates (Liu *et al.* 2012).

3.   Physiological and biochemical modifications under shade

3.1   *Photosynthetic adaptations*

The stoichiometry and morphological changes in the photosynthetic apparatus in plants grown at low-light include changes in chloroplast PSII: PSI ratio (Murchie *et al.* 2005). They have higher peripheral light-harvesting complexes per PSII, RUBISCO and cytochrome b/f complexes per unit chlorophyll (Liu *et al.* 2014). Low-light decreases RUBISCO activity, electron transfer and quantum yield of PSII. Low-light-tolerant varieties of rice showed higher chlorophyll B and reduced chlorophyll A/B in their leaves after 15 days under low-light. Low-light-tolerant varieties have been shown to maintain higher synthesis of Sedoheptulose 1,7 biphosphatase (SBPase) and Fructose 1,6 biphosphatase (FBPase), which serves to increase the carbon flux in the Calvin cycle and ultimately result in increased rate of carbon fixation than the low-light-sensitive genotypes (Tamoi *et al.* 2006).

3.2   *Physiological changes*

Low irradiance perceived by *PhyB* reduces leaf stomatal density, transpiration and photosynthesis. However, water-use efficiency and non-photochemical quenching were seen to be increased (Ruban 2016). Cryptochromes are also involved in stomatal development, and regulate leaf conductance by reducing abscisic acid. Low-light negatively regulates stomatal conductance, leading to higher concentration of CO_2 in the leaf cells (Chen *et al.* 2012).

3.3   *Reduced defence responses*

Plants grown under low-light show decreased defence response, thereby become more vulnerable to insect

herbivores. This partly happens due to reduced sensitivity to jasmonic acid (de Wit *et al.* 2013). The reduced defence response is due to the release of resources for SAS responses (Louda and Rodman 1996). The (*TOLL/INTERLEUKIN-1 NUCLEOTIDE-BINDING-SITE LEUCINE-RICH REPEAT*) *TIR-NBS-LRR* gene implicated in defence response mediates the SAS responses such as elongated hypocotyl, petioles, hyponastic leaves, early flowering and enhanced expression of shade marker genes like *HAT4* and *HFR1*. Hence, mutation at the *TIR-NBS-LRR* gene to cause truncated version in the (*Arabidopsis constitutive shade-avoidance 1*) *csa1* mutant shows constitutive SAS responses (Faigón-Soverna *et al.* 2006). The *phyB* mutant in tomato increases susceptibility to insect herbivores, reduced (*PATHOGENESIS RELATED 1*) PR1 protein expression and susceptibility to blast fungus *Magnaporthe grisea* (Casal 2012)

3.4 *Biochemical modifications*

Shade-tolerant genotypes of rice maintain high ROS scavenging enzyme activity and water potential, whereas susceptible genotypes show membrane damage. Shade-tolerant varieties have been observed with enhanced superoxide dismutase, catalase activities, decreased malondialdehyde (MDA) content and peroxidase activity (Panigrahy *et al.* 2019) under low-light conditions. MDA is a lipid peroxidation product, and hence, reflects the extent of membrane damage under stressful conditions.

Reduced soluble sugar content under low-light is associated with osmotic regulation and maintaining reactive oxygen species and water potential of cells (Liu *et al.* 2012). Leaf exposed to EODFR showed higher activities of sucrose-phosphate synthase, the enzyme-linked with carbon export from leaves. Under low-light, decreased starch, amylose and sucrose content, unchanged ADP-glucose pyrophosphorylase (AGPase) activity, reduced activity of soluble starch synthase and increased starch branching enzyme activities in rice were observed. Low-light during grain filling results in decreased carbohydrate supply to the grain and starch synthase activity, thus affects grain filling. Improper grain filling and translocation to the grain results in decreased spikelet fertility. In rice later formed florets result in pollen sterility. Poor partitioning of dry matter to panicle result in low harvest index (Liu *et al.* 2012).

Low-light-associated decreased nitrogen (N) allocation to the panicles was seen by Liu *et al.* (2014). Decreased amount of nitrogen transport from culm and sheath to panicles results in increased N percentage in leaves and column-sheaths. This results in increase of development of leaves and culm-sheath under low-light conditions (Ren *et al.* 2003).

Low-light exposure from transplanting till booting increases the head rice yield and amylose content, but increase in chalky kernels and protein content (Ren *et al.* 2003). This was proposed to be due to the marked alterations in source-to-sink ratio. The biomass of sink organs such as fertile panicle and grains per panicle were significantly reduced. In addition to the decrease in the photosynthetic ability of the plant, the rate of seed set rate and 1000-grain weight were also markedly reduced. However, in the study of Panigrahy *et al.* (2019), there was no reduction in the 100-grain weight in Swarnaprabha after prolonged exposure to low-light.

4.   Hormonal regulation under shade

Prolonged shade leads to reduced branching, loss of erect stricture, early flowering, insect herbivory, and decreased spikelet fertility. Hypocotyl elongation is regulated by PIF-governed modulation of auxin biosynthesis, transporters and signalling genes. Inhibited leaf growth is resulted by the breakdown of cytokinins due to the expression of cytokinin oxidase stimulated by auxin. Reduced branching is resulted by the accumulation of abscisic acid in young buds. Reduced jasmonate and salicylic acid levels under shade result in decreased the defence responses and altered resource allocation between growth and defence (Yang and Li 2017).

In addition to phenomena such as photo- and grav-itropism, auxin transport and concentrations are important regulators of shade-induced stem elongation. The regulatory action of auxin is also imparted towards the elongation of primary root and reduction of lateral root formation under shade. This is explained by the reorientation of auxin transport in the root along with the redistribution of specific auxin efflux carrier protein. In roots, higher lateral transport of auxin, which occurs under shade, led to decreased net polar auxin transport. This results in reduction in lateral root formation and increased root primary growth. Increased root length was also one among the observed findings under low R/FR light in studies of Panigrahy *et al.* (2019). This was also supported by the lateral root phenotype of ATHB-2, which was rescued by exogenous indole acetic acid (IAA) (Morelli and Ruberti 2000). Involvement auxin in low-light-induced changes in root architecture and patterning as evident in

different phytochrome mutants also showed synergy to the above findings (Kumari *et al.* 2019). They have identified several genes from the light, hormone pathway including PIF4, *AUXIN RESPONSE FACTOR18 (ARF18)*, *TOC1* and others involved in light-intensity-mediated root development.

When the plants are exposed to shade, their defence system is challenged. This was demonstrated by studies of de Wit *et al.* (2013), as reduced salicylic acid (SA) and jasmonic acid (JA) induced defence pathway genes under shade. Severe repression of SA-responsive transcription factor and coactivator *NONEXPRESSER OF PR GENES 1 (NPR1)* and its phosphorylation was reduced under shade. JA-dependent disease resistance was also inhibited under low R/FR accompanied by the phytochrome inactivation.

Convergent role of ethylene pathway genes under flooded condition as well as under low R/FR light condition in controlling hypocotyl elongation response in *Arabidopsis* was demonstrated by studies of Das *et al.* (2016). Genome-wide expression analysis in seedlings grown in the above two conditions revealed that they share the major cluster of a positively and negatively regulated cluster of genes and transcriptome patterns for elongation of hypocotyl and petioles.

Brassinosteroid (BR)-responsive genes are expressed in both leaf and petiole during the shade avoidance response (SAS). The transcription factors BZR1 and PIF4 regulate target gene expressions. *BR-ENHANCED EXPRESSION* (BEE), and *BES1-INTERACTING MYC-LIKE* (BIM) positively regulate SAS responses. DELLA controls to reduce the expression of BR pathway genes by (*BRASSINAZOLE-RESISTANT 1)* BZR1 binding (Yang and Li 2017)

5. Molecular characteristics

5.1 *Genomic aspects*

Whole genome studies on mutants examining the collection of phenotypic traits was done using robotic technology (Nozue *et al.* 2015). Over-representation analysis of shade-responsive genes in a large collection of mutants identified at least three subgroups of shade responses, with each subgroup sharing separate and different pathways. Auxin pathway components were required for shade avoidance responses in hypocotyl, petiole and flowering time, and Jasmonic acid pathway components were found to be required only for petiole and flowering time responses (Nozue *et al.* 2015).

Wang *et al.*'s (2018) study on floral genes in rice grown under shade revealed that shade reduced the number of secondary branches in the panicle. Panicle degeneration and slower spikelet differentiation, and downregulation of chloroplast development genes were prominent developmental changes associated with shade stress. Suppressed expression of floral gene *Oryza sativa DNA BINDING WITH ONE FINGER* (*OsDof12*), *RICE FLOWERING LOCUS 1 (RFT1)*, and induction of expressions of *HEADING DATE (Hd1)*, *HEADING DATE 3A (Hd3a), EARLY HEADING DATE (Ehd1)* under shade was found using transcriptome sequencing in rice (Wang *et al.* 2018).

The enhanced rate of panicle emergence was found to be higher in shade-tolerant Swarnaprabha rice than that of Nagina 22 (Panigrahy *et al.* 2019). Additionally, seedling traits such as rootlet number and coleoptile length were discriminating characteristic in seedlings grown under simultaneous R + FR light. Expression pattern of *PHYTOCHROME INTERACTING FACTOR LIKE-13* (*PIL-13*) and Phytochrome B in Swarnaprabha and Nagina 22 were contrasting. Significant upregulation of ethylene and cytokinin pathway genes as well as *ETHYLENE RESPONSE ELEMENT BINDING PROTEIN-2* (*EREBP 2*), *MOTHER OF FLOWERING TIME1* (*MFT1*), *SHORT PANICLE 1* (*SP1*) genes were observed in panicles of Swarnaprabha grown under shade.

Microarray expression analysis in seedlings grown under flooded and shading conditions revealed a convergent genomic cluster of genes shared under these two conditions (Das *et al.* 2016). It was concluded from the study that *Arabidopsis* seedlings under shade stimulate the synthesis of auxin in the cotyledon. Upon polar transport to hypocotyl, it interacts with GA and BR, which coordinately regulated hypocotyl elongation.

Genomic expression analysis in *phyA phyB* double mutant identified 301 unique genes to be shade responsive. It revealed that major shade-responsive genes are antagonistically regulated by *PhyA* and *PhyB* in response to shade (Devlin *et al.* 2003).

Fabre *et al.* (2016) in their study identified a quantified trait locus qTSN4 in the near isogenic lines (NILs) in two genetic backgrounds, which affected flag leaf size, photosynthesis and panicle size irrespective of the environment. Further, this observation was emphasized under low-light conditions as qTSN4-NILs did not express low-light tolerance traits. Hence, it was concluded that qTSN4 may enclose promising locus specifically for limited light conditions.

5.2   *Circadian clock regulations*

Zhang *et al.* (2020) have recently identified two negative regulators of shade avoidance syndrome (SAS), which are components of the circadian clock, i.e. *PSEUDO-RESPONSE REGULATOR 5 (PRR5)* and *PRR7*. These two factors co-bind with the promotors of several PIFs (*PIF1, PIF3, PIF4* and *PIF5*, which show enhanced expression in low R:FR) on the promoters of target genes. Co-localization of PIFs and PRRs on the target genes, for example *PIF7*, may directly or indirectly regulate auxin signalling genes. Thus, the physical interaction of *TOC1/ PRR1* (which is a transcriptional repressor) with PIFs indicate the key role of clock in modulating plant adaptation, effective resource allocation during shade.

5.3   *Non-coding RNAs*

Next-generation genomics has widened our views on the non-coding RNAs including microRNA (miR), small interfering RNAs and long non-coding RNAs. Out of these, miRNAs have been shown to mediate several photomorphomorphogenic events including cotyledon opening and photoperiod-dependent flowering, which are reported in a few recent researches (Xie *et al.* 2017). Novel concepts of regulation of shade avoidance responses under shade demonstrate the degradation of miRNA biogenesis factor *HYPONASTIC LEAVES (HYL1)* but, with an active pool of phosphorylated protein, remains stable inside the nucleus. Degraded *HYL1* leads to the onset of gene silencing, and elicitation of shade avoidance responses and dephosphorylated form of *HYL1* lead to the reactivation of miRNA biogenesis and developmental switch to maximize light uptake (Achkar *et al.* 2018).

PIFs act as positive regulators of EOD-FR responses. Several PIFs repress transcription of miR156 directly on their promotors at their PIF-binding sites. Reduction of mature miR156 levels leads to a concomitant increase of its target *SQUMOSA PROMOTOR BINDING PROTEIN LIKE* (SPL) transcript abundance (Xie *et al.* 2017). Further genetic analysis showed that miR156 acts downstream to PIF5. Thus, miR156 is required for EOD-FR responses and mediates through downregulation of SPL genes and an increase of PIFs for a portion of low R:FR responses.

6.   Conclusion

A list of genes and their functions involved in optimizing different responses to low R:FR or natural shade are listed in table 1. Low-light-tolerant varieties are equipped with mechanisms to maintain a sustainable photosynthetic rate, effective antioxidants for ROS scavenging, which are not observed in the low-light susceptible genotypes. Among several strategies for the generation of low-light-tolerant varieties, studies on identifying the low-light-sensing promotor region, association mapping among different low-light-resistant varieties, application of different nutrients such as silica to cope the low-light plant phenotypes, plants with improved translocation and grain filling characteristics are promising. Hormonal regulations for SAS may vary among different tissue types, stages of development within plants and different species. Further studies in this respect would be significant in order to unfold the spatiotemporal regulation and crosstalk among different hormones for the mechanistic understanding of SAS. Although several links of control of circadian clock including PRRs for SAS have been discovered, the role of *COP1* and *ELF3* in controlling low R:FR stem elongation is not known. Further researches uncovering the portion of the skotomorphogenesis effect controlled by COPs and their roles in SAS in synchrony with controls of the circadian clock would be interesting. Despite recent findings of the involvement of miR156 in SAS, it was shown only for EOD-FR and part of SAS controlled by PIFs. It would be interesting to find the role of miR156 in SAS under the canopy, natural shade or dense planting conditions. Numerous studies collaterally indicate the statement that prolonged exposure to low-light is an abiotic stress for the plant leading to several morpho-physiological adaptations. Low-light-induced hypocotyl elongation and flooding have been shown to share transcriptomic patterns. Further, SAS is elevated in plants in warm environments, nutrient and water inputs being sufficient (Romero-Montepaone *et al.* 2020), which indicated that SAS can be elevated at warm temperatures. Similar studies with impacts of SAS on different abiotic or biotic stresses, with global aspects, would be interesting.

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