New horizons in light control of plant photomorphogenesis and development

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Light from Sun has tremendously shaped the evolution of plants and represents one of their key triggers for proper morphogenesis and development. Energy from Sun light is converted by photosynthesis into chemical energy that ultimately drives all energy consuming processes in plants. Besides, Sun light provides information about environmental conditions or constraints and signals important parameters such as day length, time point of season, direction and intensity of illumination or spatial competition with neighbouring plants. Plants possess a sophisticated array of photoreceptors that perceive this information (photoperception) and initiate signalling pathways that control appropriate responses at developmental or physiological level. While the primary processes of photoperception are largely understood, many aspects of the subsequent signalling networks are still elusive and especially the interaction with other signalling networks is far from understood. Light represents also a highly versatile tool for scientists to study morphogenesis and development of plants by a steadily increasing number of remote sensing technologies that allow to observe plants in real time and high resolution (photodetection). Further, scientists now can even use the knowledge about photobiology and photoreceptors to construct synthetic tools that can be genetically introduced into plants to monitor internal processes (so-called biosensors). Recent technological developments in optogenetics even allow to generate tools that actively regulate gene expression or metabolism by selective illumination (photocontrol). In this perspective article we highlight progress in our understanding of light signalling and a number of selected technological improvements in photocontrol with a special focus on the areas of phytochrome signalling and plant optogenetics.

KEYWORDS

light signalling, photomorphogenesis, molecular networks, photocontrol, optogenetics

Introduction

Light is one of the most fundamental abiotic factors controlling and influencing growth, development and survival of plants. It is, however, of dual significance as it serves as reporter of environmental conditions that are detected by specific photoreceptors and, at the same time, as energy source for photosynthesis. Thus, it triggers multiple developmental responses and provides also the required energy for the underlying cellular activities. Further, both photo-controlled development and photosynthesis are affected in parallel by other external factors, notably temperature, which may change, modify or even block light-triggered cellular activities. This asks for integrated research approaches that respect the manifold spatio-temporal interactions and interceptions of various external factors with the light-controlled processes in plants. While the molecular structure and physiological involvement

of photoreceptors is largely understood, many aspects of their regulation and their effective role in molecular signalling networks are still under investigation. Here we highlight some recent breakthroughs of our knowledge in these fields of research and provide a number of perspectives on promising technological improvements in the area of plant photobiology.

Novel factors in phytochrome signalling networks

Plants sense environmental light information via an array of photoreceptors that detect specific wavelengths in the UV/blue and red light range which largely overlap with the photosynthetic active radiation (400–700 nm). The group of UV/blue light receptors comprises UVR8, Cry1-3, Phot1 and 2 and members of the ZTL family which are involved in a vast range of physiological responses including UV stress response, light intensity reactions, chloroplast movements, stomata opening control, circadian rhythmicity and photoperiodic control of flowering and development (Ponnu and Hoecker, 2022). Many of these photoreceptors have orthologues in bacteria, fungi and animals indicating a common evolutionary origin. The group of red light photoreceptors comprises the family of phytochromes, a plant specific photoreceptor family with cyanobacterial ancestry (Lamparter, 2004). They control essential developmental steps such as seed germination, photomorphogenic programs of seedling development or shade avoidance reactions in dense plant stands with high competition for incident light (Cheng et al., 2021).

Upon illumination, phytochromes (Phys) convert from their inactive Pr-to their active Pfr-form, enter the nucleus and form so-called photobodies (PBs) via interaction with other proteins (Figure 1). Phy target proteins, such as Phytochrome interaction factors (PIFs) 1 and 3, are then degraded releasing the PIF-dependent repression of photomorphogenesis (PM) genes. Simultaneously, Phys disrupt the CONSTITUTIVE PHOTOMORPHOGENIC1/SUPPRESSOR OF PHYA-105 (COP1/SPA1) mediated degradation of PM-promoting factors, such as ELONGATED HYPOCOTYL 5 (HY5) and HY5-HOMOLOG (HYH) (Lu et al., 2015; Sheerin et al., 2015). PBs can be directly observed by microscopy in *Arabidopsis* lines stably transformed with green fluorescence protein (GFP) tagged PhyB (PBG) (Yamaguchi et al., 1999). They exhibit dynamic changes in size and number during PM and likely form microdomains where
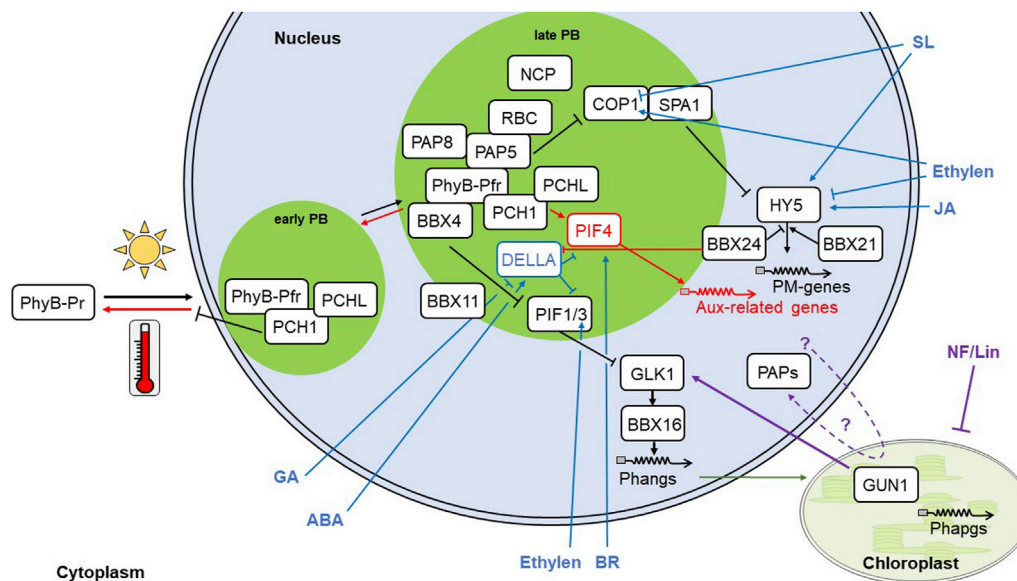

FIGURE 1
Regulators and signalling pathways in PM. Light triggers PhyB-Pr-photoconversion into its active form Pfr. Pfr translocates to the nucleus and forms early nuclear PBs. PB-formation is supported by PCH1 and PCHL, which prevents thermal backconversion of Pfr into Pr. Prolonged illumination initiates late PB formation, which is dependent on PAP5 and its interaction partners PAP8, RBC and NCP as well as the B-Box proteins BBX 4 and, likely, BBX11. Within PBs, PIFs are hampered in binding to their target genes and become degraded, thus, releasing their repression of PM genes, such as GLK1, which mediate gene expression of Phangs through BBX16. Simultaneously, COP1/SPA1 become inactivated, leading to the stabilization of HY5 protein and subsequent expression PM genes. HY5 expression is positively regulated by BBX21 and negatively by BBX24. The concerted expression of PIF and HY5 target genes leads to repression of hypocotyl elongation and activates cotyledon opening. Further, nuclear and plastid encoded photosynthesis associated genes (Phangs, green arrow; and Phapgs) are expressed and induce the build-up of chloroplasts. The PM pathway (black arrows) can be altered through other pathways that converge at distinct points. High ambient temperatures induce thermomorphogenesis (red symbols) by scaling up thermal conversion of Pfr, thus stabilizing PIF4, which in turn induces expression of auxin-related genes leading to cell elongation. This pathway largely coincides with the shade avoidance response. Retrograde signalling (violett arrow) is mediated through GUN1, which, together with GLK1 act on BBX16 and Phang expression. Phytohormones are not only regulated by the PM pathway, but regulate also PM (dark blue arrows). GA (gibberellic acid) reduces and ABA (abscisic acid) induces DELLAs, which in turn repress PIFs. Under high ambient temperatures, however, BBX24 binds to DELLAs and derepresses PIF4 action. Through BRZ1, BR promotes PIF4 action. SL (strigolactones) retain COP1 in the cytoplasm and promote HY5 expression. Ethylene promotes nuclear COP1 localization, stabilizes PIFs and leads to HY5 degradation. JA (jasmonic acid) through the MYC2 transcription factor promotes HY5 expression. Protein symbols that are in contact represent experimentally shown interaction. Lines with arrow heads represent promotion, lines with block represent repression. NF, Norflurazon; Lin, Lincomycin; Aux, auxin; BR, brassinosteroids. For other abbreviations see text.

regulator proteins condense and jointly participate in the initiation and regulation of PM. The physical nature and protein composition of PBs remained elusive for long time, but recent reports shed more light on their structure. PBs appear as discrete, but not membrane-delineated bodies within the nucleus and are formed due to liquid-liquid phase separation (LLPS) of PhyB (Chen et al., 2022). Isolation of PBG-particles using fluorescence-activated particle sorting (FAPS) combined with mass spectrometry identified proteins associated with PB formation or marked for PB-mediated degradation (Kim et al., 2023). This included direct PhyB interaction partners as well as proteins indirectly recruited to PBs. However, several PhyB interaction partners known to influence PB-formation (see below) where not identified. Either i) these proteins were too low abundant under the experimental conditions, or ii) the size-selection of FAPS was too stringent to deal with the size dynamics of PBs, or iii) PB protein composition varies in response to internal or external stimuli (light conditions/shading/daytime/daylength/temperature/hormones/tissue) (Geilen and Bohmer, 2015; Legris et al., 2016; Hahm et al., 2020) or iv) they are involved in PB-formation without being a structural component of it. Future PB-isolation from plants grown under different conditions, thus, is needed to solve these questions.

During PM-initiation, early PB formation relies on the presence of PHOTOPERIODIC CONTROL OF HYPOCOTYL1 (PCH1) and likely its homologue PCH1-LIKE (PCHL) (Huang et al., 2019). PCH1/PCHL promote PM through the stabilization of PBs by inhibiting the thermal reversion of Pfr to Pr (Enderle et al., 2017; Huang et al., 2019). Further, the formation of late PBs depends on the presence of a number of novel regulators including PLASTID-ENCODED RNA POLYMERASE (PEP) ASSOCIATED PROTEIN 5 (PAP5)/Hemera and PAP8/pTAC6 (Chen et al., 2010; Liebers et al., 2020). Inactivation of these regulators blocks the transition from early to late PBs indicating that the structural dynamics of PBs are required for PM. PAPs are 12 nuclear-encoded plastid proteins that are crucial for the formation of the PEP-complex and the proper build-up of chloroplasts (Pfannschmidt et al., 2015). However, six PAPs, including PAP5 and PAP8, contain a nuclear localization signal that permits them to enter the nucleus and to participate in PB-mediated PM control providing nucleo-plastidic regulation of chloroplast build-up (Pfannschmidt et al., 2015; Chambon et al., 2022). Interestingly, both nuclear and plastid versions of PAP5/Hemera and PAP8/pTAC6 display similar sizes suggesting a plastid passage for removal of the chloroplast transit peptide in both protein versions (Chen et al., 2010; Liebers et al., 2020). Similar observations were reported also for other proteins (Grabowski et al., 2008; Isemer et al., 2012; Yang et al., 2019; Yoo et al., 2019). Whether or not this hypothesis holds true requires further investigations and a number of potential export mechanisms from plastids have been discussed (Krause et al., 2012).

Two further dually localized proteins, NUCLEAR CONTROL OF PEP ACTIVITY and REGULATOR OF CHLOROPLAST BIOGENESIS (NCP and RCB), were identified in a genetic screen (Yang et al., 2019; Yoo et al., 2019). Both are connected to PB-controlled PM since RCB was shown to interact with PAP5/Hemera, and ncp as well as rcb mutants lost the ability to form late PBs. Furthermore, null alleles of these mutants display phenocopies of PAP-inactivation mutants. Interestingly, inactivation of all four PIFs (pifq) releases nuclear repression of hypocotyl elongation of

pap5/hemera, rcb and ncp (Qiu et al., 2015; Yang et al., 2019; Yoo et al., 2019). The build-up of the PEP-complex, however, remains impaired in pap and ncp mutants and the plants stay albino (Qiu et al., 2015; Yang et al., 2019; Liebers et al., 2020). Rcb-mutants, in contrary, are able to form a PEP-complex and start to green (Yoo et al., 2019). Thus, PAPs and NCP affect PM both, through nuclear and plastid signaling events. RCB on the contrary seems to modulate PM mainly from the nucleus.

Another group of recently identified proteins involved in PM are B-box-type zinc finger domain proteins (BBX). Arabidopsis contains 32 BBX, contributing to various pathways, such as seed germination, flowering and circadian rhythmicity, and are involved in light signaling. BBX4 and 11 are able to interact with PhyB and PIFs (Heng et al., 2019; Song et al., 2021) pointing to a basal function in early PM. Interestingly, BBX4 is recruited to PBs through its interaction with PhyB, enhancing PhyB-promoted PIF3 degradation (Heng et al., 2019). In addition, BBX4 and 11 directly interact with PIFs preventing their binding to target genes. Similar interference with transcription factors was found further downstream in PM-signaling. The positive regulator of PM, BBX21, binds to the HY5 promoter and promotes HY5 expression, while the negative regulator of PM, BBX24 interacts with HY5 in order to prevent the HY5 association to its target gene chalcone synthase (Job et al., 2018; Xu et al., 2018).

The precise functional significance of PBs, however, remains unclear, since mutants lacking PCH1, PAP5, PAP8, NCP or RCB are still able to repress hypocotyl growth, de-hook, and open cotyledons upon illumination (Chen et al., 2010; Huang et al., 2016; Yang et al., 2019; Yoo et al., 2019; Liebers et al., 2020). It is feasible that PBs represent a protein interaction platform that may facilitate rapid reactions and a lack maybe only decelerates PM. Further, similar PB dynamics can be involved in apparently conflicting physiological reactions. Light and high ambient temperatures decrease the number of PBs, while their size increases. However, light triggers also formation of Pfr, which represses elongation growth, while higher ambient temperatures promote conversion to Pr and, thus, elongation (Van Buskirk et al., 2012; Hahm et al., 2020). Shade avoidance on the other hand involves hypocotyl elongation, similar to thermomorphogenesis (TM), however, in stark contrast to TM with a multitude of small PBs, comparable to the mutants of hmr-5, pap8, rcb and ncp (Chen et al., 2010; Trupkin et al., 2014; Yang et al., 2019; Yoo et al., 2019; Hahm et al., 2020; Liebers et al., 2020). In addition, PB dynamics seem also to depend on tissue-identity (Hahm et al., 2020). It, thus, remains to be investigated whether PBs of same size but found in different conditions are comprised of identical components.

Integration of light control with other signalling networks

Light signaling is intimately linked to phytohormone signaling at multiple levels. For instance, Phys mediate the breaking of seed dormancy through PHYTOCHROME INTERACTING FACTOR 3-LIKE 5 (PIL5) that directly controls transcription regulators of gibberellic acid (GA) and abscisic acid (ABA) (Oh et al., 2009; Seo et al., 2009). Phototropism relies on Phototropin-induced changes in auxin transport and might be enhanced by PhyA (Han et al., 2008;

Liscum et al., 2014) and COP1 modulates root growth through changes in shoot-to-root auxin transport by repressing PIN1 transcription, as well as intercellular distribution of PIN 1 and 2 (Sassi et al., 2012). Interestingly, several important components of the light signaling network do not only combine light and hormone signaling, but are also responsive to both stimuli. PIF3 and PIF4 are post-translationally regulated by GA through DELLAS (de Lucas et al., 2008; Feng et al., 2008; Li et al., 2016) and by ABA through modulation of GA and DELLAS (Lorrai et al., 2018). At the transcriptional level, PIF4 was shown to be regulated by brassinosteroids via the transcription factor BRASSINAZOLE RESISTANT 1 (BZR1) (Bernardo-Garcia et al., 2014; Ibanez et al., 2018). Strigolactones retain COP1 in the cytoplasm and promote HY5 expression via MORE AXILLARY GROWTH 2 (MAX2) (Tsuchiya et al., 2010; Jia et al., 2014) and ethylene stabilizes PIFs and nuclear localization of COP1 in the light and induces HY5 degradation (Zhong et al., 2012; Yu et al., 2013). Jasmonic acid regulates HY5 transcription via the transcription factor MYC2 (Ortigosa et al., 2020). In roots, auxin negatively regulates greening due to the repression of HY5, while cytokinin promotes greening through the transcription factors GATA, NITRATE-INDUCIBLE, CARBON-METABOLISM INVOLVED -like (GNL) and GOLDEN-like 2 (GLK2) (Kobayashi et al., 2017). Further, HY5 is also involved in germination (Chen et al., 2008; Yadukrishnan et al., 2020), entrainment of the circadian clock (Andronis et al., 2008; Hajdu et al., 2018), root development (Zhang et al., 2019; Duan et al., 2021) and flowering (Bhagat et al., 2021; Chu et al., 2022).

Also BBX have multiple connections to phytohormones. For instance, BBX24 mediates shade avoidance by binding to DELLA-proteins, which are negative regulators of GA signaling, and thus, prevent PIF4 repression. Furthermore, GA-treatment can even rescue the short hypocotyl-phenotype of *bbx24* under low R:FR (Crocco et al., 2015). In rice, BBX8 and 30 expression is not only regulated in response to light-dark-cycles, but also to GA, auxin and cytokinin (Huang et al., 2012). BBX21 antagonizes ABA-induced stomata closure, since *bbx21* mutants are hypersensitive to ABA and show reduced stomata opening (Xu et al., 2014).

BBX connect light signaling also to retrograde signaling from plastids. BBX16 was reported to be regulated by GUN1 and GLK1 and to promote the expression of nuclear photosynthesis genes (Veciana et al., 2022). Interestingly, this protein was also found to be downregulated, whenever chloroplast biogenesis is blocked, either by chemical treatment or genetic inactivation (Grubler et al., 2021). Additionally, BBX16 also integrates shading signals. Thus, many PM regulators are active at key events of the light signaling cascade and seem to integrate several external and internal signals, such as light, shading, phytohormones and biogenic retrograde signals in order to fine-tune the growth response of the plant in accordance with the prevailing conditions.

Another important signal, that is integrated into the light signaling network are changes in temperatures. Thermomorphogenesis (TM) is an architectural reprogramming initiated upon high ambient temperatures that induces morphological changes, such as increased hypocotyl and petiole elongation, hyponastic growth as well as early flowering, in order to circumvent negative heat effects through cooling (Quint et al., 2023). High ambient temperatures can be sensed by PhyB due to increased kinetics of their thermal back conversion from the active Pfr to the inactive Pr form. As a consequence, repression on PIF4 is released and emanates in the PIF4-mediated elongation of hypocotyls and petioles due to the induction of auxin biosynthesis and signalling, therefore, coupling TM and hormone signalling. PIF4 regulation, however, is influenced by many factors both on the transcriptional and the (post)-translational level and many signalling pathways converge. Thus, PIF4 might represent another integrator for biotic signals and fine-tune their responses.

As an important consequence, the different signaling networks should not be viewed separately. In laboratory conditions often only one parameter (the one of researcher´s interest) is changed, while the others are kept constant by active technological regulation. In nature, however, major environmental parameters often change in conjunction with others, a connection that often is not reflected in experimental set-ups generating potentially conflicting or misleading results. For instance a prolonged increase in ambient temperature in nature is often accompanied by low water availability. This could highly affect the physiological output, because TM is accompanied by stomata opening to provide cooling (Kostaki et al., 2020). Open stomata, however, would favor higher transpiration rates, which is counterintuitive under drought. Similarly, increased temperatures have strong negative effects on light-induced repression of hypocotyl elongation (Gray et al., 1998). Also circadian gating (Salter et al., 2003) and day length impacts positively hypocotyl elongation. The *pap5/hmr* mutant exhibited strong repression of TM-induced hypocotyl elongation in continuous red light, which was partially abolished in short and long day conditions (Qiu et al., 2019).

In sum, several parallel factors should be considered in future research including the question whether some signals are more prominent than others. For instance, Pfr converts to Pr under high ambient temperatures. PCH1, however prevents thermal conversion of Pfr (Huang et al., 2019). But how both signals interact and which signal dominates remains to be investigated. It also needs to be considered that also the ecotype of the test organism could have an effect on the results. Indeed, thermal responses were shown to vary between *Arabidopsis* traits (Sanchez-Bermejo et al., 2015). It is, thus, likely that also crop plants vary in their temperature responses depending on their (ancestral) origin and line of breeding.

Light as technological tool to understand plant development and physiology

Light as carrier of information is used by plants to sense the state of critical environmental conditions and dynamic changes in it (photoperception). Light, however, also provides a tool for researchers to obtain information about endogenous processes in plants (photodetection) and to even gain control over gene expression, metabolism and development (photocontrol). In recent years, there was lot of technological progress in the areas of photodetection and photocontrol that allow to tackle scientific question by fully novel approaches.

Photonic detection technologies based on fluorescence or bioluminescence became of fundamental importance in life sciences as they allow to analyze biological processes in lifetime without

destructive impact on the object of study. A well-established method in plants represents the measurement of chlorophyll a (Chl) fluorescence (Maxwell and Johnson, 2000). It exploits the red autofluorescence of illuminated Chl to obtain *in vivo* information about the functional (and in some aspects structural) state of the photosynthetic apparatus (Kramer et al., 2004) and are also used for the physiological characterization of plants including their responses to environmental fluctuations or stressors (Kalaji et al., 2014; Kalaji et al., 2017). The invention of the pulse-amplitude modulation (PAM) technology even allowed the determination of such information in presence of ambient light (Schreiber, 1983; Bilger et al., 1995), a general problem for the usage of photonic-based research approaches (see also below). Recent development of other remote sensing technologies such as hyperspectral imaging, nuclear magnetic resonance imaging, mass spectrometry imaging and infra-red spectroscopy imaging even further expand the possibilities to investigate endogenous processes of plants providing a whole set of novel approaches for plant phenotyping (Saric et al., 2022; Borisjuk et al., 2023).

Such external photodetection of biological processes is complemented by intracellular *in vivo* monitoring of spatio-temporal variations using genetically encoded biosensors that typically are based on fluorescent proteins or enzymes catalyzing bioluminescent reactions. Such biosensors can be used to detect for instance the redox state of antioxidant metabolite pools, reactive oxygen species (ROS), Ca^{2+}, and K^+ ion concentrations, pH and many more parameters, but also the time-dependent localisation of proteins or hormone effects. This field has seen tremendous progress in the last decade and provides an extensive toolbox to study biological processes in high resolution and in all four dimensions (Isoda et al., 2021; Schwarzlander and Zurbriggen, 2021; Molinari et al., 2023).

Our understanding of functional components and mechanistic connections in light signalling at the molecular level has reached a niveau that allows to get beyond fundamental research of photoperception and to use this knowledge for the construction of optogenetic tools. While this field of science has tremendous success in various areas of the life sciences such as neuroscience or animal research, optogenetics in plants is lagging behind mostly because of interference with plant internal light-dependent processes (Christie and Zurbriggen, 2021; Konrad et al., 2023). Major obstacles in the past were the principle requirement of plants for light as energy source in photosynthesis (requiring growth under light/dark cycles) as well as the sophisticated internal light signalling networks that show high degrees of redundancy providing high compensation capabilities of genetic manipulations. More importantly, the lack of retinal in plants hampered the technological development of rhodopsin-based optical switches, e.g., the implementation of channelrhodopsins that were used with great success in neurosciences (Miller, 2006). Optogenetic tools, however, provide a number of advantages over chemical inducible systems and there is a strong interest in the establishment of such tools for plant research (Omelina et al., 2022).

Recent approaches combining the progress in LED-based illumination technologies with smart molecular solutions of synthetic biology provided several important improvements in plant optogenetics. The availability of cost-efficient LED arrays equipped with combinations of narrow band-width LEDs allowed the establishment of highly flexible and defined illumination solutions in plant growth technologies that are superior to earlier

standard light sources with coloured filters. Using these in combination with genetic constructs comprising specific light responsive *cis*-elements and corresponding *trans*-acting proteins or protein domains (either as activator or repressor) generate molecular switches that do nicely work in plants. The research field benefits a lot from the progress in synthetic biology and the principles in engineering synthetic orthogonal gene circuits with sensor, processor and actuator modules in which the components of the circuits show only minimal interaction with endogenous signalling pathways or networks (Vazquez-Vilar et al., 2023).

The reversible *cis/trans* isomerisation of phytochromes upon red/far-red illumination shifts provides a natural optoswitch that was used to engineer a first optogenetic tool for control of gene transcription in yeast (Shimizu-Sato et al., 2002). In plants the first optogenetic tool has been constructed as a split transcription factor module from the N-terminus of PHYB fused to the viral transactivator VP16 and the N-terminus of PIF6 fused to an *E. coli* repressor protein. The system restores a functional transcription factor upon red light illumination and is switched off by far-red illumination allowing to control gene expression upon corresponding illumination switches (Muller et al., 2014). It bears, however, the risk that the endogenous phytochrome system is also affected by the light regime. This can be overcome by using optogenetic switches that work in the green wavelengths range where plants do exhibit a light detection gap of their photoreceptor systems. The transcription factor CarH from *Thermus thermophilus* is naturally activated by green light. It was used to engineer a switch in *Arabidopsis* protoplasts that terminates transcription from a synthetic binding site/promoter construct upon green light illumination (Chatelle et al., 2018). Disadvantage of this system is that CarH requires adenosylcobalamin as chromophore. Since this vitamin B12 derivative is not produced in plants, it must be exogenously added preventing effective use in whole plants unless the corresponding biosynthetic pathway is engineered in them. An alternative might be the orange carotenoid protein family from cyanobacteria that perform conformational changes separating N- and C-terminal domains upon illumination with blue-green light. This behaviour was exploited to engineer a heterodimerization switch in which the domain separation allowed chloroplast transcription initiation by the plastid Sigma factor 2 in *Arabidopsis* protoplasts. However, also this system requires a chromophore not produced in plants (i.e., keto-carotenoids) and, hence, the engineering of ketocarotenoid production (Piccinini et al., 2022).

Recently, an optogenetic switch in plants could be constructed that is blind to ambient white light allowing to express genes on demand by illumination with a discrete wavelength (Ochoa-Fernandez et al., 2020). To this end two photoswitches controlling a synthetic promoter construct were combined comprising a blue-light off switch and a red-light on switch. The system allows vegetative and regenerative growth of plants in light chambers and greenhouses since the blue wavelengths in white light prevent any expression. Only under monochromatic red light the system (dubbed plant-useable light switch element (PULSE)) will be activated providing a versatile tool to control signalling and metabolic networks in whole plants and has been also successfully combined with CRISPR-Cas based tools (Ochoa-Fernandez et al., 2020). The PULSE system, therefore, provides a highly promising approach for future fundamental research and biotechnological applications under dark/white light cycles.

One major field in optogenetics is the control of ion fluxes over membranes using channelrhodopsins. Depolarization/hyperpolarization is also in plant cells of high relevance, for instance in the control of stomata aperture and plant transpiration. However, plants do not produce retinal leading to degradation of opsins (Ullrich et al., 2013). Recently, this problem could be overcome by introduction of a plastid-targeted marine bacterium dioxygenase that converts plastidial β-carotene (the precursor) into retinal. The stable chromophor availability allowed the expression of the light-sensitive anion channel GtACR1 and subsequently green-light stimulated membrane potential changes in pollen tubes and guard cells resulting in corresponding physiological reactions (pollen tube bending or stomata closure, respectively) (Zhou et al., 2021).

In sum, major obstacles for wide application of optogenetics in plants has been removed now. One highly interesting future application will be the combination of optoswitches with specific biosensors providing the possibility to study physiological effects of light-induced cellular manipulations in real time, both at cellular and tissue level. Such research may pave the avenue for future applications in the field to control decisive developmental transitions or improved acclimatory responses to environmental constraints in crop plants.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

ML: Conceptualization, Writing–original draft. TP: Conceptualization, Funding acquisition, Writing–original draft.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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