Review Article

Photoregulation of seed germination : A review

ABSTRACT

Seed germination is an important stage in the plant's life cycle, and light is a key factor in regulating this stage. The regulation of seed germination by light is an intricate process that is governed by a range of photoreceptors and signaling pathways. Photoreceptors, which include phytochromes, cryptochromes, and phototropins, are the major sensors in seeds that detect and transduce light signals. These photoreceptors regulate the expression of various sets of genes, resulting in the activation or repression of germination related activities. The phytochrome system, which consists of various phytochrome species such as phyA, phyB and phyC acts critically in controlling the seed germination in response to varying light conditions. Phytochromes break seed dormancy, promote endosperm weakening, and mobilize store reserves during germination. Cryptochromes, another form of photoreceptor, are largely involved in blue light perception and have been found to influence seed germination through numerous processes, including the modulation of hormonal pathways, such as those involving gibberellic acid (GA) and abscisic acid (ABA). In addition to the photoreceptors, there are various upstream and downstream signaling components, such as transcription factors, protein kinases, and hormonal regulators, that contribute to the complex network that regulates light induced seed germination. This review examines the current state of knowledge regarding the molecular mechanisms that govern the photoregulation of seed germination. It delves into the intricate among between photoreceptors, signaling pathways, and environmental cues that play a crucial role in this process. Moreover, it explores the possible implications of this research in enhancing agricultural practices and devising strategies for maximizing crop yields.

Keywords: Light; Photoreceptors; Phytochromes; Red and Far red light; Seed germination

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1. INTRODUCTION

Seed plays a fundamental role in plant growth and development [51]. Germination is the process by which a plant develops from a seed to seedling [8,63] (Fig. 1). According to ISTA [42], germination is defined as "the emergence and development of the seedling to a stage where the aspect of its essential structures indicates whether or not it is able to develop further into a satisfactory plant under favourable conditions in the soil".

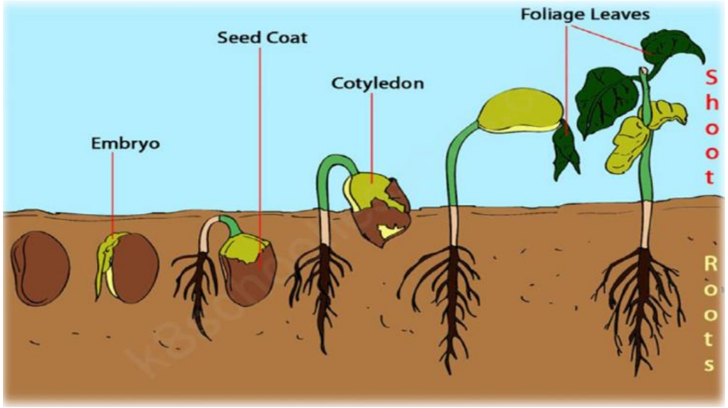

Fig. 1. Seedling growth stages
(Source: https://k8schoollessons.com/germination/)

2. PHASES OF SEED GERMINATION

Seed germination may be divided into three phases namely (i) imbibition, (ii) respiration and (iii) cell division [8,11,12,2,63]. The phase I, characterized by the rapid absorption of water by the seed, results in swelling and the initiation of metabolic activities, which also activate the essential biochemical reactions for germination [8,12,63]. The phase II, characterized by the reactivation of metabolism, hydrolysis, macromolecules biosynthesis, the mobilization of stored reserves such as starch, proteins and lipids, provides the energy and building blocks necessary for growth and development [2]. The phase III, characterized by cell division and radicle protrusion, represents the final stage of seed germination [2,63], in Fig. 2.

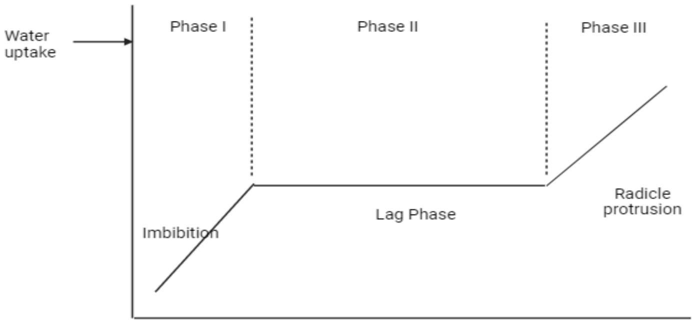

Fig. 2. Phases of seed germination
(Source: https://www.biorender.com/)

3. FACTORS REQUIRED FOR SEED GERMINATION

Seed germination depends on both internal and external factors [10,98].

Factors

External factors ↓
Internal factors ↓

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Water
Temperature
Light
Oxygen

Seed viability
Genotype
Seed maturation
Seed dormancy

3.1 LIGHT

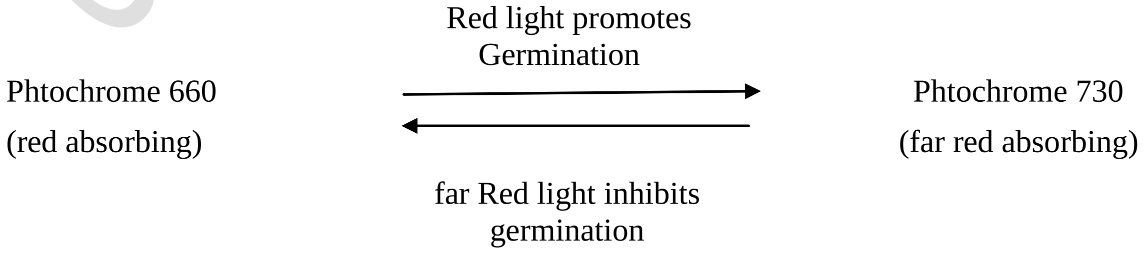
Several environmental factors influence the growth, development, and reproduction of green plants, but among them, light is perhaps the most important factors [29]. Besides its role as the energy source for photosynthesis, light also provides crucial environmental signals that control every stage of the plant life cycle, from seed germination to flowering [4,29]. It is particularly evident how light affects plant development when seedlings are grown in the absence of light. In such cases, etiolation, the response to growth in darkness, leads to the elongation of stems and a significant reduction or halt in leaf development [59].

The presence or absence of light may or may not influence germination. Environmental factors such as light or darkness, can initiate physiological dormancy in seeds, which is known as germination [16]. The most of the seeds are not sensitive to light or darkness, but many seeds, particularly those found in forest areas, will not germinate until sufficient light is available for the seedling growth [33].

3.1.1 Role of light on seed germination

Light is an important environmental factor influencing germination [99]. The certain types of seeds can only germinate when they receive an adequate amount of light. Meanwhile, other plants have methods for determining whether they are in the shade of neighbouring vegetation or direct light source [28]. Here, it is focused on two plant responses to light and explore how these responses allow plants to survive and development of the growth to their environments [28].

Light serves as a signal to initiate and regulate photoperiodism and photomorphogenesis. The two light-sensing systems are involved in these responses namely the blue light-sensitive system (photoregulation) and the red light-sensitive system (phytochrome regulation) [100]. The photochemically reactive pigment Phytochrome has been shown to be involved in the mechanism of light sensitivity in seeds [10]. The phytochrome is synthesized when seed is exposed to red light (600-760 nm) phytochrome changes to Pfr which promotes germination. When exposed to far-red light (760-800 nm), inhibits germination [60,39].



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3.1.2 Photo regulation

Photoregulation of seed germination is the process by which light, as perceived by specialized photoreceptors known as phytochromes, regulates the transition of a quiescent dry seed to a metabolically active state, thereby commencing the germination process [9]. Photoregulation is defined as regulation of plant by light or blue light systems [96]. Photoregulation involves blue light receptors like cryptochromes and phototropins that control responses like phototropism and chlorophyll synthesis [16].

Light signals are detected by photoreceptors in seeds, which include phytochromes, cryptochromes and phototropins, which plays an important role in integrating light information and controlling germination responses [16,96].

3.1.3 Phytochromes

Seed germination of plant species is significantly influenced by light, and among the various photoreceptor systems, phytochrome plays a crucial role [81]. Phytochromes are soluble, dimeric chromopeptides with 120 to 130 kD monomers that exist in two photoconvertible forms namely inactive form Pr (red light-absorbing) and active form Pfr (far-red light-absorbing) [99,73,74,17]. The Pfr form is the biologically active form that initiates signaling cascades leading to various physiological responses, including seed germination [5].

3.1.3.1 Red light

Red light enhances seed germination in many plant species. Phytochromes, a type of photoreceptor, absorb red light and undergo a conformational change, triggering a series of biochemical events that activate genes involved in germination [86].

3.1.3.2 Far-red light

Far-red light, which is present in sunlight and is also produced by neighboring plants, can inhibit seed germination. Additionally, phytochromes play a role in sensing far-red light. When seeds are exposed to far-red light, phytochromes undergo a distinct conformational change, which may counteract the effects of red light and inhibit germination. This phenomenon is referred to as phytochrome-mediated seed germination inhibition [86].

3.1.3.3 Blue light and UV light

Furthermore, blue light and UV light can influence seed germination [10], however their effects are frequently more complex and vary depending on the plant species and environmental factors [31]. While red and far-red light are the principal regulators of seed germination, blue and ultraviolet light also plays an important role. Blue light perception requires photoreceptors, such as cryptochromes, which regulate many aspects of plant growth and development, including germination. UV radiation can stimulate or inhibit germination depending on its intensity and duration of exposure. These reactions are regulated by UV-B photoreceptors and entail intricate signaling pathways.

When light is activated, the Pfr form of phytochrome translocate to the nucleus and interacts with transcription factors, causing changes in the expression of light-regulated genes involved in hormonal biosynthesis, enzyme activation and seed reserve mobilization [7,50].

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Gibberellin (GA) and abscisic acid (ABA) are the key hormones which regulate seed germination in response to light signals. In photoblastic seeds, the Pfr form of phytochrome stimulates GA production while suppressing ABA levels, resulting in a hormonal balance that promotes germination [33,83].

The classification of seeds into three types based on their sensitivity to white light, known as photoblastism [94], is linked to recent advancements in research on phytochrome forms and modes of action. This classification divides seeds into three categories namely, positive photoblastic, which germinate only under white light, negative photoblastic, which germinate only in the dark and white light inhibits germination, and light insensitive seeds, which germinate both in the dark and under white light.

Casal and Sanchez [18] revealed that phytochromes role in controlling photosensitive seeds. PHYs were the first photoreceptor proteins found in plants that detect Red and Far-Red light [92,21,22]. In dicotyledonous plants like *Arabidopsis thaliana*, five Phys encoded by small gene families have been identified were PhyA, PhyB, PhyC, PhyD, and PhyE [23,78]. However, in monocots, the phytochrome is made up of PhyA, PhyB, and PhyC. Furthermore, depending on their light stability, these phytochromes can be classed as photostable type I (PhyA is the only type I phytochrome) and photostable type II (PhyB to PhyE) [75,68]. PhyA is responsible for far-red light, while PhyB and PhyE govern red light signaling.[21] There are five distinct phytochromes such as phyA to phyE, observed in *Arabidopsis thaliana* each with its apoprotein encoded by unique and divergent genes [38,84,86,30].

3.1.4 Functions

PHYA: PHYA primarily mediates responses to far-red light and it is a light sensitive. It plays a significant role in regulating seed germination, de-etiolation of seedlings, and photoperiodic flowering. It also involved in shade avoidance responses [79].

PHYB: PHYB is the best-characterized phytochrome in Arabidopsis and mediates responses to red light. It regulates various aspects of plant growth and development, including seed germination, photomorphogenesis, shade avoidance, circadian rhythms, and flowering time control. It also plays a role in photoperiodic flowering [35].

PHYC: Its precise functions in *Arabidopsis* are not fully illuminated, but it likely contributes to light-mediated developmental processes similar to other phytochromes [35].

PHYD: It may have overlapping functions with other phytochromes in regulating plant development in response to light signals [35].

PHYE: PHYE is involved in regulating various aspects of plant growth and development, like other phytochromes. Its specific functions in *Arabidopsis* include roles in seedling de-etiolation, photomorphogenesis, shade avoidance responses, and flowering time control [79].

The physiological effects of phytochrome can be categorized into three primary mechanisms *viz.*, **Low Fluence Responses (LFR),** which involve the classical red/far red reversible responses in which the production of Pfr promotes plant responses and the removal of Pfr reverses them**, Very Low Fluence Responses (VLFR),** which represent the saturation of responses by very low fluences with reciprocity but without reversibility, as the photoequilibrium maintained by far red light or even the dim green safe light used in

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photomorphogenic experiments produces enough Pfr to saturate these responses, and **High Irradiance Responses (HIR),** which refer to the responses produced by prolonged high irradiance, which do not exhibit reversibility or reciprocity [81].

3.1.5 Structure

Phytochrome consists two proteins with each two domains. The upper one consists pigment called chromophore and regulate photoreceptors and the lower one acts as cellular response [75].

3.1.6 History

The phytochrome pigment was discovered by Sterling Hendricks and Harry Borthwick at the USDA-ARS Beltsville Agricultural Research center in Maryland during a period from 1940 to 1960 [72,14,37,76]. They also suggested that red light promotes germination which also triggers flowering. The red-light responses could be reversed by far-red light, implying the presence of a photoreversible pigment. In 1959, biophysicist Warren Butler and biochemist Harold Siegelman identified the phytochrome pigment using a spectrophotometer. Warren Butler was responsible for naming the pigment, phytochrome. In 1983, the laboratories of Peter Quail and Clark Lagarias reported the chemical purification of the intact phytochrome molecule, and in 1985, Howard Hershey and Peter Quail published the first phytochrome gene sequence [73].

4.1 CRYPTOCHROMES

Cryptochromes are blue light receptors that mediate various light induced responses in plants and animals [76,55,104,20]. Cryptochrome is a class of flavoprotein that encompass a blue light [16]. Cryptochrome is involved in the circadian clocks of plants and animals, and the sensing of magnetic fields in a number of species [16]. Cryptochrome mediated response in inhibition of the germination of dormant seeds, and hypocotyl elongation, stimulation of cotyledon expansion [56], promotion of root greening, stomata opening and development [45], regulation of shade avoidance, enhancement of biotic and abiotic stress responses, regulation of fruit development [31], and suppression of leaf senescence [98]. It also enhances photo morphogenesis in the absence of phytochromes [87].

4.1.1 Structure

The structure of cryptochrome involves a fold very similar to that of photolyase, with a signal molecule of FAD. These proteins have variable lengths and surfaces on the c-terminal end [16,55].

4.1.2 History

The cryptochrome was first documented by Charles Darwin which induce plant responses to blue light [19]. By 1995, it became clear that the products of the HY4 gene and its two human homologous did not exhibit photolyase activity and were instead a new class of blue light photoreceptor hypothesized to be circadian photo pigments [55].

4.1.3 Functions

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Cryptochromes (CRY) are photosensory receptors that regulate plant growth and development, as well as the circadian clocks of plants and animals [57,93,104,20]. Plant cryptochromes are examined in *Arabidopsis*. The *Arabidopsis* genome contains three cryptochrome genes such as CRY1, CRY2 and CRY3. CRY1 and CRY2 typically act in the nucleus [101], whereas CRY3 most likely works in chloroplasts and mitochondria.[48] Cryptochromes and other photoreceptors help plants recognize environmental cues such as irradiance, day-night transition, photoperiods, and light quality, allowing them to grow and develop. In *Arabidopsis*, CRY3 is a member of the photolyase or cryptochrome superfamily CRY-DASH and it functions as a single-stranded DNA repair enzyme [15,70]. CRY DASH (cryptochrome-Drosophila, Arabidopsis, Synechocystis, human) functions on DNA-repairing enzyme and photosensory activity [15,6].

CRY1 and CRY2: It is a blue light photoreceptor of plant which promote photomorphogenesis [53]. By comparing these two cryptochromes, CRY 1 is more stable than CRY 2 under blue light, CRY 2 degrades under blue light [1].

CRY3: It is not a blue light receptor but promote photomorphogenesis [54].

5.1 PHOTOTROPINS

Phototropins are blue-light receptors that regulate a variety of plant responses to improve photosynthetic efficiency [24]. There are two different phototropins in *Arabidopsis* that exhibits overlapping function in addition to having unique physiological role. The two phototropins are Phot1 and Phot2. Phot1 help in cotyledon or hypocotyl growth. The phot1 mutant lacks hypocotyl Phototropism in response to low-intensity blue light but retains a phototropic response at higher intensities [49,23].

5.1.1 Structure

Phototropin has two light sensing Light-oxygen-voltage (LOV) Domains, namely **LOV1** and **LOV2** [23,34]. The LOV1 and LOV2 bind a chromophore FMN (Flavin Mono Nucleotide). Blue light irradiation/photoexcitation of protein bound FMN cause a conformational change of phototropin that triggers auto phosphorylation and start the sensory transduction cascade. It directs the movement of chloroplasts optimize photosynthesis efficiency of plant [23].

6.1 ENVIRONMENTAL IMPLICATIONS

Light, an important environmental signal influences plants undergo several biological processes, including seed dormancy, germination and photomorphogenesis, phototropism, shade avoidance, and flowering [26,44].

Plants use light as both an energy source and a source of information for plants to adapt to their surroundings [102]. When buried in soil, seeds may detect the quality and strength of light signals to determine about their closeness grounds surface. Burying seeds too deep can hinder germination and prevent emerging seedlings from reaching the surface for photosynthesis before the seeds energy components are depleted [71]. As a result, light is an essential environmental component for seeds to assess about their surroundings for favourable seedling emergence [102].

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Phytochrome was first observed in lettuce *(Lactuca sativa).* The red light induce germination, while far red light has no effects on germination in seed [13,103,25]. Red light stimulates lettuce seed germination and far-red light inhibits this effect. Phytochrome exists in two forms, the Pr, is transformed by red light into Pfr. This process is reversible by far-red irradiation. The Pfr form is assumed to be the bioactive form that promotes lettuce seed germination.[91] The phytochrome B is primarily responsible for lettuce seed germination.[81] Although light is required for germination in fully matured seeds[51], the significance of light signaling in seed dormancy is unknown. Environmental factors can impact endogenous information, including the balance of ABA and GA levels, as well as the expression of delay of germination 1 (DOG1), a crucial gene for seed dormancy. These are used to regulate the seed dormancy and induce the germination with the light signals [103].

Kendrick and Frankland [46], employed negative photoblastic seeds of *Amaranthus caudatus*, concluded that phytochrome regulates germination in **High Irradiation Response** (HIR), as only continuous and or intermittent white light suppresses germination, but phyA is the phytochrome that controls germination in negative photoblastic seeds. Mc Donough [61] resulted that non photoblastic seeds of *Raphanus sativus* of white light inhibit the germination when the seeds are osmotically treated and Thanos and Mitrakos [90] in *zea mays*, Defreitas and Takaki [27] in *Raphanus sativus*, Lopes and Takaki [58] in *Phaseolus vulgaris* which has non-photoblastic seeds, that water stress promoted by polyethylene glycol, Takaki and Toledo [89] in *Oryza sativa*, are the non photoblastic seeds exhibit no germination, but under continuous light and or intermittent light showed an effect on germination, phytochrome acts through HIR and we can conclude that phyA is the form of phytochrome present in those seeds. Felippe and Polo[32] suggested that weed species of scarifying the positive photoblastic seeds can change sensitive to white light and germinated under both light and darkness conditions. Based on phytochrome, that germination of lettuce seeds is controlled by phyB (LFR), but scarification induces phyA to promote germination (VLFR) since seeds germinate under both white light and darkness. As reported above, phyA seems to be responsible for the perception by seeds of the water potential of the media inducing osmolyte synthesis to counteract the pressure needed for rupturing the seed coat [89].

7.1 SEED GERMINATION

Shinomura *et al*. [81] reported that PHYA and PHYB response germination in *Arabidopsis thalaiana*, with mutants of wild type (WT), fre1 and hy3 mutants under continuous red, far red, white and dark light. They showed that continuous red and white light exhibit the germination, whereas the continuous far red light exhibited germination in fre1 at 1%, and hy3 at 47%. These results suggest that the red-absorbing form of PhyB inhibits PhyA-dependent germination in continuous far-red light.

Neff *et al.* [64] studied with various types of lettuce varieties exposed under red, far red and dark light conditions (Table 1).

Table 1. Comparison of lettuce variety under different light treatments on germination %

S. No.	Variety	Treatment	Mean Germination %
1.	Waldmann's Dark Green	Dark	47.2

		FR	26.2
		R	98.6
		R/FR	25.6
2.	Two Star	Dark	70.4
		FR	59.8
		R	97.8
		R/FR	58.4
3.	Marin	Dark	89
		FR	60
		R	99.5
		R/FR	64.5
4.	Black Seeded Simpson	Dark	90.4
		FR	82.4
		R	92.2
		R/FR	79.4
5.	Baronet	Dark	94.6
		FR	95.6
		R	97.8
		R/FR	94
6.	Tropicana	Dark	95.6
		FR	93.2
		R	87
		R/FR	93.6
7.	Concept	Dark	96.8
		FR	91
		R	97.6
		R/FR	89.2
8.	New Red Fire	Dark	98.25
		FR	100
		R	99.25
		R/FR	94.75
9.	Red Sails	Dark	90.4
		FR	99
		R	92.8
		R/FR	91.6
10.	Vulcan	Dark	99.2
		FR	99
		R	99.5
		R/FR	95.8
11.	Galactic	Dark	98.2
		FR	98.2
		R	99.4
		R/FR	99.2
12.	Blackjack	Dark	98.8
		FR	99.6
		R	99.6
		R/FR	98.2
13.	Firecracker	Dark	99.2

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		FR	99.6
		R	100
		R/FR	99.2
14.	Simpson Elite	Dark	95.2
		FR	87.4
		R	98.6
		R/FR	98

The comparison between light and temperature was carried out under germination rate with 13, 17, 21, 25 and 30 ^{o}C of *R. niveum* (Table 2). The germination was increased with increase in temperature and decreased above 25 ^{o}C and lowest occurred at 13 ^{o}C. The optimum temperature occurred at the range between 17-21 ^{o}C, and no difference in germination was observed between at 21-25 °C, whereas the seedlings germinated at 25 °C and 30 °C under light condition were not healthy and most of them will die after radicle protrusion [85]. In Grand Raphids lettuce seeds also exposed to red light at 656 nm with temperature 20^{o} C, which promoted germination [7].

Table 2. Effect of light with temperature on seed germination % of *R. niveum*

S. No.	Temperature/ light or dark	Days required for onset of germination	Days required for completion of germination	Germination %
R. niveum				
1.	13°C, Light	30	55	14.33 ± 1.86
2.	17°C, Light	26	54	25.00 ± 1.73
3.	21°C, Light	21	50	34.33 ± 0.88
4.	25°C, Light	25	48	35.00 ± 0.58
5.	30°C, Light	36	49	33.33 ±1.76
6.	Alternate temperature (21°C in light and 10°C in dark for 12 h)	21	50	32.66 ± 3.38

Nepenthes mirabilis were treated under red, green, blue and yellow light on germination, and possessed that seedling under yellow light gave the highest germination (83.69 %) and followed by to red and white light (60.75% and 57%) respectively [42] (Table 3). Zucareli *et al*. [105] studied that *Passiflora nitida* had no significant effect on germination when exposed to light/dark conditions. Likewise, Vogel and Macedo [94] examined the light quality on in vitro germination and protocorm formation and and the effect of indole-3-acetic acid (IAA) and thidiazuron (TDZ) on proliferation of protocorm-like bodies (PLBs) in *Cyrtopodium glutiniferum* Raddi. of germination, was faster under white and blue light and highest under green light (Table 3).

Table 3. Comparison between different lights on germination of *Nepenthes mirabilis* and *C. glutiniferum.*

S. No.	Treatments	Germination	Mean germination

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1.	White	57±7.71	46±5.0
2.	Red	60.75±8.518	90±2.8
3.	Blue	31.63±11.066	50±3.7
4.	Green	36.4±2.93	64±5.1
5.	Yellow	83.69±3.372	-
6.	Dark	-	107±6.3
Reference		Jala [42]	Vogel and Macedo [94]

Panda *et al.* [69] reported that low light treatment suppresses rice seed germination, by decreasing gibberellin (GA), and proposed that FR-induced GA deficiency is resulted by upregulation of SLR1 and GA-catabolism genes, therefore increasing DELLA proteins, which further enhanced GA-responses in sprouting rice seeds. Aref (2000) resulted that *Cassia fistula*, *Enterolobium saman* and *Delonix regia* under the effect of light intensity at 100%, 50% and 25% on seed germination. The result showed that germination% were 67, 45 and 33 % for *Delonix regia, Cassia fistula* and *Enterolobium saman*, respectively.

8.1 HORMONAL EXPRESSION

PIF1 (Phytochrome Interacting Factor) is a phytochrome mediated germination. PIF1 interacts with the Pfr forms of phyA and phyB to suppress phys-induced seed germination [66]. Red light activates phyB, which enhances PIF1 degrade by the proteasome [67,26]. In low R/FR ratios, PIF1 accumulates in the nucleus and promotes DAG1 transcription, which suppress the expression of GA3ox1, blocking GA production and preventing seed germination. PIF1 suppresses a few genes required for cell wall loosening, such as Expansin (EXP) genes and XyloglucanendoTransglycosylase/Hydrolase (XTH) genes [65], which are essential for seed germination. SOMNUS also a direct gene resemblance as a PIF 1 [47]. SOM is also positively regulated germination under light [23]. In the dark, JMJ20 and JMJ22 are directly suppressed by SOM. When stimulated by light, the PHYB-PIF1-SOM pathway downregulates SOM, causing JMJ20/JMJ22 to target GA3ox1 and GA3ox2 chromatin and eliminate histone arginine methylation at their promoters. Increased expression of GA3ox1 and GA3ox2 in seeds leads to GA accumulation and germination [23].

9.1 APPLICATIONS

Phytochrome functions in *Arabidopsis* by [35], shows response in seed germination, seedling de-etiolation, and shade avoidance [36]. Phytochromes control many aspects of plant development. They regulate the germination of seeds (photoblastic), synthesis of chlorophyll, elongation of seedlings, size, shape and number and movement of leaves and timing of flowering [62,73,52].

10.1 EFFECT OF SEEDLINGS UNDER DARK AND LIGHT CONDITIONS

The seedlings grown under the dark conditions of etiolated growth shows yellow unexpanded cotyledons, apical hook, and long hypocotyl growth. Under red light cause de-etiolation growth shows green expanded cotyledons, no formation of apical hook and hypocotyl appearance of short [16].

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11.1 CONCLUSION

Photoregulation of seed germination is an important component of plant development, and it involves in the use of light, as an essential environmental signal that affects seed germination. **Photoreceptors** including **phytochromes, cryptochromes, and phototropins,** play a key role in detecting light signals and germination initiation. Different wavelengths of light, red (R) and far-red (FR) light, used to regulate seed germination through the phytochrome, and used in environment signals for promoting the germination. Understanding these photoregulation mechanisms provides invaluable views for enhancing germination conditions in agricultural practices, ultimately benefiting the sustainability of plant ecosystems and food production.

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