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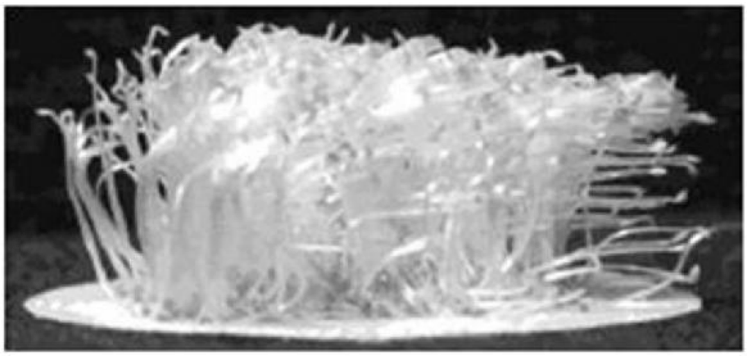
LECTURE 4: PHOTOTROPISM



LECTURE FLOW

1. INTRODUCTION
2. DEFINITION
3. INITIAL STUDY
4. PHOTROPISM MECHANISM
5. PHOTORECEPTORS

INTRODUCTION

1. Plants can sense the direction, quality (wavelength), intensity and periodicity of light that induces
   - Phototropism
   - Photomorphogenesis
   - chloroplast differentiation and
   - various other responses such as flowering and germination.
2. This behavior, called phototropism, is generally assumed to improve light harvesting for photosynthesis.
3. However, dark-grown etiolated seedlings, which lack the developed chloroplast necessary for photosynthesis, display very rapid phototropic responses.

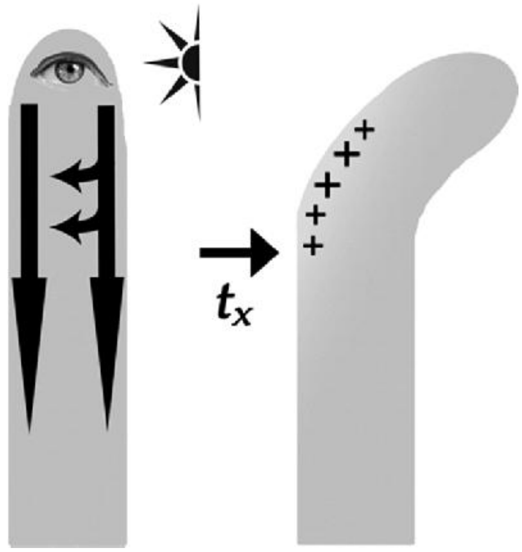
4. As such, the phototropic response of etiolated seedlings probably does not initially enhance photosynthesis.
5. Instead, the phototropic response of etiolated seedlings is more likely to assist in seedling emergence from the soil and around other obstacles.
6. Once the seedling emerges from cover and receives enough light to sustain photosynthesis, another process, called photomorphogenesis, inhibits shoot elongation and stimulates chloroplast biogenesis.

Darwin Findings

- As early as 1880, Charles Darwin had noted:
  "no one can look at the plants growing on a bank or on the borders of a thick wood, and doubt that the young stems and leaves place themselves so that the leaves may be well illuminated”
- Phototropism is especially important for germinating seedlings, whereby the emerging shoot must grow towards the light to survive by maximizing the capture of light for photosynthesis
- Darwin, together with the help of his botanist son Francis, left us an entire book, ‘The power of movements in plants’, describing his many, varied, and insightful observations on this topic.

- Darwin’s findings have provided an impetus for an entire field of study, the study of plant tropic responses, or differential growth (curvature) of plant organs in response to directional stimuli.
- Darwin proposed that
  plants could grow differentially (thus directionally) in response to external stimuli such as light or gravity.
- The part of the plant that perceives the stimulus is separate and distinct from the part that responds to that stimulus were demonstrated.
- In the case of phototropism,
  - directional light is perceived in the apical portion of a young seedling and ‘transduced’ to more basally localized portions of the shoot as a differential signal that informs the plant which side is the closest to and which is the furthest from the light source such that a bending response occurs.

- Finally, Darwin proposed that an 'influence' (though he was unable to identify it) moves from the site of stimulus perception to the area of response where bending occurs.



DEFINITION

1. PHOTOTROPISM

- Phototropism is a growth movement induced by a light stimulus
  - Growth towards a source of light is called positive phototropism, that away from the source is termed negative phototropism.
  - The tips of shoots are usually positively, that of roots negatively phototropic

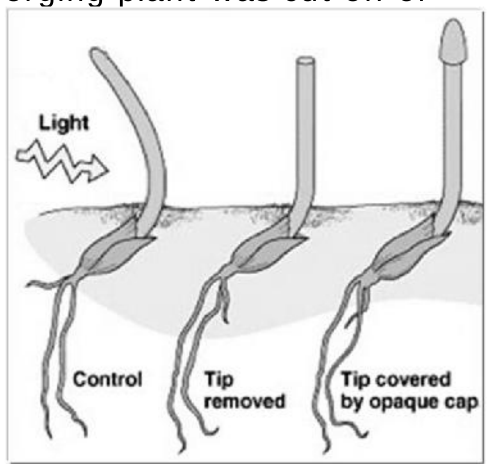
- Originally was phototropism called heliotropism, because the plant grows towards the sun.

- The name was altered when it became clear that plants react also towards artificial sources of light
- Plants utilize light not only as an energy source, but also as a vital source of temporal and spatial information
- Phototropism, or the directional growth of a plant organ in response to directional blue light (BL), represents a predominant mechanism by which plants reposition body parts as a strategy of adaptation
- Phototropic responses are distinguished from other types of light-modulated directional growth responses, such as nastic and circadian regulated leaf movements, by two criteria.

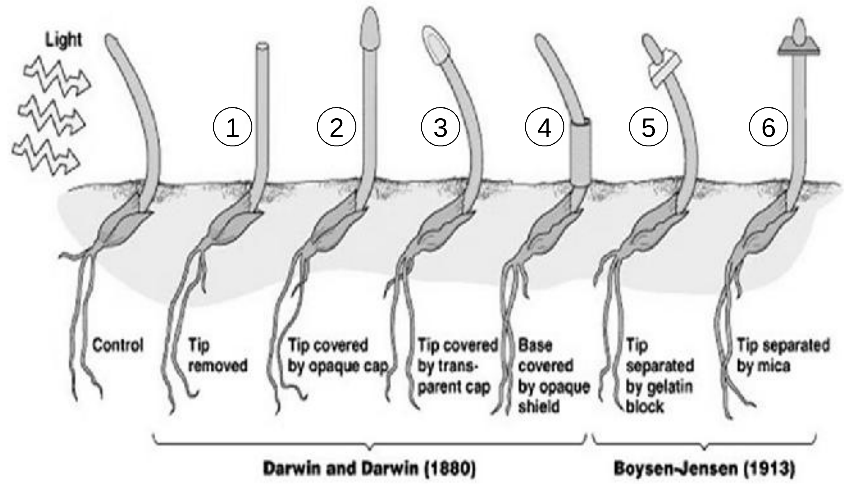
  - First, the direction of phototropic curvatures is determined by the direction of the light stimulus, while the direction of nastic and circadian-regulated movements are not
  - Second, many leaf movement responses occur as a result of reversible swelling/shrinking of specialized motor, or pulvinar, cells whereas all stem and root phototropic responses are driven by changes in cell elongation rates across the bending organ.
- With respect to phototropic responses, unidirectional irradiation of seedlings with UV-A/blue light results in enhanced growth in the stem on the flank away from the light (“shaded side”) and generally represses growth on the flank facing the incident light (“lit side”) causing it to bend towards the light

INITIAL STUDY

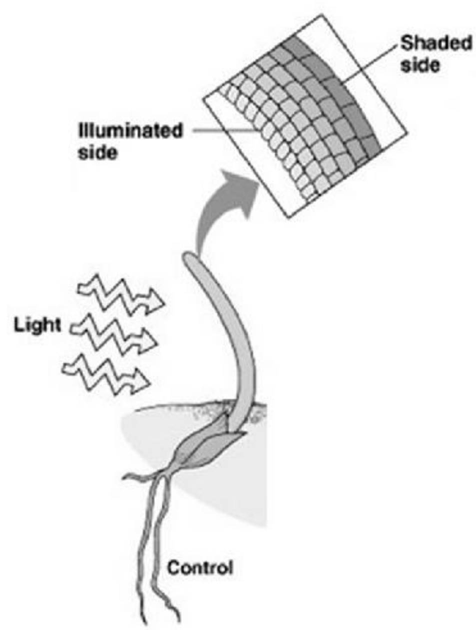
1. Darwin in 1880 showed that the phototropic response was lost when
   - the tip of the emerging plant was cut off or
   - covered with an opaque cap.



2. Covering the base of the stem did not block phototropic bending.
3. Boysen-Jensen showed in 1913 that placing a block of gelatin between the tip and the base did not block the response, showing that something was able to diffuse from the tip, through the gel, and into the base.
4. When the tip was separated from the base with a piece of mica, which blocks anything from flowing through, the response is blocked.

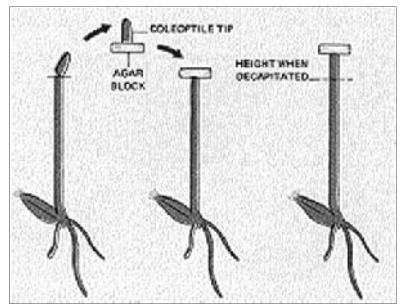


5. Note that there is more auxin growth hormone on the shaded side (green color in the small picture insert).

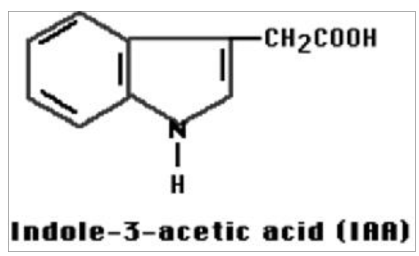


- The Discovery of Auxin

  F. W. Went extracted the growth stimulant.
  - He removed the tips of several coleoptiles of oat, Avena sativa, seedlings.
  - He placed these on a block of agar for several hours. At the end of this time, the agar block itself was able to initiate resumption of growth of the decapitated coleoptile.
  - The growth was vertical because the agar block was placed completely across the stump of the coleoptile and no light reached the plant from the side.
  - The unknown substance that had diffused from the agar block was named auxin

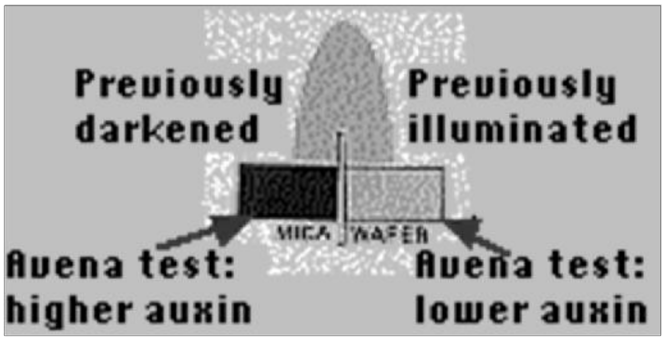


- The Avena test soon revealed that substances with auxin activity occur widely in nature. One of the most potent was first isolated from human urine.



- It was indole-3-acetic acid (IAA) and turned out to be the auxin actually used by plants.
- Went also discovered that it is the unequal distribution of auxin that causes the bending in phototropism.

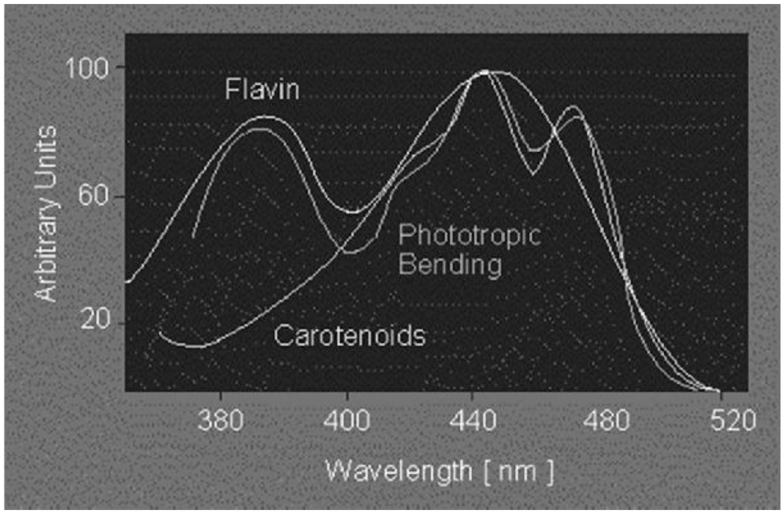
- When a coleoptile tip that has previously been illuminated from one side is placed on two separated agar blocks, the block on the side that had been shaded accumulates almost twice as much auxin as the block on the previously lighted side. Hence the more rapid cell elongation on the shady side of the plant

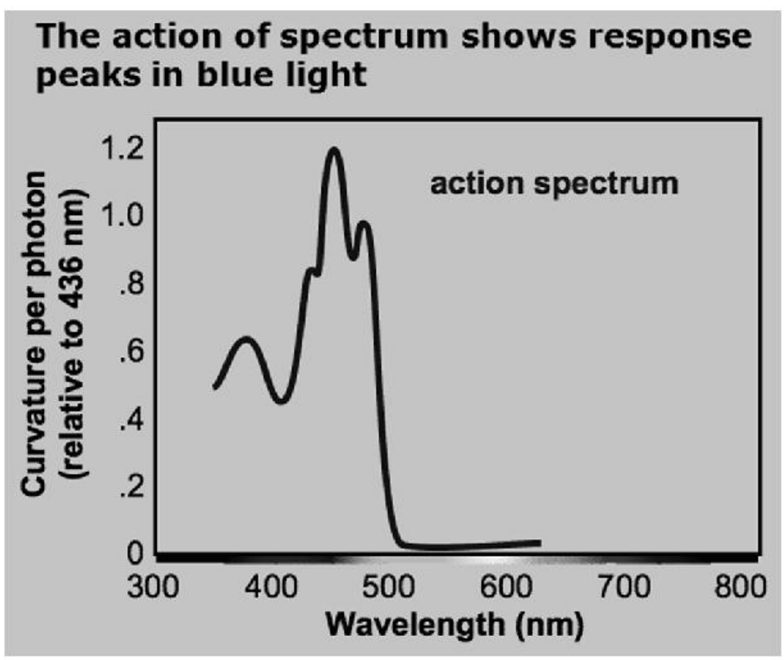


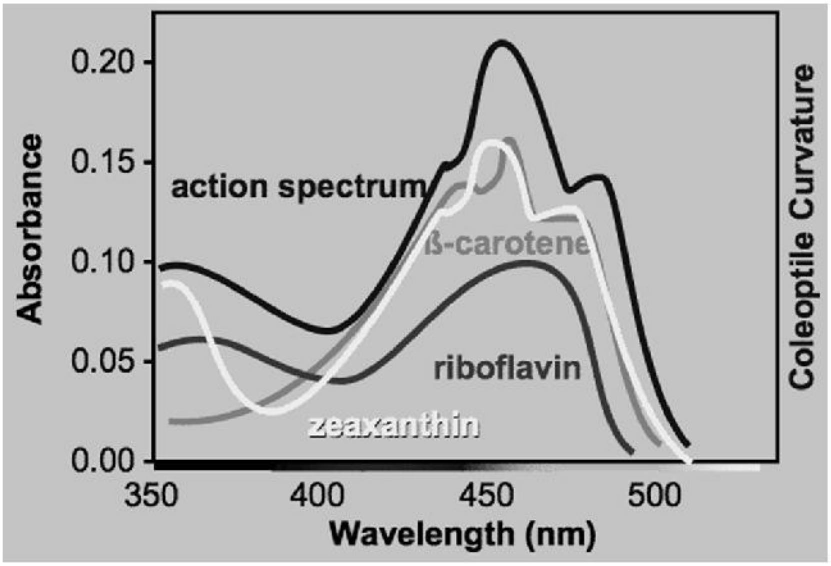
PHOTROPISM MECHANISM

- It is well accepted that lateral redistribution of the phytohormone auxin underlies the bending of plant organs towards light
- The questions arising are
  - How the light is perceived or sensed by plants?
  - How the information of light presence is transduced to Auxin
- Despite more than a century of research, it is still unresolved
  - how light regulates auxin distribution and
  - where this occurs in dicots

Comparison of the action spectrum of an *Avena* coleoptile's phototropic bending (green curve) and the absorption spectra of carotenoids (orange curve) and flavins (yellow curve; according to H. MOHR, P. SCHOPFER, 1978, according to W. SHROPSHIRE and R. B. WITHROW, 1959)






0.20
0.15
0.10
0.05
0.00
Absorbance
action spectrum
ß-carotene
riboflavin
zeaxanthin
350
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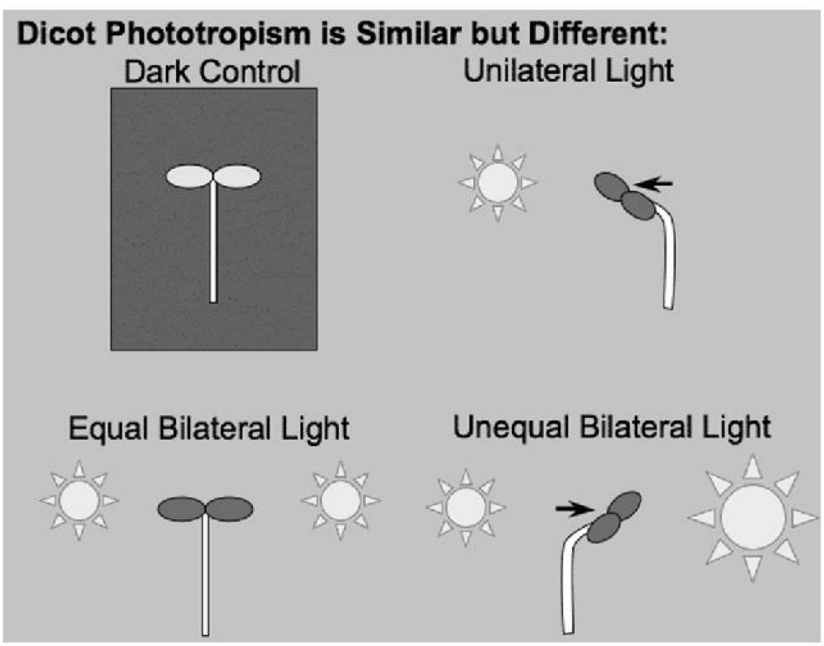
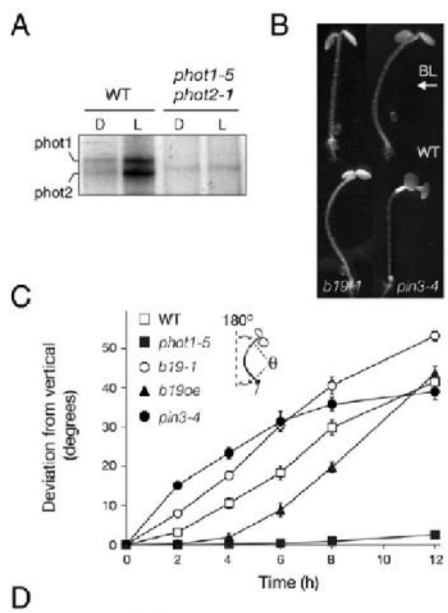
450
500
Wavelength (nm)
Coleoptile Curvature


Dicot Phototropism is Similar but Different:
Dark Control
Unilateral Light
Equal Bilateral Light
Unequal Bilateral Light

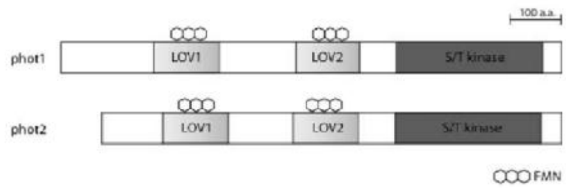
PHOTORECEPTORS

- Phototropins are the primary photoreceptors controlling phototropism in aerial organs of higher plants that perceive directional blue-light (BL) cues and then stimulate signaling, leading to relocalization of the plant hormone auxin
- Phototropins regulate not just phototropism, but a number of additional blue light responses, including stomatal opening, chloroplast movements, leaf movements and expansion, and rapid inhibition of stem growth.
- The first of these photoreceptors identified at the molecular level is phototropin 1 (phot1), originally designated NPH1 (for its non-phototropic hypocotyl mutant phenotype).

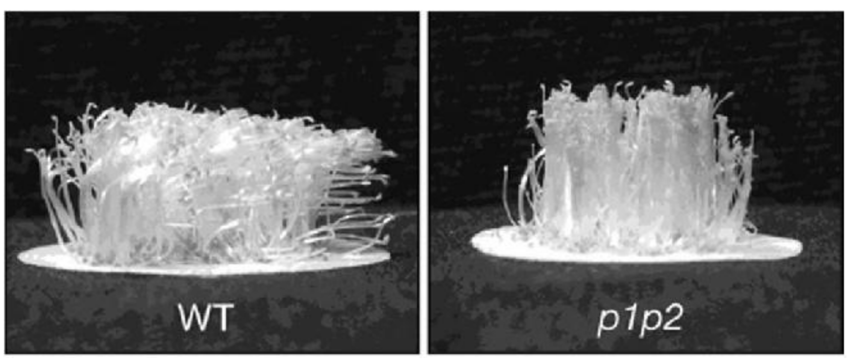
- The PHOT2 gene was subsequently identified based on its high degree of sequence homology to PHOT1



- The structure of plant phototropins can be separated into two parts:
  - LOV1: a N-terminal photosensory input region coupled to
  - LOV2: a C-terminal effector or output region that contains a classic serine/threonine kinase motif



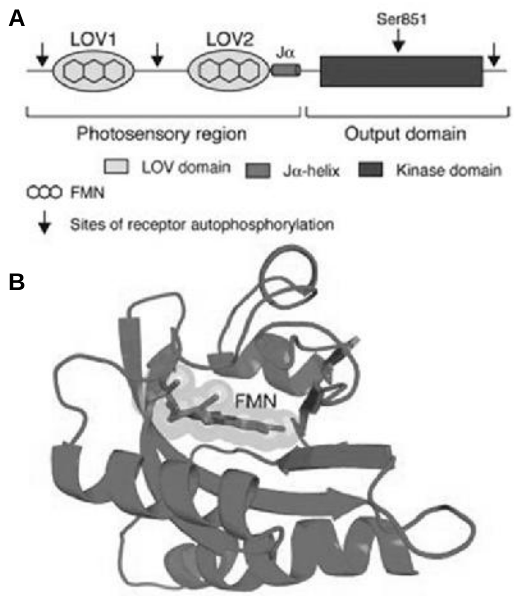
Domain structures of the phot1 and phot2 receptors. The amino terminal photosensory LOV domains are shown in blue with their associated FMN co-factor (above each LOV domain). The carboxyl-terminal protein kinase domain of each phot is shown in red.



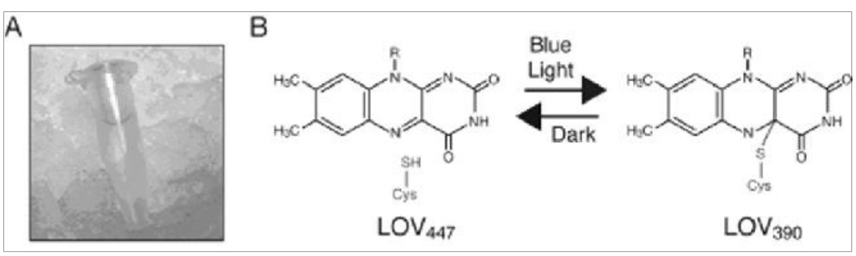
Phototropic response of wild-type Arabidopsis seedlings (WT) and a phototropin-deficient mutant (p1p2) irradiated with blue light from the right.

Phototropin structure

(A) Cartoon illustrating the domain structure of phototropin blue light receptors.
(B) Structural model of the phototropin LOV2 domain in the dark state.

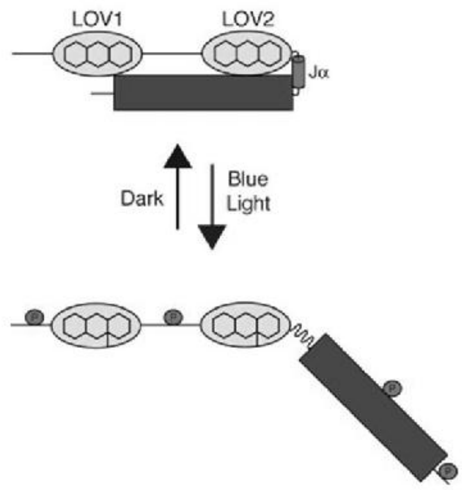


The position of the FMN chromophore is indicated.



LOV-domain photochemical reactivity. (A) Purified preparation of bacterially expressed LOV2. (B) Schematic representation of LOV-domain photochemistry. Details of the reaction are described in the text.

1. Phototropin activation by blue light. In the dark, phototropin is unphosphorylated and inactive.
2. The absorption of light invokes a photochemical reaction within the LOV domains
3. Photoexcitation of the main light sensor, LOV2, causes a disordering of the Jα-helix, and the activation of the C-terminal kinase domain, which consequently leads to autophosphorylation of the photoreceptor.



The relative positions of phosphorylation sites are indicated

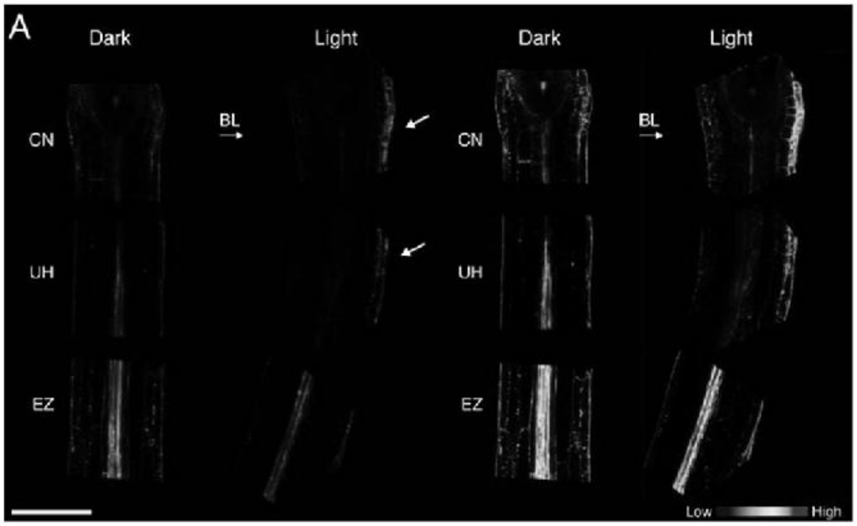
- A number of phototropin-interacting proteins have been isolated
  - NPH4/ARF7 is the auxin response factor (transcriptional activator, a key regulator of hypocotyl phototropism and gravitropism in Arabidopsis) that responds to changes in local auxin concentrations to directly mediate expression of genes likely encoding proteins necessary for development of phototropic curvatures
  - NPH3 (Non-Phototropic Hypocotyl 3, phototropin-interacting protein), a novel protein that directly interacts with phot1 or serves as a protein scaffold to assemble components of a phototropin receptor complex. NPH3 is required for optimal leaf positioning and leaf flattening in Arabidopsis.
  - RPT2 (Root Phototropism 2) = a protein closely related to NPH3 that also interacts with phot1, and is required for both phototropism and stomatal opening by blue light

- cryptochromes (crys) = BL absorber can act as modulators of phot-dependent signal-response. phytochromes (phys) = RL absorber can act as modulators of phot-dependent signal-response
- AUX1—a gene encoding a high-affinity auxin influx carrier previously associated with a number of root responses
- ABCB19 (ATPBINDING CASSETTE B19) = the auxin efflux transporter at and above the hypocotyl apex as a substrate target for the photoreceptor kinase PHOTOTROPIN 1 (phot1)
- Members of the PIN-FORMED family are the primary mediators of directional auxin fluxes that regulate plant development [8]. PIN3 = an auxin transporter that is proposed to mediate lateral auxin fluxes by differentially restricting auxin to the vascular cylinder [6].

Table 1. Genes shown to be definitively involved in phototropic signal perception, transduction, and response

Gene1	Synonym(s)[2]	AGI locus no.	Gene ID[3]	Phototropic function
ABCB19	*MDR1,PGP19*	At3g28860	822519	Regulation of auxin-transport
AXR1	*none*	At1g05180	839266	Regulation of auxin-response
NPH3	*RPT3*	At5g64330	836554	Signal transduction; phot1, RPT2 and PKS1 interacting protein
NPH4	*ARF7,BIP,MSG1,TIR5*	At5g20730	832196	Regulator of auxin-response
PHOT1	*JK224,NPH1*	At3g45780	823721	Primary photoreceptor
PHOT2	*CAV1,NPL1*	At5g58140	835926	Primary photoreceptor
PHYA	*FRE1,FHY2,HY8*	At1g09570	837483	Major secondary/modulatory photoreceptor
PHYB	*HY3*	At2g18790	816394	Minor secondary/modulatory photoreceptor
PIN1	*none*	At1g73590	843693	Relocalization of auxin
PIN3	*none*	At1g70940	843432	Relocalization of auxin
PKS1	*none*	At2g02950	814823	Signal transduction; phot1, phyA, phyB and NPH3 interacting protein
RPT2	*none*	At2g30510	817601	Signal transduction; phot1 and NPH3 interacting protein

[1]Standard gene name established by the community or the one most commonly used in conjugation with a discussion of phototropism
[2]Additional names for the genes given in the first column. Citations for the first reference to the synonocymous gene are as follows: *RPT3* (Okada and Shimura, 1994); *BIP* (GenBank only, AAD04807); *MSG1* (Watahiki and Yamamoto, 1997); *TIR5* (Ruegger et al., 1997); *JK224* (Khurana and Poff, 1989); *NPH1* (Liscum and Briggs, 1995); *CAV1* (Kagawa et al., 2001); *NPL1* (Jarillo et al., 1998); *FRE1* (Nagatani et al., 1993); *FHY2* (Whitelam et al., 1993); *HY8* (Parks and Quail, 1993); *HY3* (Koornneef et al., 1980). *MDR1* (Noh et al., 2001).
[3]Gene ID number as recorded in NCBI Entrez Gene register (Maglott et al., 2007).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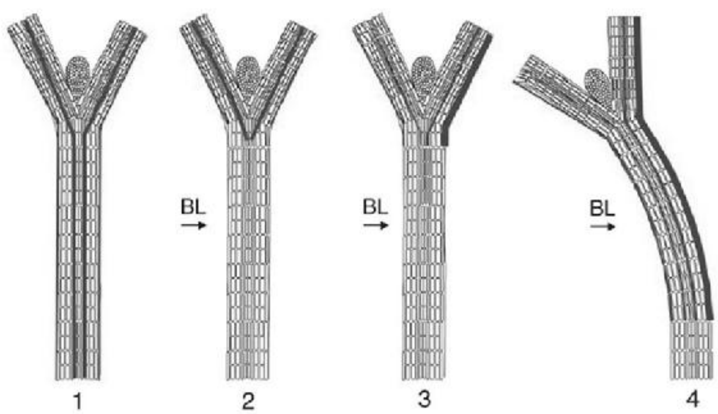
BL
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2
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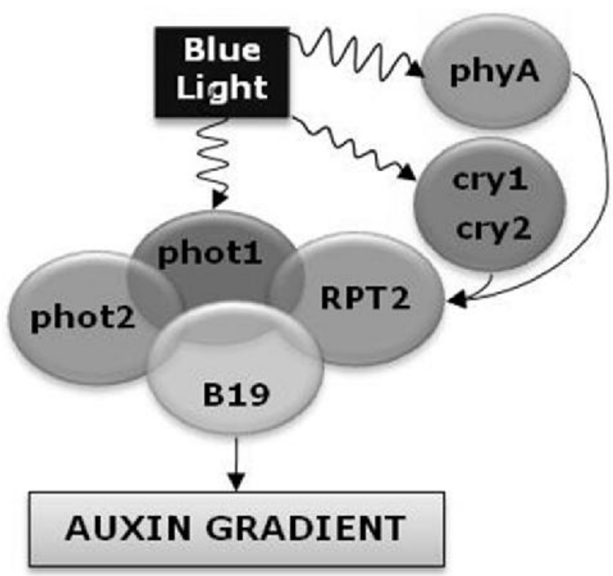
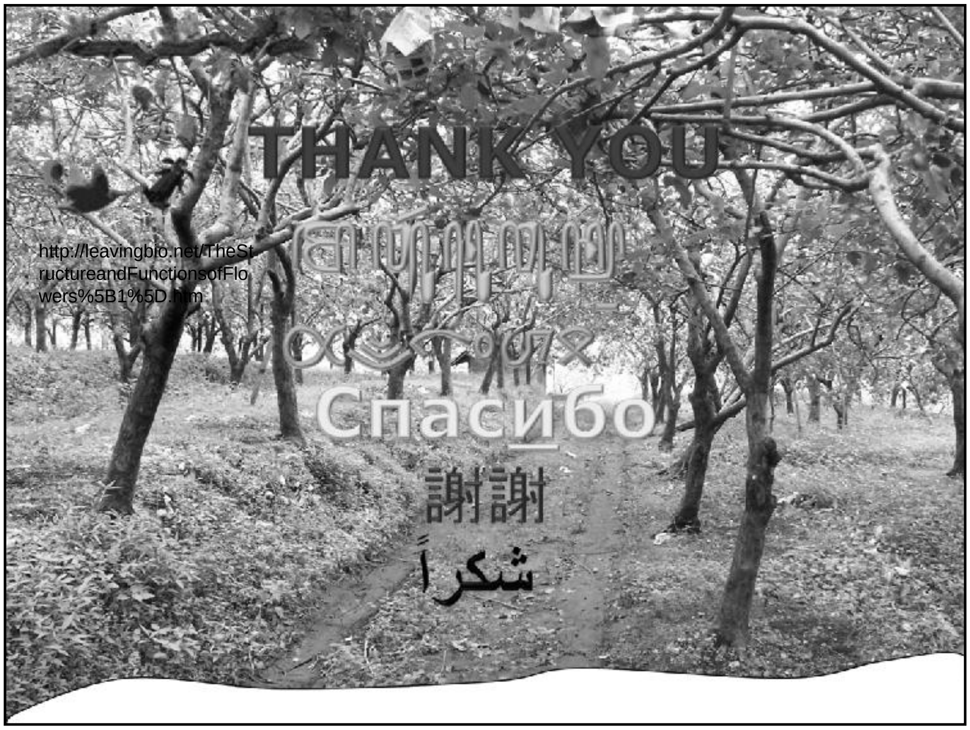
4

1. In darkness, auxin primarily moves through the vascular tissues in the petioles and hypocotyl, and also through epidermal tissues
2. Upon exposure to directional blue light, auxin movement is temporarily halted at the cotyledonary node and the seedling stops elongating vertically
3. This is followed by a redistribution of auxin at the cotyledonary node to the shaded side of the seedling and a channeling to the elongation zone below
4. Subsequent elongation of the cells on the shaded side of the hypocotyl results in differential growth and bending towards the light source

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