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Light mediated plant growth and development

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Abstract
Light is an important external stimulus that acts both as an information stimulus and energy source. Plant employs two contrasting developmental programs to succeed under prevailing light conditions: skotomorphogenesis and photomorphogenesis. Skotomorphogenesis is characterized by the closed cotyledon, elongation of hypocotyl and apical hook formation for rapid growth of young seedlings utilizing energy reserve present in seed. On the other hand, photomorphogenesis is the process where light signals prevent the speedy elongation of hypocotyl, expand the cotyledons, and encourage greening to allow light harvesting and autotrophic growth. Also, seasonal changes in photoperiod (light duration) promotes switch from vegetative to reproductive growth by inducing flowering. To monitor changes in light direction, quality, quantity and duration, plants have evolved various photoreceptors to modulate plant growth and development.

Keywords: Photoreceptors, light, phytochrome, photmorphogenesis

Introduction
Light is an electromagnetic radiation within a certain portion of the electromagnetic spectrum that produces a visual sensation. Its energy is proportional to frequency: $E = h\nu$ and inversely proportional to wavelength. Therefore, longer wavelength light has lower energy than shorter wavelength light. Light is an essential requirement for photosynthetic energy production as well as act as an environmental cue for increasing awareness and fitness to the surrounding conditions. Two contrasting developmental programs plant employ to succeed under prevailing light conditions: skotomorphogenesis and photomorphogenesis. Skotomorphogenesis is characterized by the closed cotyledon, elongation of hypocotyl and apical hook formation for rapid growth of young seedlings utilizing energy reserve present in seed. On the other hand, photomorphogenesis is the process where light signals prevent the speedy elongation of hypocotyl, expand the cotyledons, and encourage greening to allow light harvesting and autotrophic growth. To promote photomorphogenesis and actively overturn skotomorphogenic development, plants have multiple photoreceptors to detect spectrum of wavelengths prevailing in the environment. This include
UVB (280–315 nm) - UVR8 uses specific tryptophan residues from the protein itself for UVB absorption

Blue Light (350–500 nm)
1. Cryptochromes - CRY1, CRY2
2. Phototropins – PHOT1, PHOT2
3. Carotenoids – Zeaxanthin

Red Light and Far Red (680 and 750nm) – Phytochromes (Pr and Pfr)
Phytochrome is a soluble protein pigment photoreceptor for the perception of red and far red light in photo-physiological processes. They are classified as either type I or type II, which are activated by far-red light and red light respectively. Phytochromes controlled plant developmental processes include seed germination, chlorophyll synthesis, elongation of seedlings, number, size, shape and movement of leaves and timing of flowering in plants. Phytochromes are characterised by red/far red reversibility. Phytochrome has ground state P_r, the $_r$ indicates that it absorbs red light. The absorbance maximum is a sharp peak 650–670 nm. Once a red photon has been absorbed; the pigment undergoes a rapid conformational change to form the P_{fr} state. Here $_{fr}$ indicates that now far-red (also called "near infra-red"; 705–740 nm) is preferentially absorbed. In plants, red light changes it to its biologically active form, while far red light changes it to its biologically inactive form. Cryptochromes are blue light sensing receptors (cry1 and cry2) that bear a similarity with light activated DNA phytolases. It uses two chromophores a folate and flavin adenine dinucleotide (FAD).

Cryptochromes are involved in entrainment of circadian clock, control plant height, root growth, pigmentation control and fruit size.

Examples of light mediated plant growth and development

Photoperiodic flowering

Coincidence model based on genetic and molecular evidences suggests that flowering in plants is sensitive to light only at certain times of day-night cycle. A major regulatory component of the flowering pathway of Arabidopsis is CONSTANS (CO) gene which encodes a zinc finger protein that regulates transcription of other genes. Its expression is controlled by circadian clock having peak activity 12 hours after dawn. In Arabidopsis under the non- inductive short days there is no overlap between CO mRNA expression and daylight. CO protein does not accumulate up to threshold in the phloem to promote the expression of FT protein (transmissible floral stimulus) and thus the plant remains vegetative. Under inductive long days, peak abundance of CO mRNA coincides with light allowing accumulation of CO protein which activates FT mRNA expression in phloem. This results in flowering when FT protein translocate to apical meristem causing floral evocation. CO is post transcriptionally regulated. During dark, CO protein is degraded by ubiquitin proteasome pathway. During morning, phytochrome B mediated signaling enhances CO degradation. During evening, both phytochrome A and cryptochrome prevent degradation of CO protein. This explains why flowering is promoted only when mRNA expression coincides with light period. In short day plants like rice lack of overlap between Hd1 mRNA expression and light period prevents Hd1 protein accumulation which acts as a repressor of gene encoding transmissible floral stimulus Hd3a. In the absence of repressor Hd1 protein, Hd3a mRNA is translated to produce transmissible floral stimulus that leads to floral evocation at apical meristem. PtFT1 is the *Populus trichocarpa* ortholog of FT which along with CO regulates the timing of flowering.

Phototropism

Plant growth directionally in response to light is called phototropism. Positive phototropism is growth towards the light source e.g. shoot and negative phototropism is growth away from light source e.g. root. Growth of shoot towards light is advantageous for higher production of photosynthates for plant growth.

Phototropins and auxin: Evidences accumulated so far suggests the involvement of blue light photoreceptor called phototropins. When a coleoptile is exposed to light, phototropins gets activated more on the side exposed to light compared to shady side causing more auxin to flow down the shady side. Thus the shady side with more auxin has more elongated cells compared to other side causing bending towards the light.

Seed germination

Experimental evidences suggest that blue light mediated inhibition of seed germination in barley coincides with increased activity of ABA biosynthetic gene 9-cis-epoxycarotenoid dioxygenase (NCED1) and subsequently ABA content. In CRY1a/b RNAi grain, NCED1 was no longer induced and ABA catabolic gene was upregulated during germination in blue light. Thus, ABA content declined faster in the CRY1a/b RNAi line than in its null sibling. This suggests that CRY1 photoreceptor mediates the effects of blue light on grain dormancy in barley by increasing ABA content. REVEILLE1 (RVE1) and RVE2 transcription factors uphold primary seed dormancy and suppress red/far-red light reversible seed germination downstream of phytochrome B (phyB). RVE1 and RVE2 are downregulated upon imbibtion and by phyB. RVE1 binds to the GIBBERELLIN 3-OXIDASE 2 promoter and prevent its transcription and thus inhibits the synthesis of bioactive gibberellins.

Shade avoidance response

Plant manifests various shade avoidance responses collectively called as shade avoidance syndrome when subjected to shade by another plant. It includes increased apical dominance, elongation, altered flowering time and altered partitioning of resources. In recent decades plant breeders have selected lines with reduced shade avoidance syndrome to produce high yields.

How plants sense shade: Plants can differentiate between the shade of another plant and shade of a lifeless objects (e.g. a rock), as well as the presence of nearby plants that may compete with it for light in future. When shaded by plant, far red light is predominant as a result of absorption of red light by photosynthetic pigments. On the other hand, a nearby plants lead to an intermediate ratio. Plants uses phytochrome to measure ratio of red to far red light, and thus sense whether the plant is shaded or not and based on it alter its growth. Phytochromes exist in two forms: P_R and P_{FR}. Plant synthesis it as $P_{R,}$ but red light absorption converts it to P_{FR} and far converts it back to $P_{R.}$ Thus far red enrichment leads to elevated levels of P_R which when present above threshold induces the shade avoidance response.

Shade avoidance response of a seedling is most well studied in *Arabidopsis thaliana.* Water imbibed seeds when shaded by excess of soil depth, seedling display a faster hypocotyl elongation and push up and out of ground. If shaded outside the soil, its petiole and internodes elongate.

Pathway: It is the quality of light and ratio available to seedling is sensed by the cotyledeons that upregulates the auxin production. PIF (Phytochrome Interacting Factor) has been shown to be involved in auxin biosynthesis. PIFs are basically transcription factors involved in shade avoidance and suppressing germination. PIF4, PIF5 and PIF7 encode enzymes involved in auxin biosynthesis. Under shaded conditions, P_R induces dephosphorylation of PIF proteins which allows them to bind the promoter region of genes involved in shade avoidance response. The auxin so produced is transported to hypocotyl to promote its elongation.

Adult plants show more complex shade avoidance response patterns compared to seedlings. Shade avoidance response of adult plants include repositioning of its leaves, hyponasty and flattening of leaves to increase surface area for light absorption. If mature plant becomes shaded, it leads to early flowering.

Pathway: Shade avoidance response of adult plants involves various mechanisms acting together. Petiole elongation is a result of cell expansion and cell division. Cell division is a primary factor in newly formed leaves while cell expansion in fully formed petiole and leaves. It is the family of cell wall modifying protein, Xyloglucan endotransglucosylase / hydrolases (XTHs) hydrolyzes and weaken the cell wall resulting in expansion of petiole cells. Curling of leaves is a response to phytochrome B converting to P_R in shade conditions which promotes differential cell growth on upper and lower leaf surfaces.

Conclusion
Multiple repressors synergistically suppress photomorphogenesis suggests that photomorphogenesis is a default pathway. Light activated photoreceptors mediate the gradual progression towards photomorphogenesis through various signal transduction pathways. Understanding of light sensing and signaling will allow strategic manipulate plant growth and development.

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