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Phytochrome mediated regulation of plant growth and development: Molecular mechanisms, physiological responses, and applications in crop improvement

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Abstract

Phytochromes are red and far red light sensing photoreceptors that play a central role in regulating plant growth, development, and environmental adaptation. These photoreceptors function as molecular switches by interconverting between inactive (Pr) and active (Pfr) forms, thereby controlling multiple physiological and developmental processes through light mediated signaling pathways. Phytochromes regulate important traits such as seed germination, photomorphogenesis, flowering time, shade avoidance, pigment biosynthesis, plant architecture, biomass accumulation, and stress tolerance. They exert their effects mainly through interaction with Phytochrome Interacting Factors (PIFs), HY5, and hormone signaling networks involving auxins, gibberellins, and abscisic acid. Recent studies have demonstrated that phytochromes also function as thermosensors, integrating light and temperature cues to regulate cold tolerance and adaptive responses under changing environmental conditions. Advances in molecular biology, genomics, and biotechnology, including CRISPR based genome editing and marker assisted breeding, have enhanced the understanding and utilization of phytochrome mediated pathways in crop improvement programs. Manipulation of phytochrome signaling offers significant opportunities for developing high yielding, climate resilient, stress tolerant, and resource efficient crop varieties suitable for sustainable agriculture. This review summarizes the molecular mechanisms of phytochrome signaling, their physiological functions, and their emerging applications in modern plant breeding and crop improvement strategies.

Keywords: Seed germination, photo morphogenesis, flowering time, shade avoidance, plant architecture, biomass production

Introduction

Light is one of the most important environmental factors influencing plant growth and development. Plants have evolved specialized light sensitive pigments called phytochromes, it can detect by red, far red light and regulate various physiological and developmental processes. it acts as molecular switches that enable plants to respond dynamically to changing light environments, there by controlling seed germination, stem elongation, leaf expansion, and flowering time (Rockwell *et al* ., 2006, Franklin and Quail, 2010) [13, 47]. In plant breeding, understanding the role of photochromic has become increasingly important for improving crop productivity and adaptability. Phytochrome mediated responses influence key agronomic traits such as plant architecture, biomass accumulation, and stress tolerance. These photoreceptors regulate shade avoidance responses and optimize plant performance under dense planting conditions and it is critical for modern agriculture (Casal, 2013, Ballaré and Pierik, 2017) [2, 4]. Recent advances in molecular biology and biotechnology, including CRISPR based gene editing and marker assisted selection, have enhanced the ability to manipulate phytochrome related pathways for crop improvement. Targeting downstream components such as Phytochrome Interacting Factors (PIFs) has further expanded opportunities to fine tune plant responses to light and temperature. Therefore, the study of phytochrome signaling provides a strong foundation for developing high yielding, climate resilient, and sustainable crop varieties, making it a key focus area in modern plant breeding (Leivar and Monte, 2014; Pham *et al* ., 2020) [30, 44].

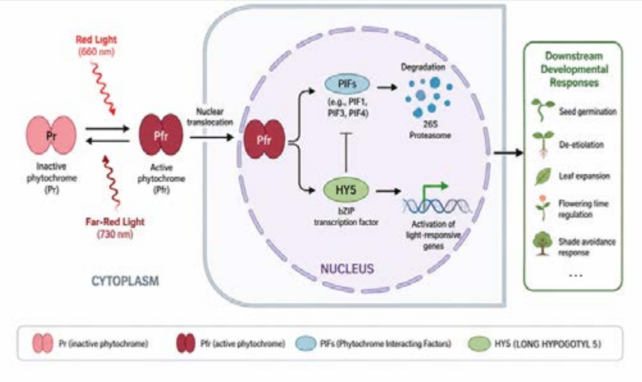

Fig 1: General Phytochrome Signaling Pathway Suggested image:

The figure illustrates the photoconversion of phytochrome from the inactive Pr form to the active Pfr form, followed by its translocation into the nucleus, degradation of PIF proteins, activation of HY5, and regulation of downstream developmental responses. Adapted from John C. Rockwell *et al.* (2006) [47] and Pilar Leivar and Elena Monte (2014) [30].

The different functions of Phytochrome

The Photochromic is a light sensitive pigment found in plants that helps regulate growth and development according to light conditions. It exists in two interconvertible forms Pr (absorbs red light) and Pfr (absorbs far red light). Through these forms, phytochrome controls many physiological processes in plants as detailed in table 1.

Table 1: Functions of Phytochrome Interacting Factors (PIFs) with Crop Details and Key Findings

PIF	Crop / Species	Major Functions	Key Findings	References
PIF1	*Arabidopsis thaliana*; Rice (*Oryza sativa*)	Suppression of seed germination; repression of chlorophyll biosynthesis; regulation of early seedling development	Demonstrated repression of light mediated germination via GA/ABA balance; regulates protochlorophyllide accumulation to prevent photooxidative damage	Oh *et al* ., 2004, Huq *et al* ., 2004[16], Kim *et al* ., 2011[25]
PIF2	*Arabidopsis thaliana*	Negative regulation of shade avoidance; modulation of transcription	Identified as modulator of light signaling redundancy with other PIFs; contributes to fine tuning photomorphogenesis	Salter *et al* ., 2003[51], Roig *et al* ., 2006
PIF3	*Arabidopsis thaliana*; Maize (*Zea mays*)	Inhibition of photomorphogenesis; chloroplast development; stress responses	Shown to directly interact with phytochromes; regulates chloroplast biogenesis genes and integrates ethylene signaling	Kim *et al* ., 2003, Stephenson *et al* ., 2009, Liu *et al* ., 2013[26, 35, 57]
PIF4	*Arabidopsis thaliana*; Tomato *(Solanum lycopersicum*); Wheat (*Triticum aestivum*)	Hypocotyl elongation; thermomorphogenesis; shade avoidance; senescence	Established as central regulator of temperature responses; controls auxin biosynthesis genes (YUC family); improves understanding of heat adaptation in crops	Koini *et al* ., 2009, Kumar *et al* ., 2012, Sakuraba *et al* ., 2014[28, 29, 50]
PIF5	*Arabidopsis thaliana*; Tomato	Hypocotyl elongation; shade avoidance; leaf senescence; fruit development	Works redundantly with PIF4; regulates senescence associated genes and hormone signaling pathways	Fujimori *et al* ., 2004, Lorrain *et al* ., 2008[14, 38], Xie *et al* ., 2017
PIF6	*Arabidopsis thaliana*	Seed dormancy; inhibition of elongation	Identified role in seed dormancy regulation and interaction with light dependent germination pathways	Penfield *et al* ., 2010, Leivar *et al* ., 2008[31, 43]
PIF7	*Arabidopsis thaliana;* Soybean (*Glycine max*)	Shade avoidance; thermomorphogenesis; stress response	Key regulator of low R signaling; controls rapid elongation growth under canopy shade; important for crop density adaptation	Li *et al* ., 2012, Mizuno *et al* ., 2015, Fiorucci *et al* ., 2020[12, 39]
PIF8	*Arabidopsis thaliana*	Far red light response; seedling development	Less characterized; recent studies suggest role in phyA signaling and early photomorphogenesis	Pham *et al* ., 2020[44]

1. Role of phytochromes in Regulating Cold Tolerance

Cold stress adversely affects plant growth, metabolism, and productivity. Plants perceive low temperature through multiple signaling pathways, among which phytochromes play a crucial role by integrating light and temperature cues. Phytochromes, especially phytochrome B (phyB), function as thermosensors that regulate plant responses to ambient temperature changes (Jung *et al*., 2016) [19].At low temperatures, phyB remains in its biologically active form for a longer duration, which influences downstream transcriptional networks. One of the key targets of phytochrome signaling is the family of Phytochrome Interacting Factors (PIFs). PIFs generally act as negative regulators of stress responsive pathways. Under cold conditions, photochromic mediated inhibition or degradation of PIFs leads to activation of cold responsive genes (Leivar and Monte, 2014) [30] in table 2.

A central component of cold tolerance is the CBF (C repeat Binding Factor) genes signaling pathway. Activation of CBF genes induces the expression of COR (cold responsive) genes that enhance freezing tolerance by stabilizing cell membranes, promoting osmolyte accumulation, protecting proteins and cellular structures (Kidokoro *et al* ., 2009) [24] as in fig 1. Phytochromes indirectly promote this pathway by suppressing PIF activity, thereby enhancing cold acclimation. In addition; phytochromes regulate hormonal pathways such as abscisic acid and gibberellins, which are important for stress adaptation. They also modulate reactive oxygen species (ROS) balance by enhancing antioxidant enzyme activity, reducing oxidative damage during cold stress (Franklin and Quail, 2010) [13]. From a crop improvement perspective, manipulation of phytochrome signaling and its downstream components offers significant potential to enhance cold tolerance in crops such as wheat, rice, and maize. This is particularly valuable for improving yield stability under low temperature stress and changing climatic conditions (Pham *et al*., 2020) [44].

Table 2: Phytochrome Mediated Regulation of Cold Tolerance in Crops

Crop	Phytochrome / Gene Involved	Mechanism of Cold Tolerance	Key Findings	References
Wheat (*Triticum aestivum*)	phyB, PIFs, CBF genes	Regulation of cold responsive (COR) genes via CBF pathway	Phytochrome signaling enhances frost tolerance by activating CBF mediated cold acclimation	Kidokoro *et al* .,2009, Franklin and Quail, 2010[13, 24]
Rice (*Oryza sativa*)	phyB, OsPIFs	Modulation of ROS balance and stress responsive genes	OsPIFs regulate chilling tolerance through interaction with light and temperature signaling	Pham *et al* ., 2020, Liu *et al* ., 2018[33, 44]
Maize (*Zea mays*)	phytochrome	Regulation of antioxidant	Improved cold tolerance associated with	Wang *et al* ., 2016[62]

	system, PIFs	enzymes and membrane stability	enhanced antioxidant activity and reduced oxidative damage	
Barley (*Hordeum vulgare*)	phyB, CBF pathway	Activation of cold acclimation genes	Phytochrome influences vernalization and cold tolerance pathways	Casal, 2013[4]
Arabidopsis (model plant)	phyB, PIF4, PIF7, CBF genes	Thermosensory regulation and gene expression control	phyB acts as thermosensor; PIF repression activates cold response genes	Jung *et al* ., 2016, Leivar and Monte, 2014[19, 30]
Tomato (*Solanum lycopersicum*)	phyB, PIF4	Hormonal regulation and stress signaling	Phytochrome mediated pathways regulate chilling tolerance and growth under low temperature	Koini *et al* ., 2009[28]
Soybean (*Glycine max*)	phyA/phyB, PIFs	Regulation of shade and stress responses	Light signaling pathways linked with improved cold adaptation and stress tolerance	Li *et al* ., 2012

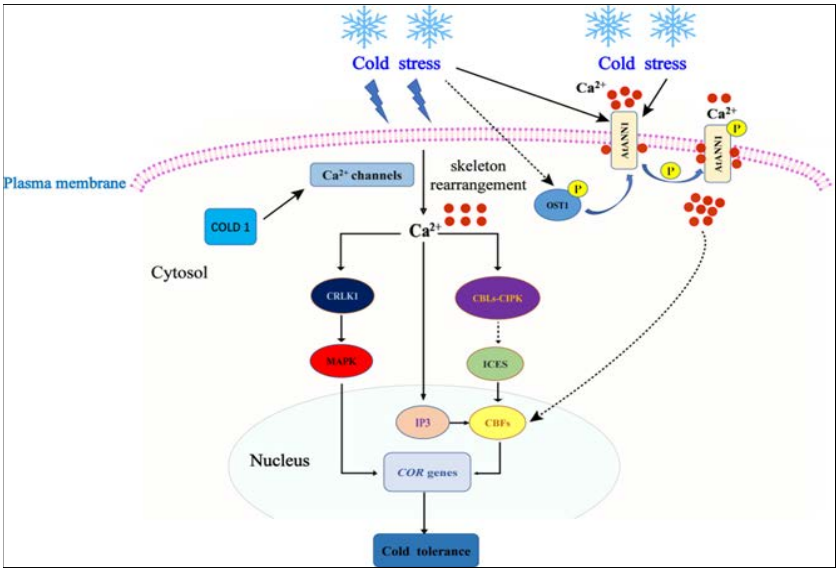

Fig 2: Cold stress signaling and regulation of cold tolerance in plants.

Cold stress is perceived at the plasma membrane, leading to Ca^{2+} influx through channels such as COLD1 and annexins. The elevated cytosolic Ca^{2+} activates several signaling pathways, including CBL–CIPK networks, MAPK cascades, and IP_3-mediated signaling. These pathways regulate CBF transcription factors, which subsequently induce the expression of COR (cold-responsive) genes, ultimately enhancing cold tolerance in plants. Adapted from Yun Xia *et al*., 2015[23].

2. Role of Phytochrome regulating in Pigment production

Phytochrome indirectly influences pigment production in plants by regulating light responsive pathways (Taiz et *al*., 2015) [58]. Although phytochrome itself is a light sensitive pigment, it controls the synthesis of other important pigments such as chlorophyll, carotenoids, and anthocyanins (Franklin and Quail, 2010) [13]. Under red and far red light conditions, phytochrome activates specific genes involved in pigment biosynthesis, leading to increased chlorophyll production for efficient photosynthesis and enhanced anthocyanin accumulation for protection against environmental stress (Chory, 2010) [9] as in table 3.

Table 3: Phytochrome Signaling and Pigment Accumulation in Plants

Pigment Type	Crop / Plant System	Role of Phytochrome	Molecular Mechanism	Key Outcome	References
Chlorophyll	Arabidopsis, Rice, Wheat	Promotes chlorophyll biosynthesis during light exposure	Light activated phytochrome degrades Phytochrome Interacting Factors (PIFs), activating chlorophyll biosynthetic genes	Greening of seedlings, enhanced photosynthesis	Franklin and Quail 2010[13]
Anthocyanins	Grapevine, Arabidopsis, Maize	Enhances anthocyanin accumulation under light/stress	Activates HY5 transcription factor; suppresses PIF mediated repression	Red/purple pigmentation, stress protection	Lloyd *et al* ., 2017[37]
Carotenoids	Tomato, Carrot, Maize	Increases carotenoid biosynthesis under light	Light signaling upregulates carotenoid biosynthetic genes	Yellow/orange pigmentation, photoprotection	Rodríguez Villalón *et al* .,2009[48]
Chlorophyll and flavonoids	Shade grown crops (soybean, rice)	Reduces pigment under shade (low R:FR light)	PIF accumulation represses pigment biosynthetic genes	Etiolation, reduced pigmentation	Casal 2013, Leivar and Monte 2014[4, 30]
Anthocyanins (stress condition)	Tomato, Arabidopsis	Enhances pigment under abiotic stress (light + temperature)	Crosstalk with ABA and stress signaling pathways	Increased antioxidant capacity	Lorrain *et al* ., 2008[38]

3. Role of Phytochrome regulating in shade avoidance

Phytochrome plays a crucial role in regulating plant responses to shade conditions by sensing the ratio of red to far red light also Casal *et al* ., 1997[5] reported by In light grown seedings, phytochrome A modulates the extent of response to reductions in red/far red ratio perceived by phytochrome B. Under shaded environments, the level of far red light increases due to absorption of red light by neighboring plants, which is detected by phytochrome also Park *et al* ., 2017[37] reported by far red light (700–800 nm) mediates plant growth and developmental processes, especially in shaded environments. This triggers physiological and molecular changes that help plants adapt to low light conditions

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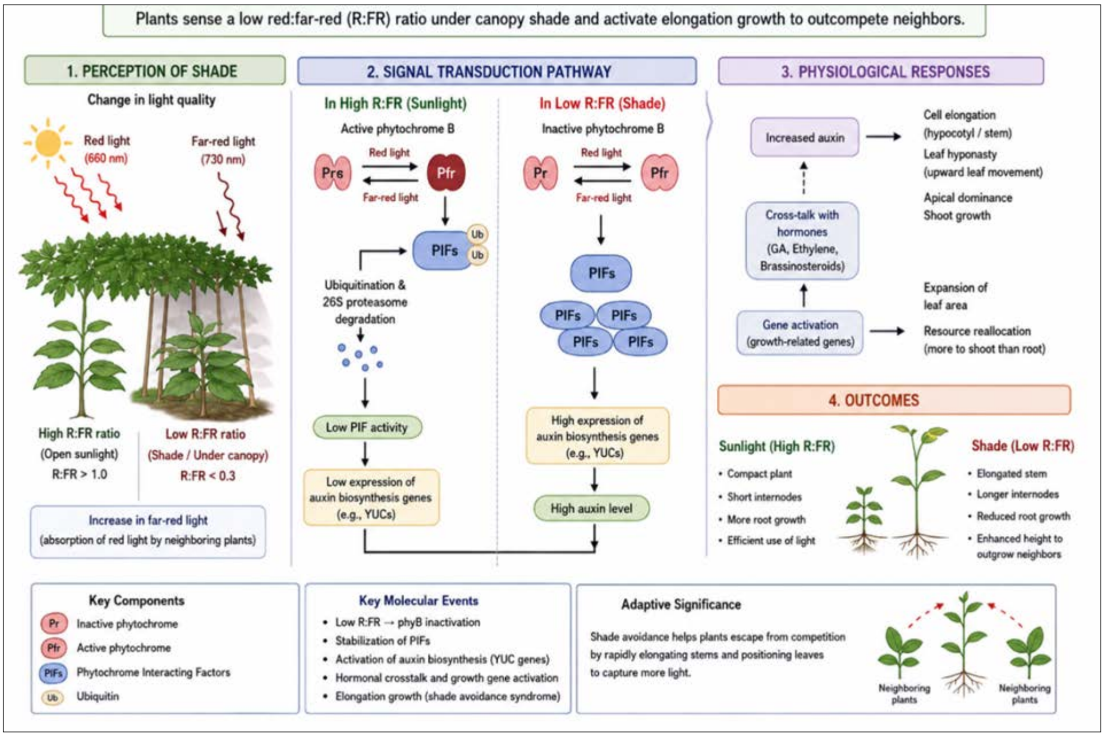

Fig 3: Shade Avoidance Syndrome (SAS)

The diagram illustrates how plants perceive nearby competitors and modify their growth patterns to capture more sunlight. Adapted from Carlos L. Ballaré and Ron Pierik 2017 [2].

In shade tolerant plants, phytochrome helps maintain efficient photosynthesis, optimal leaf expansion, and chlorophyll production instead of excessive stem elongation as in fig 3 and table 3. It also regulates gene expression to improve light capture and energy use efficiency also Pashkovskiy *et al*., 2026[42] reported by tomato were grown for two weeks under controlled light regimes with RL/FRL ratios of 2/1, 1/1, and 1/2, simulating different levels of shade stress. Plants lacking all three phytochromes (phya, b1, b2) showed pronounced decreases in biomass, photosynthetic pigments, and photosynthetic activity, accompanied by increased ascorbic acid and phenolic levels, indicating compensatory antioxidant responses.

Table 3: Phytochrome Controlled Shade Avoidance Mechanisms in Plants

Aspect of Shade Avoidance	Crop / Plant System	Role of Phytochrome	Molecular Mechanism	Key Outcome	References
Perception of shade (low R:FR light)	Arabidopsis, maize, rice	Detects reduction in red:far red ratio under canopy shade	Inactivation of phytochrome B (phyB) under shade conditions	Initiation of shade avoidance response	Casal 2013[4]
Hypocotyl/ stem elongation	Arabidopsis, soybean	Promotes elongation growth under shade	Stabilization of Phytochrome Interacting Factors (PIFs) (PIF4, PIF5, PIF7)	Increased stem elongation to outgrow neighbors	Lorrain *et al* ., 2008[38]
Auxin biosynthesis activation	Arabidopsis, tomato	Enhances auxin production under shade	PIFs activate YUC auxin biosynthesis genes	Cell elongation and shoot growth	Franklin and Quail 2010[13]
Leaf angle (hyponasty)	Rice, maize	Regulates leaf upward movement to capture light	Shade induced phyB inactivation triggers hormonal signaling (auxin/ethylene)	Improved light capture efficiency	Casal 2013[4]
Biomass allocation changes	Wheat, barley	Alters resource allocation under dense planting	Shade signaling modifies GA and auxin pathways	Reduced root growth, increased shoot elongation	Pierik and Testerink 2014[45]
Suppression under full light	All major crops	Prevents unnecessary elongation in high light	Active phyB degrades PIFs, repressing shade genes	Compact plant architecture	Leivar and Monte 2014[30]

4. Role of Phytochrome regulating in photomorphogenesis

Phytochrome plays a central role in photomorphogenesis, is the light mediated development of plants. It acts as a photoreceptor that detects red and far red light and regulates various growth processes accordingly as in table 4. In the presence of light, phytochrome becomes active and promotes normal plant development, including inhibition of stem elongation, expansion of leaves, chlorophyll synthesis, and chloroplast development (Kendrick and Kronenberg 1994, Taiz and Zeiger, 2015) [22, 58]. Also, Wang reported that this ligase inhibits plant photomorphogenesis and promotes hypocotyl elongation by degrading phosphorylated phya and the positive regulator HY5 (LONG HYPOCOTYL 5) by Wang *et al*., 2018 [33] and far red light also reduced stomatal density in leaves of cucumber (Shibuya *et al*., 2010) [9].

Table 4: Phytochrome Controlled Photomorphogenic Responses in Plants

Developmental Process	Plant/Crop Examples	Role of Phytochrome	Molecular Mechanism	Key Outcome	References
Seed germination	Arabidopsis, rice, wheat	Promotes light dependent germination	Active phyB inhibits ABA signaling and suppresses PIFs	Initiation of germination under light	Franklin and Quail 2010[13]
Seedling de etiolation	Arabidopsis, maize	Controls transition from dark grown to light grown form	Light activated phytochromes degrade Phytochrome Interacting Factors (PIFs)	Development of green, short hypocotyl seedlings	Leivar and Monte 2014[30]
Hypocotyl elongation	Arabidopsis, tomato	Suppresses excessive elongation in light	phyB inhibits PIF4/PIF5 (reduces auxin biosynthesis) for YUC genes	Short, sturdy seedlings in light	Lorrain *et al* ., 2008[38]
Cotyledon opening and expansion	Arabidopsis, rice	Promotes leaf expansion under light	Activation of photomorphogenic genes (HY5 pathway)	Expand ed cotyledons for photosynthesis	Chen *et al* ., 2004[7]
Chloroplast development	Arabidopsis, wheat	Induces chloroplast differentiation	phytochrome signaling activates chlorophyll biosynthesis genes	Functional chloroplast formation (greening)	Stephenson *et al* ., 2009[57]
Shade suppression of photomorphogenesis	Rice, soybean	Inhibits photomorphogenesis under shade	Low R:FR (phyB inactive and PIF accumulation)	Etiolated growth under canopy shade	Casal 2013[4]
Flowering regulation	Arabidopsis	Influences flowering time under light conditions	phytochrome interacts with CO/FT pathway	Proper photoperiodic flowering control	Franklin and Quail 2010[13]

5. Role of Phytochrome regulating in Plant architecture

Phytochrome plays a significant role in regulating plant architecture by controlling traits such as plant height, branching pattern, leaf size, and stem elongation. It acts as a photoreceptor that senses red and far red light signals and adjusts plant growth accordingly, especially under crowded or shaded conditions. Active phytochrome suppresses excessive stem elongation and promotes compact growth, whereas low phytochrome activity under shade conditions induces elongation and reduced branching, a phenomenon known as the shade avoidance response (Lincoln *et al* ., 2015, Carlos 1999). Phytochrome also influences the distribution and activity of plant hormones such as auxins and gibberellins, which regulate apical dominance and lateral bud growth, thereby shaping overall plant architecture (Peter, 2003) [26]. Furthermore, overexpression of the *Arabidopsis thaliana* PHYTOCHROME A (*PHYA*) gene in a commercially important indica rice variety (*Oryza sativa* L. cv. Pusa Basmati 1) demonstrated significant architectural modifications. The transgene expression, driven by a light regulated and tissue specific rice *rbcS* promoter, resulted in homozygous T5 transgenic lines accumulating high levels of PHYA protein under light conditions. Under both red and far red light, these transgenic plants exhibited a significant reduction in plant height, internode length, and internode diameter (including variations in cell size and number), along with an increased number of panicles per plant under greenhouse conditions (Wang *et al* ., 2018) [33] in table 5.

6. Role of Phytochrome regulating in Seed germination

Phytochrome plays a vital role in regulating seed germination by sensing red and far red light. It exists in two interconvertible forms Pr (inactive) and Pfr (active). When seeds are exposed to red light, phytochrome converts from Pr to the active Pfr form, which promotes germination by activating genes responsible for enzyme production and embryo growth. In contrast, far red light converts phytochrome back to the inactive form, inhibiting germination. Phytochrome also interacts with plant hormones such as gibberellins, it stimulates germination, and abscisic acid, inhibits it in **table 5**.

This light dependent regulation ensures that seeds germinate under favorable environmental conditions reported by Shinomura 1997[53] that seed germination of Arabidopsis thaliana (L.) with phytochrome deficient mutants showed for the first time that phytochrome A and phytochrome B modulate the timing of seed germination in distinct actions. Perception of R: FR ratio has ecological importance for seeds (Smith 1995). Botto *et al* ., 1996[3, 54] showed that, in contrast to seeds of the wild type and the phyB mutant of Arabidopsis, phyA mutant seeds germinated poorly under the low R : FR ratios (e.g. less than 0.15) of canopy shade light, suggesting that PhyA mediates the induction of germination under dense canopies table 5.

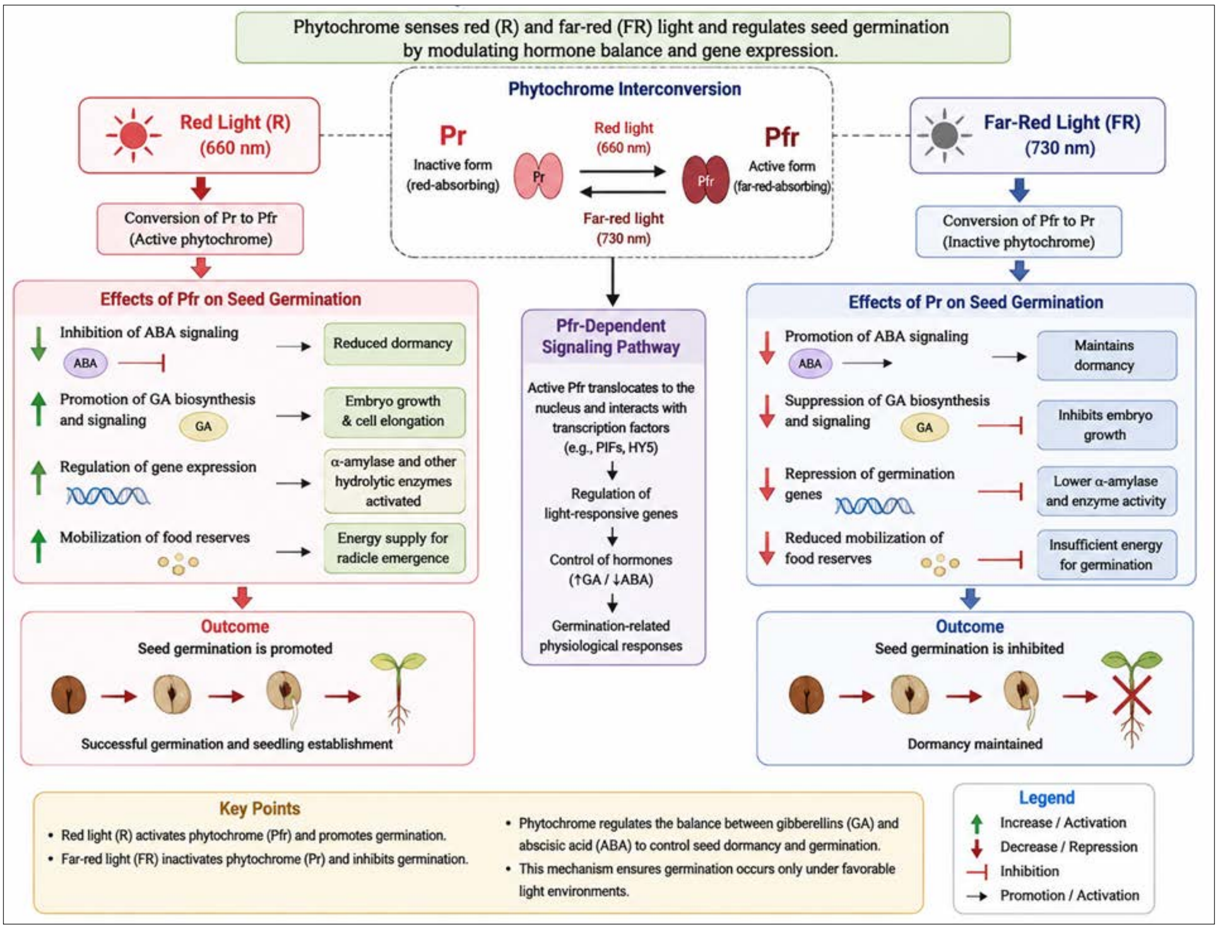

Fig 4: Phytochrome dependent Seed Germination Responses

The figure illustrates red light-mediated conversion of phytochrome from the inactive Pr form to the active Pfr form, which promotes gibberellic acid (GA) synthesis and initiates seed germination. Adapted from Keara A. Franklin and Peter H. Quail 2010[13].

Table 5: Phytochrome Mediated Regulation of Plant Architectural and Seed germination Traits under Different Light Conditions

Architectural Trait	Plant/Crop Examples	Role of Phytochrome	Molecular Mechanism	Key Outcome	References
Stem/hypocotyl elongation	Arabidopsis, rice, wheat	Suppresses excessive elongation in light	Active phyB degrades Phytochrome Interacting Factors (PIFs) → reduced auxin biosynthesis	Compact, sturdy plants in light	Lorrain *et al* ., 2008, Franklin and Quail 2010[13, 38]
Shade avoidance growth	Maize, soybean, rice	Promotes elongation under shade (low R:FR)	Inactive phyB → PIF4/PIF5/PIF7 accumulation → auxin signaling activation	Tall plants to escape shade	Casal 2013[4]
Branching / tillering	Rice, wheat	Regulates shoot branching and tiller number	Phytochrome controls auxin and strigolactone pathways	Balanced tiller/branch formation	Kebrom *et al* ., 2010[21]
Leaf angle (hyponasty)	Rice, maize	Controls leaf orientation toward light	Shade perception alters phyB signaling → auxin redistribution	Upright leaves for better light capture	Pierik and Testerink 2014[45]
Internode elongation	Sorghum, maize	Enhances stem elongation in dense planting	Shade induced phyB inactivation activates growth genes	Increased plant height under competition	Casal 2013[4]
Biomass allocation	Wheat, soybean	Controls root–shoot balance	Light signaling regulates GA and auxin pathways via phytochromes	More shoot growth under low light	Franklin and Quail 2010[13]
Plant density adaptation	Cereals (rice, wheat, maize)	Adjusts architecture under high planting density	Low R:FR triggers shade avoidance syndrome via PIFs	Adaptation to crowded conditions	Casal 2013[4]
Light perception in seeds	Arabidopsis, lettuce, rice	Detects red (R) and far red (FR) light to trigger germination	Conversion of phytochrome from inactive Pr to active Pfr form	Initiation of germination under light	Franklin and Quail 2010[13]
Promotion of germination	Lettuce, Arabidopsis	Promotes seed germination in light conditions	Active phyB suppresses ABA signaling and promotes GA biosynthesis	Breaks seed dormancy	Finch Savage and Leubner Metzger 2006

Reversal by far red light	Lettuce, weed seeds	Inhibits germination under shade (low R:FR)	Pfr (Pr conversion leads to reduced phytochrome activity)	Maintains dormancy in darkness/shade	Casal 2013[4]
Regulation via PIFs	Arabidopsis, rice	Controls hormonal balance during germination	Phytochrome Interacting Factors (PIFs) repress GA and promote ABA action in dark	Prevents premature germination in dark	Leivar and Monte 2014[30]
Seed dormancy release	Wheat, barley	Breaks dormancy under favorable light	Phytochrome signaling activates GA related genes	Synchronized germination in suitable conditions	Kami *et al* ., 2010[20]
Agricultural control	Crop seeds (cereals, vegetables)	Used to control germination timing	Manipulation of red light exposure regulates phytochrome activity	Improved crop establishment	Franklin and Quail 2010[13]

7. Role of Phytochrome regulating in Flowering time

Phytochrome plays a key role in regulating flowering time by sensing changes in day length (photoperiod) through red and far red light signals (Franklin and Quail, 2010, Smith, 2000) [13, 55]. It enables plants to distinguish between long day and short day conditions, thereby controlling the transition from vegetative growth to flowering (Quail, 2002, Thomas and Vince Prue, 1997) [5, 46]. The active form of phytochrome (Pfr) influences the expression of key flowering genes such as CONSTANS (CO) and FLOWERING LOCUS T (FT), which promote flowering under appropriate light conditions (Jiao *et al* ., 2007, Chen *et al* ., 2004) [7, 18]. In long day plants, phytochrome promotes flowering by stabilizing these regulatory pathways, whereas in short day plants it may inhibit flowering under extended light exposure (Kami *et al* ., 2010) [20].

Further molecular evidence is provided by Cerdán and Chory 2003[6] reported that PFT1 (PHYTOCHROME and FLOWERING TIME 1), a nuclear protein acting in the phyB signaling pathway, induces flowering under suboptimal light conditions. PFT1 functions downstream of phyB to regulate the expression of FLOWERING LOCUS T (FT), supporting the existence of a light quality pathway controlling flowering time in plants (Cerdán *et al* ., 2008, Fankhauser and Chen, 2008) [10, 31]. Phytochrome also interacts with the plant circadian clock to ensure flowering occurs at the appropriate season, synchronizing internal biological rhythms with environmental light cycles (Rockwell *et al* ., 2006) [47]. In plant breeding, manipulation of phytochrome signaling pathways is therefore important for developing early or late flowering varieties adapted to different environmental and cropping systems (Taiz *et al* ., 2015) [58].

8. Role of Phytochrome in Regulating Biomass Production

Phytochrome plays an important role in biomass production by regulating light mediated growth and photosynthetic efficiency in plants (Franklin and Quail, 2010, Smith, 2000) [13, 55]. By sensing red and far red light, phytochrome controls plant architecture, leaf expansion, and chlorophyll synthesis, which directly influence the plant's ability to capture light and produce energy (Quail, 2002, Chen *et al* ., 2004) [7, 46]. Active phytochrome promotes balanced growth by reducing excessive stem elongation and enhancing leaf development, leading to increased photosynthetic area and higher biomass accumulation (Rockwell *et al* ., 2006, Kami *et al* ., 2010) [20, 47]. It also regulates the allocation of resources between shoots and roots, improving overall plant productivity (Jiao *et al* ., 2007) [18]. Additionally, phytochrome interacts with hormonal signaling pathways to optimize plant growth under varying environmental conditions (Fankhauser and Chen, 2008, Taiz *et al* ., 2015) [10, 58]. Experimental evidence further supports its role in biomass regulation. Phytochrome A deficient (phyA) mutants of Solanum lycopersicum showed reduced photosynthetic activity in isolated chloroplasts along with decreased shoot biomass in adult plants, highlighting the essential role of phytochrome A in maintaining photosynthetic efficiency and growth (Kharshiing *et al* ., 2015) [23] present in table 6.

Table 6: Phytochrome Mediated Regulation of Flowering time and Biomass production Traits under Different Light Conditions

Aspect of Flowering Time	Plant/Crop Examples	Role of Phytochrome	Molecular Mechanism	Key Outcome	References
Photoperiod sensing	Arabidopsis, rice, soybean	Measures day length (red/far red light ratio)	phyA/phyB regulate light signaling pathways controlling CONSTANS (CO)	Determines flowering under long day or short day conditions	Franklin and Quail 2010[13]
Promotion of flowering	Arabidopsis (long day plant)	Promotes flowering under long day conditions	Active phyB stabilizes CO protein and activates FT gene expression	Early flowering in favorable seasons	Song *et al* ., 2015[56]
Inhibition of flowering	Rice (short day plant)	Prevents flowering under non inductive light	phytochrome signaling represses Hd1 and Hd3a pathways	Delayed flowering in unsuitable conditions	Izawa *et al* .,2003[17]
Shade regulation of flowering	Arabidopsis, tomato	Alters flowering under canopy shade	Low R:FR inactive phyB and accumulation of Phytochrome Interacting Factors (PIFs)	Accelerated flowering under shade stress	Casal 2013[4]
Integration with temperature	Arabidopsis	Links light and temperature signals for flowering time control	phyB acts as thermosensor and modulates FT expression	Adjusted flowering in seasonal environments	Jung *et al* ., 2016[19]
Hormonal regulation	Wheat, rice	Coordinates flowering hormones	Interaction with gibberellin and florigen pathways (FT/Hd3a)	Synchronised reproductive transition	Turck *et al* ., 2008[59]
Shoot growth regulation	Arabidopsis, rice, wheat	Controls balance between elongation and compact growth	Active phyB suppresses Phytochrome Interacting Factors (PIFs) → reduces excessive elongation	Optimized shoot biomass allocation	Franklin and Quail 2010[13]

Photosynthetic capacity	Maize, wheat, rice	Enhances leaf development and chloroplast formation	Phytochrome signaling activates chlorophyll biosynthesis and photosynthetic genes	Increased biomass via higher photosynthesis	Stephenson *et al* ., 2009[57]
Shade avoidance biomass shift	Soybean, maize, rice	Alters biomass distribution under canopy shade	Low R:FR → inactive phyB → PIF activation → stem elongation	Increased stem biomass, reduced root biomass	Casal 2013[4]
Leaf expansion	Arabidopsis, tomato	Promotes leaf area development in light	Light activated phytochromes regulate auxin and GA pathways	Higher leaf biomass and surface area	Koini *et al* ., 2009[28]
Root–shoot allocation	Wheat, barley	Regulates biomass partitioning between roots and shoots	Light signaling affects hormone balance (auxin, gibberellin)	Enhanced shoot biomass under light conditions	Pierik and Testerink 2014[45]
High density planting response	Cereals (rice, wheat, maize)	Adjusts biomass production in crowded conditions	Shade signals modify phyB–PIF module	Increased shoot biomass but reduced yield stability if excessive	Casal 2013[4]

Conclusion

Phytochromes are important photoreceptors that regulate plant growth and development by sensing red and far red light signals. They play central roles in controlling key physiological processes such as seed germination, photomorphogenesis, flowering time, shade avoidance, plant architecture, and biomass production. Through reversible conversion between Pr and Pfr forms, phytochromes regulate downstream signaling pathways and gene expression networks associated with plant development and environmental adaptation. Phytochromes also interact with plant hormones including auxins, gibberellins, and abscisic acid to regulate growth responses such as stem elongation, chlorophyll synthesis, and leaf expansion. These processes contribute directly to photosynthetic efficiency and biomass accumulation, thereby improving crop productivity. In modern agriculture, manipulation of phytochrome signaling pathways provides significant opportunities for developing high yielding, stress tolerant and climate resilient crop varieties. Therefore, understanding phytochrome mediated signaling mechanisms is essential for sustainable crop improvement and climate smart agricultural development

Future Thrust

Future research on phytochrome mediated regulation of plant growth and development should focus on understanding the complex interaction between light signaling, temperature sensing, and hormonal regulation under changing climatic conditions. Advanced molecular approaches such as CRISPR/Cas genome editing, RNA sequencing, proteomics, and functional genomics can be utilized to identify novel phytochrome associated genes and signaling components involved in stress tolerance, biomass production, and yield improvement. Special emphasis should be given to the manipulation of Phytochrome Interacting Factors (PIFs), HY5, and downstream transcriptional networks to develop crops with improved shade tolerance, enhanced photosynthetic efficiency, and better adaptation to dense planting systems. Future studies should also explore the role of phytochromes in regulating abiotic stress responses such as cold, drought, salinity, and heat stress through integration with ROS scavenging systems and hormonal pathways.

The application of marker assisted selection, genomic selection, and transgenic technologies can accelerate the incorporation of favorable phytochrome related traits into elite crop varieties. In addition, research on phytochrome mediated regulation of flowering time and plant architecture will be highly useful for developing climate resilient cultivars suitable for different agro ecological regions and cropping systems. Integration of phytochrome biology with artificial intelligence, precision agriculture, controlled environment agriculture, and smart farming technologies may further improve crop productivity and resource use efficiency. Understanding light quality management in protected cultivation systems such as greenhouses and vertical farming will also provide new opportunities for optimizing plant growth and secondary metabolite production. Therefore, future advancements in phytochrome research will play a significant role in sustainable agriculture, food security, and climate smart crop improvement programs.

Reference

1. Ballaré CL. Keeping up with the neighbours: Phytochrome sensing and other signalling mechanisms. Trends in Plant Science,1999:4(3):97–102.
2. Ballaré CL, Pierik R. The shade avoidance syndrome: Multiple signals and ecological consequences. Plant, Cell & Environment,2017:40(11):2530–2543. https://doi.org/10.1111/pce.12914
3. Botto JF, Sánchez RA, Whitelam GC, Casal JJ. Phytochrome A mediates seed germination responses. Plant Physiology,1996:110:439–444.
4. Casal JJ. Photoreceptor signaling networks in plant responses to shade. Annual Review of Plant Biology,2013:64:403–427. https://doi.org/10.1146/annurev-arplant-050312-120221
5. Casal JJ, Sánchez RA, Deregibus VA. The effect of plant density on phytochrome-mediated responses. Plant, Cell & Environment,1997:20(6):769–775.
6. Cerdán PD, Chory J. Regulation of flowering time by light quality. Nature,2003:423(6942):881–885.
7. Chen M, Chory J, Fankhauser C. Light signal transduction in higher plants. Annual Review of Genetics,2004:38:87–117. https://doi.org/10.1146/annurev.genet.38.072902.092259
8. Choi DM, Kim SH, Han YJ, Kim JI. Regulation of plant photoresponses by phytochrome A kinase activity. International Journal of Molecular Sciences,2023:24(3):2110. https://doi.org/10.3390/ijms24032110
9. Chory J. Light signal transduction: An integrated view. Annual Review of Plant Biology,2010:61:219–239. https://doi.org/10.1146/annurev-arplant-042809-112308
10. Fankhauser C, Chen M. Transducing light signals in plants. Nature Reviews Molecular Cell

Biology,2008:9(5):357–371. https://doi.org/10.1038/nrm2346

11. Finch-Savage WE, Leubner-Metzger G. Seed dormancy and germination control. New Phytologist,2006:171(3):501–523. https://doi.org/10.1111/j.1469-8137.2006.01787.x
12. Fiorucci AS, Galvão VC, Ince YÇ, et al. Phytochrome B and PIF7 regulate shade avoidance. Nature Plants, 2020. https://doi.org/10.1038/s41477-020-0636-1
13. Franklin KA, Quail PH. Phytochrome functions in *Arabidopsis* development. Journal of Experimental Botany,2010:61(1):11–24. https://doi.org/10.1093/jxb/erp304
14. Fujimori T, Yamashino T, Kato T, Mizuno T. Circadian-controlled PIF5 regulates plant growth responses. Plant and Cell Physiology,2004:45(7):913–920.
15. Hedden P. The genes of the Green Revolution. Trends in Genetics,2003:19(1):5–9.
16. Huq E, Al-Sady B, Quail PH. PIF1 is a critical regulator of chlorophyll biosynthesis. Nature, 2004. https://doi.org/10.1038/nature02692
17. Izawa T, Takahashi Y, Yano M. Comparative biology of flowering time regulation in rice. Plant Physiology, 2003.
18. Jiao Y, Lau OS, Deng XW. Light-regulated transcriptional networks in plants. Nature Reviews Genetics,2007:8(3):217–230. https://doi.org/10.1038/nrg2049
19. Jung JH, Domijan M, Klose C, et al. Phytochromes function as thermosensors in *Arabidopsis*. Science,2016:354(6314):886–889. https://doi.org/10.1126/science.aaf6005
20. Kami C, Lorrain S, Hornitschek P, Fankhauser C. Light-regulated plant growth and development. Current Opinion in Plant Biology,2010:13(5):571–578. https://doi.org/10.1016/j.pbi.2010.05.001
21. Kebrom TH, Brutnell TP, Finlayson SA. Phytochrome B regulates branching and tillering responses. Plant Physiology,2010:154(2):768–776.
22. Kendrick RE, Kronenberg GHM. Photomorphogenesis in plants (2nd ed.). Springer, 1994.
23. Kharshiing E, Sinha SP, Sharma R. Phytochrome A regulates photosynthesis and growth in tomato. Plant Physiology and Biochemistry,2015:97:193–201.
24. Kidokoro S, Maruyama K, Nakashima K, et al. The phytochrome-interacting factor PIF7 negatively regulates DREB1 expression under circadian control. Plant Physiology,2009:151(4):2046–2057.
25. Kim J, Yi H, Choi G, Shin B, Song PS, Choi G. Functional characterization of phytochrome interacting factor 1 in light signaling and chlorophyll biosynthesis. The Plant Cell,2011:23(4):1230–1243.
26. Kim J, Yi H, Choi G, Shin B, Song PS, Choi G. Functional characterization of phytochrome interacting factor 3. The Plant Journal, 2003.
27. Kim K, Shin J, Lee SH, Kweon HS, Maloof JN, Choi G. Phytochromes inhibit hypocotyl negative gravitropism by regulating the development of endodermal amyloplasts through phytochrome-interacting factors. Proceedings of the National Academy of Sciences of the United States of America,2011:108(4):1729–1734. https://doi.org/10.1073/pnas.1011066108
28. Koini MA, Alvey L, Allen T, et al. High temperature-mediated adaptations require PIF4. Current Biology, 2009. https://doi.org/10.1016/j.cub.2009.03.046
29. Kumar SV, Lucyshyn D, Jaeger KE, et al. Transcription factor PIF4 controls thermosensory activation. Science, 2012. https://doi.org/10.1126/science.1220843
30. Leivar P, Monte E. PIFs: Systems integrators in plant development. The Plant Cell,2014:26(1):56–78. https://doi.org/10.1105/tpc.113.120857
31. Leivar P, Tepperman JM, Cohn MM, Monte E, Al-Sady B, Erickson E, et al. Dynamic antagonism between phytochromes and PIF family in seedling development. The Plant Cell,2008:20(2):337–352.
32. Li L, Ljung K, Breton G, et al. Linking photoreceptor excitation to auxin distribution. Nature, 2012. https://doi.org/10.1038/nature11131
33. Liu H, Wang Y, Xu J, Zhang H. OsPIF-mediated regulation of cold stress tolerance in rice. Plant Molecular Biology,2018:97(1–2):91–105.
34. Liu X, Chen CY, Wang KC, et al. PHYTOCHROME INTERACTING FACTOR3 associates with the histone deacetylase HDA15 in repression of chlorophyll biosynthesis and photosynthesis in etiolated *Arabidopsis* seedlings. The Plant Cell,2013:25(4):1258–1273. https://doi.org/10.1105/tpc.113.109710
35. Liu Z, Zhang Y, Liu R, Xing J, Wang X. Phytochrome interacting factors integrate environmental signals in chloroplast development. Plant Physiology,2013:162(2):1063–1075.
36. Liu Z, Zhang Y, Liu R, Xing J, Wang X. PIF4 negatively regulates anthocyanin accumulation. Plant Science,2021:303:110788. https://doi.org/10.1016/j.plantsci.2020.110788
37. Lloyd A, Brockman A, Aguilar-Martinez J. Light-regulated anthocyanin accumulation in plants. Plant Journal,2017:89(6):1130–1142.
38. Lorrain S, Allen T, Duek PD, Whitelam GC, Fankhauser C. Phytochrome-mediated shade avoidance involves PIF4 and PIF5. Genes & Development,2008:22(18):2457–2467. https://doi.org/10.1101/gad.1706208
39. Mizuno T, Oka H, Yoshimura F. PIF7 regulates thermomorphogenic and shade responses in plants. Plant Signaling & Behavior,2015:10(8):e1044194.
40. Oh E, Yamaguchi S, Hu J, et al. PIL5 regulates gibberellin responsiveness. The Plant Cell, 2004. https://doi.org/10.1105/tpc.104.025163
41. Park Y, Runkle ES. Far-red radiation promotes growth of seedlings by increasing leaf expansion and whole-plant net assimilation. Environmental and Experimental Botany,2017:136:41–49.
42. Pashkovskiy P, Khudyakova A, Ashikhmin A, et al. Phytochrome-dependent photosynthetic and antioxidant responses of tomato under shaded conditions induced by red/far-red light ratios. Plant Science,2026:367:113090. https://doi.org/10.1016/j.plantsci.2026.113090
43. Penfield S, Josse EM, Halliday KJ, Graham IA. Cold and light regulation of seed germination. Plant Physiology,2010:152(2):915–926.
44. Pham VN, Kathare PK, Huq E. Phytochromes and phytochrome interacting factors. Plant

Physiology,2020:176(2):1025–1038. https://doi.org/10.1104/pp.19.01468

45. Pierik R, Testerink C. Plant responses to shade. Plant Physiology,2014:166(1):10–21.
46. Quail PH. Phytochrome photosensory signalling networks. Nature Reviews Molecular Cell Biology,2002:3(2):85–93. https://doi.org/10.1038/nrm728
47. Rockwell NC, Su YS, Lagarias JC. Phytochrome structure and signaling mechanisms. Annual Review of Plant Biology,2006:57:837–858. https://doi.org/10.1146/annurev.arplant.57.032905.105212
48. Rodríguez-Villalón A, Gas E, Rodríguez-Concepción M. Regulation of carotenoid biosynthesis by light. Plant Physiology,2009:150(1):209–220.
49. Roig-Villanova I, Bou J, Sorin C, Devlin PF, Martínez-García JF. Identification of primary target genes of phytochrome signaling. Plant Physiology,2006:141(1):85–96.
50. Sakuraba Y, Jeong J, Kang MY, Kim J, Paek NC, Choi G. Phytochrome interacting transcription factors PIF4 and PIF5 induce leaf senescence. Nature Communications,2014:5:4636. https://doi.org/10.1038/ncomms5636
51. Salter MG, Franklin KA, Whitelam GC. Gating of the rapid shade avoidance response by the circadian clock in plants. Nature,2003:426(6967):680–683. https://doi.org/10.1038/nature02174
52. Shibuya T, Endo R, Yuba T, Kitaya Y. Effects of red:far-red ratio on cucumber. Biologia Plantarum,2015:59:188–200.
53. Shinomura T. Phytochrome regulation of seed germination. Plant and Cell Physiology,1997:38(12):1341–1348.
54. Smith H. Physiological and ecological function within the phytochrome family. Annual Review of Plant Physiology and Plant Molecular Biology,1995:46:289–315.
55. Smith H. Phytochromes and light signal perception by plants. Plant, Cell & Environment,2000:23(7):755–767. https://doi.org/10.1046/j.1365-3040.2000.00579.x
56. Song YH, Shim JS, Kinmonth-Schultz HA, Imaizumi T. Photoperiodic flowering control. Annual Review of Plant Biology,2015:66:501–522.
57. Stephenson PG, Fankhauser C, Terry MJ. PIF3 controls chloroplast development. Plant Physiology, 2009. https://doi.org/10.1104/pp.109.139667
58. Taiz L, Zeiger E, Møller IM, Murphy A. Plant physiology and development (6th ed.). Sinauer Associates, 2015.
59. Turck F, Fornara F, Coupland G. Regulation of florigen FT. Science,2008:321(5888):1650–1654.
60. Wang JG, Chen CH, Chien CT, Hsieh HL. FAR-RED INSENSITIVE219 regulates hypocotyl elongation. Plant Physiology,2011:156:631–646.
61. Wang J, Chen CH, Chien CT, Hsieh HL. A ubiquitin ligase regulates phytochrome signaling and photomorphogenesis. Plant Physiology,2018:176(1):559–573.
62. Wang X, Liu F, Jiang Y, Li Z. Regulation of antioxidant metabolism under cold stress in maize. Plant Physiology and Biochemistry,2016:108:367–376.