

REVIEW ARTICLE

Modulation of Phototropin Signalosome with Artificial Illumination Holds Great Potential in the Development of Climate-Smart Crops

Sunita Sharma¹, Sibaji K. Sanyal¹, Kumari Sushmita¹, Manisha Chauhan², Amit Sharma², Gireesh Anirudhan³, Sindhu K. Veetil¹ and Suneel Kateriya^{1,*}

¹Lab of Optobiology, School of Biotechnology, Jawaharlal Nehru University, New Delhi 110067, India; ²Multidisciplinary Centre for Advanced Research and Studies, Jamia Millia Islamia, New Delhi-110025, India; ³Integrated Science Education and Research Centre (ISERC), Institute of Science (Siksha Bhavana), Visva Bharati (A Central University), Santiniketan (PO), West Bengal, 731235, India

Abstract: Changes in environmental conditions like temperature and light critically influence crop production. To deal with these changes, plants possess various photoreceptors such as Phototropin (PHOT), Phytochrome (PHY), Cryptochrome (CRY), and UVR8 that work synergistically as sensor and stress sensing receptors to different external cues. PHOTs are capable of regulating several functions like growth and development, chloroplast relocation, thermomorphogenesis, metabolite accumulation, stomatal opening, and phototropism in plants. PHOT plays a pivotal role in overcoming the damage caused by excess light and other environmental stresses (heat, cold, and salinity) and biotic stress. The crosstalk between photoreceptors and phytohormones contributes to plant growth, seed germination, photo-protection, flowering, phototropism, and stomatal opening.

Molecular genetic studies using gene targeting and synthetic biology approaches have revealed the potential role of different photoreceptor genes in the manipulation of various beneficial agronomic traits. Overexpression of PHOT2 in *Fragaria ananassa* leads to the increase in anthocyanin content in its leaves and fruits. Artificial illumination with blue light alone and in combination with red light influence the growth, yield, and secondary metabolite production in many plants, while in algal species, it affects growth, chlorophyll content, lipid production and also increases its bioremediation efficiency. Artificial illumination alters the morphological, developmental, and physiological characteristics of agronomic crops and algal species. This review focuses on PHOT modulated signalosome and artificial illumination-based photo-biotechnological approaches for the development of climate-smart crops.

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1. INTRODUCTION

Light is one of the key environmental factors regulating the growth and development of plants and influencing crop productivity. In plants, it elicits different functions like phototropism, seed germination, circadian rhythm, chloroplast relocation, stomatal opening, and photomorphogenesis. To regulate various developmental and physiological processes in plants, there are several light-sensing proteins (photoreceptors) that are capable of perceiving and responding to different light conditions. These are Phytochrome (PHY), Cryptochrome (CRY), Phototropin (PHOT), and UVR8 [1] that sense and adapt to the diverse environmental cues and translate the information to signalling cascades for plant development [2]. Among the light conditions, quality and quantity of light are of utmost importance as prolonged exposure can damage plant parts, and specific cellular responses are acti-

vated or repressed by a particular wavelength of light. In plants and algae, red/far-red (600-800nm) light is sensed by PHY that exists in two interconvertible forms *viz.* red light-absorbing P_r form and far-red light-absorbing P_{fr} form. UV-B is sensed by UVR-8, a seven-bladed β -propeller photoreceptor using four intrinsic tryptophan residues as chromophores [3]. Blue light is sensed by CRYs and LOV containing photoreceptors- LOV histidine kinase (LOV-HK) and PHOT. CRYs consist of the N-terminal (PHR) domain homologous to DNA Photolyase and a C-terminal domain.

Blue light is responsible for multiple cellular responses in plants and other organisms. In various algae, blue light mediates developmental processes, phototaxis and eyespot development [4], photoprotection [5], growth and photosynthesis [6], gametogenesis [7], and surface adhesion [8]. In higher plants, blue light mediates chloroplast relocation, hypocotyl growth inhibition, phototropism, growth and photosynthesis, circadian clock, leaf expansion, stomatal movement, and photomorphogenesis (extensively reviewed in other studies [9, 10]). It regulates photoprotection, photosyn-

*Address correspondence to this author at the Lab of Optobiology, School of Biotechnology, Jawaharlal Nehru University, New Delhi 6 110067, India; E-mail: skateriya@jnu.ac.in

thesis, phototaxis, gene expression, and biofilm formation in cyanobacteria [11-14]. The current review emphasizes the role of PHOT, a blue-light photoreceptor, in various physiological processes and stress tolerance in plants. PHOT functions in coordination with other photoreceptors in various physiological processes. PHOT exists in two interconvertible forms, consists of two Light Oxygen Voltage (LOV) domains (a type of PER-ARNT-SIM domain that binds to flavin mononucleotide (FMN) as a chromophore) and a serine/threonine kinase domain [15-17]. PHOT affects several critical signalling pathways involving phytohormones [18] and metabolite biosynthesis [19, 20]. Recent advances in technology have offered several strategies in photoreceptor engineering like alteration in gene sequence or expression level through genome editing and application of synthetic biology tools like cluster regularly interspaced short palindromic repeat and CRISPR-associated protein (CRISPR-Cas), transcription activator-like effector nucleases (TALEN), zinc finger nuclease (ZFN), *etc.* for crop improvement [21-24]. Various advanced technological approaches of photoreceptor engineering for crop improvement will also be discussed in detail.

Crop yield and quality are strongly influenced by various environmental conditions and gene constitution. The alteration in the genetic make-up of different crop species had been tried using various breeding strategies to improve crop yield [25]. In agriculture, researchers mainly focus on regulating various features of crop varieties such as increased shelf life, early ripening, fruiting, fruit size and quality, high plant yield, and increased stress resistance. In plants, various physiological processes are regulated through photoreceptors sensing different light intensities [26]. Both high and low light intensities influence crop yield, like Excess Light (EL) exposure causes photodamage and the very low light intensity decreases the rate of photosynthesis, as reviewed extensively in other studies [2, 27]. Thus, light quality, intensity, and duration influence both plant growth and yield, a very critical factor of agricultural productivity. This review discusses the effect of artificial illumination using Light-Emitting Diode (LED) technology in agriculture regarding the regulation of crop yield and photosynthesis [28]. In algae and crops, this technology could be used to modulate various important metabolic pathways involving photosynthetic efficiency [29-32], plant development [33, 34], fruit quality and size [28, 35-40], metabolite accumulation [41-44], and stress tolerance [45-48]. We have also summarized the applications of other photo-biotechnological approaches and LED illumination for the modulation of various photoreceptor signalling pathways that result in the production of climate-smart crops in agriculture.

2. PHOTOTROPIN REGULATES VARIOUS PHYSIOLOGICAL RESPONSES IN PLANTS

PHOT is well conserved among algae and plants. However, it is absent in the cyanobacterial group, though possesses a notable number of LOV domain proteins, due to which it was anticipated that these organisms might contain PHOT [49]. In *Synechocystis sp.* PCC 6803, *slr0359* gene and in *An-*

abaena sp. PCC 7120, *all2875*, *alr3170*, and *alr1229* genes encode for LOV domain proteins [50]. In *Synechocystis sp.* PCC 6803, LOV domain protein (Slr0359) encoded by gene *slr0359* is consisting of cGMP phosphodiesterase Adenylcyclase FhIA (GAF), Gly-Gly-Asp-Glu-Phe (GGDEFF), and Glu-Ala-Leu (EAL) domains beside LOV domain [51]. LOV domain proteins (All2875 and Alr3170) encoded by *al-12875* and *alr3170* are GGDEF domain-containing proteins possessing conserved cysteine, bind to FMN, and exhibit photocycle similar to PHOT [52]. LOV domain proteins in cyanobacteria contain diverse effector domains like GGD-EFF, GAF, EAL, and histidine kinase (HK). LOV domain containing HK is also present in algal groups, and in *O. tauri*, it regulates the circadian clock [53, 54]. Therefore, LOV domain proteins have been seen to be conserved throughout the green lineage during evolution.

PHOT senses the UV-A/blue region (370-450 nm) of the light spectrum. Structurally, PHOT consists of two photoactivated LOV (LOV1 and LOV2) domains at the N-terminal region; the serine/threonine kinase domain at the C-terminal region with a J- α helix present between LOV2 and kinase domain. LOV domain binds noncovalently to FMN as a chromophore in the dark and exists as an inactive singlet state LOV₄₄₇. In the dark, the kinase domain remains inactive in contact with the LOV2 domain. Blue light illumination activates singlet state LOV₄₄₇ that decays into short-lived triplet state LOV₆₆₀, which gets converted into photoactivated state LOV₃₉₀. Activation of the LOV domain converts noncovalent interaction between flavin and LOV domain into covalently bound flavin-cysteinyl adduct, leading to a conformational change in J- α helix [55]. N414 and Q513 residues of the active site of the LOV domain affect solvent accessibility and the electrostatic nature of FMN, which controls the time for completion of the photocycle. Mutation of these two residues slows the photocycle by regulating the deprotonation of FMN and breaking the bond between FMN and cysteine of the LOV domain [15-17]. The light-dependent unfolding of the J- α helix is induced by a conformational transition in conserved glutamine residue of flavin binding pocket through the dynamic shifting in main β -sheet of LOV domain core and A' α helix [56, 57]. In higher plants, LOV2 domain C-terminus (J- α helix) unfolding and N-terminus (A' α helix) extension and deletion regulate activation of the kinase domain. Extension of A' α helix causes attenuated structural change in J- α helix and deletion of A' α helix eliminate the J- α helix unfolding [58]. The conformational change in the J- α helix and extended linker region between J- α helix and kinase induce a change in the tertiary structure of the kinase domain, which regulates different photo-physiological processes [59-61]. The physiological role of PHOT in higher plants is discussed below.

2.1. Growth and Photosynthesis

PHOTs function in different physiological processes like leaf expansion, stomatal opening, chloroplast repositioning, pigment accumulation, and phototropism that enhance photosynthesis and growth [6, 10]. In tomato, blue light exposure

increases dry matter, chlorophyll, flavanol, leaf area, and the number of leaves [62]. In *Arabidopsis*, *phot1* single mutation and *phot1phot2* double mutation lead to leaf curling which causes a decrease in photosynthesis than the wild type due to CO₂ fixation in photosynthetic active radiation (PAR) [63]. Moreover, stomatal opening and chloroplast movement also get impaired in *phot1* mutant and *phot1phot2* double mutant, which cause a decrease in photosynthesis by impaired transpiration, CO₂ fixation, chlorophyll and carotenoid accumulation, photodamage, excessive light capture, and an increase in the abscisic acid (ABA) [63-65]. PHOTs also contribute to the optimization of photosynthesis in low-light environments like dense forests, canopies, and shaded areas [66].

2.2. Phototropism

In *Arabidopsis*, blue light induces FMN-binding and auto-phosphorylation of the kinase. Non-phototropic hypocotyl 1 (NPH1) is reported to have a main role in root and hypocotyl curvature and was later renamed as PHOT1. The action spectrum for phototropism in *Arabidopsis* looks similar to NPH1. Therefore, NPH1 was suggested to be a blue light-controlled auto and phosphorylating serine/threonine kinase that functions in phototropism [67]. In *Arabidopsis*, the *phot1* mutant does not show phototropic movement at a low light intensity, but it shows normal phototropic movement at a high light intensity, indicating the presence of another photoreceptor, *i.e.*, NPH1-LIKE (NPL1), later renamed as PHOT2 for high-intensity phototropic movement in plants. However, *phot1phot2* double mutant failed to show phototropism even at high light intensity [67]. PHOT2 functions exclusively at a high light intensity, whereas PHOT1 functions both in low and high light intensities. Therefore, in *Arabidopsis*, PHOT1 regulates negative root curvature and positive hypocotyl curvature in low light intensity, but at a high light intensity, PHOT1 and PHOT2 cumulative response regulates phototropism [66, 68].

2.3. Chloroplast Repositioning

PHOTs control chloroplast repositioning, playing an important role in photoprotection in crop plants. In *Arabidopsis*, *npl1* (*phot2*) mutant does not show chloroplast repositioning in strong light, indicating that PHOT2 is important in mediating chloroplast avoidance response in strong blue light exposure. In low light intensity, *npl1* mutant shows normal chloroplast accumulation response, but *npl1/npl1* double mutant is impaired in both chloroplast avoidance and accumulation response [65, 67]. Therefore, PHOT1 (NPH1) and PHOT2 (NPL1) function redundantly during chloroplast accumulation response in low light intensity [67].

2.4. Stomatal Opening

PHOTs regulate stomatal movement, essential for gaseous exchange during photosynthesis in plants. Stomatal opening is controlled through the surrounding guard cells, and these guard cells open in response to different stimuli, including blue light. PHOTs regulate stomatal opening

through phosphorylation of serine and threonine residues at the C-terminus of H⁺ATPase in *Vicia faba* (VHA1 and VHA2). The blue light stimulus causes the accumulation of K⁺ ions in guard cells in response to negative potential generated through phosphorylation of H⁺ATPase in the plasma membrane [69]. The activity of H⁺ATPase is enhanced in response to blue light exposure by the binding of protein 14-3-3 with phosphorylated H⁺ATPase for the optimization of photosynthesis [69]. The EARLY FLOWERING 3 (ELF-3) protein is a negative regulator of stomatal opening and interacts with H⁺ATPase. Mutation in *elf-3* causes stomata to remain open and increase H⁺ATPase activity in blue light [70]. Moreover, ROOT PHOTOTROPISM 2 (RPT2) protein consists of N-terminal broad complex, tram track, bric a' brac/poxvirus, and zinc finger (BTB/POZ) domain and a coiled-coil C-terminal domain that is important for PHOT1 signalling. It interacts with the N-terminal domain of PHOT1 and acts as signal transducer for PHOT in mediating stomatal closure and other functions by interacting with other proteins like COP1 (CONSTITUTIVELY PHOTOMORPHOGENIC 1) and PHYs [71, 72]. In *Arabidopsis*, a single mutant of *phot1* or *phot2* showed a decrease in stomatal opening response compared to the wild type, whereas in *phot1/phot2* double mutant, stomata remained shut, suggesting that PHOT1 and PHOT2 function redundantly in stomatal opening [69].

2.5. Photomorphogenesis

PHOTs inhibit hypocotyl elongation in dark-grown seedlings after blue light exposure, known as the photomorphogenic response in plants. The inhibition of hypocotyl elongation is divided into two phases. The first phase is rapid, transiently controlled through PHOT, and occurs within 30 sec of illumination with blue light, whereas the second phase is slow, persistently controlled through CRYs (CRY1 & CRY2), and occurs after 30 minutes to 120 minutes of blue light exposure [66]. Membrane depolarization through anion channel activation within seconds of blue light exposure is the initial response for CRY-regulated growth inhibition, and it replaces the PHOT rapid growth inhibition response [73]. Membrane depolarization and slow phase inhibition response are delayed in *nph1cry1* mutant in comparison to *cry1* mutant, indicating that CRY controlled inhibition response is influenced by blue light activation of PHOT. CRY1 and CRY2 function non-redundantly for hypocotyl growth inhibition and membrane depolarization [73]. In crops, photomorphogenic responses play a very important role in seed germination, plant growth, and de-etiolation. In addition to PHOT, other photoreceptors like PHYs in maize function in mesocotyl growth inhibition and C4 photosynthetic differentiation photomorphogenic responses [74].

2.6. Photoreceptor-Mediated Thermomorphogenesis

Elevation in ambient temperature results in morphological changes (hypocotyl, petiole, root elongation, and hypostatic response) in plants termed thermomorphogenesis. Phytochrome Interacting Factor 4 (PIF4), a transcription factor,

is a major signalling component of thermomorphogenesis [75]. Among photoreceptors, PHYA/B is well known as a thermosensor and promotes thermomorphogenesis by regulating PIF4 activity, as reviewed in other studies [76-79]. CRY1 suppresses the PIF4 activity in blue light and thus the thermomorphogenesis [79, 80]. UVR8 inhibits thermomorphogenesis in UV-B light [79, 81]. PHOT also perceives temperature and affects the temperature-dependent lifetime of the photoactivated chromophore state in PHOT [82]. The lifetime of activated LOV2 lengthens at a lower temperature (5°C), leading to cold-avoidance response through re-positioning of chloroplasts towards the periphery in *Marchantia polymorpha* [82]. Although the role of PHOT in photomorphogenesis is well established, its role in thermomorphogenesis is not yet reported. Recently, physical interaction between PHYA and PHOT1 at the plasma membrane was reported in *Physcomitrella patens* [83]. This indicates the crosstalk among photoreceptors, suggesting the possibility where PHOT may indirectly contribute to thermomorphogenesis through PHY.

2.7. Metabolite Accumulation

Blue light in combination with red light increases the production of pigments like xanthophyll, carotenoids, chlorophyll, glucosinolates, macro and micronutrients, and secondary metabolites content in crop plants. It has been reported in crops like broccoli (*Brassica oleracea* var. *Italica*) and kale (*Brassica oleracea* var. *acephala*) that PHOT in combination with other blue light receptors increases the chlorophyll amount after small blue light exposure with red light [29, 63, 84]. Tomato plants exposed to 12% blue light in combination with 88% red light increase chlorophyll and secondary metabolites like flavanols content as compare to tomato plants with 100% red light exposure [62].

The role of PHOT is well established in *Arabidopsis thaliana*. It regulates chloroplast relocation, stomatal opening [63], phototropism [85], leaf flattening, photomorphogenesis, and de-etiolation [29, 86] in *Arabidopsis thaliana* and *Oryza sativa*. To find the molecular partners of PHOT involved in various responses in rice (*Oryza sativa*) and soybean (*Glycine max*), the STRING database was used. Some of the key proteins are discussed here (Fig. 1), and detailed information is provided in Table 1. Predictions indicated that PHOT could putatively interact with several other photoreceptors such as PHYs, CRYs, UVR8, and signalling proteins for regulation of various physiological functions in different plants like rice (monocot) and soybean (dicot) (Fig. 1). PHY and CRY (OsPHYA, OsPHYB, and OsCRY1, OsCRY2) in rice interact with proteins like GIGANTEA (GI) and mediate flowering [87]. GI is a nuclear protein highly conserved in seed plants like *Oryza sativa* (OsGI) [88] and *Glycine max* (GmGI1, GmGI2, GmGI3) [89]. Some other photoreceptor proteins like CRY3 and Deoxyribodipyrimidine Photolyase (PhrB) function to repair local DNA lesions and photoreactivation mechanism [90, 91]. Transcription factor PIF is involved in PHY signalling and freezing tolerance [92]. Proteins like Sugars Will Eventually

Be Exported Transporter 6B (SWEET6B) and Monosaccharide transporter 6 (MST6) are suggested to be sugar transporters that might be involved in seed filling, germination, and photosynthesis in crop plants through interaction with other photoreceptors like PHOT and CRY [93-95]. In rice, coleoptile phototropism 1 (CPT1), the homolog of Non-phototropic hypocotyl 3 (NPH3), induces phototropism through auxin redistribution in the plants [96]. COP1, an E3-ubiquitin ligase, interacts with UVR-8 to regulate various photomorphogenic responses in plants [97]. Proteins like SUPPRESSOR OF PHYA (SPA) and SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 (SOC1) are involved in photoperiodic flowering and flowering meristem activity, respectively [98, 99]. In addition to this, several other proteins like Adagio, HEADING DATE (HD2 & HD3) and pseudo-response regulator-7 (GHD7), Rieske, RPT (RPT2 & 3), TIMELESS C (TMC) were observed in the PHOT interactome, indicating their involvement in the regulation of PHOT mediated physiological functions. Therefore, PHOT works with other photoreceptors in an integrated manner for the regulation of different physiological processes. PHOT is involved in various important physiological functions contributing to plant growth and development. Apart from that, PHOT also functions in plants to sense and adapt to diverse environmental conditions influencing plant growth and yield, which is explained in detail below.

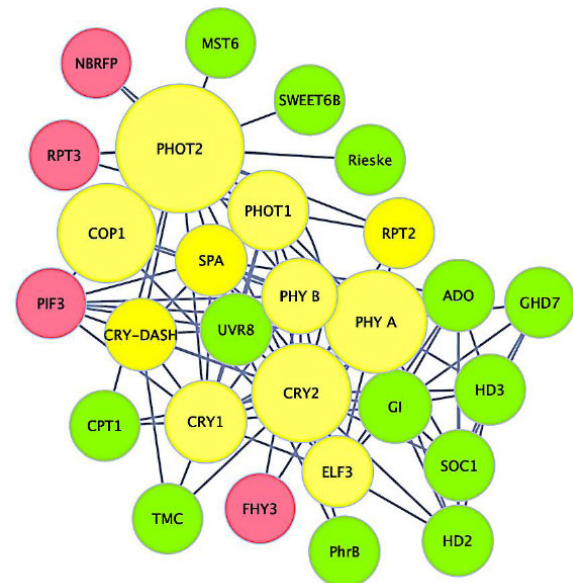


Fig. (1). Photoreceptor interactome analysis in *Oryza sativa* (rice) and *Glycine max* (soybean). The protein-protein interaction network has been predicted in String version 11 (<https://string-db.org/>) and visualized using Cytoscape 3.7.2. with Compound Spring Embedder (CoSE) layout. The network analysis was performed using the betweenness centrality algorithm, where the sizes of nodes (circles) indicate betweenness values. Proteins shown by dark red colour represent proteins interacting with Phototropin in soybean, light green colour in rice, and yellow colour in both rice and soybean. (A higher resolution / colour version of this figure is available in the electronic copy of the article).

Table 1. Biochemical properties and role of proteins interacting with Phototropin (PHOT) in different physiological processes in *Glycine max* and *Oryza sativa*.

Proteins in Interactome	Interacting Proteins	Biological Functions of the Interacting Proteins	References
CRY2*	Cryptochrome 2	Hypocotyl growth inhibition, de-etiolation, flowering, leaf senescence	[100, 101]
CRY1*	Cryptochrome 1	Hypocotyl elongation inhibition, seedling development, photoperiodic flowering	[102, 103]
CRY-DASH*	DASH (Drosophila, Arabidopsis, Synechocystis, Human)-type Cryptochrome, (CRY3)	Transcriptional regulation, repair of unwounded DNA region	[90, 104]
COP1*	CONSTITUTIVE PHOTOMORPHOGENESIS 1	Regulate photomorphogenesis, stress tolerance, shade avoidance response, hypocotyl and leaf petiole elongation	[97]
PHYA*	Phytochrome A	Plant architecture, grain yield, suppression of internode elongation, root gravitropism, leaf de-etiolation, fertility, long day flowering	[105-108]
PHYB*	Phytochrome B	Leaf area, stomatal density, drought tolerance, light period related repression of flowering, fertility regulation, suppression of internode elongation, fertility, seed germination, root gravitropism, leaf de-etiolation	[107, 109, 110]
ELF3*	E74 LIKE ETS TRANSCRIPTION FACTOR 3 like protein	Regulation of flowering time, H ⁺ ATPase, stomatal opening, circadian rhythm	[70, 111]
PHOT2*	Phototropin 2	Phototropism, chloroplast avoidance response, stomata opening, viral defense	[112-114]
PHOT1*	Phototropin 1	Phototropism, chloroplast accumulation response, stomata opening, viral defense	[112-114]
SPA*	SUPPRESSOR OF PHYA	Photoperiodic flowering, photomorphogenesis	[98, 115]
RPT2*	ROOT PHOTOTROPISM PROTEIN 2	Phototropism, stomatal opening	[116]
FHY3 [#]	FAR-RED ELONGATED HYPOCOTYL 3	Chlorophyll biosynthesis, growth and development, circadian clock	[117-119]
PIF3 [#]	PHYTOCHROME INTERACTING FACTOR 3	Phytochrome signalling, freezing tolerance, anthocyanin biosynthesis	[92, 120]
RPT3 [#]	ROOT PHOTOTROPISM PROTEIN 3	Disease resistance	[121]
NBRFP [#]	NAD(P)-BINDING ROSSMANN-FOLD SUPERFAMILY PROTEIN	Role in secondary metabolism, developmental pathway	[122]
TMC	TIMELESS C, Timeless domain containing protein	Circadian rhythm	[123]
Rieske	Rieske [2Fe-2S] domain-containing protein	Increases CO ₂ assimilation and photosynthesis	[124]
CPT1	COLEOPTILE PHOTOTROPISM PROTEIN 1	Phototropism and lateral translocation of auxin	[96]
SWEET6B	SUGARS WILL EVENTUALLY BE EXPORTED TRANSPORTERS 6B, bidirectional sugar transporter	Involved in sugar efflux and uptake across the plasma membrane, resource allocation, plant defense	[93, 94]
MST6	MONOSACCHARIDE TRANSPORTER 6, SUGAR TRANSPORT PROTEIN	Involved in active uptake of hexoses by sugar-proton symport, transport glucose, fructose, mannose, galactose, xylose, and ribose	[94, 95]
UVR8	Putative UV B-RESISTANCE 8 protein	Photosynthesis, biomass production, photomorphogenesis, hypocotyl growth inhibition, circadian clock, secondary metabolite production	[97, 125]
ADO3	ADAGIO-LIKE PROTEIN 3, a component of an E3 ubiquitin ligase complex	Circadian clock	[126]
GI	Protein GIGANTEA	Circadian rhythm, photoperiodic flowering, herbicide, cold and drought tolerance	[127]
HD2	HEADING DATE 2	Heading date, plant height	[128]
HD3	HEADING DATE 3	Flowering, heading date	[129]
GHD7	PSEUDO-RESPONSE REGULATOR-7 like protein	Plant height, grain yield, adaptation	[130]
PhrB	DEOXYRIBODIPYRIMIDINE PHOTOLYASE domain protein	Photoprotection	[91]
SOC1	SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1	Floral meristem activity	[99]

*-indicate proteins found to interact with PHOT in both *Glycine max* and *Oryza sativa* using String program.

[#]-indicate proteins found to interact with PHOT only in *Glycine max* and without # for proteins found to interact with PHOT only in *Oryza sativa* using String program.

3. PHOTOTROPINS ARE INVOLVED IN STRESS RESPONSES IN PLANTS

Plants are sessile organisms, and hence, there is a strong influence of environmental factors on plant growth and development. To sense various environmental cues efficiently, plants have adapted different signalling pathways that convert information perceived from external cues to affect various physiological processes. Plants respond to diverse environmental conditions (heat, cold, salinity, and light) via light-sensing proteins called photoreceptors [2]. PHOTs, in coordination with other photoreceptors like CRYs and PHYs, are involved in the perception and modulation of various physiological processes in response to external cues.

3.1. Light Stress

Excess light causes photo-oxidative damage and the formation of ROS (Reactive Oxygen Species) in the plants [131]. To avoid photo-oxidative stress, different plants and algae have evolved photoreceptors to sense excess light exposure. PHOT is one of the major photoreceptors in algae and plants, involved in many adaptive responses like chloroplast avoidance response, non-photochemical quenching, and carotenoid biosynthesis (extensively reviewed in [132]). *Arabidopsis* possesses two *phot* genes, encoding PHOT1 and PHOT2. In low light conditions, both PHOT1 and PHOT2 control chloroplast accumulation response, and during excess light conditions, PHOT2 shows chloroplast avoidance response to avoid photo-oxidative stress in high-intensity blue light [133]. In fern *Adiantum capillus-veneris*, PHOT2 is important for chloroplast avoidance response against strong blue light [134]. In *Marchantia polymorpha*, a liverwort, single copy *phot* gene mediates chloroplast avoidance response in strong blue light for protection from photo-damage [135]. *Chlamydomonas reinhardtii* possesses a single *phot* gene involved in modulation of gene expression of enzymes for Light-Harvesting Complex (LHC) proteins, chlorophyll, and carotenoid biosynthesis upon light exposure [136]. In *Adiantum capillus-veneris*, *Physcomitrella patens* (moss), and *Mougeotia scalaris* (a green alga), PHOT mediates chloroplast avoidance response in both blue and red light. The photo-adaptive response is reversed using far-red light, indicating the role of a red-light photoreceptor, PHY. The photophysiological response is controlled by a chimeric photoreceptor having both the LOV domain and PHY domain, called Neochrome (NEO). It consists of a PHY domain binding bilin chromophore at N-terminus and a full-length PHOT at the C-terminus. Photo-adaptive responses in red and blue light are modulated by four NEO encoding genes in *Physcomitrella patens* [137]. In addition to PHOT, other photoreceptors like UV-B, PHYs, CRYs, and photolyase also contribute to photoprotection in the strong light environment. PHOT-mediated photoprotection in algae and plants is discussed in the next section.

3.2. Heat and Cold Stress

Plants exposed to adverse temperature conditions display diverse changes in important signalling proteins and en-

zymes [138]. Various thermosensory molecules like PHYs, CRYs, PHOTs contribute to temperature tolerance in plants. In plants like *Adiantum* and *Arabidopsis*, PHOTs regulate light-induced chloroplast relocation in a temperature-dependent manner [82, 139]. In fern gametophyte, chloroplasts accumulate along the periclinal wall at 25°C temperature in low light intensity, whereas PHOT2 induces chloroplast shifting from periclinal to an anticlinal position called cold positioning response, and this response is enhanced under high-intensity white light [139]. Recently, it has been reported in *Marchantia polymorpha* (a bryophyte) that chloroplast relocation is dependent on transitional light intensity and not on intrinsic PHOT level. Overexpression of PHOT decreases the transitional light intensity, as it occurs during cold positioning response, but PHOT endogenous level remains the same [140]. In addition to PHOT, other photoreceptor proteins like PHYs and CRYs, are also helpful in plants for adapting to diverse temperature conditions [82, 141, 142]. PHYB perceives temperature through the thermal reversion from the active Pfr (far-red light-absorbing) state to the inactive Pr (red light absorbing) state. Exposure of *Arabidopsis* seedlings to a warm environment increases the thermal reversion and reduces the level of active Pfr-Pfr dimer of PHYB and associated nuclear bodies in plant cells even in day-light time [141]. PHYB acts as a thermo-sensor, associated with the promoter of important thermo-morphogenetic genes in a temperature-dependent manner over the night time [140]. Under a low R/FR light ratio, a decrease in PHY activity has been linked to an increase in cold acclimation in plants. In low-temperature conditions, freezing tolerance is achieved through increased expression of CRT/DRE BINDING FACTOR (CBF) family of proteins (CBF1,2,3), resulting in up-regulation of Cold-Responsive genes (COR) containing CBF regulated promoter [143]. PHYB and two PIFs (PIF4, PIF7) repress freezing tolerance and CBF pathways during the long day condition. The high transcript level of PIF4 and PIF7 during long-day warm conditions downregulates the CBF pathway [144], suggesting the role of PHY as a connection point in the light and temperature signalling in plants [145]. High temperature modulates the gene expression for heat shock proteins (HSPs) via the PHY-dependent pathway. In rice, *phyAphyB* double mutation results in alteration of gene expression for HSPs, leading to impaired pollen and anther development process [146]. CRY has been reported to suppress auxin synthesis and induce several morphological changes in plants under heat stress through interaction with PIF4 [80]. In *Arabidopsis*, CRYs also play role in cold acclimation through regulation of Elongated Hypocotyl 5 (HY5), COP1, and Z-box (ATACGTGT; a likely Z-DNA forming nucleotide sequence), which is mediated by CRYs through interaction with other photoreceptors and signalling proteins [147]. Therefore, plants might involve an integrated signalling mechanism for heat and cold tolerance however, the details about the signalling mechanism remain to be studied.

3.3. Drought Stress

Drought is considered to be one of the most critical factors for crop productivity [148]. PHOT functions in plant sur-

vival under water-deficient conditions through influencing the root architecture and increasing root growth to increase water absorption in dry soil. PHOT1 expresses in the root elongation zone of the primary and lateral root of etiolated *Arabidopsis* seedlings and mediates negative phototropism in root in relation to light intensity [114]. It is expressed in the upper shallow portion of the root where soil dryness is severer and blue light intensity is higher. In *A. thaliana*, plants with *phot1* mutation showed less root growth efficiency and drought tolerance in dry conditions in comparison to wild-type plants [149]. PHOT also functions in light-mediated leaf heliotropism to avoid heat and drought stress in high light intensity environmental conditions (as reviewed in a study [150]). PHOTs, in combination with other photoreceptors like PHYs, CRYs, are involved in the stomatal opening, leading to transpiration regulation in plant cells [69]. PHYs function in seed germination, leaf area, stomatal density and transpiration, and regulation of drought-responsive gene expression to increase drought tolerance in plants [109, 151-153]. ABA plays a very important role in drought tolerance, and PHY regulates the metabolic expression level of ABA in the cell [154]. CRY acts in combination with PHOT for drought stress tolerance [155]. In *Arabidopsis*, plants with *cry1cry2* double mutation were more tolerant to drought stress in comparison to wild type, and plants showing overexpression of CRY (CRY1-ovx) display higher transpiration as compared to wild type (CRY1) plants. This is due to COP1, the repressor of stomatal opening acting downstream of CRY [156, 157]. CRY also influences ABA metabolism in plants. In *Arabidopsis*, transgenic plants overexpressing wheat TaCRY1 and TaCRY2 show less drought tolerance to osmotic stress and ABA treatment [158]. In addition to that, its interaction with various stress-related genes like LATE EMBRYOGENESIS ABUNDANT PROTEIN 4-1 (LEA4-1), ASCORBATE PEROXIDASE 1 (APX1), NITRITE REDUCTASE 1 (NIA1), and DEHYDRIN FAMILY PROTEINS (RAB18) in *Brassica napus* has been reported to increase drought tolerance [159]. Therefore, the molecular mechanism of drought tolerance in plants is still unclear because its regulation depends on a number of factors like ABA, other hormones, and the interaction of different photoreceptors like CRYs, PHOTs, and PHYs.

3.4. Salt Stress

Excess light and heat stress accompany the salt stress leading to lower water potential and accumulation of mineral nutrients in plants. Blue light has been reported to antagonize the salt stress-mediated ABA-induced responses like stomatal closure and photosynthetic growth, suggesting the role of blue light photoreceptors in salt stress tolerance [160]. In *Physcomitrella patens* (bryophyte), PHOT works in combination with 14-3-3 protein by regulating H⁺ATPase and hence control the stomatal opening and ion channels to maintain the ionic balance in plant cells [65, 161]. In addition to PHOT, other photoreceptors like PHY, CRY, also contribute significantly to salt stress tolerance. Drought and salt tolerance share several common physiological changes due to solute accumulation. In *Arabidopsis*, plants overex-

pressing wheat CRYs (TaCRY1 and TaCRY2) show less salt tolerance in comparison to wild-type (CRY) plants, and also plants overexpressing TaCRY1 are observed to be more sensitive than plants overexpressing TaCRY2 [158]. In addition, sweet sorghum plants with *cry1* mutation show great germination and salt tolerance in seedlings, whereas plants overexpressing SbCRY1 show higher sensitivity to salt stress in comparison to wild-type plants. CRY mediates salt tolerance through LONG HYPOCOTYL 5-ABCISSIC ACID INSENSITIVE 5 (HY5-AB15) regulation, inducing expression of RD29A and RD22 ABA [159, 162]. The PHY action reduces the salt tolerance in plants after red light treatment through reduced expression of salt-tolerant (STO) protein. STO interacts with other important signalling proteins like HY5 and COP1 [163, 164]. Therefore, salt stress tolerance is regulated through the integrated signaling mechanism involving various photoreceptors and phytohormones like ABA, but the detailed pathway is not known so far.

3.5. Biotic Stress

Light is very important for plant growth and development in diverse environmental conditions. It also has a significant role in cell death and activation of several defense responses against viruses and various pathogens in plant cells [165, 166]. In *Arabidopsis*, resistance to the Turnip crinkle virus (TCV) is regulated by a number of genes encoding proteins like lipase (EDS1 and PAD4), a member of the MATE transporter family (EDS5), through SID2 dependent Salicylic acid (SA) pathway [167]. However, the expression of TCV induced hypersensitive response (HR) and pathogenesis-related (PR) genes are not affected through mutations in the SA pathway, suggesting the SA independent regulation of this response. TCV resistance is controlled through HRT and an R protein consisting of coiled-coil, nucleotide-binding, and leucine-rich repeat domain [168]. However, this HRT protein requires a recessive allele of an unidentified locus *rrt* for resistance against TCV [167]. Plants after inoculation with TCV accumulate SA and activate the defense genes expression under the influence of HRT and *rrt* [167, 169], whereas plants deficient in HRT produce symptoms like crinkled leaf appearance that leads to plant death due to systemic spread of viral infection [169]. The HR and PR-1 induced gene expression is not dependent on the SA pathway and *rrt* like resistance response. PHOT2 with CRY2 confers stabilization of HRT protein. However, CRY1 and PHOT1 play an important role in HRT resistance but without influencing HRT stabilization. Protein HRT, with CRY2 and PHOT2, interacts with an E3 ubiquitin ligase, COP1, and inhibits proteasomal mediated degradation of HRT that provides resistance in blue light against TCV. Therefore, CRY2 and PHOT2 restore HRT levels in plant cells through negative regulation of COP1 [113]. In addition to this, PHY also has a role in providing defense against pathogens. Plants with a mutation at either *phyA* or *phyB* site show the impaired response of cell death localized to pathogen entry site called hypersensitive response (HR) [170]. Plants having a mutation in *phyA* and *phyB* also show impaired expression of SA induced PR genes [171]. The impact of light ex-

posure and photoreceptors on plant defense and photomorphogenesis has already been reviewed in previous studies [172], however, understanding the detailed molecular mechanism needs further research. Thus, PHOTs are not only involved in plant growth and development but also help plants to survive and grow in diverse environments including biotic stress.

It suggests the role of light in the regulation of plant growth, physiology, and survival through different photoreceptors, sensing different light intensities in varying environmental conditions. However, different light parameters like quality, quantity, and duration influence plant yield, like low light decreases the photosynthetic rate, and excess light exposure causes the photo-oxidation of the photosynthetic machinery. Therefore, plants adopt various photoprotection mechanisms involving different photoreceptors like PHOTs, CRYs, PHYs, and UVR8 to mitigate the photodamage effects in plants. PHOT functions in combination with other photoreceptors in different photoprotection mechanisms are discussed below in detail.

4. PHOTOTROPIN MEDIATES PHOTOPROTECTION IN ALGAE AND PLANTS

Light is essential for performing various functions like phototropism, photomorphogenesis, etc., playing an important role in enhancing the crop yield. However, excess light produces ROS (reactive oxygen species), causing damage to photosynthetic apparatus and photo-oxidation of chlorophyll in algae and plants [131]. To cope up with the detrimental effects of excess light, plants have adapted the photoprotective mechanism against regulation of excess light absorption by chloroplast avoidance response and dissipation of excess absorbed light in the form of energy (qE) through NPQ (non-photochemical quenching) and by increasing zeaxanthin synthesis [173]. In plants, photoprotection is regulated through an integrated signalling pathway involving several photoreceptors like CRYs, PHOTs, UVR8, and PHYs that mitigate photodamage through different photoprotective mechanisms. PHOTs are functionally conserved across different green lineages like algae and plants for regulating light-induced movements in coordination with other photoreceptors. In *Chlamydomonas*, PHOT functions in the regulation of phototaxis, in combination with another photoreceptor Channelrhodopsin (ChR1 and ChR2) [4]. Moreover, PHOT is also responsible for the accumulation of LHCSR3 protein, qE, in response to high light intensity in algae [6] and different photoprotection mechanisms like avoidance, scavenging, and quenching mechanism in higher plants. Blue light-induced PHOT activity work in combination with chloroplast signalling for photoprotection, suggesting photoreception and photosynthesis work in a coordinated manner for adaptation in high light intensity conditions [6, 133]. CRYs mediate expression of EARLY LIGHT INDUCED PROTEINS (ELIP1 & ELIP2) encoded by *eli1* and *eli2* genes in *Arabidopsis* on excess light exposure, but its detailed mechanism of functional regulation is not yet confirmed [174]. It has been reported in blue-green algae that HLiD (HLIP, a high light-induced protein) binding with chlorophyll A and β -

carotene in excess light conditions causes thermal dissipation and increases photosynthetic growth in algae [175]. *Chlamydomonas* contains ten ELIP encoding genes induced via two independent signalling pathways, one is the UV-B light which induces the ELIP1, ELIP5, and ELIP6, and the other is white light which induces ELIP2, ELIP3, ELIP4, ELIP 9, ELIP10 encoding genes [174]. UVR-8 interacts with COP1 and induces PSBS, LHCSR (LHCSR1 & LHCSR3) signalling pathway and proteins of qE like PHOT but via a different mechanism from PHOT [174]. So, the actions of both photoreceptors are complementary to each other, and CRYs regulate photoprotection through an indirect role in the PHOT signalling pathway of photoprotection. In higher plants, chloroplast relocation is mediated in blue light through PHOT. However, in moss *Physcomitrella patens*, not only blue light but even red light also causes chloroplast relocation by coordinated signalling between PHY and PHOT [176]. In algae, PHY is not present but retains genes encoding HEME OXYGENASE (HMOX1) involved in the conversion of heme to biliverdin (BV) and Ferredoxin-dependent bilin reductases (PCYA) involved in the conversion of BV to phycocyanobilin (PCB). Bilin production downregulates the expression of photosynthesis-associated nuclear genes [177]. UV (200-300 nm) radiation predominantly causes photodamage by producing photo-dimers like CPDs (cyclobutene pyrimidine dimers) and 6-4PPs (6-4 photoproducts), causing blockage of DNA replication and transcription [178]. Plants also have adapted the photoreactivation mechanism using CPDs and 6-4PPs specific photolyase to repair photo-dimer formation [27, 179]. However, UV radiation photoreactivation work in combination with the signalling pathway of different photoreceptors like PHYs, CRYs, and UVR8 [180]. To cope up with excess light exposure, various photoprotective mechanisms adopted by algae and higher plants have been discussed below (Fig. 2, Table 2).

4.1. Excess Light Avoidance Mechanism

To regulate light absorption in excess light, plants have adapted excess light screening mechanism, leaf positioning response, and chloroplast avoidance [150, 173].

4.1.1. Screening Mechanism

Excess sunlight consisting of UV and visible light damage photosynthetic machinery, predominantly PSII (photosystem II), which is the major target of photodamage (reviewed in a study [150]). To avoid photodamage from UV and high-intensity visible radiations, plants synthesize screening compounds like plant secondary metabolite that include polyamines, waxes, alkaloids, phenolic compounds (anthocyanins, flavonols, and carotenoids) in leaf epidermis, and Mycosporine-like Amino Acids (MAA) in algae [150]. The rosy periwinkle (*Catharanthus roseus*) plant produces terpenoid indole alkaloids (TIA) to increase UV-B tolerance in plants [181]. In UV light exposure, plants synthesize phenolic compounds in the cell cytoplasm and later accumulate them in the vacuole. UV radiation primarily photo-oxidizes PSII and increases the degradation of D1 protein [182]. High-intensity visible light also photo-oxidizes PSII

of the electron transport chain in photosynthesis. To avoid visible light photo-oxidation, plants highly accumulate anthocyanins in the leaf epidermis [150]. Agriculturally important crops like *Sorghum bicolor*, *Zea mays*, and *Sinningia cardinalis* synthesize 3-deoxyanthocyanins to reduce photo-oxidative damage [183]. It has been suggested that blue light irradiation along with red light increases the accumulation of se-

condary metabolites like flavonoids, phenolic acids in *Rosa hybrida* (Rose), *Chrysanthemum morifolium* (Chrysanthemum), and *Campanula portenschlagiana* (Campanula) [184]. Therefore, blue light-activated PHOT elevates the production of secondary metabolites like flavonols, anthocyanins, and alkaloids, having a major contribution to the mitigation of photo-oxidative damage.

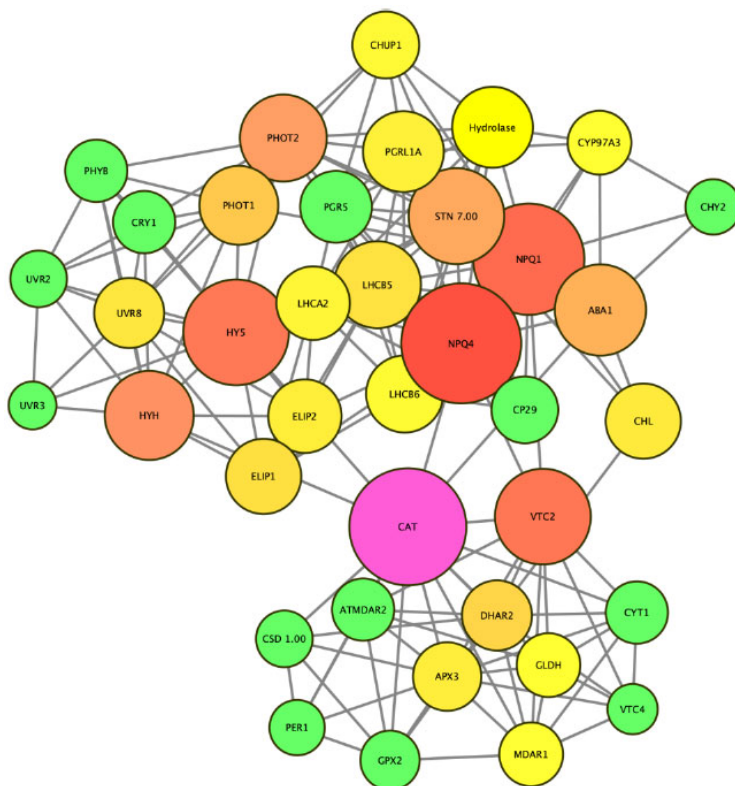


Fig. (2). Interactome showing the crosstalk of different photoreceptors, photosynthetic components, photolyase, photoprotection components in *Arabidopsis*. The protein-protein interaction network has been predicted in String version 11 (<https://string-db.org/>) and visualized using Cytoscape 3.7.2 with Compound Spring Embedder (CoSE) layout. The network analysis was performed using the betweenness centrality algorithm where the sizes and color range from green-yellow-orange-red to pink of the nodes (circles) indicate betweenness values. (A higher resolution / colour version of this figure is available in the electronic copy of the article).

Table 2. Biochemical nature and role of proteins involved in photoprotection of *Arabidopsis thaliana*.

Proteins in Interactome	Properties of Interacting Proteins	Biological Function	References
NPQ1	VIOLAXANTHIN DE-EPOXIDASE (chloroplastic) belongs to the Lipocalin family	Controls zeaxanthin concentration, non-photochemical quenching	[201]
CSD 1.00	COPPER/ZINC SUPEROXIDE DISMUTASE CSD1 (cytosolic)	Detoxify superoxide radicals	[191]
UVR2	DEOXYRIBODIPYRIMIDINE PHOTOLYASE	Involved in repair of UV-induced DNA damage in plants through monomerization of CPDs (cyclobutyl pyrimidine dimers) in a light-dependent manner	[178, 179]
LHCB6	LHCBM6, Chlorophyll a/b binding protein of LHCI type I	Light-harvesting complex protein, photosynthesis, photoprotection	[202-204]
CYP97A3	Cytochrome P450, family 97, subfamily A, polypeptide 3	Involved in the biosynthesis of xanthophylls, specific for beta-ring hydroxylation of alpha- and beta-carotene	[205]

Proteins in Interactome	Properties of Interacting Proteins	Biological Function	References
NPQ4	Encodes CP22 (PSII-S), a ubiquitous pigment-binding protein, belongs to the ELIP/PSBS family	Involved in non-photochemical quenching (qE)	[133]
PER1	Thiol-specific peroxidase (1-cysteine peroxiredoxin 1)	Involved in germination inhibition during stress <i>via</i> the reduction of hydrogen peroxide and organic hydroperoxides to water and alcohol	[206]
Hydrolase	Haloacid dehalogenase-like hydrolase family protein	Involved in maintaining the light-harvesting efficiency during non-photochemical quenching recovery <i>via</i> the regulation of chlorophyll excited-state lifetime	[207]
STN 7.00	Serine/threonine-protein kinase STN7 (chloroplastic)	State transition and phosphorylation of LHCII, minor light-harvesting protein LHCB4.2/CP29 and in the light-dependent phosphorylation of TSP9, growth, adaptation in high light	[208, 209]
DHAR2	DEHYDROASCORBATE REDUCTASE belongs to the DHAR family	Involved in the ascorbate recycling system, redox homeostasis, scavenging of ROS (reactive oxygen species) under oxidative stresses	[210]
PGR5	Protein PROTON GRADIENT REGULATION 5 (chloroplastic)	Regulate cyclic electron flow (CEF) around Photosystem I and PGRL1A reduction by ferredoxin (Fd) and for the photoprotection	[211, 212]
PHYB	Phytochrome B	Chloroplast relocation, photoreactivation, expression of the small subunit of ribulose- bisphosphate carboxylase, chlorophyll A/B binding protein	[176,177,180]
GPX2	Probable glutathione peroxidase 2 belongs to the glutathione peroxidase family	May be involved in glutathione peroxidase-like protective system against oxidative stresses	[206]
CYT1	Glucose-1-phosphate adenyltransferase family protein	Ascorbate biosynthesis, plant growth and development and cell-wall architecture in plants, sugar accumulation, starch biosynthesis	[213, 214]
VTC4	L-GALACTOSE-1-PHOSPHATE PHOSPHATASE (GPP), Inositol monophosphatase family protein (vitamin C 4)	Ascorbate biosynthesis, biomass accumulation	[192, 215]
UVR3	DNA PHOTOLYASE family protein	Involved in repair of UV-induced DNA damage and catalyzes the photoreactivation of pyrimidine [6-4] pyrimidine photoproduct (6-4 products)	[27]
HYH	TRANSCRIPTION FACTOR ELONGATED HYPOCOTYL 5 (HY5)- LIKE belongs to the bZIP family	Involved in photomorphogenesis, transcription, and activation of light-induced genes, regulate expression of photolyase	[180, 216]
ELIP1	EARLY LIGHT-INDUCED PROTEIN 1(chloroplastic)	Regulate the chlorophyll biosynthesis pathway involved in pigments incorporation into light-harvesting pigment-protein complexes	[217, 218]
CHUP1	CHLOROPLAST UNUSUAL POSITIONING PROTEIN 1, Hydroxyproline-rich glycoprotein family protein	Regulates localization of chloroplast by anchoring chloroplasts to the plasma membrane	[186, 219]
PHOT1	Phototropin-1	Membrane depolarization and blue light mediated growth inhibition, chloroplast accumulation, leaf positioning and growth, accumulation of photosystem proteins, root phototropism	[64,69,71]
CHL	LIPOCALIN (chloroplastic)	Prevents thylakoidal membrane lipids peroxidation, oxidative stress, and seed longevity	[220]
GLDH	L-GALACTONO-1,4-LACTONE DEHYDROGENASE, mitochondrial	Involved in the biosynthesis of ascorbic acid, accumulation of respiratory complex I	[192, 210]
MDAR1	MONODEHYDROASCORBATE REDUCTASE 1, peroxisomal	Catalyzes the conversion of monodehydroascorbate to ascorbate	[191, 210]
CP29	Photosystem II chlorophyll-a/b protein, chloroplastic	Stability of chloroplast mRNAs, non-photochemical quenching, and normal chloroplast development under cold stress	[221]
LHCA2	Photosystem I chlorophyll a/b-binding protein 2, chloroplastic	Captures and delivers excitation energy to closely associated photosystems (PS I)	[222]
CRY1	Cryptochrome-1	Expression of photoprotective genes, transcriptional upregulation of ROS responsive genes, non-photochemical quenching, and anthocyanin biosynthesis	[223-225]
LHCB5	Chlorophyll a-b binding protein CP26, chloroplastic	Light reception, energy transfer, and non-photochemical quenching	[194, 226]
ELIP2	EARLY LIGHT-INDUCED PROTEIN 2, chloroplastic	Involved in pigments incorporation into light-harvesting pigment-protein complexes important in photoprotection	[217]
PGRL1A	A transmembrane protein present in thylakoids belongs to the PGR5 family	Role in cyclic electron flow	[211]

Proteins in Interactome	Properties of Interacting Proteins	Biological Function	References
VTC2	GDP-L-galactosephosphorylase 1	In the Smirnoff-Wheeler pathway, ascorbate biosynthesis, phosphorylase, leaf size, and biomass accumulation	[192, 227]
APX3	ASCORBATE PEROXIDASE	Act as hydrogen peroxide (H ₂ O ₂) scavenger	[191, 210]
CAT	CATALASE-2, peroxisomal	Act as hydrogen peroxide (H ₂ O ₂) scavenger	[191]
ATMDAR2	PYRIDINE NUCLEOTIDE-DISULPHIDE OXIDOREDUCTASE family protein	Involved in the conversion of monodehydroascorbate to ascorbate, detoxification of H ₂ O ₂	[228]
HY5	ELONGATED HYPOCOTYL 5, Basic leucine zipper (bZIP) transcription factor	Role in light-induced (blue & far-red light) anthocyanin accumulation, Phytochrome A-mediated of hypocotyl elongation inhibition	[180, 200, 216]
CHY2	BETA-CAROTENE 3-HYDROXYLASE 2, chloroplastic belongs to the sterol desaturase family	Involved in the biosynthesis of xanthophylls	[205]
PHOT2	Phototropin-2, membrane-bound	Involved in stomatal opening, chloroplast movement, phototropism, photomorphogenesis, and non-photochemical quenching	[137]
UVR8	UV RESISTANCE-8, a regulator of chromosome condensation (RCC1) family protein	Acts as UV-B photoreceptor, a role in establishing UV-protective responses in plants	[180]
ABA1	ZEAXANTHIN EPOXIDASE, chloroplastic	Zeaxanthin and abscisic acid (ABA) biosynthesis, osmotic and drought stress tolerance, defense, disease resistance, non-photochemical quenching (NPQ)	[193]

4.1.2. Leaf Movement Response

Some plants in strong light conditions move their leaves called heliotropism. In strong light, plants move their leaves parallel to the direction of light to minimize light absorption called para-heliotropism, and in low light conditions, they move their leaves perpendicular to the direction of light called dia-heliotropism. In *Phaseolus vulgaris* (kidney bean), the diurnal movement of leaf lamina avoids photoinhibition [150]. Here, PHOT present in pulvinar motor cells of the leaf has been reported to be involved in the leaf movement upon blue light exposure [185].

4.1.3. Chloroplast Avoidance Response

In strong light illumination, chloroplasts are arranged along the periclinal wall, parallel to the incident light to reduce photodamage, called chloroplast avoidance response. Different PHOT mutants defective in chloroplast avoidance response show photodamage of photosynthesis PSII (photosystem II), leaf necrosis, bleaching of leaf color, and decrease in quantum yield [186]. In higher plants, PHOT2, in coordination with other proteins like actin-binding protein, CHLOROPLAST UNUSUAL POSITIONING 1 (CHUP1), is involved in chloroplast avoidance response activated during excess light exposure [186]. In fern, *Adiantum capillus-veneris*, PHOT2 regulates chloroplast avoidance response [134]. In bryophytes (*Marchantia polymorpha*), a single PHOT is present to regulate chloroplast avoidance response [135]. In green algae *Mougeotia scalaris* [187], fern *Adiantum capillus-veneris* [188], and moss *Physcomitrella patens*, PHOT mediates chloroplast avoidance response in blue light as well as in red light [176]. The adaptive photo-response is reversed using far-red light, indicating the role of a red-light photoreceptor, PHY. The photophysiological response is thereby controlled by a chimeric photoreceptor NEO in *Mougeotia scalaris* and fern *Adiantum capillus-veneris* [189]. In *Physcomitrella patens*, NEO has not been isolated and characterized, and here PHOT functions

downstream of PHY signalling to regulate chloroplast positioning [176].

4.2. Scavenging and Dissipation Mechanism

In excess light, plastoquinone (PQ) pool changes oxidation/reduction state of thiol compounds like glutathione and thioredoxin, and change in pH of thylakoid lumen acts as sensing molecules to activate photoprotection mechanism in plants [173]. Plants have adapted the scavenging mechanism and non-photochemical quenching mechanism to avoid the production of ROS and dissipation of excess absorbed energy by the production of different types of antioxidants and carotenoids.

4.2.1. ROS Scavenging Mechanism

In excess light environmental conditions, PSI and PSII in chloroplast get photo-oxidized and produce ROS in photosystems. The free and PS1 & II bound fractions of carotenoids present in chloroplast act as ROS scavengers [173]. PSII Reaction Center (RC) binds β -carotene, and the light-harvesting complex binds xanthophylls like zeaxanthin, violaxanthin, lutein, and neoxanthin [190]. Photo-oxidation of PSII and PSI produces H₂O₂ via O₂⁻ and excitation of 3O₂ to 1O₂ by triplet excited chlorophyll (3Chl*), respectively [191]. For detoxification of these ROS, plants have adapted constitutive photoprotective scavenging mechanism by the production of several antioxidative enzymatic compounds that include SUPER-OXIDE DISMUTASE (SOD), ASCORBATE PEROXIDASE (APX), GLUTATHIONE PEROXIDASE, PEROXIREDOXIN, and CATALASE (CAT), antioxidative non-enzymatic compounds like prenylquinols, ascorbate, and glutathione, in addition carotenoids like zeaxanthin, lutein, neoxanthin, and tocopherol [173]. It has been reported that blue light treatment increases the accumulation of ascorbic acid in citrus fruits through upregulation of ascorbic acid (ascorbate) biosynthetic genes (CitGLDH, CitVTC1, CitVTC2, and CitVTC4) and

ascorbic acid regeneration genes (CitDHAR, CitMDAR1, and CitMDAR2) and reduces glutathione (GSH) producing genes (CitGR and CitchGR), suggesting the role of blue light receptor photoreceptor PHOT or CRY or integrated signalling pathway in increasing ascorbic acid in citrus fruits [192].

4.2.2. Non-Photochemical Quenching Mechanism

In plants, excess light absorption constitutively produces chlorophyll triplet excited state (3Chl*) from chlorophyll singlet excited state (1Chl*) causing photodamage. To prevent photodamage, the production of chlorophyll triplet state is prevented through a set of photoinducible mechanisms called non-photochemical quenching (NPQ). NPQ converts excess photodamaging energy into non-photodamaging heat through thermal dissipation (qE) [150]. Excess light condition activates VIOLAXANTHIN DE-EPOXIDASE (VDE) and substitutes violaxanthin (viola) to zeaxanthin primarily in proteins CP24 and CP26 [193]. It has been studied in *Arabidopsis* that mutants having *npq1* mutation are unable to convert viola to zeaxanthin and show reduced NPQ as compared to wild type, indicating that zeaxanthin possesses enhanced capacity of NPQ for ROS [150, 194]. Different components of the xanthophyll cycle like zeaxanthin and violaxanthin bind to light-harvesting proteins and mediate NPQ of Chl singlet excited state (1Chl*) by energy transfer to (1-Car*) carotenoids. It has been reported that PHOT induces light-harvesting complex stress-related protein-3 (LHCSR3), a light-harvesting protein present predominantly in plants and algae [6]. It senses acidic pH of thylakoid lumen by protonation of amino acid residues exposed towards thylakoid lumen in excess light condition and controls non-photochemical quenching energy dissipation (qE) [173]. This protonation is controlled by specific gene product LHCSR in algae and PSBS in both plants and mosses. Excited-state carotenoid molecules dissipate energy in the form of heat and reach a ground state (Car) [173].

4.2.3. Photoreactivation Mechanism

This mechanism is functionally conserved from algae to higher plants to avoid photodamage from pyrimidine dimers produced in UV-B light, using photolyase. In *Phaeodactylum tricorutum* photolyase, CPF1 (cryptochrome/photolyase family) and CRYP are involved in the modulation of expression of LHCX1, LHCX2, LHCX3 [195] but not LHCX4 that is upregulated in longer dark duration [196]. LHCX1 plays a very important role in NPQ and gets expressed even in very low light duration [197]. However, here, the PHOT function is done by bZIP transcription factor Aureochrome (AUREO) [198]. Plants have evolved photoreactivation mechanisms using CPDs and 6-4PPs specific photolyase to repair photo-dimer formation. Photolyases bind the photo-dimer and reverse the photodimer to original single bases in near UV (300-500 nm) using a photo reversal mechanism [178]. In *Oryza sativa* mutant of *uvr-2* (*phr1*) shows impaired repair mechanism of cyclobutene pyrimidine dimers during UV-B light illumination condition [199]. CPD-photolyase (*phr1*) expression is induced in UV-B or

white light, and 6-4PP photolyase (*uvr-3*) is constitutively expressed [199]. CPD photolyase expression is regulated by both HY5 and HY5-HOMOLOG (HYH) dependent pathways under the control of CRY, PHY, and UVR8 photoreceptors and UVR8 independent manner due to accumulation of PHR1 after UV-B light exposure [180, 200]. Photodamage repair in UV radiation is coordinated by integrated signalling pathways of different photoreceptors like PHY, CRY, and UVR8 [180].

Photoreceptors including Phototropin (PHOT) in combinations with other photoreceptors and signalling proteins are involved in the regulation of plant adaptation and metabolism in diverse environmental conditions. Apart from that, photoreceptors also interact with phytohormones, having a major role in plant growth and metabolism, suggesting the contribution of light in plant growth and morphogenesis. Photoreceptors crosstalk to various phytohormones, involved in various signalling pathways, is discussed next in detail.

5. CROSSTALK OF PHOTORECEPTORS AND PHYTOHORMONES IN PLANT GROWTH AND DEVELOPMENT

Through the course of evolution, plants have adopted the phytohormone network as an efficient means of communicating within the cell. It is now well established that plants have evolved from green algae (Streptophytes). During the evolution and gradual terrestrialization of the early plant ancestors, they had to adapt themselves to new challenges (e.g., various abiotic stresses, UV irradiation, temperature fluctuations, and nutrient scavenging). The photoreceptors and the phytohormones network can extensively crosstalk to help plants respond to challenging environmental cues.

5.1. Crosstalk of Photoreceptors and Phytohormones During Seed Germination and Stomatal Opening

Two very important phenomena in plant life are seed germination and regulation of the stomata. The PHYs (both PHYA and PHYB) can induce seed germination [18, 229]. ABA and gibberellic acid (GA) play a crucial role during seed germination and, PHYA and PHYB modulate these two phytohormones to facilitate seed germination. An early pulse of far-red (FR) inactivates PHYB and activates PHYA. In the endosperm, PHYB inactivation leads to the stabilization of PIF1, resulting in the repression of GA and stimulation of ABA. In the embryo, the PHYA activation meanwhile leads to - (a) PIF1 destabilization; (b) PIF1-dependent stimulation of SOMNUS (SOM), Gibberellic Acid-insensitive (GAI), and repressor of GA1-3 (RGA) expression; (c) SOM-dependent repression of GA and stimulation of ABA expression; (d) GA-dependent further destabilization of GAI and RGA; and (e) GAI- and RGA-dependent stimulation of ABA synthesis. The ABA from the endosperm moves and joins the embryonic ABA and over-rides the PHYA signalling in the embryo, leading to the repression of GA signalling and repression of germination. However, the embryonic ABA signalling weakens over time, and a second

FR-pulse can reverse the condition. In this case, the GA signalling (modulated by the PHYA) in the embryo dominates, leading to seed germination [230].

ABA also plays a crucial role during the modulation of stomata. The ABA signalling pathway in stomata is well worked out. In the absence of ABA, a very important kinase (open stomata 1 (OST1)) remains bound to its regulator PP2C phosphatase. As a result, several downstream channels/transporters remain inactivated. As soon as ABA is produced (due to stress), the ABA-bound receptors of PYL/PYR/RCAR bind to PP2C and allow the OST1 kinase to phosphorylate and activate the downstream channels/transporters. ROS and Ca²⁺ signalling also crosstalk with this pathway to modulate the stomata. The PHOT plays an important role in the modulation of stomata [231], and they mediate stomatal opening. The PHOTs, in their activated form, are autophosphorylated, and phosphatase (PP2A in the case of PHOT2) dephosphorylates and negatively regulates it. They can separately regulate an H⁺ATPase to mediate stomatal opening. The PHOT pathway mediates stomatal opening during the day, but when plants sense drought signal, the ABA pathway can suppress the PHOT pathway [232].

5.2. Crosstalk of Photoreceptors and Phytohormones During Plant Growth

The plant germination follows two strategies - initial skotomorphogenesis (development in the dark, where plants have maximum hypocotyl elongation, limited root growth, closed cotyledons with an apical hook) followed by photomorphogenesis (development in light, that is, plants have inhibition of hypocotyl elongation, root growth, opening and greening of cotyledons with an apical hook) [233]. The photoreceptors PHYA, PHYB, CRY1, CRY2, UVR8, and PHOT are positive regulators of photomorphogenesis [18]. These photoreceptors communicate with COP, DE-ETIOLATED (DET), and FUSCA (FUS) to modulate plant growth. The COP1 and SPA form an E3 ubiquitin ligase complex to regulate photomorphogenesis, promoting transcription factors. The PHY inactivates the COP1-SPA complex, which leads to the accumulation of HY5, which is a positive regulator of photomorphogenesis (*i.e.*, negative regulator of cell elongation). In the dark, The PIFs are stable and cause the typical hypocotyl elongation observed during the skotomorphogenesis (and also during normal growth) [18].

Ethylene plays a crucial role in regulating the hypocotyl along with PIFs. In the dark, ETHYLENE RESPONSE FACTOR 1 (ERF1) is unstable due to degradation. As the etiolated seedlings are obstructed, ERF1 becomes abundant and blocks hypocotyl elongation and a closed apical hook. In light, initially, the PIFs are degraded, and the cotyledons unfold. Later PIFs are again accumulated and, together with ERF1, result in proper plant growth [18]. The PHYB, after getting activated in light, can act as a “molecular glue” to allow the interaction between transcription factors Ethylene-Insensitive 3 (EIN3) and SCF E3 ligase complexes. This promotes the degradation of EIN3, controlling ethylene sig-

nalling [234, 235]. Auxin can also regulate cell elongation through modulating the Auxin Response Factor (ARF) family of transcription factors. The photoreceptors can directly connect with the auxin-signalling pathway to modulate the hypocotyl elongation [235]. In the dark, both PHYB and CRY remain inactive, and as a result, the ARF promotes hypocotyl elongation. In light, these photoreceptors get to activate, and they interfere with the degradation of AUX/IAA. The proteins (CRY1-AUX/IAA or PHYB-AUX/IAA) can then repress the ARF and auxin-signalling [236]. PHYA and AUX/IAA similarly cause hypocotyl elongation in the deep shade [237]. Brassinosteroids (BR) and GA can also modulate cell elongation by cross-talking with the photoreceptor pathway [233]. The UVR8 photoreceptor, after sensing UV-B, moves inside the nucleus. Here, it interacts with transcription factors BRI1-EMS-SUPPRESSOR1 (BES1) and BES1-INTERACTING MYC-LIKE 1 (BIM1). These events block the BR signalling and promote photomorphogenesis in plants [238]. CRY1 can also interact with BES1 to inhibit BR signalling under light [239]. The BZR1, PIF4, ARF6, and their inhibitor DELLA (BAP/D) circuits are responsible for modulating the crosstalk between photoreceptors and abiotic stress [233].

5.3. Crosstalk of Photoreceptors and Phytohormones During Plant Movement Towards Light

The orientation of plants towards the light (phototropism) is an important facet for the survival of sessile plants. The PHOTs are the main photoreceptors driving phototropism and, together with auxin (AUX), play a critical role in phototropism. The relation between PHOTs and auxin transporters PIN-FORMED (PIN) needs more experimental evidence. But the H⁺ATPase, discussed earlier, indicate that there is a direct connection between PHOTs and auxin. Another phenomenon related to light is shade avoidance. Here different photoreceptors crosstalk with auxin to help in plant development. PHYB, when activated by ample light, inactivates the PIFs, thereby stopping the elongation of plants. When plants experience low light (shade), PHYB gets inactivated, and this results in the activation of PIFs. The PIFs activate downstream targets, which result in the transcription of YUCCA (YUC), AUXIN (AUX)/INDOLE-3-ACETIC ACID INDUCIBLE (IAA), and PIN. This results in an increase of the hypocotyl length to avoid shade [18].

5.4. Crosstalk of Photoreceptors and Phytohormones During Flowering

Flowering is another important phenomenon in plants, and again, we can see crosstalk between photoreceptors and phytohormones for its modulation. In short days, CONSTANS (CO) is regulated by COP1-SPA and PHYB, and as a result, FLOWERING LOCUS T (FT) is not expressed. In long days, FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 (FKF1)-GI together with PHYA and CRY2 help in stabilizing CO and subsequently FT. In parallel, the photoreceptors may also suppress the TEMPRANILLO 1 (TEM1) and TEM2 resulting in the accumulation of GA. As a result,

DELLA proteins are degraded and hence allow further FT accumulation. The FT and the GA can induce flowering genes in shoot apical meristems. Here the FT downregulates SHORT VEGETATIVE PHASE (*svp*) gene, which in turn affects the GA and DELLA. TEMs are also downregulated (their modulation is independent of FT), and as a result, they separately affect the GA and DELLA. These components together play a role in modulating flowering [18].

5.5. Photoreceptors Inspired Metabolic Engineering

The photoreceptors govern the metabolite (both primary and secondary) biosynthesis in plants [19, 20]. Photoreceptors are important regulators of chlorophyll abundance [19, 240-245], photosynthesis-related genes [19], and photosynthetic capacity by directly affecting the proteins involved in the Calvin cycle and electron transport [246]. Supporting the hypothesis that photoreceptors regulate photosynthesis, there are reports on a reduction in CO₂ uptake in photoreceptor mutants [245, 247, 248]. The carbon acquired during photosynthesis is used in other metabolic pathways, thus linking the photoreceptors with primary and secondary metabolism [19]. Any alterations in photoreceptors directly affect the sugar levels in plants (reports vary on the concentration-oscillating between high and low) [19]. When carbon is used, other biochemical pathways are also activated, and some of them generate metabolites that can be used for the biosynthesis of amino acids. Again, like carbon, the amino acid levels also vary in photoreceptor mutants [19]. Apart from the primary metabolites, secondary metabolites such as anthocyanins, carotenoids, and flavonols can also be affected by photoreceptors [20]. UV light can affect the concentration of anthocyanin and flavanols [20, 249]. Carotenoids are affected by blue, red, and UV-B lights [20]. These reports show evident crosstalk between the photoreceptors and plant metabolites.

Photoreceptors have a major role in various signalling pathways contributing to plant growth, development, and longevity. Therefore, the applications of various novel biotechnological approaches such as genome editing and synthetic biology, and artificial illumination can be utilized to optimize crop growth and yield and are discussed extensively below.

6. APPROACHES INVOLVING PHOTORECEPTORS FOR CLIMATE-SMART CROP PRODUCTION

Since the growth and development of plants are mediated through photoreceptors, various biotechnological approaches have been used to improve the growth and yield of plants by targeting the photoreceptor genes. Photoreceptors are excited by particular wavelengths; light parameters in terms of light intensity, duration, and wavelength are optimized (artificial illumination) for particular plants. Insertion/deletion/mutation of single base pair in photoreceptor has been used for crop improvement. Methods to alter gene expression have also been applied for enhancing crop yield and growth (Fig. 3).

6.1. Artificial Illumination

It is well-established that continuous illumination could be deleterious to the algal and crop systems. The natural defense mechanisms, such as the degradation of PSII [250], movement of a mobile pool of LHCII from PSII to PSI to equilibrate imbalance of light excitation in two photosystems [251], dissipation of excess light by antenna complexes [252], carotenoid-based photoprotection [253, 254], and ultrafast time scale quench in reaction centers [255] are the adapted measures that protect the photosynthetic apparatus from getting degraded. However, due to all these approaches, the light that is otherwise channelized for biomass accumulation gets compromised, and most of the energy gets dissipated in the form of heat and fluorescence.

Algal growth under natural conditions gets impacted by regular changes in light conditions. Similar observations have been seen for the microalgal cultivations; herein, algal cells usually travel between the saturating light at the surface of the reactors and the dark depths of the culture. Hence, the cells experience more of the flashing-light conditions than continuous lights. Such travels through light/dark cycles lead the cells to adapt to the light dosage conditions (intensity and frequency of the light flashes) for optimal photosynthesis and growth [256]. Several experiments have been carried out where the use of artificial illuminations with different continuous and flashlight conditions are exploited to study their effects on algal growth and production. Effects on growth and metabolic contents have been studied through varying different light parameters such as intensity, wavelength, photoperiod (light/dark period), flash frequency (*f*, number of light flashes per second), and duty cycle (ratio of light flash duration and total (light + dark) flash duration). Continuous white light at different intensities and photoperiods (light/dark periods (h/h) imparts differential responses in different algal species, as summarized in Table 3. For *Scenedesmus* sp. the use of continuous white light at 400 $\mu\text{mol}/\text{m}^2/\text{s}$ enhanced the biomass production to as high as 3.8 g/L [109]. Maximum cellular growth rates are seen for *Nannochloropsis* sp. at 100 $\mu\text{mol}/\text{m}^2/\text{s}$ and 18/6 hr light/dark cycle [257]. Usage of white light illumination at photoperiods of 12/12 L/D for *Scenedesmus* sp. enhanced its lipid contents to 37% [109], to 67% for *Ankistrodesmus falcatus* [258], and to ~54% for *Botryococcus braunii* KMITL 2 [259]. Flashing white light conditions also have differential effects on growth and metabolic accumulation. For *Dunaliella salina*, the combination of flashing light with continuous background light can potentially improve the energy-harvesting efficiency of algal cultures by >50% [260]. Pre-acclimation of *Scenedesmus obliquus* promotes better growth at pulsed light than continuous illumination [261]. Although the biomass and lipid contents of *Chlamydomonas reinhardtii* remain unaffected under flashing illumination conditions (0.5 duty cycle at 100 and 200 $\mu\text{mol}/\text{m}^2/\text{s}$), it helps to save up to 62.5% of energy [262].

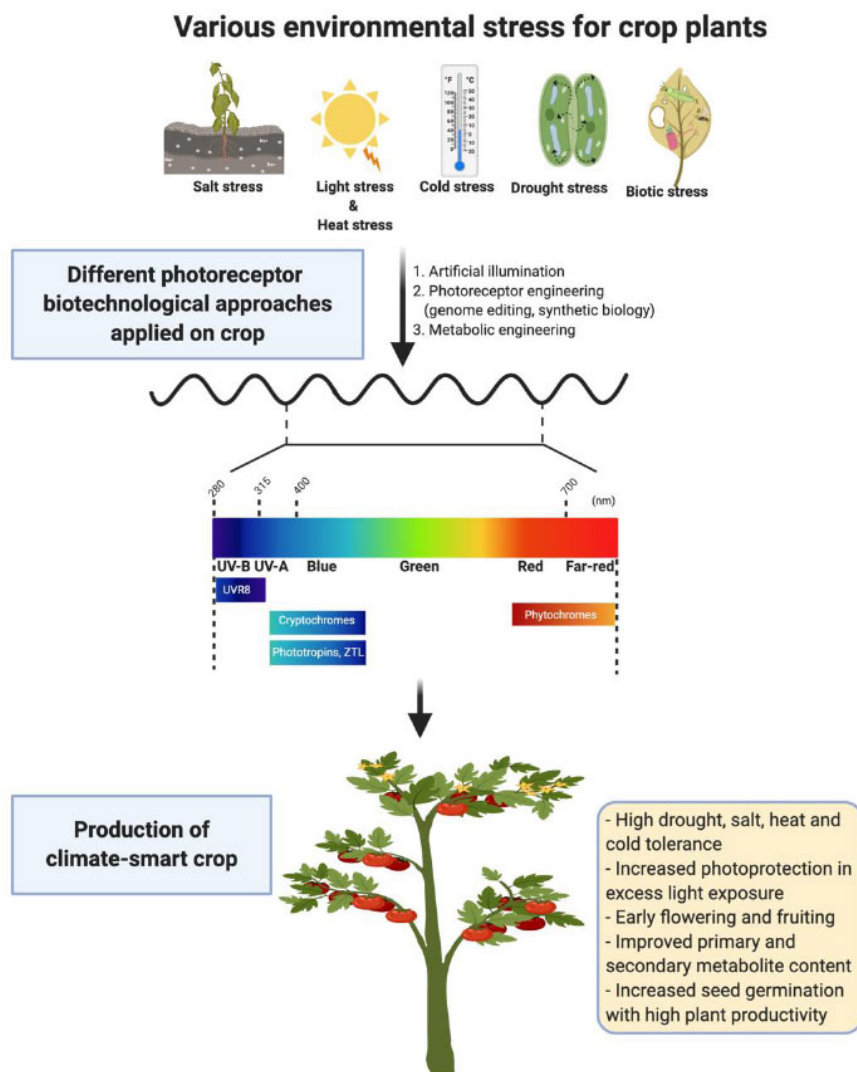


Fig. (3). Schematic representation of the application of artificial illumination and photoreceptor biotechnological approaches for the production of climate-smart crops. (A higher resolution / colour version of this figure is available in the electronic copy of the article).

Additionally, specific wavelengths also impact growth, metabolites, pigments, soluble proteins, and lipid accumulation in algae [263]. However, these effects vary among different algal species. Metabolite and soluble proteins are exploited by nutraceutical, pharmaceutical, and cosmetic industries, and the higher lipid content of algae form the basis for biofuel production. Algal cultures are also used in wastewater treatment and biogas production. These properties are enhanced by varying the color, photoperiod, and intensity of light. Continuous illumination with yellow light ($1500 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) led to highest productivity ($54 \text{ g m}^{-2} \text{ d}^{-1}$) in *C. reinhardtii* [264]. *Oscillatoria* sp. SRA (collected from stagnant rainwater) growth was enhanced in blue light, while the growth of *Oscillatoria* sp. CWA (collected from coom water) gets enhanced by white and yellow light illumination [265]. Growth of *Ankistrodesmus* sp. SoA (isolated from the soil) was observed to get enhanced in green light [265]. Blue

light enhances the Chl A content in *Oscillatoria* sp. SRA and carotenoid in *Ankistrodesmus* sp. SoA [265]. Lipid accumulation in *Ankistrodesmus* sp. SoA and *Oscillatoria* sp. CWA increased when cultivated in yellow light [265]. Cell counts and dry mass of *Chlorella kessleri* were the highest in red LED illumination, while cell size was the largest in blue LED [266]. The cell density of *Chlorella vulgaris* in different light illuminations (white, red, and fluorescent) was found to vary with the culturing times [267]. In white light, cell density was the highest on day 14, while in red light, the cell density was highest on day 3 [267]. Another report suggests that in red light, Chl A content was enhanced in *C. vulgaris* [268]. Blue light increased the biomass and chlorophyll content for *Scenedesmus quadricauda* while its photon yield remained independent of the spectral composition of light. However, the photon yield decreased with the increase in biomass content [269].

Table 3. Effect of light on growth and metabolite production in different algal species.

Species	Light Parameters	Impact
<i>Scenedesmus</i> sp.	Continuous white light with light/dark cycle-12/12 hr	Enhanced biomass and lipid content [109]
	Blue light	Removed phosphorus from medium (wastewater treatment) [275]
	Red + blue in the ratio 7:3	Removed phosphorus and nitrogen (wastewater treatment) [275]
<i>Scenedesmus quadricauda</i>	Blue light	Increases biomass and chlorophyll content [269]
<i>Scenedesmus obliquus</i>	Continuous red light with 12/12 hr light/dark cycle	Higher biomass yield [268]
	Continuous green light with 12/12 hr light/dark cycle	Higher accumulation of chlorophyll b [268]
	Continuous blue light with 12/12 hr light/dark	Affect carbohydrate content; enhance lipid content [268]
	Continuous blue + green light with 12/12 hr light/dark	Affect protein content [268]
	Pre-acclimation to white pulsed light; Flash /dark time-10/90 ms; flash frequency-10 Hz	Promotes better growth [261]
<i>S. obliquus</i> (FACHB-12)	Continuous blue light with 18/6 hr light/dark cycle	Accumulation of astaxanthin and higher biomass yield [273]
	Continuous blue light with 24/0 hr light/dark cycle	Removal of phosphorus from the medium (wastewater treatment) [273]
	Continuous blue + green light with 24/0 hr light/dark cycle	Removal of nitrogen from the medium (wastewater treatment) [273]
<i>Haematococcus pluvialis</i>	Continuous red light with 20/4 hr light/dark cycle	Increased cell growth [274]
	Continuous blue light post-cell growth with 20/4 hr light/dark cycle	Increased astaxanthin production [274]
<i>Botryococcus braunii</i>	Continuous white light with light/dark cycle 16/8 hr	Enhanced lipid content [259]
<i>Dunaliella salina</i>	Flash + continuous light White light, flash frequency-50 Hz, Flash /dark time=10/10 ms	Improves the energy-harvesting efficiency [260]
<i>Chlamydomonas reinhardtii</i>	Flash light with 0.5 duty cycle at 100 and 200 $\mu\text{mol}/\text{m}^2/\text{s}$	Saves up to 62.5% of energy [262]
	Continuous yellow light	Increased biomass specific light absorption rate [264]
<i>Oscillatoria</i> sp. SRA	Continuous blue light with light/dark cycle 8/16 hr	Enhanced growth and chlorophyll a content [265]
<i>Oscillatoria</i> sp. CWA	Continuous white/yellow light with light/dark cycle-8/16 hr	Enhanced growth [265]
	Continuous yellow light with 8/16 hr light/dark cycle	Enhanced lipid content [265]
<i>Ankistrodesmus</i> sp.	Continuous green light with 8/16 hr light-dark cycle	Enhanced growth and carotenoid content [265]
	Continuous yellow light with 8/16 hr light-dark cycle	Increased lipid content [265]
<i>Chlorella kessleri</i>	Red light	Increased cell count and dry mass [266]
	Blue	Increased cell size [266]
<i>Chlorella vulgaris</i>	Continuous white, red, and fluorescent light with 12/12 hr light/dark cycle	It affected the cell growth, and it varied with the culturing time [267]
	Continuous red light with 12/12 hr light/dark cycle	Enhanced biomass yield and chlorophyll a content [268]
	Continuous green light with 12/12 hr light/dark cycle	Higher accumulation of chlorophyll b [268]
	Continuous blue light with 12/12 hr light/dark cycle	Affect carbohydrate content and enhance lipid content [268]
	Continuous blue + green light with 12/12 hr light/dark cycle	Affect protein content [268]
	Continuous blue and red light with 12/12 hr light/dark cycle	Degraded effluents from the dye industry [277]
<i>Chlorella</i> sp.	Blue + red light	Enhanced biomass productivity [271]
	Red	Enhanced lipid content [271]
	Continuous red light with 12/12 hr light/dark cycle	Reduce nutrient from digestate and upgrade biogas production [276]

Species	Light Parameters	Impact
<i>Phaeodactylum tricornutum</i>	Continuous blue + red light with 12/12 hr light/dark cycle	Enhanced biomass yield [272]
	Continuous green light post-biomass yield with 12/12 hr light/dark cycle	Enhanced lipid accumulation [272]
<i>Isochrysis galbana</i>	Continuous blue + red light with 12/12 hr light/dark cycle	Enhanced biomass yield [272]
<i>Arthrospira platensis</i>	Continuous red light with 12/12 hr light/dark cycle	Higher biomass yield [268]
	Continuous green light with 12/12 hr light/dark cycle	Higher accumulation of chlorophyll b and carotenoid [268]
	Continuous blue light with 12/12 hr light/dark cycle	Affect carbohydrate content [268]
	Continuous blue + green light with 12/12 hr light/dark cycle	Affect protein content [268]
<i>Nannochloropsis salina</i>	Continuous + pulsed light, flash frequency-10 Hz, flash /dark time-10/90 ms	Enhanced biomass content [278]
	Continuous blue + red light with 12/12 hr light/dark cycle	Enhanced biomass yield [272]
<i>Nannochloropsis</i> sp.	Continuous light with 18/6 hr light/dark cycle was used	Enhanced lipid content [257]
	Continuous blue light with 12/12 hr light/dark cycle	Increased biomass and fatty acid methyl esters (FAME) [270]
<i>Nannochloropsis oceanica</i>	Continuous blue + red light with 12/12 hr light/dark cycle	Enhanced biomass yield [272]

Abbreviations: SRA-collected from stagnant rainwater; CWA-collected from Cooum water.

Biomass of the volumetric Fatty Acid Methyl Esters (FAME), which are the source of biofuel from *Nannochloropsis* sp., is the highest when cells are cultivated under blue light [270]. In *Chlorella* sp. biomass productivity is found to be maximum when illumination is a combinatorial effect of the blue and red light, while its lipid contents were maximum when illuminated solely with the red light [271]. The combination of blue and red light also led to higher biomass yield in *Nannochloropsis oceanica*, *Isochrysis galbana*, *Nannochloropsis salina*, and *Phaeodactylum tricornutum* [272]. Exposure to green light post-biomass yield led to the accumulation of lipid content in these algal species, the highest being in *P. tricornutum* [272]. Higher biomass in *Arthrospira platensis*, *Chlorella vulgaris*, and *Scenedesmus obliquus* was found when exposed to red light, while exposure to green light led to a higher accumulation of Chlorophyll B (Chl B) in these three species and carotenoid in *A. platensis* [268]. Though carbohydrate contents of these species get affected only by the blue light, both blue and green lights mark their effects on the protein contents [268]. Blue light also enhances lipid contents in *S. Obliquus* and *C. vulgaris* cultures [268]. Accumulation of astaxanthin (widely used in the pharmaceutical and cosmetic industry) and biomass in *S. obliquus* (FACHB-12) was enhanced in blue light using an 18/6 hr light/dark cycle [273]. Cell growth of *Hematococcus pluvialis* (the best source of astaxanthin) was increased using red light, and then switching to blue light significantly increased the astaxanthin production [274]. In addition to being a source of biomass and metabolites, algae are also useful for the environment in several other scenarios, such as in the degradation of organic compounds to sources like nitrogen and phosphorus that are supplements for plant growth and also help in wastewater treatments. Thus, the algal cultivation under the artificially tuned wavelength illuminations also has an impact on these useful scenarios. Blue light treatment given to *S. obliquus* culture efficiently re-

moved phosphorus from the medium, while the mixture of blue and green light was efficient in removing nitrogen from the medium and can thus be useful in wastewater treatment [273]. The blue light was efficient in reducing phosphorus from the medium using *Scenedesmus* sp. and the mixture of red and blue light (7:3) reduced phosphorus and nitrogen content from the medium, increasing the growth rate of *Scenedesmus* sp [275]. *Chlorella* sp. grown in digestate culture with the supplement of biogas was found to upgrade the biogas production and reduce nutrient from digestate under red LED (1200-1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$) [276]. Nutrient reduction of digestate suggests that *Chlorella* sp. under red light could be used for wastewater treatment. Effluent from the dye industry was efficiently degraded by *C. vulgaris* in blue and white LED under laboratory conditions [277].

Light provides input for various physiological responses via photoreceptors. It affects the secondary metabolite accumulation and biochemical compositions that impact the quality and quantity of food. Factors like differences in light intensity and its availability across the different regions greatly impact the crop yield. The seasonal variations and other factors like biotic and abiotic stress restrict the cultivation of several fruits and crops throughout the year. Plant growth under the controlled environmental conditions (light, temperature, CO₂, and humidity) within a small area has come up as an alternative measure to tackle these restrictions, though the control of light parameters through artificial illumination remained a major challenge [278]. Initially, fluorescent lamps, metal halides, low and high-pressure sodium lamps were used as a source of artificial illumination. However, with these lighting systems, a large amount of heat was generated, and irradiance over a narrow wavelength range remained difficult to achieve. However, these issues got resolved with the advent of LEDs. Another advantage that LED provides is precise control over intensity and wavelength [279, 280].

Photoreceptors are key players in mediating various cellular, physiological and morphological responses in plants. CRYs and PHOTs mediate a suite of morphological changes in blue, red, and far-red light and determine the active and inactive state of PHY, directing various responses. UVR8 senses UV-B light and mediates various photomorphogenic responses. UV light treatment has been used to reduce microbial infection. Therefore, optimization of light wavelength, intensity, and duration could greatly increase the production, nutritional value, taste, growth, and flowering time of fruits, vegetables, and crops. Existence of crosstalk among photoreceptors and their pathway suggest that a combination of different wavelength of light will affect the growth parameters of plants. Recently, PHYA and PHOT1 had been shown to interact directly at the plasma membrane in *Physcomitrella patens* [83]. Therefore, maintaining the ratio of blue, red, and far-red will help to improve the plant growth and thus the plant products. Also, the ratio of blue and red light varies during dawn, mid-day, and dusk, and therefore illumination with a specific wavelength at a particular time will also determine the quantity and quality of plant products. Reports suggest that photoreceptors sense not only the light but also the temperature. PHOTs and PHYs both sense temperatures on the basis of a photoactivated state of the chromophore part. Thus, controlling temperature along with light will help

to maximize the yield and quality of plant products. Understanding photoreceptor and their signalling pathway will provide the link between light quality and physiological responses and will enable to define the parameters more accurately.

Lights of different wavelengths in specific or in combinations have been applied to many plant species, and their effects are reported. In most cases, the varying ratio of blue and red has profoundly increased the growth, biomass, nutritional value, phenolic compounds, and antioxidant capacity. Although no photoreceptors are known yet to be able to sense green light, supplementation of green light in some plant species promotes growth. Green light also controls the flowering in ornamental plants like petunia, ageratum, chrysanthemum, and marigold [281]. Flowering in *Arabidopsis* under green light is mediated by CRY2 [281]. Short pulses of UV light not only increased the yield and content of bioactive compounds but also reduced the infection during the storage of potato, tomato, and almonds. The varying ratio of red, blue, and green light increased plant growth, phytochemical content, and nutritional value in microgreens of the Brassicaceae family [282-286]. Parameters like light intensity, wavelength, and duration have been optimized for different groups of plants to enhance the quality of products. Parameters utilized and their effect on a particular plant are summarized in Table 4 below.

Table 4. Effect of light on plant quality and quantity.

Plants	Light Parameters	Effect on Plant
Spinach (<i>Spinacia oleracea</i>)	High light intensity for short period (R:B = 4:1, PPFD = 150 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$, photoperiod = 9/15 hr)	Enhanced taste and nutritional value [287]
	Low light intensity for long period (R:B = 4:1, PPFD = 100 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$, photoperiod = 13/11 hr)	Higher yield [287]
Tomato (<i>Solanum lycopersicum</i> L.)	HSL (420 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$) + R:B = 80%:20%, intensity = 70 Wm^{-2} , duration = 4-22 hr	Faster fruit growth, increased fruit size, and weight [35]
	Supplemental high-intensity red and red + blue light	Increased biomass, yield, higher sweetness, and lycopene content, reduced growing time [28, 36-38]
	Alternate blue (12 hr) and red (12 hr) supplemental light	Improved growth and yield and protected from injury [288, 289]
	Yellow LED (590 nm) during storage	Increased phenolic compound [43]
	UV-B irradiation post-harvest; UV-B treatment during different harvesting stage- mature green and turning	Increased carotenoid and ascorbic acid content; affected the color parameters [290]
	Supplemental UV-B irradiation	Increased flavanol quercetin-3-O- rutinoside (rutin) content [39]
	UV-B irradiation prior to inoculation of ToMV (Tomato mosaic virus) onto leaves of tomato	Suppressed the viral disease without having a damaging effect on plant [291]
	Supplemental UV-A irradiation pre-harvest	Enhanced flavor, aroma, and acidity [39]
Soyabean (<i>Glycine max</i>)	Blue light, PPFD = 150 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$, duration = 16 hr for 3-7 DAS	Enhanced secondary metabolite accumulation [293]
	Far-red light after harvest at 110°C	Enhanced secondary metabolite accumulation [293]
	B: R = 80% : 20%	Promoted plant growth and yield [32]
Strawberry (<i>Fragaria x ananassa</i>)	Blue LED	Enhanced yield [294]

Plants	Light Parameters	Effect on Plant
Lettuce (<i>Lactuca sativa</i>)	R:G+Y:B = 77.1:17.9:5; PPFD = 165.89 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, duration = 14 hr	Enhanced quality and yield [295]
	Supplementation of green to blue and red light	Promotes growth and helps to overcome light stress or unfavorable condition [48]
	Blue, red, and mixture of blue and red	Enhanced photosynthetic efficiency and stomatal characteristics [29]
	Blue, green	Regulates secondary metabolite production [44]
Potato (<i>Solanum tuberosum</i> L.)	%R:B:G = 45:35:20	Increase the number, fresh and dry weight of tubers [40]
	R and FR at low and high irradiance, respectively	Inhibited the elongation of tuber sprouts [296]
	Moderate UV-C treatment when tubers started to sprout	Suppressed the sprout growth [297]
	Treatment of tubers with UV-C followed by storage under fluorescent light	Suppressed the infection by <i>Pectobacterium carotovorum</i> sub sp. <i>carotovorum</i> (wet rot) [47]
	1 hr UV-C treatment followed by storage at 4°C	Prevented the oxidative injury during storage; content of reducing sugar was lowered, and thus cold-induced sweetening (CIS) was reduced [46]
Kale (<i>Brassica oleracea</i> var. <i>acephala</i>)	UV-A (385 nm) treatment for 5 days	Increased dry weight and elevated the level of phenolic compounds and thus antioxidant activity [298]
Sweet red pepper (<i>Capsicum annuum</i> L.)	Red LED	Increased phenolic compounds and plant growth [299]
	Blue light	Increased plant growth, enhanced anthocyanin, and chlorophyll amount [299]
	Yellow LED (590 nm) during storage	Increased antioxidant capacity and bioactive compounds [43]
	R:B = 4:1 for 3 hr	Improved plant growth [300]
Apple (<i>Malus domestica</i>)	Yellow LED (590 nm) during storage	Increased phenolic compounds and antioxidant capacity [43]
Cherry radish (<i>Raphanus sativus</i> L.)	R:B = 2:1, PPFD = 240 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, photoperiod = 16/8 hr	Root diameter and volume were increased; increased biomass and yield [301]
	Red and blue dim lighting (PPFD = 15+/-2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at root-zone)	Enhanced the shoot fresh and dry weight and root dry weight [30]
Rice (<i>Oryza sativa</i> L.)	%R:B:G = 62.5:25:12.5	Root and shoot growth were improved [34]
	%R:B:G = 50:25:25	Root growth and grain yield were improved [34]
	R:B = 4:1, PPFD = 380 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, duration = 12 hr	Increased biomass production [31]
	White and blue light	Enhanced shoot biomass and leaf area; porphyrin metabolite were decreased [302]
Wheat (<i>Triticum aestivum</i> ssp. <i>Aestivum</i> cv. 'MvKikelet')	R:B = 1:1	Shorten flowering time [33]
	B and FR	Affected redox potential mediated by glutathione and proline in leaf [33]
	B, P, and low R	Improved flour quality via maintaining the ratio of glutenins and glutens [33]
Wheat (<i>Triticum aestivum</i> L.)	Continuous spectra (maxima at 445 and 600 nm), PPFD = 82 to 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Increases growth [303]
Welsh onion (<i>Allium fistulosum</i> L.)	W and B LED (PPFD = 300 to 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Photosynthetic efficiency was improved [304]
Hazelnut (<i>Corylus avellana</i> L.)	R and FR	Increased biomass and flavonoid content [41]
Mustard (<i>Brassica juncea</i> L. cv. "Red Lion")	UV-A LED (402 nm, independent of duration)	Increased leaf area and phenolic compound [42]
	UV-A (366 nm for 10 hr and 399 nm for 16 hr)	Increased β -carotene, lutein/zeaxanthin content [42]
Grapes (<i>Vitis vinifera</i> L.)	B-LED	Increased quality of the plant, gene-related to sugar metabolism, chlorophyll synthesis was upregulated; gene related to resistance and auxin repression were downregulated [305]
Almonds (<i>Prunus dulcis</i>)	405 nm LED	Reduced pathogenic and non-pathogenic infection [45]

Abbreviations: R: Red, B: Blue, G: Green, Y: Yellow, P: Pink, W: White, FR: Far-red, PPFD: Photosynthetic photon flux density, DAS: Day after sowing, HSL: High sodium lamp.

6.2. Photoreceptor Engineering for Climate-synchronized Crops

Photoreceptors have a very important role in light sensing and signalling mechanism for different physiological processes. Therefore, to fulfill the needs of the increasing population, biotechnological approaches have been adopted for photoreceptor-engineering to modify agronomically beneficial traits in crops. Details about different approaches applied to photoreceptor engineering are discussed below.

6.2.1. Gene Targeting for Crop Improvement

Since various developmental processes in plants are regulated *via* light, and this suggests that modulation of genes involved in light signalling pathways could be one of the potential methods for seeking enhancements in agricultural crop production [26]. Photoreceptor genes involved in developmental processes are the most suitable target for gene manipulation and crop improvements (Table 5) [306]. Functional genomic studies and other strategies like eco-tilling and broad-scale sequencing have contributed towards the identification of diverseness between various cultivars and landraces [307, 308]. These studies have provided large datasets of molecular heterogeneity among crop plants. Through the identification of natural alleles for a number of photomorphogenic genes and those resulting from crop breeding programs, upregulation/downregulation or transgenics could be helpful in improving agronomic value. Different genome projects for important agronomic crops like rice, soybean, tomato, maize, and others are progressively providing information regarding the use of photoreceptors and/or components signalling pathway to achieve the enhanced yield, fruiting regulation, targeted dwarfing, alteration of shade avoidance response, and ripening of food crops. Genetically Modified (GM) crops also have to face the problem regarding bioethics and safety in the countries that have permitted to utilize the GM crops. Therefore, the acceptance of GM crops has improved productivity and food security to cope with the rapidly increasing demands of the population. However, a lack of global consensus regarding safety concerns to encourage GM crops presents the challenge for increasing crop productivity through other strategies apart from transgenics. Several reports on mutational studies suggested that the upregulation and downregulation of genes could modify the traits without the introduction of any foreign gene. During the past many years, crops have been modified through mutation in a given gene resulting in the change of worthwhile traits [27]. Mutation-derived crop varieties show remarkable traits like shorter growth cycles [25], semi-dwarf habit, drought tolerance, and high disease resistance [309]. Gene targeting strategy is utilized in the study of gene function, moreover also in producing gene knockout or point mutation through the use of different tools such as CRISPR/Cas9, TALEN, *etc.* for crop breeding approach. Apart from transgenics, other screening strategies on a large scale, such as TILLING [307, 308] could couple both random mutagenesis and targeted mutagenesis approaches for

the selection of the desired mutations in different photoreceptor genes for further analysis.

6.2.2. Synthetic Biology Strategies and Biotechnology

For a long time, plant traits that were predominantly focused on increasing yield were targeted to crop improvement. However, the increasing food security issue for the growing population presents a challenge to crop improvement for food and non-food applications. Currently, the traditional approach in connection with mutation-based strategies is being adapted for increasing yield. However, other biotechnological approaches should be included to achieve the multifaceted goal. Synthetic biology has emerged as an achievable strategy for increasing food production, resistance to environmental stress, and biotic agents [24]. Synthetic biology allows the modification of the biological system through the control of gene expression on DNA, RNA, or protein level to show desired phenotypic traits. Gene-editing tools discussed in previous reviews [21, 23, 320, 321] allow DNA sequence manipulation at specific target sites, thereby helping researchers to engineer plant genome with much higher precision than earlier. Recently in the last few years, many crops were successfully engineered for important traits through the synthetic biology approach (Table 6). While designing engineered photoreceptors can be a novel approach for agriculture, it would need different systems for its optimal function [322]. Thus, such a photoreceptor could be utilized to study the effect of light on agronomically important traits.

Therefore, the myriad advancements in photoreceptor engineering strategies have allowed the researchers to modify several beneficial traits in crops through the modulation of different light-mediated signalling pathways. The artificial illumination and genome editing approaches provide a major opportunity for the revolution of agronomic traits in the direction of increasing crop yield and productivity. The emerging technology of artificial illumination using LEDs has improved the production of algal biomass and crop productivity (Tables 4 and 5) by controlling the light pulse and spectral composition [263, 279, 280]. In recent years, photoreceptor engineering technology has made a major contribution in the improvement of key agronomic traits like nutritional quality, disease and herbicide resistance, environmental stress resistance, yield, and productivity of both food and non-food crops (Tables 4-6). The targeted, robust, and more precise genome editing technologies and the novel approach of artificial illumination have provided a new direction in the development of major agronomic traits in food crops like rice, soybean, and a special interest in tomato. The genome-editing technology has enabled the researchers to modify beneficial traits like growth and yield [288, 289, 292], flowering and fruiting time [35, 316, 323], herbicide and disease resistance [291, 324], and improve nutritional status [28, 36-39, 43, 225, 290] in tomato.

Table 5. Agricultural beneficial traits modified in some important crops by altered expression or mutation at a certain locus in photoreceptor genes.

Crop	Photoreceptor	Gene Locus Alteration/Influenced	Traits
<i>Oryza sativa</i>	<i>PHYB</i>	Insertion of single base	Increase in drought tolerance, alleviation of chilling induced photoinhibition [109]
	<i>PHYA</i>	Insertion of <i>Tos17</i> retrotransposon	Resistance from blast fungus related to plant age [310]
	<i>PHYB</i>	Insertion of single base	Reduction in plant height and increase in grain yield [106] Delay in flowering under long and short-day condition [100]
	<i>PHYC</i>	Insertion of <i>Tos17</i> retrotransposon	
	<i>PHYA</i>	Transgene at PHY, an overexpression	
	<i>CRY2</i>	Gene silencing of CRY2	
<i>Zea mays</i>	<i>PHYB2</i>	Deletion	Acceleration of long and short day flowering [311]
<i>Triticum</i> sp.	<i>PHYC</i>	Nonsense mutation single base substitution	Acceleration of long day flowering [312]
<i>Hordeum vulgare</i>	<i>CRY1a/b</i>	Downregulation of gene expression	Increased germination percentages [313]
<i>Solanum tuberosum</i>	<i>PHYA</i>	Increase in gene expression	Increased tuber formation [314]
	<i>PHYB</i>	Enhancement of gene expression	Increased yield of tuber at high densities of planting [315]
<i>Solanum lycopersicum</i>	<i>CRY2</i>	Increase in gene expression	Enhanced fruit pigmentation and lycopene content [225] Accelerating transition of fruit ripening stages [316]
	<i>PHYA</i>	Transition of single base	
	<i>PHYB1</i>	Nonsense mutation	
	<i>PHYB2</i>	Nonsense mutation, three base substitutions	
<i>Glycine max</i>	<i>PHYA3</i>	Deletion of 40 bp	Early plant flowering and fruit (pod) maturation [317]
	<i>CRY1a</i>	Enhancement of gene expression	Early plant flowering [103]
<i>Fragaria ananassa</i>	<i>PHOT2</i>	Overexpression of Fa PHOT2	Increase in anthocyanin content in leaves and fruits [318]
<i>Brassica</i> sp.	<i>CRY1</i>	Increase in gene expression	Reduction in plant height [159]
<i>Pisum sativum</i>	<i>PHYA</i>	Substitution of single base	Early photoperiod-independent flowering [319]

Table 6. Agronomically beneficial traits in some important crops modified by the application of genome editing technologies.

Crop	Tool Used	Gene Targeted	Traits
<i>Oryza sativa</i>	Transcription activator-like effector nucleases (TALENs)	Rice bacterial blight susceptibility gene (<i>Os11N3</i>) mutation	Disease resistance [322]
<i>Solanum lycopersicum</i>	Cluster regularly interspaced short palindromic repeat and CRISPR-associated protein 9 (CRISPR/Cas9)	Self-pruning 5G (<i>SP5G</i>) gene with a null mutation Downy mildew resistance 6 gene orthologue with frameshift deletion in exon 2 & 3 in tomato (<i>SIDMR6-1</i>)	Early flowering, early fruit ripening [323] Broad-spectrum disease resistance [324]
<i>Solanum tuberosum</i>	TALENs	Vacuolar invertase gene (<i>Vinv</i>) knockout	Improve reducing sugar amount and cold storage in tubers [325]
<i>Glycine max</i>	TALENs	Fatty acid desaturase 2 genes (<i>FAD2-1A</i> & <i>FAD2-1B</i>) mutation	Improve the soil quality [326]
<i>Triticum</i> sp.	TALENs	Mildew resistance locus gene homoallele knockout in wheat (<i>TaMLO-1</i> , <i>TaMLO-2</i> , <i>TaMLO-3</i>)	Heritable resistance to powdery mildew [327]
<i>Zea mays</i>	Zinc finger nuclease (ZFN)	Inositol-1,3,4,5,6-penta-kisphosphate-2-kinase encoding gene (<i>IPK1</i>) insertional disruption Phosphinothricin acetyltransferase (<i>pat</i>), aryloxy alkanoate dioxygenase (<i>aad1</i>) encoding herbicide resistance genes stacking	Multiple herbicides tolerance [328] Multiple herbicides resistance [329]
	Meganuclease	Maize sterility gene (<i>MS26</i>) with a mutation in 5 th exon	Male sterile plants production [330]
<i>Gossypium</i> sp.	Meganuclease	4-hydroxyphenylpyruvate dioxygenase gene (<i>hppd</i>), enol-pyruvylshikimate-3-phosphate synthase gene (<i>epsps</i>) stacking	Herbicide tolerance [331]

Photoreceptor engineering using synthetic biology tools produces targeted modification (TagMo) in the plant genome. TagMo engineered crops are categorized according to regulation: with foreign DNA insertion from sexually compatible or incompatible species, no DNA inserted and having the deletion in part of chromosome or inactivation of the gene, modified gene or alteration in gene sequence [332]. Crops modified using TagMo with the insertion of the foreign gene are similar to the genetically modified (GMO) crops; however, it allows the insertion of foreign DNA at the target site, and if the target site of foreign gene insertion is characterized for not having any negative consequence on crops, then regulatory requirements to characterize gene insertion site can be restructured [332]. TagMo engineered crops with gene knockout and altered gene, providing great importance in the elimination of undesired traits; however, the gene knockout and altered gene sequence might produce a non-sense RNA or truncated polypeptide in some cases. Therefore, further research is mandatory in this direction to study the off-targets modification and toxicity tests. To study undesired modification in the genome, whole-genome profiling, gene surveillance, and post-release monitoring could be adopted [333, 334].

TagMo technology could provide better acceptability with desirable features for improved crop yield and productivity; however, it produces indistinct boundaries with genetically modified organism regulation. Therefore, the crops modified through genome editing may present major issues regarding safety concerns for social acceptance [332, 335]. The genome editing technologies allow plant breeding to have genetically modified crops without having “foreign” transgenes, hence avoiding the unwanted gene integration in the plant genome and bypassing the GMO regulations. Countries like Argentina adopted a resolution in 2015 to rule out the crops that are not having foreign DNA from product-based GMO regulation. However, contrary to that, New Zealand amended its process-based regulations based on court judgment in 2016 for the regulation of gene-editing without the integration of foreign DNA [334]. It is not appropriate to consider all gene-editing produced crops for the subject of GMO regulations as there is no health risk associated with some TagMo-derived crops. Therefore, amendments are required in GMO regulations on the scientific basis for the social acceptance of crops produced from the gene-editing approach. Amendments should include social deliberations for increasing awareness and clarity about the crops derived from different approaches like old transgenic, random-mutagenesis, and new gene-editing among consumers [334]. The advancements in the development of key beneficial traits in crops through the engineering of various photoreceptors provide an efficient strategy for increasing crop yield and productivity.

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

Previous findings have demonstrated the role of light in modulating various important signalling pathways in plants. Here, we have reviewed the role of PHOT in plants and its

associated signalling processes like metabolite accumulation, phytohormone biosynthesis [18, 19], and its cross-talk with other photoreceptors. Photoreceptor engineering with various advanced strategies has been used as a novel approach for regulating plant growth and development. Photoreceptor biotechnology through the genome editing method is proved to be a highly significant tool in the development of various beneficial traits in crop varieties [21, 22, 24]. The emergence of the artificial illumination approach has led to the adaptation of LED technology for modulating light exposure to plants [279] for biotechnological avenues. Combinatorial strategies for light quality, quantity, and duration using sustainable LED technology result in the alteration of plant morphological, physiological, and yield [28, 279]. Photoreceptor signalling is well studied in *Arabidopsis*, few crops, and green algae, and hence, photoreceptor modulation can be further applied for the development of useful traits in crop varieties. Safe genome editing could also be used in the future for the manipulation of other photoreceptor encoding genes in order to study signalling mechanisms of different photo-physiological processes in important crops. Photoreceptor(s) modulation through artificial illumination technology holds the sustainable potential for the manipulation of metabolic pathways in plants and the development of climate-smart crops.

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CONFLICT OF INTEREST

The authors declare no conflict of interest, financial or otherwise.

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