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Review article

Brassinosteroids (BRs) and photomorphogenesis: Hormonal regulation of light-mediated plant development

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ABSTRACT

To adapt to varying environmental conditions, plants have developed complex mechanisms to optimize growth and development throughout their lifecycles. Light is the primary energy source that drives photosynthesis and act as an environmental signal, which is involved in regulating various plant physiological functions. Plants detect changes in external light conditions through multiple photoreceptors. Photomorphogenesis is characterized by the opening and expansion of the cotyledon, suppression of hypocotyl elongation, and the development of proplastids into fully mature chloroplasts in response to light. The Brassinosteroids (BRs) are polyhydroxylated steroidal hormones—important for plant growth, development, and productivity, including photomorphogenesis. While promoting hypocotyl elongation, BRs fine-tune light-responsive photomorphogenesis in plants. Since BRs are eco-friendly and non-toxic phytohormones, they promote plant adaptability to changing environmental conditions and various biotic and abiotic stresses, thereby maintaining ecological equilibrium. Light and BR antagonistically regulate the transition from skotomorphogenesis in darkness to photomorphogenesis in light. Photomorphogenic repressors, such as Arabidopsis (*Arabidopsis thaliana*) G-protein β subunit (AGB1), PHYTOCHROME-INTERACTING FACTORS (PIFs), and CONSTITUTIVELY PHOTOMORPHOGENIC PROTEIN 1 (COP1), have been reported to enhance BR response, whereas factors that promote photomorphogenesis, including NF-YCs, *bzr1–D* suppressor1 (BZS1), and ELONGATED HYPOCOTYL 5 (HY5), have been reported to inhibit BR signaling. BRASSINAZOLE RESISTANT 1 (BZR1) and BRASSINOSTEROID-INSENSITIVE 2 (BIN2) cross-talk with the transcription factors (TFs), playing a crucial role in the light signaling pathway to orchestrate photomorphogenesis. This review discusses BRs, photomorphogenesis, and the interaction between photoreceptors and BRs. It outlines the physiological roles of BRs in plant development during photomorphogenesis and elucidates the molecular mechanism of BRs in regulating photomorphogenesis.

1. Introduction

Light is one of the essential elements to sustain the normal growth, development, and survival of plants. In addition to the primary source of energy for photosynthesis in plants, light governs various processes throughout their lifecycle, including seed germination, stem elongation, seedling photomorphogenesis, seedling etiolation, lateral root growth, phototrophic growth, flowering time, shade response, and circadian rhythm (Dai et al., 2024; Hao et al., 2023; Heijde and Ulm, 2013; Kami et al., 2010; Wu et al., 2025). Light-mediated growth allows plants to adjust to challenging environmental conditions (Wu et al., 2025). Upon germination, plants have developed two distinct and complex strategies to adapt to a variety of dark and light conditions (Jiao et al., 2007; Kami et al., 2010). In the dark, plants experience skotomorphogenesis (etiolation/dark-grown development), characterized by closed cotyledons, elongated hypocotyls, apical hooks, and etioplasts. On the other hand, plants that are exposed to light undergo a process called photomorphogenesis (de-etiolation/light-grown development), which is characterized by opened and expanded cotyledons, short hypocotyls, formation of mature chloroplasts for greening, autotrophic growth, and the production of photosynthetic energy (Cao et al., 2022; Howe, 2024; Jiao et al., 2007; Kami et al., 2010; Liu et al., 2020).

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Plants utilize a minimum of five types of photoreceptors to detect and convert various wavelengths of light signals (Kami et al., 2010). Upon the absorption of visible light, these active photoreceptors inhibit photomorphogenic repressors, allowing light-promoting transcription factors (TFs) to be released. In Arabidopsis (*Arabidopsis thaliana*), CONSTITUTIVELY PHOTOMORPHOGENIC PROTEIN 1 (COP1), functioning directly downstream of several photoreceptors, is responsible for targeting numerous substrates for ubiquitination and subsequent degradation through the 26S proteasome system (Han et al., 2020; Huang et al., 2014; Lau and Deng, 2012). In darkness, COP1 accumulates in the nucleus of plant cells, where it facilitates the ubiquitination and breakdown of factors that promote photomorphogenesis, such as basic zipper (bZIP) TF ELONGATED HYPOCOTYL 5 (HY5), thus promoting skotomorphogenic development (Huang et al., 2014; Lau and Deng, 2012). Mutations that consistently cause a loss-of-function of COP1 result in short hypocotyls and expanded cotyledons under darkness, resembling the phenotype of light-grown wild-type seedlings (Deng et al., 1991, 1992). The HY5 serves as a primary positive regulator of light signaling. A loss-of-function of HY5 leads to significantly elongated hypocotyls under all light conditions and partially rescues the short hypocotyl phenotypes associated with the weak allele *cop1* (Ang et al., 1998; Oyama et al., 1997). In darkness, HY5 undergoes rapid degradation by COP1; however, it becomes abundant in light, mainly due to the suppression of COP1 activity by various light-activated molecular regulatory mechanisms (Hoecker, 2017; Kim et al., 2017; Podolec and Ulm, 2018). The COP1–HY5 module serves as a pivotal component of the light signal transduction pathway. A group of key components, which play n essential role in the developmental processes mediated by COP1-HY5 in plants (Cao et al., 2022; Heng et al., 2019; Xu, 2020).

Under light conditions, photoreceptors are activated, which are involved in triggering light and Brassinosteroids (BRs) signaling pathways, leading to the suppression of BR-mediated growth response. These profound morphological changes are induced by cross-talk between light and BR signaling pathways, which trigger several target genes related to plant growth and development (Razzaq and Du, 2024). BRs modulate growth and development and are involved in environmental adaptation in plants (Gómez-Ocampo et al., 2024; Manghwar et al., 2022). Since their discovery, the signaling mechanism and biosynthesis of BRs have been considerably studied in plants, providing a thorough understanding of their signaling pathways and biosynthesis (Tong and Chu, 2018; Zebosi et al., 2024). The BR signaling pathway is initiated when BL, the most active BR compound, is detected by receptor BR-INSENSITIVE 1 (BRI1) and the co-receptor BRI1-ASSOCIATED RECEPTOR KINASE (BAK1), which subsequently inactivates the BR-INSENSITIVE 2 (BIN2). This inactivation of BIN2 leads to accumulate unphosphorylated forms of BRI-EMS-SUPPRESSOR 1 (BES1) and BRASSINAZOLE-RESISTANT 1 (BZR1). The unphosphorylated forms of both TFs bind to the gene targets and facilitate cell elongation (Li et al., 1996; Wang et al., 2002). BZR1 and BES1 are involved in regulating the expression of numerous genes associated with plant growth, and also play a role in feedback inhibition by directly binding to the promoters of various BR biosynthesis genes, thereby suppressing their expression (He et al., 2005; Yu et al., 2011).

The interaction between BR singnaling and light involves various mechanisms, including the phosphorylation and cytoplasmic retention of BZR1/BES1. This process not only accelerates the degradation of BR-responsive proteins but also inhibits transcription of genes related to BR biosynthesis (Jing and Lin, 2020; Luo et al., 2010). At the molecular level, BRs frequently counteract light signals and adjust the function of essential signaling proteins to fine-tune plant responses to varying light conditions. For instance, in darkness, BRs facilitate skotomorphogenesis by inhibiting photomorphogenic growth, working synergistically with auxin and gibberellins to promote rapid cell elongation and development. When exposed to light, photoreceptors, including phytochromes (PHYs), cryptochromes (CRYs), and others, interact with BR signaling components, such as BES1 and BZR1, frequently diminishing their ability to bind to DNA, which results in redirecting the developmental process towards photomorphogenesis. This interaction ensures that the plant's structure is precisely adapted to its surroundings, enhancing growth and survival (Kim and Russinova, 2020; Nolan et al., 2020; Wang et al., 2012). Understanding the interaction between BRs and photomorphogenesis not only deepens our understanding of plant biology but also presents opportunities to enhance crop performance and adaptability by strategically manipulating hormonal and light signaling pathways (Nolan et al., 2020; Wang et al., 2012). This review aims to enhance our current understanding of how BRs regulate photomorphogenesis. It highlights recent advances and discusses the broader significance of this hormone-light signaling cross-talk for plant growth and development. Moreover, the molecular mechanism of BRs in regulating genes and proteins associated with photomorphogenesis in plants is discussed.

2. Brassinosteroids and their roles in plants

BRs were initially identified as a crude lipid extract from the pollens of rapseed (*Brassica napus* L.), and the extract was first referred to as "brassins". To further analyze the role of brassins, they were applied exogenously to bean seedlings, which significantly promoted internode elongation compared with gibberellic acid and lanolin treatments (Mitchell et al., 1970). However, the structure of BRs was first reported in 1979 for brassinolide (BL), a BR characterized as a polyhydroxyl lactone with a 5α-cholestane structure, showing similarity to animal steroids (Grove et al., 1979). They have been identified in almost all plant tissues and organs and across diverse plant species, including bryophytes, lycophytes, mosses, green algae, angiosperms, and gymnosperms (Bajguz et al., 2020; Zebosi et al., 2024).

BRs play multiple roles in smoothly regulating various critical physiological processes, e.g., reproductive development, seed germination, differentiation, response to light (skotomorphogenesis and photomorphogenesis), xylem differentiation, cell division and expansion, and differentiation (Chakraborty et al., 2025; Chaudhuri et al., 2022; Manghwar et al., 2022; Nolan et al., 2020). Additionally, BRs are involved in regulating stress tolerance, flowering, and stomatal development (Li et al., 2021; Lin, 2020). BRs also play a variety of roles against diverse abiotic and biotic stresses (Manghwar et al., 2022; Sadura and Janeczko, 2021; Yao et al., 2023). Due to their immobility, plants must adjust their development and growth in response to environmental stimuli (Liu et al., 2018; Yang and Guo, 2018). The application of BRs as stress alleviators can reduce the adverse effects of high temperature, drought, salinity, cold, and other external environmental stresses (CHEN et al., 2019; Shakirova et al., 2016) by enhancing biomass and photosynthesis, strengthening antioxidant enzymes and detoxification capabilities, and stimulating the expression of associated genes (Rajewska et al., 2016; Shahzad et al., 2018) (Fig. 1).

Due to their vital role in diverse developmental and physiological functions, BRs have attracted the focus of plant researchers in recent decades. BRs are non-toxic and environmentally benign, which facilitate plants in adaptation to adverse environmental conditions without disrupting ecological balance. Loss-of-function mutants in BR biosynthesis or signaling pathways exhibited constitutive photomorphogenesis. Whereas the BR signaling gain-of-function mutation led to longer leaf petioles and hypocotyls, along with early leaf senescence phenotypes (Wang et al., 2019).

3. Photomorphogenesis: key processes and regulatory mechanisms

Photomorphogenesis refers to the light-mediated developmental changes in plants throughout their lifecycle (Zhang et al., 2021b). This process involves numerous physiological and structural changes triggered by specific wavelengths of light, including seed germination, stem

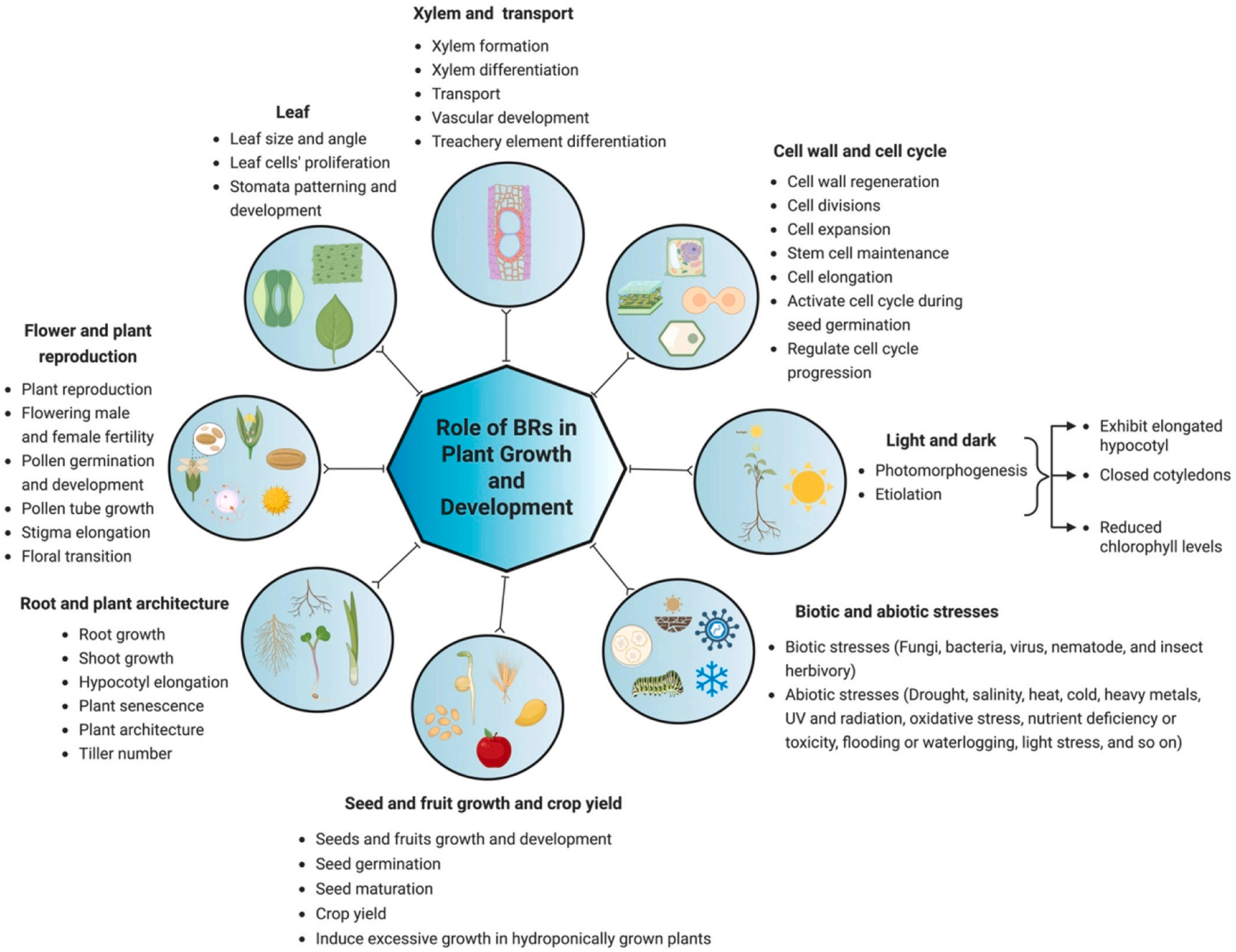

Fig. 1. BRs are involved in regulating the complex processes of plant growth and development. In seeds, BRs mediate seed growth, development, maturation, and germination. In root and plant architecture, they are involved in root and shoot growth, hypocotyl elongation, plant senescence, and tiller number. In flowering and reproduction, BRs are involved in plant reproduction, fertility of male and female flowers, tube growth and germination and development of pollens, stigma elongation, and floral transition. In leaves, BRs determine the leaf size and angle, as well as the proliferation of leaf cells and the patterning and development of stomata. BRs contribute to xylem formation and differentiation, transport, vascular development, and treachery element differentiation. They regulate multiple processes of the cell wall and the cell cycle, including cell wall regeneration, maintenance of the stem cell, cell elongation, division, and expansion, as well as the activation of the cell cycle during seed germination and the progression of the cell cycle. They play a significant role in light and dark responses, including photomorphogenesis and de-etiolation, characterized by elongated hypocotyls, closed cotyledons, and reduced chlorophyll levels. BRs also play an essential role in fruit and crop yield, including the growth and development of fruits and crops. BRs also contribute to excessive growth in hydroponically grown plants. Moreover, BRs play a crucial role in mitigating a variety of biotic and abiotic stresses.

elongation, flowering, leaf development, and de-etiolation (Liu et al., 2020; Razzaq and Du, 2024; Wang et al., 2022). After germination in dark conditions, seedlings undergo photomorphogenic growth upon exposure to light (De Wit et al., 2016; Ma et al., 2024). Moreover, the light intensity is an essential element that governs different physiological functions in plants, like seed germination, photosynthesis, cell division, proliferation and expansion of leaves, and stomatal development (Bialevich et al., 2022; Bueno and Vendrame, 2024; Xu et al., 2024). In addition to light intensity, plants also optimize their growth and development in response to photoperiods, influencing various functions, including fruit ripening and flowering. Photoperiods also enable plants to respond to stresses and adapt to various seasonal variations (Bao et al., 2024; Chen et al., 2024; Shibaeva et al., 2024).

Under low-light conditions, plants experience a decrease in photosynthetic rate, stomatal conductance, stem thickening, dry matter accumulation, and transpiration (Huang et al., 2024; Jin et al., 2023). Conversely, plants grown in darkness develop etiolated phenotypes, characterized by elongated hypocotyls and small, yellowish cotyledons. The transition from darkness to light primarily induces the accumulation of HY5 protein, which activates downstream gene cascades (Burko et al., 2020; Gangappa and Botto, 2016; Wang et al., 2020b). Plants have developed various photoreceptors to detect a broad spectrum of wavelengths, thereby actively promoting photomorphogenesis and suppressing skotomorphogenesis (Galvão and Fankhauser, 2015).

Plants perceive changes in external light conditions through photoreceptors, which are associated with developmental signaling pathways that regulate their growth and development (Huang et al., 2024). Photoreceptors are essential for responding to environmental stimuli, particularly light. Plants have developed several photoreceptors to detect and differentiate different wavelengths of light (Franklin et al., 2004). These include PHYA-E, which perceive red and far-red light, CRYs detect blue/ultraviolet (UV)-A light (Cashmore et al., 1999; Wang and Lin, 2020), UV resistance locus 8 (UVR8), which is involved in UV-B detection (Paik and Huq, 2019), phototropins (PHOTs), which respond to blue light (Briggs and Christie, 2002), while ZTL (ZEITLUPE) family members—FLAVIN-BINDING KELCH REPEAT-BOX (FKF1) and light/-oxygen/voltage (LOV) KELCH PROTEIN2 (LKP2) perceive blue light (Galvão and Fankhauser, 2015; Li et al., 2022). These photoreceptors exhibit structural variations and integrate distinct light signals to promote plant growth and development (Kami et al., 2010; Wang et al., 2018a) (Fig. 2, Table 1).

PHYs photoreceptors mediate photomorphogenesis or light-dependent growth and shade avoidance responses. The red light induces the transition of PHY proteins from their inactive red light-absorbing Pr form (localized to the cytoplasm) to the active far-red light-absorbing Pfr form. This active Pfr form reverts back to the inactive Pr form when exposed to far-red light, which triggers the response to shade avoidance (Howe, 2024; Klose et al., 2020). Consequently, the Pr to Pfr ratio at daybreak serves as a measure of day length, which regulates plant growth that depends on the season (Hendricks, 1960). However, the active Pfr enters the nucleus and interacts with the TFs from the PHYTOCHROME-INTERACTING FACTOR (PIF) family. In the absence of light, for instance, in underground seeds, PIFs suppress photomorphogenesis and promote skotomorphogenesis, or growth in the dark, including the elongation of the hypocotyl as the seedlings grow toward the surface. Conversely, upon exposure to sufficient light, red light–activated Pfr triggers the phosphorylation and ubiquitination events, resulting in the degradation of PIFs by the proteasome, which enables the activation of light-responsive genes that enhance photomorphogenesis (Cai and Huq, 2025; Howe, 2024).

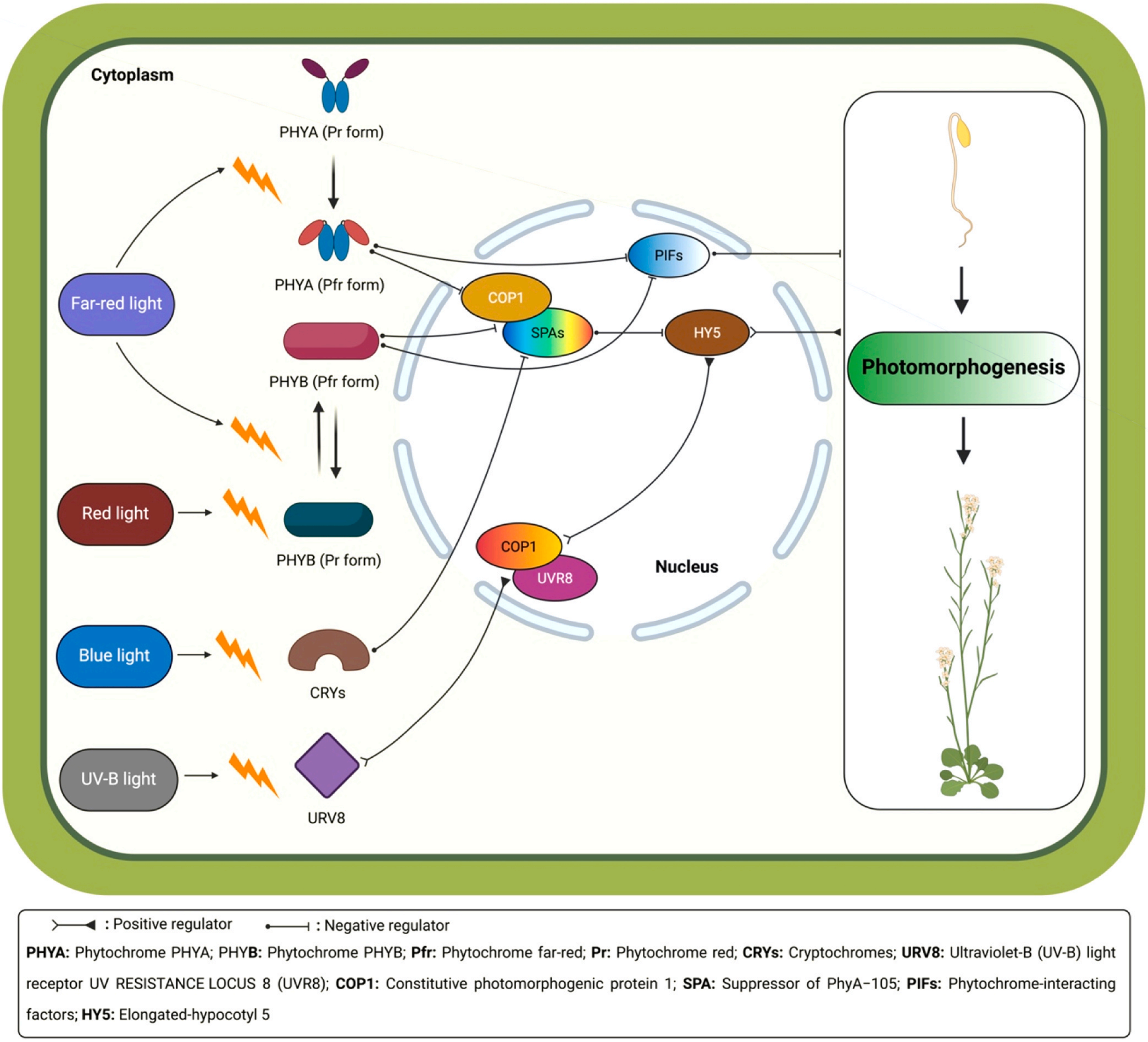

Fig. 2. Plants undergo photomorphogenesis through the light signaling pathways. Different light wavelengths, which include far-red, red, blue, and UV-B, activate specific photoreceptors, triggering downstream signaling events. Far-red light transforms PHYA to the active Pfr form from its inactive Pr form, which then enters the nucleus. Similarly, PHYB is activated by red light, converting it to its active Pfr form from its inactive Pr form, which also enters the nucleus. CRYs and UVR8 photoreceptors, which recognize the blue light and UV-B light, and inside the nucleus, these activated photoreceptors modulate the function of important regulatory proteins, such as COP1, PIFs, and SPAs. Typically, COP1, along with SPAs, negatively regulates the photomorphogenesis by promoting the degradation of positive regulators, such as HY5. However, upon exposure to light, active photoreceptors inhibit COP1-SPA complexes, which results in stabilizing HY5 and other transcription factors that promote photomorphogenesis. This signaling ultimately results in the activation of genes related to developmental processes that are dependent on light, leading to normal plant growth and the de-etiolation of seedlings. Blunted lines and arrows represent negative and positive regulatory effects, respectively.

Table 1
Involvement of different photoreceptors in photomorphogenesis.

Photoreceptor	Characteristic	Role in photomorphogenesis	Reference
Phytochrome PHYA	Far-red light photoreceptor	PHYA serves as a primary photoreceptor for far-red light, promoting photomorphogenesis when exposed to far-red light	(Quail, 2002)
Phytochrome PHYB	A primary red light photoreceptor	PHYB acts as a main photoreceptor for red light, which mediates photomorphogenesis triggered by red light exposure	(Quail, 2002)
Phytochrome PHYC	Phytochrome red (Pr), the active form is known for absorbing red light, whereas phychrome far-red (Pfr), the active form, which absorbs far-red light. In the absence of PHYB, PHYC is unable to fully mediate red light responses, indicating that it plays a supportive role rather than acting independently	PHYC regulates seedling de-etiolation under the exposure of continuous red-light	(Lymperopoulos et al., 2018)
Phytochrome PHYD	A main regulator of red/far-red responses	PHYD plays a role similar to that of PHYE and PHYB, particularly in regulating the elongation of hypocotyls, flowering time, and shade avoidance	(Tripathi et al., 2019)
Phytochrome PHYE	Primarily mediates red/far-red reversible low-fluence responses under conditions of continuous red light or white light	PHYE is involved in in avoiding shade and germination of seeds	(Kami et al., 2010; Lymperopoulos et al., 2018)
Cryptochromes (CRYs, CRY1, and CRY2)	Blue/ultraviolet-A (UV-A) light receptors	CRY1 is responsible for regulating photomorphogenesis, the accumulation of anthocyanin, and development of a mature plant. In contrast, CRY2 reduces the leght of the hypocotyl and internode when exposed to blue light	(Cashmore et al., 1999; Giliberto et al., 2005; Weller et al., 2001)
Phototropins (PHOTs, PHOT1, and PHOT2)	PHOTs detect both temperature and blue light	In the liverwort *Marchantia polymorpha*, PHOTS detects temperature and blue light, facilitating the arrangement of chloroplasts for efficient photosynthesis while reducing the risk of photodamage	(Briggs et al., 2001; Fujii et al., 2017)
Ultraviolet-B (UV-B) light receptor UV RESISTANCE LOCUS 8 (UVR8)	UVR8 perceives UV-B light	CRYs and UVR8 interact with TFs BES1-INTERACTING MYC-LIKE1 (BIM1) and BRI1-EMS-SUPPRESSOR1 (BES1), play a role in mediating BRgene expression and plant growth through BR regulation. This interaction inhibits their ability to bind to DNA, thereby suppressing transcription and reducing hypocotyl elongation	(Liang et al., 2018; Wang et al., 2018c)
FLAVIN-BINDING KELCH REPEAT F-BOX 1 (FKF1)	A blue light receptor	It plays a role in promoting flowering in Arabidopsis when exposed to long-day conditions	(Galvão and Fankhauser, 2015; Shibuya et al., 2021)
ZEITLUPE (ZTL) family members ZTL	A blue light receptor	Primarly affect the circadian clock and photoperiodic flowering, while also modulating development that is regualted by light	(Baudry et al., 2010)
Light/oxygen/voltage (LOV) KELCH PROTEIN 2 (LKP2)	A blue light receptor	LKP2 regulates the photoperiodic flowering and circadian clock. In Arabidopsis, it positively regulates the elongation of hypocotyls under white light	(Miyazaki et al., 2016, 2011)

CRYs and blue light receptors orchestrate photomorphogenesis by regulating TFs and interacting in hormone signaling pathways. These receptors interact with the same downstream networks to adjust light responses, especially in environments rich in blue light (Nemhauser and Chory, 2002). The COP1/SPA E3 ubiquitin ligase complex serves as a key suppressor of photomorphogenesis in darkness by targeting positive regulators, such as HY5, for degradation. Exposure to light results in the inactivation or dissociation of COP1/SPA, facilitating the accumulation of HY5 and other light-responsive TFs, thereby activating photomorphogenic genes (Chen and Chory, 2011; Nemhauser and Chory, 2002). HY5 enhances the transcription of numerous light-induced genes associated with photoprotection, chloroplast development, and metabolism. Its function is modulated by upstream controllers (e.g., COP1/SPA, B-Box Protein (BBX) family regulators) and by PHY and CRY signaling, coordinating the light response on a genome-wide scale (Chen and Chory, 2011; Nemhauser and Chory, 2002; Tripathi et al., 2019). BBX proteins, which are B-box Zn finger proteins, are involved in either positive or negative regulation of photomorphogenesis by modulating the expression of HY5. The balance of BBX family members determines the intensity and direction of the photomorphogenic response, with certain BBXs acting either upstream or downstream of HY5 in response to light signals (Tripathi et al., 2019).

4. Photoreceptors and their interactions with BRs

Plants have developed several photoreceptors to sense and transduce signals, enabling them to recognize and respond to a broad spectrum of light wavelengths (Kathare et al., 2020). CRYs are involved in regulating photomorphogenesis, stomatal development and closure, and photoperiodic flowering (Kang et al., 2009; Mao et al., 2021). Arabidopsis proteins CRY1 and CRY2, homologs of CRYs, inhibit hypocotyl elongation in response to blue light (Wang et al., 2022). The cross-talk between CRY2 and CIB1 (basic helix–loop–helix (bHLH)) TF initiates transcription and induction of flowering. Whereas CRY1 forms a physical interaction with HBI1, a close homolog of CIB1, which functions downstream of gibberellic acid (GA) and BR signaling pathways to facilitate blue light-dependent hypocotyl elongation (Wang et al., 2018b).

The UVR8 photoreceptors mediate responses to UV-B light and suppress plant growth by inhibiting BR-promoted growth (Fang et al., 2022). UVR8 interacts directly with functionally dephosphorylated BES1 and BES1-INTERACTING MYC-LIKE 1 (BIM1) TFs, responsible for mediating plant growth and gene expression regulated by BR, to inhibit their activities (Liang et al., 2018, 2020). PHOTs control various plant responses, including stomatal opening, phototropism, and chloroplast

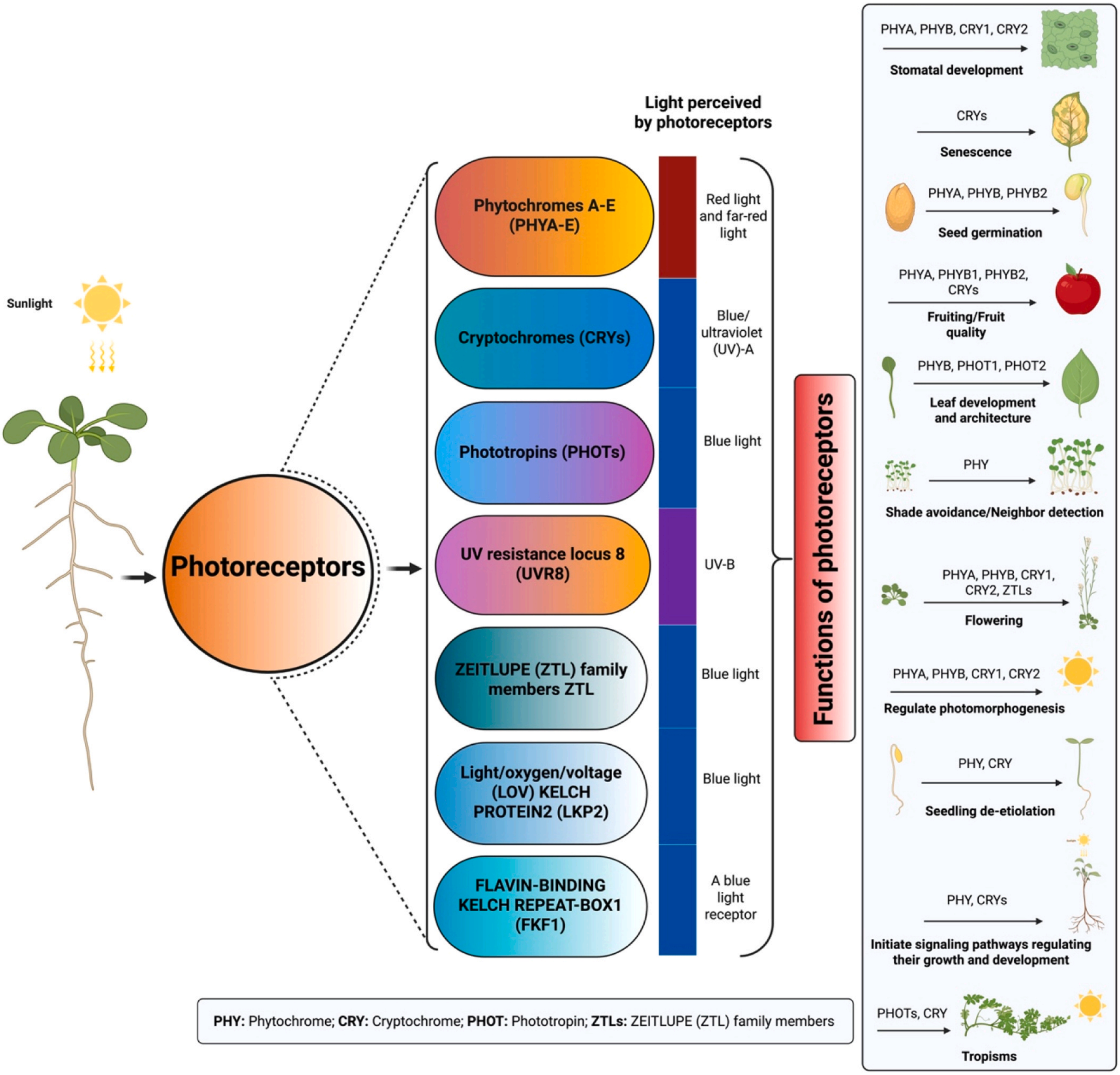

Fig. 3. Schematic representation of photoreceptors, the specific light wavelengths they detect, and their related physiological functions. Plants possess several photoreceptors that detect different light spectra and regulate a wide range of developmental processes. PHYA-PHYE recognize red and far-red lights, whereas CRYs recognize blue/UV-A light. ZTLs, PHOTs, KF1, and LKP2 are responsible for recognizing blue light. UVR8 recognizes UV-B light. These photoreceptors regulate various plant responses, such as stomatal development (PHYA, PHYB, CRY1, and CRY2), the process of senescence (CRYs), germination of seeds (PHYA, PHYB, and PHYB2), fruiting and fruit quality (PHYA, PHYB1, PHYB2, CRYs), and the development and architecture of leaves (PHYB, PHOT1, and PHOT2), shade avoidance and neighbor detection (PHY), and the flowering process (PHYA, PHYB, CRY1, CRY2, and ZTLs). They also play crucial roles in regulating photomorphogenesis (PHYA, PHYB, CRY1, and CRY2), as well as the de-etiolation of seedlings (PHY and CRY). PHYs and CRYs are involved in activating signaling pathways that regulate overall plant growth and development. The PHOTs and CRYs mediate the tropic responses. This interconnected photoreceptor network enables plants to adjust their growth and reproduction in response to light.

relocation. PHOTs regulate the phototropic curvature of seedlings (e.g., coleoptiles and hypocotyls) under unilateral blue light exposure (Dou and Niu, 2020). In Arabidopsis, the red light receptor PHYB inhibits BR signaling by directly interacting with BES1 (Fig. 3, Table 2). The *phyB* mutant exhibited increased sensitivity to BR, a response suppressed in transgenic plants overexpressing PHYB, which indicates that PHYB negatively regulates the BR signaling pathway (Wu et al., 2019).

Light-activated photoreceptors inhibit the function of COP1, an E3 ubiquitin ligase that ubiquitinates various TFs (Podolec and Ulm, 2018), thereby repressing photomorphogenesis. Under dark conditions, COP1 accumulates in the nucleus; upon exposure to light, it is exported from the nucleus. This relocation allows TFs to accumulate, which promotes photomorphogenesis (Podolec and Ulm, 2018; Xu et al., 2016). All light signals perceived by various photoreceptors converge downstream of the HY5 TF that regulates multiple growth programs. For example, skotomorphogenesis occurs in dark-grown seedlings, which results in elongated hypocotyls and closed yellowish cotyledons (Wang et al., 2020b).

5. How BRs play physiological roles in photomorphogenesis?

BRs modulate various physiological processes during photomorphogenesis, including hypocotyl elongation, chloroplast development, and leaf expansion to fine-tune plant growth in the light response. The light and BR pathways are two essential factors that control photomorphogenesis. BRs are crucial for regulating photomorphogenesis, playing diverse physiological roles by balancing light-mediated development and skotomorphogenesis via tightly integrated signaling networks. Their function is facilitated by their interaction with light signaling pathways, transcriptional regulators, and direct modulation of gene expression associated with growth, cell wall development, and stress responses (Lin et al., 2021; Percio et al., 2025; Wang et al., 2012). BRs and light signals function antagonistically to shape seedling growth patterns. In darkness, BR signaling induces skotomorphogenesis and in the presence of light, photomorphogenesis is induced. At the molecular level, BRs are detected by the cell-surface receptor BRI1, which triggers signaling cascades that include kinases, such as CONSTITUTIVE DIFFERENTIAL GROWTH1 (CDG1), brassinosteroid signaling kinases (BSKs), and the *bri1* SUPPRESSOR1 (BSU1) phosphatase family, which activate the BZR1/BES1 family of TFs. When light is present, photoreceptors, including PHYs and CRYs, directly interact with and inhibit components of the BR signaling pathway to facilitate photomorphogenesis. For example, CRY1 and PHYB interact with BES1/BZR1, inhibiting their DNA binding and target gene expression (Li et al., 2017; Lin et al., 2021; Zhai et al., 2020).

Numerous studies have demonstrated substantial crosstalk between light signaling and BR in plants (Li and He, 2016). The first BR-deficient mutants, de-etiolated-2 (*det2*) and constitutive photomorphogenesis and dwarfism (*cpd*), were identified due to obvious phenotypes of extreme dwarfism and constitutive photomorphogenesis (Li et al., 1996; Szekeres et al., 1996), revealing a significant role of BR in light-regulated development. BRs are closely related to photomorphogenesis; BR biosynthesis- or signaling-defective mutants, such as *cpd*, *dwf4*, *det2*, *bin2*, and *bri1*, exhibit photomorphogenesis phenotypes (Choe et al., 1998; Li et al., 1996; Szekeres et al., 1996; Wang et al., 2012).

BRs modulate the activity and stability of central regulators, such as BZR1, BES1, and PIFs. Light promotes photomorphogenic TFs, including HY5, B-box21 (BBX21), and *bzr1*–1D suppressor1 (BZS1), which suppress BR signals. BR signaling activates BZR1 and by inhibiting BIN2, stabilizes and activates PIFs, and together these factors promote skotomorphogenesis or dark-type growth. In the absence of BR, BIN2, a GSK3-like kinase, phosphorylates and deactivates BZR1/BES1, thereby facilitating photomorphogenesis. However, when BR levels are high, usually in darkness, BIN2 is inactivated, allowing the dephosphorylation and activation of BZR1/BES1, which in turn triggers the expression of skotomorphogenic genes (Flynn, 2023; Li et al., 2017; Lin et al., 2021; Wang et al., 2022; Zhu et al., 2013).

BRs are essential for plant growth, development, and their ability to withstand stress. They achieve this by influencing the structure and composition of the cell wall, primarily by regulating gene expression involved in the biosynthesis and metabolism of primary and secondary cell walls. This regulation affects the deposition of cellulose, lignin, and other components, altering internal architecture of wall and enabling it to adapt to developmental changes and environmental conditions (Percio et al., 2025).

BR signaling interacts with environmental light signals that facilitate dynamic adjustments in plant structure, metabolism, and stress resilience. In shaded or dark conditions, BRs promote rapid elongation, enabling seedlings to seek light. Conversely, under bright light, the light signals override BR effects, triggering photomorphogenesis that optimizes photosynthetic tissue formation and improves survival. The balance orchestrated by BRs and photoreceptor interactions facilitates adaptable growth and competitiveness in changing environments (Lin et al., 2021; Manghwar et al., 2022; Wang et al., 2012). BRs serve as key regulators of photomorphogenesis, which function through complex networks that integrate light responsiveness, hormonal signaling, and gene regulatory mechanisms to determine plant morphology, growth strategies, and environmental adaptation. This intricate coordination of

Table 2
Interaction of BRs with photoreceptors to regulate photomorphogenesis.

Photoreceptor	Characteristic	Plant	Function	References
Cryptochrome 1 (CRY1)	CRYs share a similar amino acid sequence with photolyases, which are flavoproteins, involved in mediating light-dependent DNA repair	Arabidopsis	The interaction of CRY1 and BES1 induced by BR is a tightly regulated mechanism that enable plants to optimize photomorphogenes in response to internal BR signals and external light	(Wang et al., 2018c)
Cryptochromes (CRYs); CRY1 and CRY2	CRYs are photoreceptors that detect blue light and involved in mediating a wide range of response induced by light in plants and animals	Arabidopsis	CRY1 forms a physical interaction with HBI1, a close homolog of CIB1, which acts downstream in the signaling pathways of gibberellin acid (GA) and BR signaling pathways, promoting blue light-dependent mannered hypocotyl elongation	(Wang et al., 2018b)
Phytochrome B (PHYB)	PHYB is a primary photoreceptor, which promotes photomorphogenesis under red light	Arabidopsis	PHYB negatively regulates BR responses by direcly interacting with dephosphorylated BES1 *in vivo*	(Wu et al., 2019)
Phytochrome PHYA	PHYA plays a role in enhancing BIN2 accumulation, which promotes BES1 phosphorylation in far-red light. BIN2 regulates photomorphogenesis under far-red light by acting genetically downstream from PHYA	Arabidopsis	PHYA and PHYB function to suppress BR signaling by inhibibing BIN2 degradation induced by BR and protomote BES1 phosphorylation	(Zhao et al., 2022)
UV-B light photoreceptor UV RESISTANCE LOCUS 8 (UVR8)	It is involved in mediating the UV-B light responses in plants	Arabidopsis	UV-B suppresses plant growth by inhibiting plant growth promoted by BR	(Liang et al., 2018, 2020)

BR and light signals is crucial for plant development and advancements in agriculture (Lin et al., 2021; Percio et al., 2025; Wang et al., 2012).

6. BR-mediated regulatory mechanism of genes and proteins involved in photomorphogenesis

BRs mediate gene regulation during photomorphogenesis through crosstalk between TFs in light and BR signaling pathways. Photosignaling TFs like HY5, COP1, GATA2, and PIFs interact with BIN2 and BZR1 in the BR signaling pathway to regulate photomorphogenesis (Ravindran et al., 2021; Yang et al., 2023). BR signaling activates BZR1, a TF essential for inhibiting photomorphogenesis in darkness (Fan et al., 2012). A study discovered a physical link between light signaling pathways and BR in Arabidopsis, which was mediated by BZR1 and HY5 (Li and He, 2016). The HY5 binds to dephosphorylated BZR1 to suppress its function and regulates the opening of cotyledons in seedlings in the dark. HY5 antagonizes the transcriptional activity of BZR1 in order to regulate the genes related to the development and opening of cotyledons (Li and He, 2016). Moreover, HY5 interacts with a BIN2, which is involved in enhancing the kinase activity of HY5. This interaction reduces BZR1 accumulation, which results in inhibiting the hypocotyl elongation (Li et al., 2020). Further studies revealed that HY5 modulates the BR signaling pathway for regulating cotyledon opening, where light influences BZR1 protein's abundance and phosphorylation status (Li and He, 2016; Li et al., 2017) (Fig. 4, Table 3).

In a study, GOLDEN2-LIKE1 (GLK1/GLK2) was identified as a BIN2 substrate, and a mechanism was elucidated by which BIN2 regulates chloroplast development. A physical interaction of BIN2 with GLK1 and GLK2 was confirmed. BIN2-mediated phosphorylation activates and stabilizes the GLKs, which is involved in the regulation of chloroplast development in response to light signals and BR (Zhang et al., 2021a). In Arabidopsis, NF-YC homologs, including *NF-YC1*, *NF-YC3*, *NF-YC4*, and *NF-YC9*, were found to play essential and redundant functions in the light-induced suppression of the BR biosynthesis and signaling pathways. Under light conditions, NF-YCs play a role in inhibiting BR biosynthesis by directly downregulating the expression of *BR6ox2*—a BR biosynthesis gene. Additionally, NF-YCs engages in a physical interaction with with BIN2, promoting its autophosphorylation, consequently inhibiting its degradation through the 26S proteasome pathway (Zhang et al., 2021b).

The BZS1 overexpression results in short hypocotyls in light, de-etiolation in the dark, decreased sensitivity to BR treatment, and downregulation of various BR-activated genes. BZS1 knockdown, achieved through co-suppression, partially suppressed the short hypocotyl phenotypes of the BR-insensitive mutants. Plants overexpressing BZS1 exhibit increased sensitivity to different light wavelengths. In contrast, loss-of-function of BZS1 reduces plant light sensitivity and partially inhibits the COP1 mutant in darkness, indicating that BZS1 enhances light

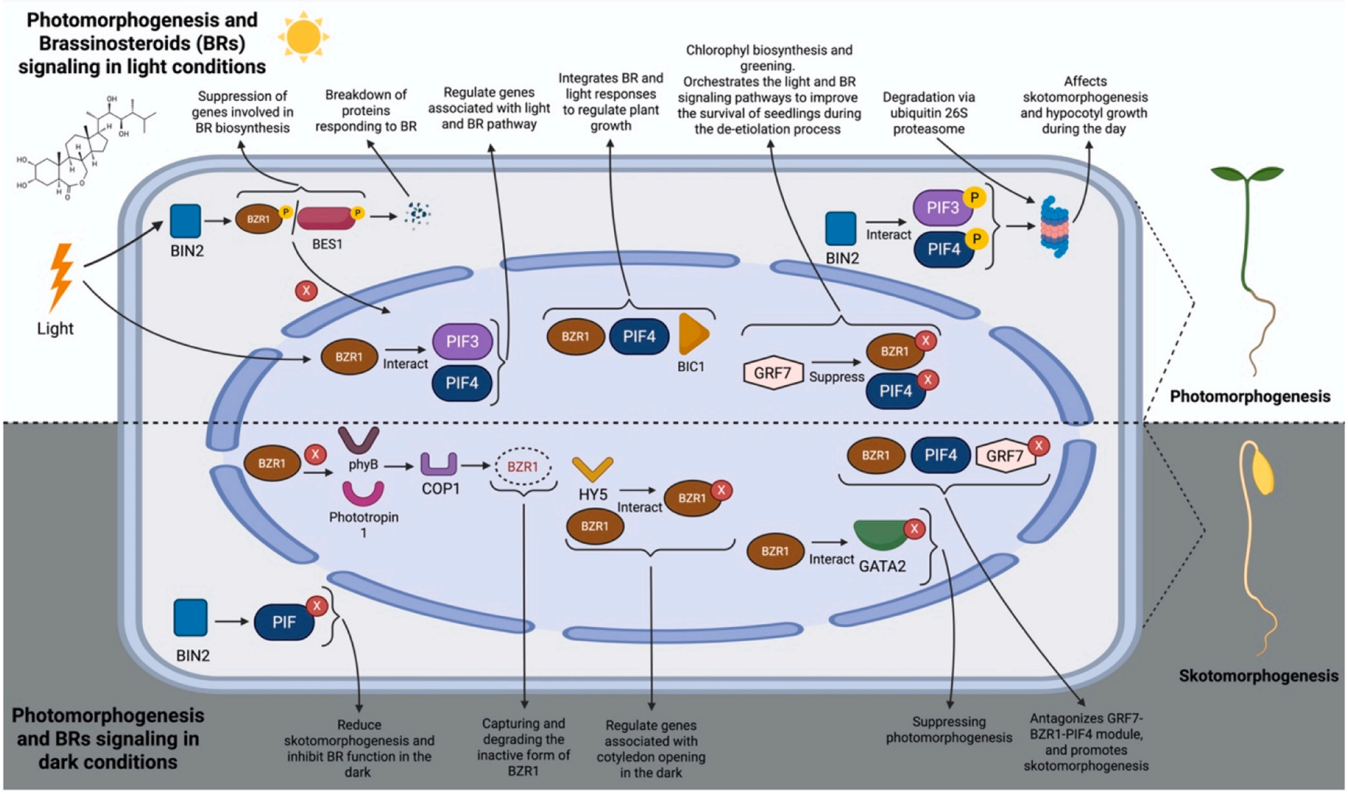

Fig. 4. Regulatory mechanism of BRs in photomorphogenesis. In light (upper section), photoreceptors are activated, promoting photomorphogenesis and inhibiting BR signaling. BR-responsive TFs BZR1/BES1 are phosphorylated and inactivated by GSK3-like kinase BIN2, leading to the degradation of the BR-responsive proteins and the repression of BR biosynthesis genes. Phosphorylated BZR1 and BES1 are either degraded or retained in the cytoplasm. BIN2 also phosphorylates PIF3 and PIF4, targeting them for ubiquitin-mediated degradation, which interferes with skotomorphogenesis and hypocotyl elongation during the day. When BZR1 is dephosphorylated, it can translocate to the nucleus and interact with PIF3 and PIF4, regulating genes involved in both BR and light signaling pathways, which are crucial for chlorophyll biosynthesis, greening, and seedling survival during de-etiolation. The BIC1-BZR1-PIF4 complex integrates BR and light signals to regulate plant growth and development. GRF7 interacts with BZR1 and PIF4, inhibiting their activity, thereby modulating the greening process by regulating genes responsible for chlorophyll biosynthesis. Consequently, the GRF7-BZR1-PIF4 module coordinates light and BR signaling to improve seedling survival during de-etiolation. In darkness (lower section), BZR1 downregulates the expression of PHYB and Phototropin 1, while upregulating the expression of COP1, a negative regulator of photomorphogenesis. The COP1 captures and degrades BZR1's inactive form. HY5 binds to dephosphorylated BZR1 to inhibit its function and regulates cotyledon opening in seedlings under dark conditions. Activated BZR1 binds tightly to the GATA2 promoter in the dark, inhibiting its transcription by suppressing photomorphogenesis. BIN2 remains active and inhibits PIFs, thereby reducing skotomorphogenesis and BR function.

Table 3
Involvement of various BR-regulated genes and proteins in photomorphogenesis.

Gene	Characteristic	Plant	Function	References
Suppressor of PHYB-4 7 (SOB7)	A homolog of BAS1	Arabidopsis	Encodes the cytochrome P450 CYP72C1, and is functionally redundant to BAS1 in that they both inactivate BRs and modulate photomorphogenesis	(Turk et al., 2005)
Membrane Steroid Binding Protein 1 (MSBP1)	MSBP1, a membrane steroid binding protein	Arabidopsis	MSBP1 has the ability to bind steroids *in vitro* and exerts a negative regulatory effect on BR signaling, as well as cell expansion and elongation	(Shi et al., 2011)
bzr1–1D suppressor1-Dominant (bzs1–D)	bzs1–D mutant	Arabidopsis	The overexpression of BZS1 results in short hypocotyls in the light, de-etiolation in darkness, decrease sensitivity of plants to BR treatment, and inhibit the expression of multiple genes that are usually activated by BR	(Fan et al., 2012)
COP1	A dark-activated ubiquitin ligase	Arabidopsis	Involved in capturing and degrading the inactive form of BZR1	(Kim et al., 2014)
ATAF2	NAC TF	Arabidopsis	*ATAF2* regulates root growth and hypocotyl elongation by suppressing BR catabolism	(Peng et al., 2015)
HY5	ELONGATED HYPOCOTYL 5 (HY5)	Arabidopsis	Involved in mediating the light and BR-regulated cotyledon opening	(Li and He, 2016)
(SINATs)	SINA OF Arabidopsis thaliana are RING finger E3 ubiquitin ligases	Arabidopsis	Light accumulates SINATs, which have a direct interaction with BES1 and BZR1	(Yang et al., 2017)
AGB1	Arabidopsis G-protein β subunit	Arabidopsis	AGB1, a photomorphogenic repressor, which positively regulates the BR response. AGB1 plays a role as a junction between BR pathways and light	(Zhang et al., 2018)
GRF7-BZR1-PIF4	GROWTH REGULATED FACTOR 7 (GRF7)-BRASSINAZOLE RESISTANT 1 (BZR1)-PHYTOCHROME INTERACTING FACTOR 4 (PIF4)	Arabidopsis	It coordinates the light and BR signaling pathway to improve seedling survival during the process of de-etiolation	(Wang et al., 2020a)
Golden 2-like (GLK) TFs (GLKs); GLK1 and GLK2	GLKs play an essential role in abscisic acid response, disease defense, and chloroplast development in plants	Arabidopsis	They play a role in regulating the development of chloroplasts in response to light and BR	(Zhang et al., 2021a)
NUCLEAR FACTOR-Y C proteins (NF-YCs)	NF-YCs are critical components of the NF-Y heterotrimeric complex. They serve as essential regulators for plant growth and development that is governed by phytohormones	Arabidopsis	They play essential and redundant roles in the light-induced suppression of biosynthesis and signaling pathways of BRs	(Zhang et al., 2021b)
BIC1	BLUE-LIGHT INHIBITOR OF CRYPTOCHROMES 1	Arabidopsis	It acts as a suppressor of photomorphogenesis and flowering by inhibiting CRY2 phosphorylation and serves as a transcriptional coactivator of PIF4 and BZR1 to activate BR-responsive genes, thereby promoting the elongation of the hypocotyl	(Yang et al., 2021)
BBX32	B-box protein	Arabidopsis	BBX32 serves as a crucial node for integrating light and BR signaling, thereby modulating the cotyledon closure during the process of de-etiolation	(Ravindran et al., 2021)

responses (Fan et al., 2012). Darkness increases the activity of BZR1 by reducing its phosphorylated (inactive) form via a proteasome-dependent process.

In addition, various genes are negatively regulated by BR and light (Luo et al., 2010). BZR1 inhibits the expression of PHYB and phototropin 1, which facilitates light signaling, while it enhances the expression of negative regulators of photomorphogenesis, including COP1 and its associated partners (Yu et al., 2011). Conversely, COP1, a ubiquitin ligase that is activated in darkness, is involved in capturing and degrading the inactive form of BZR1. The phosphorylated BZR1 removal in darkness increases the dephosphorylated to phosphorylated BZR1 ratio, consequently enhancing the likelihood of active homodimer formation between dephosphorylated BZR1 proteins (Kim et al., 2014).

COP1 can directly regulate other critical components in the BR signaling pathway, including BIN2, which functions as a negative regulator of the BR signaling (Yin et al., 2002). BIN2 reduces skotomorphogenesis by inhibiting PIF activity and suppressing BR function in darkness. Besides binding with PIF3-BIN2, the SPA/COP1 complex has the ability to interfere with PIF phosphorylation by BIN2 (Ling et al., 2017; Wang et al., 2019). Membrane Steroid-Binding Protein 1 (MSBP1) binds to steroids *in vitro* and acts as a negative regulator of BR signaling, along with elongation and expansion of cells. Light induces the expression of MSBP1 via direct interaction with and activation by HY5 Homolog (HYH) and HY5, which results in suppressing the hypocotyl elongation (Shi et al., 2011).

Peng et al. discovered that the NAC TF, *Arabidopsis thaliana ACTIVATING FACTOR2* (*ATAF2*) binds to the promoters of SOB7 and BAS1, which results in suppressing their expression. *ATAF2* is involved in inhibiting the tissue-specific expression of SOB7 and BAS1 in plants. *ATAF2* regulates hypocotyl growth in a light-dependent manner. When plants are treated with the BR biosynthesis inhibitor Brassinazole (Brz), the photomorphogenic phenotypes of *ATAF2* gain-of-function and loss-of-function seedlings are suppressed. Furthermore, disrupting SOB7 and BAS1 eliminated the short-hypocotyl phenotype of *ATAF2* loss-of-function seedlings under low fluence-rate white light, revealing an association between photomorphogenesis and BR catabolism mediated by *ATAF2* (Peng and Neff, 2020; Peng et al., 2015). Arabidopsis seedlings treated with the Brz showed a light-grown phenotype (Ruan et al., 2021). Moreover, CRY1 signaling suppresses BR signaling by directly interacting with BES1 in Arabidopsis (Wang et al., 2018c).

BZR1 directly interacts with E3 ubiquitin ligases, COP1 and MAX2, elucidating the mechanisms of BZR1 degradation (Kim et al., 2014; Wang et al., 2013). It is widely recognized that BR can affect the activity of BZR1 by altering its phosphorylation status, which impacts the retention of BZR1 in the cytoplasm and its DNA-binding ability (Cao et al., 2024). Moreover, the modulation of BZR1 stability plays a crucial role in affecting BR signaling output (Kim et al., 2014; Li and He, 2016).

In addition to HY5 and COP1, BZR1 interacts with another significant light-signaling TF, GATA2. GATA2 binds GATA motifs and functions as a positive regulator of photomorphogenesis (Luo et al., 2010). In dark conditions, GATA2 undergoes COP1-dependent degradation, and COP1 can directly ubiquitinate GATA2 *in vitro* (Luo et al., 2010). Besides light signaling, BZR1 also regulates GATA2 (He et al., 2005). Activated BZR1 binds tightly to the GATA2 promoter in darkness, thereby inhibiting its transcription and suppressing photomorphogenesis (Luo et al., 2010). Thus, GATA2 plays a pivotal role in the interaction between BR signaling and light (Wang et al., 2019).

Light also suppresses BR biosynthesis through regulation mediated by PIF (Martínez et al., 2018a; Wei et al., 2017). BZR1 forms a direct interaction with PIF4 to co-regulate nearly 2000 common target genes (Li et al., 2017). PIF3 and PIF4 interact with BZR1 to regulate genes associated with BR pathways and light signaling (Oh et al., 2012). PIF4 is also recognized for changing BES1's binding activity within the BR pathway. The interaction of BES1 and PIF4 with each other promotes cell elongation and activates genes associated with the regulation of auxin (such as ARF6) and GA, while inhibiting the expression of photosynthesis-related genes (Martínez et al., 2018b). BIN2 also interacts with PIF3 and PIF4, phosphorylating them and resuliting in their degradation via the ubiquitin-26S proteasome, which in turn affects skotomorphogenesis and hypocotyl growth during the day (Ling et al., 2017).

BZR1 and PIF4 were found to enhance the expression of GROWTH REGULATED FACTOR 7 (*GRF7*) and *GRF8* genes, which results in repressing chlorophyll biosynthesis. The interaction between PIF4, BZR, and GRF7 leads to precisely modulating the greening process through the regulation of genes associated with chlorophyll biosynthesis. As a result, the PIF4-BZR1-GRF7 module coordinates BR signaling and light to improve seedling survival during de-etiolation (Wang et al., 2020a). BIC1, known as BLUE-LIGHT INHIBITOR OF CRYPTOCHROMES 1 (BIC1), is recognized as a suppressor of photomorphogenesis and flowering by phosphorylation inhibition of CRY2, which functions as a transcriptional coactivator of PIF4 and BZR1, which in turn activate BR-responsive genes, thereby promoting hypocotyl elongation. The BIC1-PIF4-BZR1 complex integrates BR response and light to regulate plant growth (Yang et al., 2021).

Arabidopsis G-protein β subunit—AGB1 is recognized for its role in repressing photomorphogenesis, which contributes to the partial de-etiolation phenotype of the *agb1* mutant (Jones et al., 2003). AGB1 interacts with BES1 to enhance the dephosphorylated-to-phosphorylated BES1 ratio. It synergistically regulates the expression of BES1 target genes, including *SAUR, DWF,* and *CPD* family members, which are essential for cell elongation. This indicates that the photomorphogenic repressor AGB1 positively regulates the BR response (Zhang et al., 2018). BBX32, a box protein that suppresses light signaling and enhances BR signaling, subsequently prevents hypocotyl opening (Holtan et al., 2011). A study revealed that BBX32 interacts with PIF3 to promote cotyledon closure mediated by BR during the transition from darkness to light. Furthermore, BBX32 interacts with BZR1, elevating BBX32 expression and forming a positive feedback loop. Consequently, this interaction indicates that BBX32 serves as a node for integrating BR signaling and light to modulate cotyledon closure during de-etiolation (Ravindran et al., 2021). RING finger E3 ubiquitin ligases, SINA OF Arabidopsis thaliana (SINATs), undergo degradation in darkness, whereas light facilitates the accumulation of SINATs that directly interact with BZR1and BES1. The biochemical evidence suggests that light-stabilized SINATs preferentially bind to dephosphorylated BES1, promoting its degradation and ubiquitination, which in turn inhibits the BR cascade and hypocotyl elongation (Yang et al., 2017).

7. Concluding remarks and future perspectives

Light functions as a vital energy source for photosynthesis in plants and as an essential environmental signal that affects numerous plant developmental processes. Photomorphogenesis is an essential developmental process that enables plants to optimize their morphology in response to light signals. BRs have been identified as significant regulators of photomorphogenic responses, influencing a variety of processes, including cotyledon expansion, hypocotyl elongation, chloroplast development, and gene expression reprogramming. The responses of BRs are highly context-dependent, sensitive to dosage, and their interactions with other hormones make their practical use in agriculture. The interaction between BR and light signaling pathways is crucial for plant development, as it regulates the essential balance between plant growth, development, and environmental adaptability. BR and light signals enable plants to optimize their developmental transitions, such as seedling morphogenesis, by balancing growth between skotomorphogenesis and photomorphogenesis (light growth), thereby improving overall plant performance. Recent progress in synthetic biology, molecular biology, and high-resolution imaging has significantly improved our understanding of BR-mediated photomorphogenesis. Despite these advancements, several challenges remain to be overcome. For example, there is much to explore regarding the dynamics of tissue-specific BR signaling and its spatial coordination with photoreceptor pathways. The interaction between BR signaling and light-responsive pathways, primarily through the regulation of essential TFs like BZR1, PIFs, BES1, and HY5, demonstrates the complex hormonal crosstalk that facilitates plant adaptability and growth optimization. At the molecular level, these key TFs serve as essential nodes that integrate BR and light signals, providing valuable genetic targets for molecular breeding and genome-editing approaches. By understanding and harnessing these interactions, breeders can design climate-resilient, resource-efficient cultivars that combine high productivity with strong adaptability—an essential objective for sustainable agriculture under changing environmental conditions. Moreover, future research should aim to explore the detailed regulatory networks and molecular mechanisms underlying the interaction between BR and light signaling in various crop species, which will enable the precise manipulation of these pathways to improve yield and stress resilience. The use of genetic engineering and genome-editing technologies, such as CRISPR/Cas9, holds significant potential for developing BR-sensitive plant varieties with tailored growth patterns and enhancing stress tolerance. Moreover, cutting-edge technologies, such as optogenetics and synthetic biology, offer the potential to create regulatory modules that respond to light and BR, enabling unprecedented precision in controlling plant growth and development. Furthermore, combining systems biology with AI-driven predictive modeling could further expedite the application of BR-based solutions in sustainable crop enhancement strategies. Exploring the full potential of BRs in photomorphogenesis offers a significant advancement in plant developmental biology and agricultural innovation. Continued interdisciplinary efforts will be crucial for translating core scientific discoveries into practical solutions for developing crops that are both climate-resilient and high-yielding. Overall, harnessing the interaction between BR and light signaling offers promising prospects for crop improvement programs aimed at producing resilient and high-yielding plants that can thrive in dynamic and challenging environments. Further elucidating the complexities of BR-mediated hormonal regulation in photomorphogenesis will be crucial for developing innovative solutions to promote sustainable agriculture and food security.

CRediT authorship contribution statement

Hakim Manghwar: Writing - review & editing, Writing – original draft, Visualization, Supervision, Software, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Amjad Hussain:** Writing - review & editing, Validation, Formal analysis, Conceptualization. **Intikhab Alam:** Validation, Methodology. **Siqi Fan:** Methodology, Data curation. **Guanghua Sun:** Methodology, Data curation. **Fen Liu:** Writing - review & editing, Resources, Investigation, Funding acquisition.

Authors agreement

All the authors of this manuscript have agreed to submit this manuscript to Environmental and Experimental Botany.

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Declaration of Competing Interest

The authors declare no potential conflict of interest.

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