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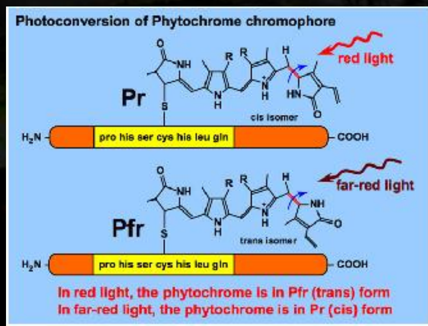
LECTURE 04: PHYTOCHROME



Photoreversibility is the most distinctive property of phytochrome

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LECTURE OUTCOMES

After the completion of this lecture and mastering the lecture materials, students should be able to

1. explain phytochrome including its discovery and initial studies.
2. explain the phytochemistry and biochemistry of phytochrome
3. explain characteristics of phytocrome-induced responses
4. explain structure and function of phytochrome proteins
5. explain signaling pathways of phytochrome
6. explain ecological functions of phytochrome

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LECTURE OUTLINE

1. INTRODUCTION
2. PHYTROCHEMISTRY AND BIOCHEMISTRY OF PHYTOCHROME
3. CHARACTERISTICS OF PHYTOCROME-INDUCED RESPONSES
4. STRUCTURE AND FUNCTION OF PHYTOCHROME PROTEINS
5. SIGNALING PATHWAY
6. ECOLOGICAL FUNCTIONS

1. C

1. INTRODUCTION

1. Initial Studies

- The discovery of phytochrome is closely associated with studies on flowering.
- **Phytochrome** is a blue protein pigment with a molecular mass of about 125 kDa that plants, and some bacteria and fungi, use to detect light.
  - The term phytochrome ("plant color") was originally coined to describe the proteinous pigment that controls photoperiod detection and floral induction of certain short-day plants (e.g. cocklebur and soybean) (Garner and Allard, 1920).

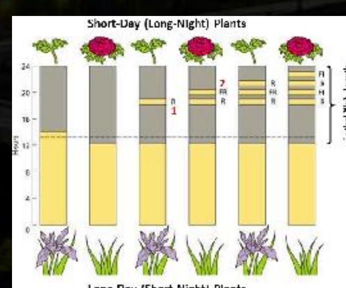


Fig. 24.22 A flash of red (R) light during the dark period induces flowering in an LDP but prevents flowering in an SDP (1), and the effect is reversed by a flash of far-red (Fr) light (2). This response indicates the involvement of phytochrome.

- Essentially all proteins absorb light in the near-UV region due to the presence of aromatic amino acids, and proteins that sense visible light possess chromophore cofactors that confer the desired wavelength sensitivity.

- In 1932, Beltsville research group of the USDA headed by Borthwick and Hendricks showed that red light (630 to 680 nm) elicits the germination of lettuce seeds, whereas far-red light (710 to 740 nm) inhibits the process.

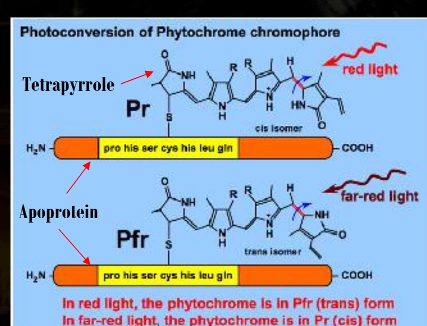
Irradiations	Germination (%)
R	88
R, Fr	22
R, Fr, R	84
R, Fr, R, Fr	18
R, Fr, R, Fr, R	72
R, Fr, R, Fr, R, Fr	22

R = red, Fr = Far red

Fig. 17.2 Lettuce seed germination

2. Chemical Structure

- Phytochromes are soluble proteins and exist as homodimers. Each monomer of phytochrome molecule has two components: a protein part (the apoprotein) and a chromophore.
- The chromophore is an open–chain tetrapyrrole which is covalently linked to the protein moiety through a cysteine residue (a sulfur linkage).
  - Apoprotein consists of a 60 kDa amino-terminal domain, and a 55 kDa carboxyl-terminal domain.



- On absorption of light, the Pr chromophore undergoes a *cis-trans* isomerisation of the double bond between carbons 15 and 16 and the rotation of the C14 and C15 single bond.
- The absorption of red light appears to provide the energy required to overcome high activation energy for rotation around double bond, a transition that is not possible at normal temperature.

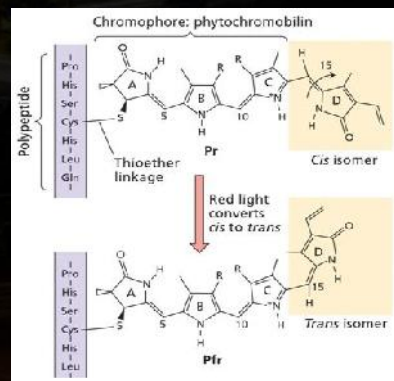


Fig. 17.6 Structure of the Pr and Pfr forms of the **chromophore** (phytochromobilin) and the peptide region bound to the chromophore through a thioether linkage. The chromophore undergoes a *cis-trans* isomerization at carbon 15 in response to red and far-red light. (After Andel et al. 1997.)

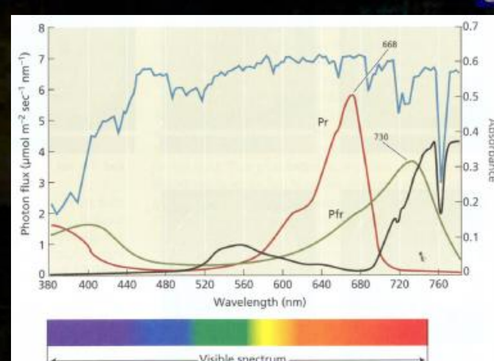
2. PHYTOCHEMISTRY AND BIOCHEMISTRY OF PHYTOCROME

1. Photoreversibility

- **Photoreversibility** is the conversion/reconversion of phytochrome which is the most distinctive property of this pigment, and it may be expressed in abbreviated form as follows:

- It is important to note that the phytochrome pool is never fully converted to the Pfr or Pr forms following-red or far-red irradiation, because the absorption spectra of the Pfr and Pr forms overlap.
- Thus, when Pr molecules are exposed to red light, most of them absorb the photons and are converted to Pfr, but some of the Pfr made also absorbs the red light and is converted back to Pr (Fig. 17.3).
- The proportion of phytochrome in the Pfr form after saturating irradiation by red light is only about 88%.
- Similarly, the very small amount of far-red light absorbed by Pr makes it impossible to convert Pfr entirely to Pr by broad-spectrum far-red light. Instead, an equilibrium of 98% Pr and 2% Pfr is achieved. This equilibrium is termed the **photostationary state**.

Fig. 17.3 Absorption spectra of purified oat phytochrome in the Pr (red line) and Pfr (green line) forms overlap. At the top of the canopy, there is a relatively uniform distribution of visible spectrum light (blue line), but under a dense canopy much of the red light is absorbed by plant pigments, resulting in transmittance of mostly far-red light.



The black line shows the spectral properties of light that is filtered through a leaf. Thus, the relative proportions of Pr and Pfr are determined by the degree of vegetative shading in the canopy. (After Kelly and Lagarias 1985, courtesy of Patrice Dubois.)

- In addition to absorbing red light, both forms of phyto-chrome absorb light in the blue region of the spectrum that can convert Pr to Pfr and vice versa.
- Blue-light responses can also result from the action of one or more specific blue-light photoreceptors.

2. The Physiologically Active Form of Phytochrome

- Because phytochrome responses are induced by red light, hypothetically they could result from either the appearance of Pfr or the disappearance of Pr.
- In most cases studied, a quantitative relationship holds between the magnitude of the physiological response and the amount of Pfr generated by light,.
- No such relationship holds between the physiological response and the loss of Pr.

- Evidence such as this has led to the conclusion that Pfr is the physiologically active form of phytochrome.
- The use of narrow waveband red and far-red light was central to the discovery and eventual isolation of phytochrome.
- However, a plant growing outdoors is never exposed to strictly "red" or "far-red" light, as are plants used in laboratory-based photobiological experiments.
- In natural settings plants are exposed to a much broader spectrum of light, and it is under these conditions that phytochrome must work to regulate developmental responses to changes in the light environment.

Table 17.1 Typical photoreversible responses induced by phytochrome in a variety of higher and lower plants

Group	Genus	Stage of development/Effect of red light
Angiosperms	Lactuca (lettuce)	Seed/Promotes germination
	Avena (oat)	Seedling (etiolated)/Promotes de-etiolation (e.g., leaf unrolling)
	Sinapis (mustard)	Seedling/Promotes formation of leaf primordia, development of primary leaves, and production of anthocyanin
	Pisum (pea)	Adult/Inhibits internode elongation
	Xanthium (cocklebur)	Adult/Inhibits flowering (photoperiodic response)
Gymnosperms	Pinus (pine)	Seedling /Enhances rate of chlorophyll accumulation
Pteridophytes	Onoclea (sensitive fern)	Young gametophyte/Promotes growth
Bryophytes	Polytrichum (moss)	Germling/Promotes replication of plastids
Chlorophytes	Mougeotia (alga)	Mature gametophyte/Promotes orientation of chloroplasts to directional dim light

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3. CHARACTERISTICS OF PHYTOCROME-INDUCED RESPONSES

1. Variety of Phytochrome Responses

- The variety of different phytochrome responses in intact plants is extensive, in terms of both the kinds of responses (see Table 17.1) and the quantity of light needed to induce the responses.
- These phytochrome-induced responses, for ease of discussion, may be logically grouped into two types:
  - Rapid biochemical events
  - Slower morphological changes, including movements and growth
- Such responses can be classified into various types depending on the amount and duration of light required and on their action spectra.

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2. Lag and Escape Time of Phytochrome Responses

- Morphological responses to the photoactivation of phytochrome may be observed visually after **a lag time**-the time between stimulation and observed response.
- The lag time may be as brief as a few minutes or as long as several weeks.
- The more rapid of these responses are usually reversible movements of organelles or reversible volume changes (swelling, shrinking) in cells, but even some growth responses are remarkably fast.
- Variety in phytochrome responses can also be seen in the phenomenon called **escape from photoreversibility**.
  - Red light-induced events are reversible by far-red light for only a limited period of time, after which the response is said to have "escaped" from reversal control by light.

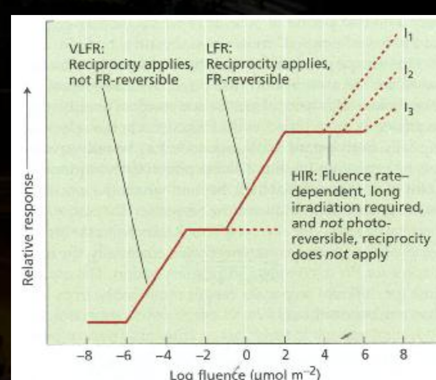
- This escape phenomenon can be explained by a model based on the assumption that phytochrome-controlled morphological responses are the end result of a multi-step sequence of linked biochemical reactions in the responding cells.
- Early stages in the sequence may be fully reversible by removing Pfr, but at some point in the sequence a point of no return is reached, beyond which the reactions proceed irreversibly toward the response.
- Therefore *the escape time represents the amount of time it takes before the overall sequence of reactions becomes irreversible*; essentially, the time it takes for Pfr to complete its primary action.
- The escape time for different responses ranges remarkably, from less than a minute to hours.

4. Phytochrome Responses and Light Quantity

- Phytochrome responses can be distinguished by the amount of light required to induce them.
- The amount of light is referred to as the **fluence**, *the number of photons impinging on a unit surface area*.
  - The standard units for fluence are micromoles of quanta per square meter (μmol m^{-2}).
  - Some phytochrome responses are sensitive not only to the fluence, but also to the **irradiance*** or **fluence rate** of light. The units of irradiance are micromoles of quanta per square meter per second (μmol m^{-2} s^{-1}).
- Phytochrome responses fall into three major categories based on the amount of light required: very low-fluence responses (VLFRs), low-fluence responses (LFRs), and high-irradiance responses (HIRs) (Fig. 17.4).

- ***VLFRs are nonphotoreversible***
  - Some phytochrome responses can be initiated by fluences as low as 0.0001 μmol m^{-2} (one-tenth of the amount of light emitted by a firefly in a single flash), and saturated (i.e., reach a maximum) at about 0.05 μmol m^{-2}. For example, Arabidopsis seeds can be induced to germinate with red fight (0.001 to 0.1 μmol m^{-2}).

Fig. 17.4 Three types of phytochrome responses, based on their sensitivi-ties to fluence. The relative magni-tudes of representative responses are plotted against increasing fluences of red light. Short light pulses activate VLFRs and LFRs. Because HIRs are proportional to irradiance as well as to fluence, the effects of three different irradiances !aiven continuously are illustrated (11 > 12 > 1 3). (After Briggs et al. 1984.)



- ***LFRs are photoreversible***.
  - These phytochrome responses cannot be initiated until the fluence reaches 1.0 μmol m^{-2}, and are saturated at about 1000 μmol m^{-2}.
  - These include most of the red/far-red photoreversible responses, such as the promotion of lettuce and Arabidopsis seed germination (Fig. 17.5).
  - LFR spectra include a main peak for stimulation in the red region (660 nm), and a major peak for inhibition in the far-red region (720 nm).

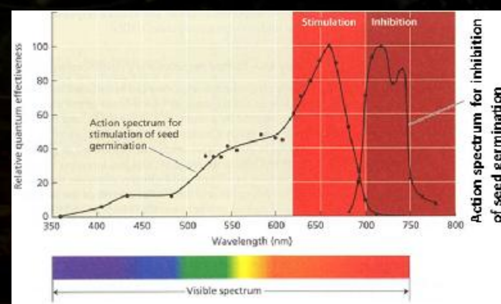


Fig. 17.5 LFR action spectra for the photoreversible stimulation and inhibition of seed germination in Arabidopsis. (After Shropshire et al. 1961.)

- Both VLFRs and LFRs can be induced by brief pulses of light, provided that the total amount of light energy adds up to the required fluence.
- The total fluence is a function of two factors: the fluence rate (μmol m^{-2} s^{-1}) and the time of irradiation.
  - Thus, a brief pulse of red light will induce a response, provided that the light is sufficiently bright, and conversely, very dim light will work if the irradiation time is long enough.
- This reciprocal relationship between fluence rate and time is known as the **law of reciprocity**, which was first formulated by R. W. Bunsen and H. E. Roscoe in 1850.
- VLFRs and LFRs both obey the law of reciprocity; *the magnitude of the response* (e.g. % germination or degree of inhibition of hypocotyl elongation) *is dependent on the product of the fluence rate and the time of irradiation*.

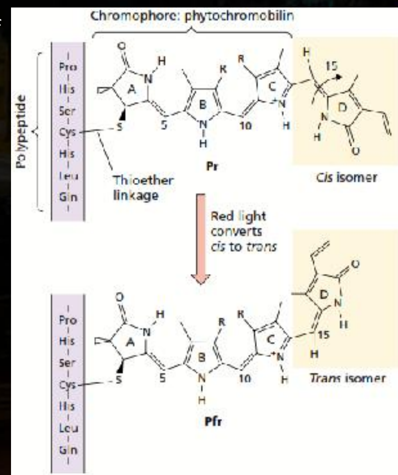
- HIRs require prolonged or continuous exposure to light of relatively high irradiance. The response is proportional to the irradiance until the response saturates and additional light has no further effect.
- These responses are proportional to fluence rate–the number of photons striking the plant tissue per second–rather than fluence–the total number of photons striking it in a given period of illumination that leads to the term of HIRs (high-irradiance responses).
- HIRs saturate at much higher fluences than LFRs–at least 100 times higher.
- HIRs obey the law of reciprocity as suggested by inhibition of hypocotyl elongation in response to short pulses of FR light, suggesting that photoperception by phytochrome is rate-limiting for this response.

4. STRUCTURE AND FUNCTION OF PHYTOCHROME PROTEINS

1. Chemical Structure

- Native phytochrome is a soluble protein with a molecular mass of about 250 kDa.
- It occurs as a dimer (a protein complex composed of two subunits). Each subunit consists of two components: a light-absorbing pigment molecule called the chrornophore, and a polypeptide chain called the apoprotein (Fig. 17.6).
- The apoprotein monomer has a molecular mass of about 125 kDa and is encoded in angiosperms by a small family of genes. Together, the apoprotein and its chromophore make up the **holoprotein**.

Fig. 17.6 Structure of the Pr and Pfr forms of the chromophore (phytochromobilin) and the peptide region bound to the chromophore through a thioether linkage.



The chromophore undergoes a *cis-trans* isomerization at carbon 15 in response to red and far-red light. (After Andel et al. 1997.)

- In higher plants the chromophore of phytochrome is a linear tetrapyrrole called **phytochromobilin**.
- Light (R or FR) cannot be absorbed by the phytochrome apoprotein alone, and can be absorbed only when the polypeptide is covalently linked with phytochromobilin to form the holoprotein.
- Phytochromobilin, synthesized inside plastids, is derived from heme via a pathway that branches from the chlorophyll biosynthetic pathway.
  - The phytochromobilin is exported to the cytosol where it attaches to the apoprotein through a thioether linkage to a cysteine residue (Fig. 17.6).
  - Assembly of the phytochrome apoprotein with its chromophore is **autocatalytic**; that is, it occurs spontaneously when purified phytochrome polypeptide is mixed with purified chromophore in the test tube, with no additional proteins or cofactors (Li & Lagarias 1992).

2. Functional Domains of Phytochrome

- Several of the structural domains in phytochrome have been identified including the diversity of cellular changes mediated in response to light (Fig. 17.7).
- The N-terminal half of phytochrome contains a **PAS domain***, a **GAF domain** with bilin-lyase activity, which is necessary for autocatalytic assembly of the chromophore, and the **PHY domain**, which stabilizes phytochrome in the Pfr form.
- A hinge region separates the N-terminal and C-terminal halves of the molecule and plays a critical role in conversion of the inactive, Pr form of phytochrome to the active, Pfr form.
- Downstream of the hinge regions are two **PAS-related domain** (**PRD**) repeats that mediate phytochrome dimerization.

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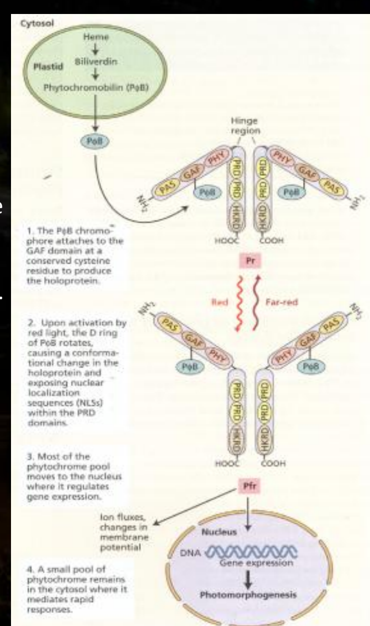
Fig 17.7 After synthesis and assembly (1), phytochrome is activated by red light (2) and moves into the nucleus (3) to modulate gene expression. A small pool of phytochrome remains in the cytosol, where it may regulate rapid biochemical changes (4). Several conserved domains within the phytochrome are shown: PAS, GAF (contains bilin-lyase domain), PHY, PRID (PAS-related domain), and HKRD (HIS kinase-related domain). POB, phytochromobilin. (After Montgomery and Lagarias 2002.)



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- Within the PRD are two **nuclear localization sequences** (**NLSs**) that when exposed, direct the active, Pfr form of phytochrome to the nucleus.
- A major breakthrough in phytochrome research was achieved with the three-dimensional structure for the N-terminal region of a bacterial phytochrome bound to its chromophore, biliverdin, from the radiation-resistant, extremophilic bacterium *Deinococcus radiodurans* (Wagner et al. 2005).
- Unlike plant phytochromes, bacterial phytochromes utilize a range of tetrapyrrole chromophores and likely mediate very different downstream responses.
- Nevertheless, the structure of the chromophore-binding pocket is likely to be highly conserved, and the chromophore is tightly associated with a pocket in the GAF domain (Fig. 17. 8).

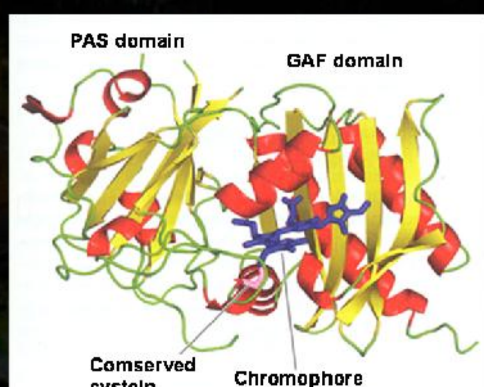

Fig. 17.8 A three-dimensional crystal structure is shown for the N-terminal portion of a bacterial phytochrome from Deinococcus radiodurans. The chromophore, biliverdin (shown in purple), is covalently attached to a conserved cysteine residue (shown in pink) and is closely associated with the protein backbone of the GAF domain. (After Wagner et al. 2005.)

3. Phytochrome as a Light-Regulated Protein Kinase

- Phytochrome is a light-regulated protein kinase that is necessary for its the activation.
- Higher-plant phytochromes, having some homology with the histidine kinase domains (bacterial phytochromes), are *serine/threonine kinases* (Fig. 17.9B) and likely phosphorylate other proteins.

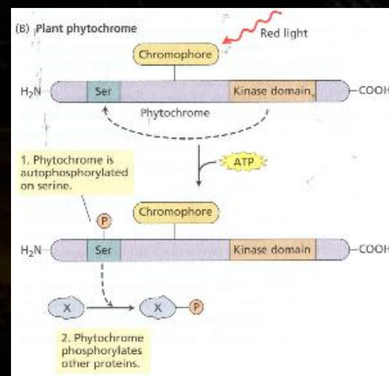

Fig. 17.9 (B) Plant phytochrome is an autophosphorylating serine/threonine kinase that phosphorylates other proteins (shapes containing X).

4. Cytosol and Nucleus Phytochrome

- In the cytosol, phytochrome holoproteins dimerize in the inactive Pr state.
  - Upon absorption of light, the Pr chromophore undergoes a *cis-trans* isomerization of the double bond between carbons 15 and 16 and rotation of the C14–C15 single bond (Fig. 17.16).
  - During the conversion of Pr to Pfr, the protein moiety of the phytochrome holoprotein also undergoes a conformational change in the hinge region that exposes a nuclear localization signal (NLS) in the C-terminal half of phytochrome resulting in the movement of phytochrome molecules from the cytosol to the nucleus (Fig. 17.7).
- The movement of phytochromes from the cytosol to the nucleus is light quality-dependent, in that the Pfr form of phytochrome is selectively imported into the nucleus (Fig. 17.10).

5. Multigene Family of Phytochrome

- Early biochemical studies provided hints that there were different forms of phytochrome.
- Two different classes of phytochrome have been found; the light-labile form (Type I) and the light-stable form (Type II). Actually, it is the Pfr form of Type I phytochromes that is unstable.
  - In Arabidopsis the family is composed of five structurally related members: *PHYA, PHYB, PHYC, PHYD,* and *PHYE* (Sharrock and Quail 1989). In rice, a monocot, there are only three phytochrome-encoding genes: *PHYA, PHYB,* and *PHYC* (Mathews and Sharrock 1997).
- The apoprotein by itself (without the chromophore) is designated PHY; the holoprotein (with the chromophore) is designated phy.

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4. SIGNALING PATHWAYS

1. Early Steps in Phytochrome Action

- All phytochrome-regulated changes in plants begin with absorption of light by the pigment.
- After light absorption, the molecular properties of phytochrome are altered, probably affecting the interaction of the phytochrome protein with other cellular components that ultimately bring about changes in the growth, development, or position of an organ.
- The early steps in phytochrome action and the signal transduction pathways that lead to physiological or developmental responses fall into two general categories:
  - Ion fluxes, which cause relatively rapid turgor responses
  - Altered gene expression, which result in slower, long-term processes.

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2. Phytochrome and Membrane Potentials

- Phytochrome can rapidly alter the properties of membranes, within seconds of a light pulse.
- Such rapid modulation has been measured in individual cells and has been inferred from the effects of red and far-red light on the surface potential of roots and oat (*Avena*) coleoptiles, in which the lag between the production of Pfr and the onset of measurable hyperpolarization (membrane potential changes) is 4.5 seconds.
- Changes in the bioelectric potential of cells imply changes in the flux of ions across the plasma membrane and suggest that some of the cytosolic responses of phytochrome are initiated at or near the plasma membrane.

3. Phytochrome and Gene Expression

- Phytochrome regulates gene expression, and the stimulation and repression of transcription by light can be very rapid, with lag times as short as 5 minutes.
- Some of the early gene products that are rapidly upregula-ted following a shift from darkness to light are transcript-tion factors that activate the expression of other genes.
- The genes encoding these rapidly up-regulated proteins are called **primary response genes**.
- Expression of the primary response genes depends on *signal transduction pathways* and is independent of protein synthesis.
- In contrast, the expression of the late genes, or **secondary response genes**, requires the synthesis of new proteins.

4. Phytochrome Interacting Factors (PIFs)

- Several **phytochrome-interacting factors** (**PIFs**) have been identified in Arabidopsis by two methods (yeast two-hybrid library screens and co-immunoprecipitation).
- One of the most extensively characterized of these factors is **PIF3**, a basic helix-loop-helix (bHLH) transcription factor that interacts with both phyA and phyB.
- Recent studies of PIF-family members have indicated that they act primarily as negative regulators of phytochrome response.
- Phytochromes appear to initiate the degradation of PIF proteins through phosphorylation, followed by degradation through the proteasome complex.

5. Protein Kinases and Phosphatases

- In addition to nucleus-localized transcription factors, two-hybrid screens also identified cytosolic proteins as potential partners for phy proteins.
- **Phytochrome kinase substrate 1** (**PKS1**) is capable of interacting with phyA and phyB in both the active Pfr and inactive Pr form.
- This protein can accept a phosphate from phyA, further highlighting the importance of phosphorylation in phytochrome signaling.
- **Phytochrome-associated protein phosphatase 5** (**PAPP5**) is another factor that interacts with phytochromes and is probably involved in accentuating phytochrome response through dephosphorylation of the active phytochrome.

- A possible model for the regulation of phy activity by phosphorylation is shown in Fig. 17.13.

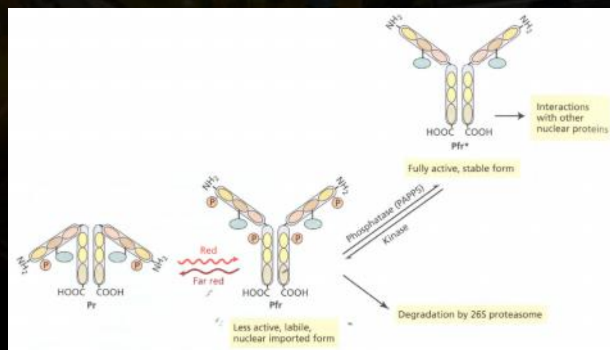


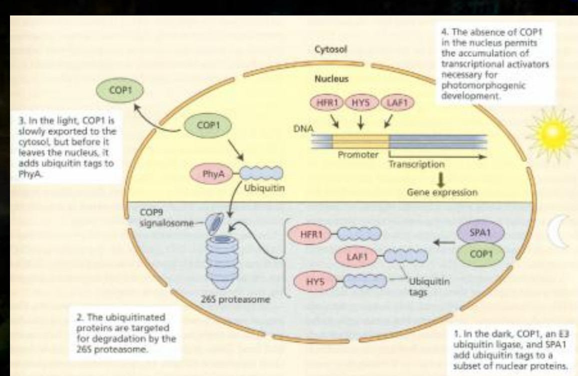
Fig. 17.13 Phytochrome activity is modulated by phosphorylation status. Following activation by red light, the phytochrome-associated phosphatase PAPP5 and as-yet unidentified kinases modulate phytochrome activity in response to the intensity or quality of light. (After Ryu et al. 2005.)

6. Gene Expression and Protein Degradation

- The cloning of several COP/DET/FUS genes has revealed an essential role for protein degradation in the regulation of the light response.
- **COP1** encodes an E3 ubiquitin ligase that is essential for placing a small peptide tag known as *ubiquitin* onto proteins.
- Once tagged by ubiquitin, the proteins are transported to the 26S proteasome, a cellular garbage disposal that chews up proteins into their constituent amino acids.
- COP9 and several other COP proteins compose the **COP9 signalosome** (**CSN**), which forms the lid of this garbage disposal, helping to determine which proteins enter the complex.

- COP1 has been shown to interact with several proteins involved in the light response, including the transcription factors HFRI, HY5, and LAFI, targeting them for degradation in the dark (Fig. 17.14,).
- In the light, COP1 is exported from the nucleus to the cytosol (Fig. 17.14), excluding it from interaction with many of the nucleus-localized transcription factors.
- These transcription factors can then bind to promoter elements in genes that mediate photomorphogenic development.
- COP1 is also responsible for the degradation of the flowering regulators CO and GI as well as proteins involved in auxin and GA response.

Fig. 17.14 COP proteins regulate the turnover of proteins required for photomorphogenic development. During the night, COP1 enters the nucleus, and the COP1/SPA1 complex adds ubiquitin to a subset of transcriptional activators. The transcription factors are then degraded by the COP9 signalosome-proteasome complex.



During the day, COP1 exits the nucleus, allowing the transcriptional activators to accumulate. Blue tails represent ubiquitin tags on proteins destined for the COP9 signalosome complex (CSN) that serves as the gatekeeper of the 26S proteasome.

5. ECOLOGICAL FUNCTIONS

1. Plant Adaptation to Light

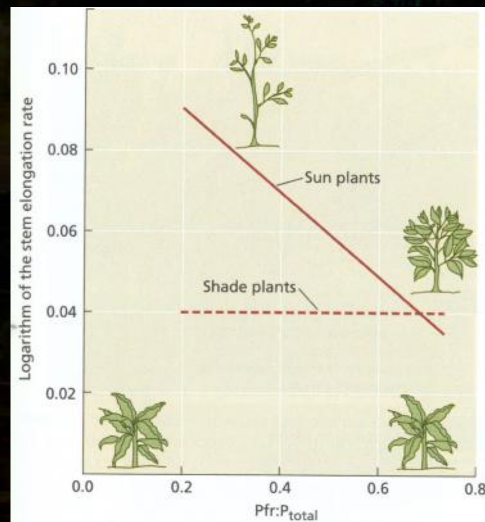
- The ratio of red light (R) to far-red light (FR) varies remarkably in different environments (Table 17.3).
  - As shading increases, the R:FR ratio decreases, and a higher proportion of FR light converts more Pfr to Pr, and the ratio of Pfr/P_{total} decreases.
- An important function of phytochrome is that it enables plants to sense shading by other plants.
- Plants that increase stem extension in response to shading are said to exhibit a **shade avoidance response**.
- When sun plants were grown in natural light with natural F:FR ratio, stem extension rates increased in response to a higher FR content (i.e., a lower $Pfr:P_{total}$ ratio) (Fig. 17.16).

Table 17.3 Ecologically important light parameters

Light type and Environment	Fluence rate («mol $m^{-2}s^{-1}$)	R:FRa
Daylight	1900	1.19
Sunset	26.5	0.96
Moonlight	0.005	0.94
Ivy canopy	17.7	0.13
Lakes, at a depth of 1 m		
Black Loch	680	17.2
Loch Leven	300	3.1
Loch Borralie	1200	1.2
Soil, at a depth of 5 mm	8.6	0.88

Source: Smith 1982, p. 493.
Note: The light intensity factor (400-800 nm) is given as the photon flux density, and phytochrome-active light is given as the RTR ratio.
*Absolute values taken from spectroradiometer scans; the values should be taken to indicate the relationships between the various natural conditions and not as actual environmental means.

Fig.17.16 Phytochromes appear to play a predominant role in controlling stem elongation rate in sun plants (solid line), but not in shade plants (dashed line). (After Morgan and Smith 1979.)

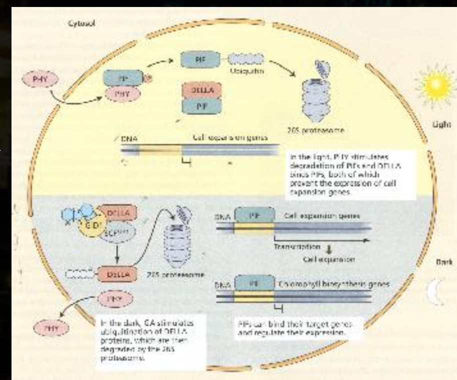


2. Role of Hormones in Shade Avoidance

- Evidence is also emerging for the integration of a number of hormonal pathways in the control of shade avoidance responses including those of auxin, gibberellins, and ethylene.
- Several recent reports have suggested that the PIF proteins play important roles in mediating responses to shade and at least some of these responses are mediated through GA signaling pathways (Fig. 17.17).
- When plants are grown under high R:FR, as in an open canopy, phy proteins become nuclear localized and inactivate PIF proteins.
- In darkness or under low R:FR, a pool of phytochrome is excluded from the nucleus, enabling the accumulation of PIF proteins that promote elongation responses.

Convergence of light and hormone signaling.

Fig. 17.17 In the dark, the growth-promoting hormone gibberellic acid (GA) binds to its receptor and mediates the ubiquitination of DELLA proteins. The DELLA proteins are then targeted to the 26S proteasome for degradation. In the absence of the DELLA proteins, PIFs can act as both positive and negative regulators of gene expression, likely through interaction with different partners, perhaps mediated through different *cis*-regulatory elements upstream of target genes.



In the light, DELLA proteins bind PIF proteins, preventing them from interacting with genes. PHY proteins also target PIF proteins, through phosphorylation, eventually leading to their ubiquitination and degradation. In the absence of PIF proteins, genes required for cell expansion are not expressed, and plant growth is retarded.

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3. Crop Yield and Shade Avoidance

- In recent years, yield gains in crops such as maize have come largely through the breeding of new maize varieties with a higher tolerance to crowding (which induces shade avoidance responses) than through increases in basic yield per plant.
- As a consequence, today's maize crops can be grown at higher densities than older varieties without suffering decreases in plant yield (Fig. 17.18).

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QUESTIONS

1. What is the light that prevents flowering in shortday plants?
2. What is the active form of phytochrome that results in germination in lettuce seeds?
3. What is the chromophore of phytochrome?
4. What does it happened to Pr chromophore on absorption of light?
5. What is photoreversibility of phytochrome?
6. What is the proportion of phytochrome Pfr form after saturating irradiation by red light?

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