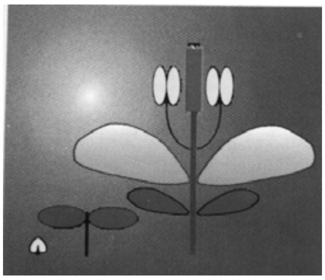
第九章　光形态建成

(PHOTOMORPHOGENESIS)



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1　光形态建成的概念、生物学意义及其特点

1.1　概念：形态建成又叫形态发生，是指形态结构的发生与构建过程，亦即生长与发育过程。**光形态建成或光形态发生是指由光所调控的植物生长与发育过程。**

图示、举例如下:

光信号
（光质、光长、光强、光向）
↓
光信号受体
↓
光信号转导
↓
基因表达
↓
代谢生理反应
↓
形态建成反应

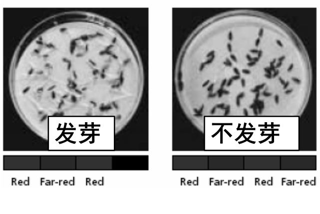
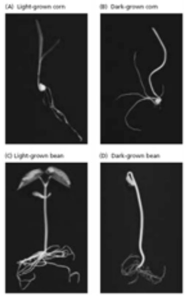


FIGURE 17.2 Lettuce seed germination is a typical photoreversible response controlled by phytochrome. Red light promotes lettuce seed germination, but this effect is reversed by far-red light. Imbibed (water-moistened) seeds were given alternating treatments of red followed by farred light. The effect of the light treatment depended on the last treatment given. (Photos © M. B. Wilkins.)



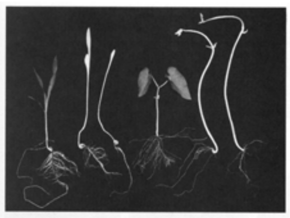


Figure 20-1 Effects of light on seedling development in a monocot (maize) and a dicot (bean). The plant at the left of each group was germinated and grown in a greenhouse, whereas the other representatives of each were grown in continuous darkness for 8 days. (Photograph by Frank B. Salisbury.)

Symptoms of etiolation in corn： the absence of greening, reduction in leaf size, failure of leaves to unroll, and elongation of the coleoptile and mesocotyl.

In bean： absence of greening, reduced leaf size, hypocotyl elongation, and maintenance of the apical hook.

黄化现象有以下的表现:

(1) 叶片小,侧枝不发育; 失绿黄化;

(2) 节间伸长;

(3) 顶芽形成钩头状弯曲,不能直线伸长;

(4) 茎的机械组织特别是导水组织不发达,因而不牢固;

(5) 叶组织不分化,全部由薄壁细胞组成,细胞间隙小;

(6) 一般地说,细胞细长,细胞壁较薄;

(7) 根的发育不良(在图中没有表现出来)。

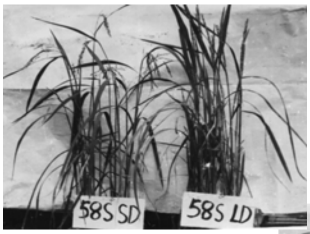
图：光对遗传上完全相同的两株马铃薯生长发育的影响

研究表明：在黑暗条件下，大部分基因不表达。在黑暗条件下的形态建成称为暗形态建成(skotomorphogenesis)。

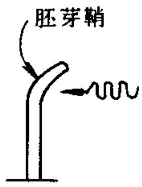
图 4　美洲烟草的开花试验

A. 在冬季的自然日照(短日照)条件下的植株；

B. 在冬季的自然日照加上人工光照(长日照)下的植株



图：长日照诱导湖北光敏核不育水稻农垦58S（ 58S ）雄性不育



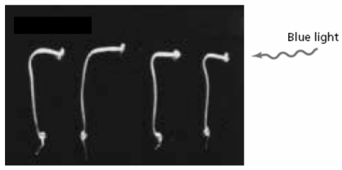


FIGURE 18.4 Phototropism in *Arabidopsis* seedlings. Unilateral light was applied from the right.

1．2　生物学意义：是植物适应环境的一种重要机制,也是植物完成正常生长发育所必需。 例如：黑暗条件下（土壤深处）萌发的种子，表现为黄化现象，有限的营养主要用于胚轴与茎的伸长以便快速出土，因为其它都不重要。此外,没有光形态建成,植物不可能完成正常的个体过程。

1．3　特点：光只起信号作用，直接调控植物的生长发育。 与光合作用中光的作用不同（光起能源作用，间接调控植物的生长发育）。

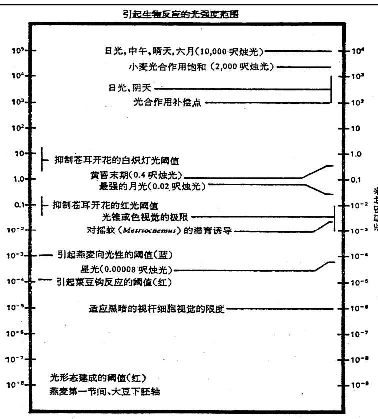


图 7　能引起某些生物反应的光强度　注意有效光强度的范围分布于13个数量级(引自 F. B. Salisbury, 1963, The Flowering Process).

2 参与光形态建成的光受体类型

目前已发现3类光受体参与光形态建成，它们是:

2.1 光敏色素(phytochrome)：又称红光/远红光受体，强烈吸收红光与远红光。目前已发现5种类型的光敏色素，分别为**phyA**、**phyB**、**phyC**、**phyD**、**phyE**，由不同基因编码，其中phyA由*PHYA*基因编码，见光易分解，光下合成少，而phyB-E为组成型表达,不受光暗影响。不同的光敏色素其作用不同。

2.2 蓝光-紫外光A受体(blue-UV-A receptor)：吸收蓝光与近紫外光（长波紫外光,320~400nm）.

隐花色素（ Cryptochrome ）:抑制下胚轴伸长、控制开花的受体,包括两个,一个感受强光(Cry1)，一个感受弱光(Cry2),生色团可能为黄素腺嘌呤二核苷酸(FAD)和蝶呤(pterin);

向光素或趋光反应受体（Phototropins）:也包括两个,一个感受弱光(Phot1)，一个感受强光(Phot2),生色团为黄素单核苷酸(FMN);

玉米黄质(Zeaxanthin/**ziə'zænθin/**):参与气孔开放的受体.

2.3 紫外光—B受体(UV-B receptor):吸收B区紫外光(280~320nm)的受体。

UVR8是在模式植物拟南芥中发现的一种特异性吸收UV-B的光受体,自然状态下UVR8二聚体在UV-B下解聚成单体，并与COP1结合,调控下游基因的转录表达。

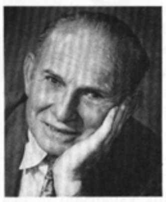
表3 不同类型光受体的吸收峰

光受体	phytochrome	blue / UV-A	UV-B
吸收峰（nm）	660；730；	420；450；480；370~380	290~300

3 光敏色素的发现与分布

3.1 The Discovery of Phytochrome （光敏色素）

Sterling B. Hendricks



The discovery of a new process in the biological world is always exciting, and when it proves to be an important one, it may be epochal. This was true for the discovery of phytochrome. In 1970, we asked Sterling B. Hendricks to tell us of the discovery. Sterling Hendricks died on January 4, 1981.

In 1945, Harry A. Borthwick, Marion W. Parker, and I set out to find out something about how plants recognize day lengths. Our method was to note changes in flowering induced by breaking long nights with periods of light of various wavelengths and intensities—or, more exactly, to measure action

FIGURE 24.17 Maryland Mammoth mutant of tobacco (right) compared to wild-type tobacco (left). Both plants were grown during summer in the greenhouse. (University of Wisconsin graduate students used for scale.) (Photo courtesy of R. Amasino.)

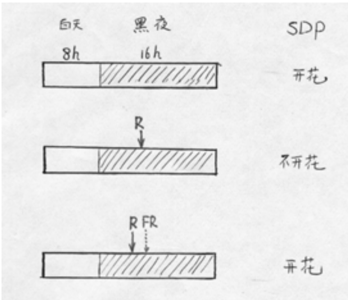
Plants Can Be Classified by Their Photoperiodic Responses

Numerous plant species flower during the long days of summer, and for many years plant physiologists believed that the correlation between long days and flowering was a consequence of the accumulation of photosynthetic products synthesized during long days.

This hypothesis was shown to be incorrect by the work of Wightman Garner and Henry Allard, conducted in the 1920s at the U.S. Department of Agriculture laboratories in Beltsville, Maryland. They found that a mutant variety of tobacco, Maryland Mammoth, grew profusely to about 5 m in height but failed to flower in the prevailing conditions of summer (Figure 24.17). However, the plants flowered in the greenhouse during the winter under natural light conditions.

1920年， W W Garner & H A Allard发现光周期现象(美国农业部Beltsville试验站)。

1938年，人们为了探索植物感受日照长短的机制，进行了暗期间断试验，发现暗间断能阻止短日植物开花，促进长日植物开花，红光最有效。



图示暗间断试验

1945年，Harry A. Borthwick,Marion W. Parker,and Sterling B.Hendricks 也开展了植物感受日照长短的机制研究。

他们还与Frits W. Went 合作，以大麦为材料，研究光对黄化现象的抑制作用，结果发现抑制大麦茎伸长、促进叶片展开最有效的光也是红光。

植物两种不同的形态建成反应，却具有相同的作用光谱，基于这一事实，他们推测植物体内光形态建成的原初反应很可能是一样的。

由于某些种子需光萌发是很久以前（100多年前）就发现了，他们便以需光萌发的莴苣种子为材料继续试验。结果 1952年，Beltsville试验站的Borthwick & Hendricks发现红光促进莴苣种子发芽，而远红光逆转这个过程。

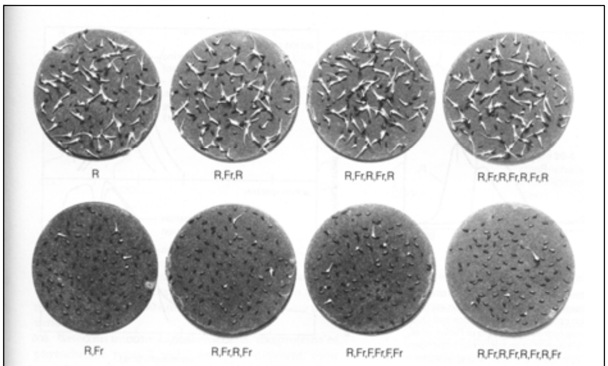


Figure 20-2 Reversal of lettuce-seed germination with red (R) and far-red (Fr) light. Red exposures were for 1 min and far-red for 4 min. If the last exposure is to red light, seeds germinate; if it is to far-red light, they remain dormant. Temperature during the half hour required to complete the treatments was 7°C; at all other times it was 19°C. (Courtesy Harry Borthwick.)

不久证明，开花过程也有类似的可逆效应。

基于上述试验，他们认为植物体内存在一种蓝颜色的色素，它可能以两种互变的形式存在。

为了直接证明这种色素的存在，开始了这种色素的提取、分离与测定工作。但遇到两个问题:

第一，植物组织中这种色素以很稀的浓度存在，而且干扰色素（如叶绿素）大量存在于植物组织中;

第二，当照射红光后，它就转变成几乎不吸收红光的形式，反之，当照射远红光后，它就转变成几乎不吸收远红光的形式。

解决这两个问题的办法是：用黄化苗提取色素、用特制的双波长分光光度计去检测 。

1959年，该试验站的Butler(生物物理学家)用特制的双波长分光光度计测定黄化玉米幼苗的吸收光谱。发现用红光照射后，红光区域吸收减少，而远红光区域吸收增多；用远红光处理后，则红光区域吸收增多，远红光区域吸收消失。红光远红光轮流照射后，这种吸收光谱可多次地可逆变化(图8）。

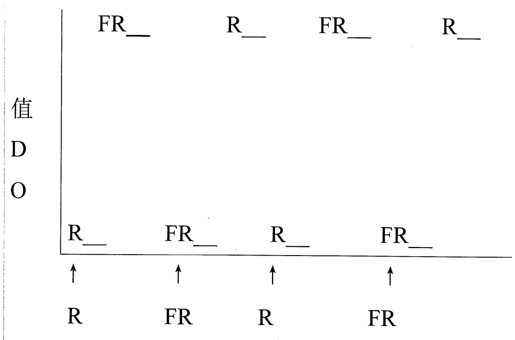


图 8 红光与远红光处理对黄化玉米幼苗地上部分提取液吸收这些光的影响

1960s早期，H.W.Siegelman 及其他一些蛋白质化学家应用色谱等技术成功地分离出这种光受体蛋白， Borthwick等称之为光敏色素(Phytochrome)。以两种可逆转的形式存在:

$$\mathrm{Pr} \underset{\text{远红光}}{\overset{\text{红光}}{\rightleftharpoons}} \mathrm{Pfr}$$

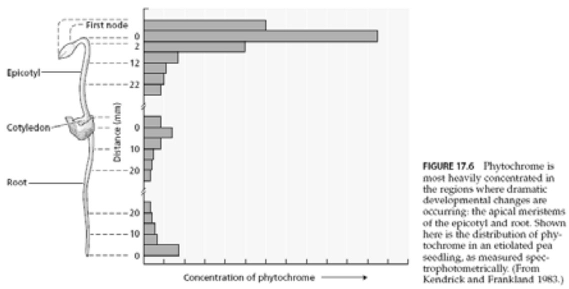
从而证明基于生理试验的推测。

3.2 光敏色素的分布

①光敏色素广泛存在于植物界：被子植物、裸子植物、蕨类植物、苔藓植物、地衣、甚至红藻、褐藻、绿藻。

②分布于植物的各器官(图9)。

③光敏色素在细胞中的分布：黑暗条件下定位于细胞质中，照光后可进入细胞核中。



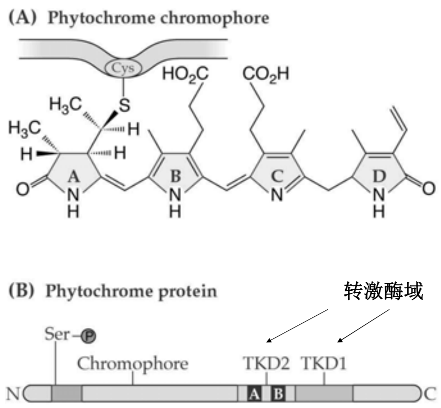
4 光敏色素的分子结构、吸收光谱特征及其光化学转换

有关光敏色素的研究绝大部分是以从黄化苗中提取的光敏色素作为研究对象，其原因有二：一是黄化苗中光敏色素含量很高,是绿苗的10～100倍，二是没有叶绿素干扰（叶绿素吸收红光与蓝紫光），只有到了上世纪80年代中期才有从绿苗中提取的光敏色素研究报道。

4.1 分子结构
4.1.1 化学结构

●**光敏色素＝生色团+脱辅基蛋白**。为二聚体，相对分子量为250KD左右。

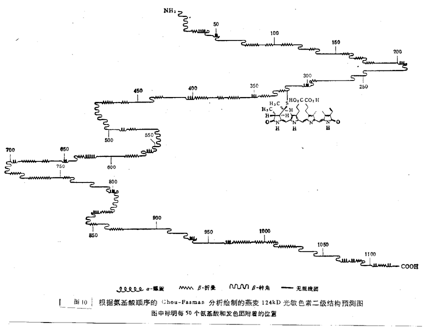
- ●生色团为链状四吡咯环，分子量为612D。
- ●脱辅基蛋白质单体分子量为120～127KD。
- ●生色团通过硫醚键与脱辅基蛋白相连。



4.1.2 空间结构

●**二级结构**：包含α螺旋、β折叠、β转角及无规线团(图10　根据AA顺序预测的燕麦124KD光敏素二级结构)。

● 1985年，揭示了燕麦黄化苗光敏色素全部氨基酸顺序，包含 1128个氨基酸残基，链状四吡咯生色团以硫醚键连接在N-端321位的半胱氨酸残基上(图)。



●**三级结构**(图11)：自然的PI光敏素（黄化苗中）多肽折绕成两个主要部分：一个球状的具发色团的大约74KD的氨基末端部分和一个比较开放的大约55KD的羧基末端部分，这两个部分由易受蛋白酶分解的肽链连接在一起。

●**四级结构**(图11)：生理状态下以二聚体形式存在（2个亚基）。

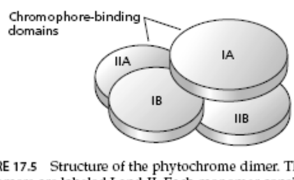


FIGURE 17.5 Structure of the phytochrome dimer. The monomers are labeled I and II. Each monomer consists of a chromophore-binding domain (A) and a smaller nonchromophore domain (B). The molecule as a whole has an ellipsoidal rather than globular shape. (After Tokutomi et al. 1989.)

4.2 吸收光谱特征

强烈吸收红光与远红光，也可吸收蓝光、紫外光。但在低辐射强度下，吸收蓝光、紫外光引起的形态建成反应没有红光与远红光有效。

黄化苗光敏素（Type 1）的吸收光谱曲线（图）：其中Pr的红光区最大吸收峰为660 nm，Pfr的远红光区最大吸收峰为730 nm，但在660 nm附近有一红肩。

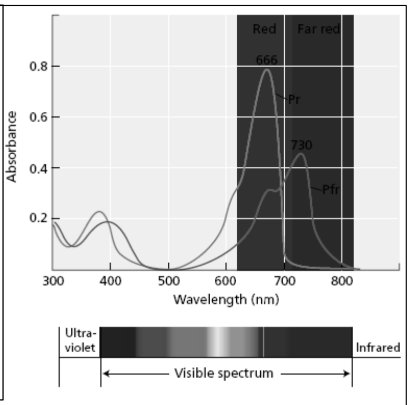
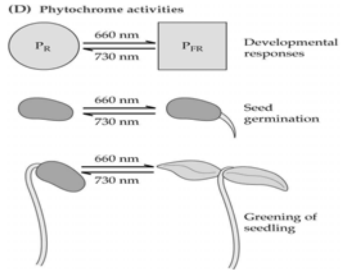


FIGURE 17.3 Absorption spectra of purified oat phytochrome in the Pr (green line) and Pfr (blue line) forms overlap. (After Vierstra and Quail 1983.)

4.3 光敏色素的光化学转换

4.3.1 光敏色素的两种存在形式可以发生光可逆转换



红光吸收型(Pr) 为生理失活型

远红光吸收型(Pfr) 为生理活化型

●在两种形式的光逆转中,构象发生改变。

当P_r吸收红光后， C14与C15之间的单键旋转，使得C15与C16之间的双键、吡咯环D进行顺反异构化，这种变化导致四吡咯环构象发生改变，从而导致脱辅基蛋白构象变化，即整个光敏色素构象发生改变。

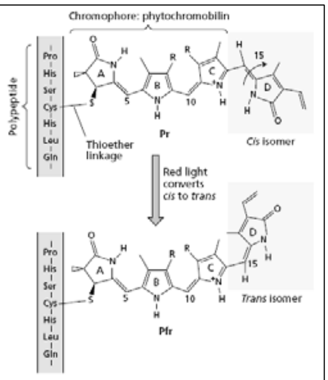


FIGURE 17.4 Structure of the Pr and Pfr forms of the chromophore (phytochromobilin) and the peptide region bound to the chromophore through a thioether linkage. The chromophore undergoes a *cis–trans* isomerization at carbon 15 in response to red and far-red light. (After Andel et al. 1997.)

4.3.2 光稳定平衡

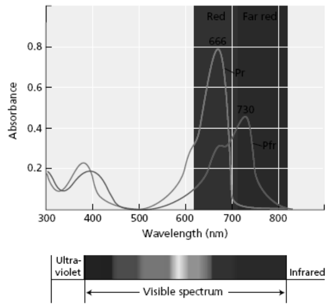


FIGURE 17.3 Absorption spectra of purified oat phytochrome in the Pr (green line) and Pfr (blue line) forms overlap. (After Vierstra and Quail 1983.)

如图所示在小于**700nm**的各种光波下,**Pr**与**Pfr**均有不同程度的吸收,会形成某种平衡。

在一定光照条件下，在红光吸收型与远红光吸收型之间形成的平衡叫光稳定平衡.

①光稳定平衡(φ,phi)＝Pfr / Pr+Pfr
＝ Pfr / Ptot。

其中Ptot(=Pr+Pfr)代表总光敏素含量，Pr代表红光吸收型的含量，Pfr代表远红光吸收型的含量。

②不同波长的红光与远红光照射，可以得到不同的φ值(图)。例如：

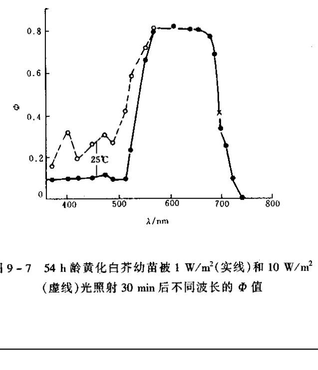


图 9－7 54 h 龄黄化白芥幼苗被 1 W/m²(实线)和 10 W/m²(虚线)光照射 30 min 后不同波长的 Φ 值

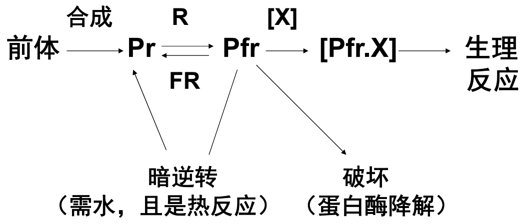
660nm的红光可以使80％的白芥光敏素转变成Pfr型，故φ＝0.80;

718nm的远红光则可使97.5%的光敏素转变成Pr型，故φ=0.025。

太阳光中红光与远红光的比例为1.1~1.2（红光占主导），加上红光吸收型吸收红光比远红光吸收型吸收远红光更有效，故形成更多的Pfr,其φ≈0.6。

自然条件下，只要φ值达到0.01～0.05，就可引起很显著的生理生化变化。

4.4 光化学转换导致形态建成反应的设想模式



4.3.3 光化学转换导致的形态建成反应

①快反应： 从吸收光量子到诱导出形态变化的反应迅速，以分秒计，受红光远红光可逆调节。

②慢反应：从吸收光量子到诱导出形态变化的反应慢，以小时或天数计，反应终止后不能逆转。

5 光敏色素的生理作用与反应类型

5.1 光敏色素介导的形态建成反应

光敏色素通过调节代谢与生理过程（可直接调节，也可通过基因表达调节），从而调节植物的形态建成反应，其作用非常广泛，贯穿植物一生，从种子萌发、幼苗生长，直至开花、结实、衰老脱落（表）。

表9-2 高等植物中一些由光敏色素控制的反应

1. 种子萌发	6. 小叶运动	11. 光周期	16. 叶脱落
2. 弯钩张开	7. 膜透性	12. 花诱导	17. 块茎形成
3. 节间延长	8. 向光敏感性	13. 子叶张开	18. 性别表现
4. 根原基起始	9. 花色素形成	14. 肉质化	19. 单子叶植物叶片展开
5. 叶分化和扩大	10. 质体形成	15. 偏上性	20. 节律现象

5.2 光敏色素调节某些酶或蛋白质的合成

① 叶绿素a/b脱辅基蛋白(LHCP) 、Rubisco大小亚基、磷酸甘油醛脱氢酶、转酮醇酶(与光合作用有关)。

② RNA聚合酶、RNA酶、氨基酸激活酶(与核酸、蛋白质代谢有关)。

③ NAD激酶、脂肪氧化酶、抗坏血酸氧化酶、淀粉酶、NR酶 (与中间代谢有关)。

④ PAL酶、肉桂酸羧化酶(与次生物质代谢有关)。

5.3 光敏色素调节植物内源激素水平

①红光处理：植物内源生长素含量减少。原因有多种报道：影响合成、运出、促进向C－IAA转化。

②红光促进GA合成,从而促进莴苣种子萌发;照射黄化大麦叶片后，GA急剧增加；但也有相反报道说红光可减少多花菜豆幼苗的GA含量。

③红光照射可提高细胞分裂素的含量。

④红光抑制幼苗弯钩乙烯生物合成，而远红光促进。红光可能通过调节内源生长素水平而间接影响乙烯。

⑤红光对脱落酸的影响研究不多，无定论。

●此外，光敏色素还作为环境中红光:远红光比率的感受器传递不同光质、不同照光时间的信息，调节植物的发育。例如，植物叶片含有叶绿素而吸收红光，透过或反射远红光。当植物受到周围植物的遮荫时，R:FR值变小，阳生植物在这样的条件下，茎向上伸长速度加快，以获取更多的阳光，这种现象叫做避阴反应(shade avoidance response)。

6 光敏色素的作用机理

6.1 膜假说(Hendricks & Borthwick 1967年提出)
6.1.1 基本内容：

认为光敏色素位于膜上，发生光转换时，可引起跨膜离子流与膜上酶的分布改变，影响代谢，经过一系列的生理生化变化，最终表现出形态建成的改变。

6.1.2 支持此假说的证据：

①含羞草、合欢叶片的昼夜运动(白天小叶张开，晚上合拢，图)；
②棚田效应(图)；
③转板藻带状叶绿体运动(图)等快反应。

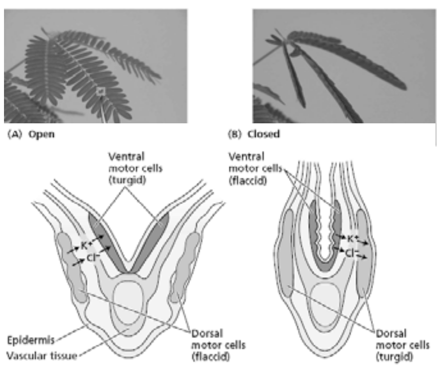


FIGURE 17.14 Ion fluxes between the dorsal and ventral motor cells of *Albizia pulvini* regulate leaflet opening and closing. (After Galston 1994.)

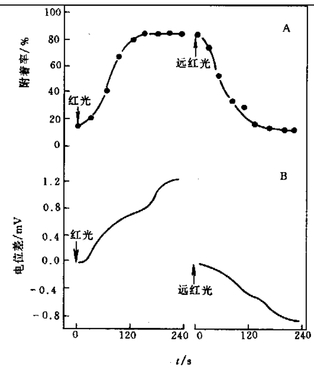


图9－11　红光或远红光处理后,绿豆根尖粘在带负电荷的玻璃表面的动力学(A)和根尖电位差(B)的变化

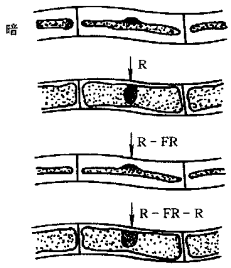


图 9－9　弱红光和远红光对转板藻叶绿体运动的影响
（红光使叶绿体面向光照方向）

6.1.3 光控转板藻带状叶绿体运动的可能信号传递链

红光 ⟶ Pfr增多 ⟶ 跨膜Ca^{2+}流动 ⟶ 细胞质中Ca^{2+}浓度增加 ⟶ 钙调素活化 ⟶ 肌动球蛋白轻链激酶活化 ⟶ 肌动球蛋白收缩运动 ⟶ 叶绿体转动。

6.2 基因调节假说(Mohr 1966年提出)
6.2.1 基本内容

接受红光后，Pfr经过一系列过程，将信号转移到基因， 活化或抑制某些特定基因，使mRNA的形成速度、种类发生改变，通过mRNA的翻译(蛋白质或酶)，最后表现出形态建成。

图示如下:

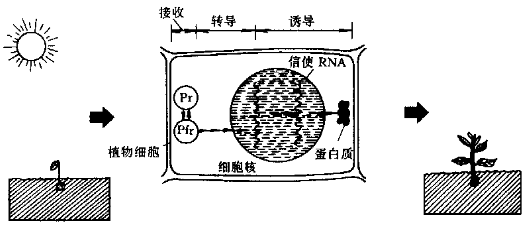


图 9－12　光形态建成过程中基因活化的 3 个步骤

6.2.2 支持此假说的证据：

①红光促进莴苣种子发芽;
②红光抑制茎的伸长;
③成花诱导;
④育性调控;
⑤多种酶及蛋白质的合成受光敏素调控等慢反应过程。

近年来,在光敏素的作用机理研究方面取得了很大进展:

Phytochrome Moves to the Nucleus

It has long been a mystery as to how phytochrome could act in the nucleus when it is apparently localized in the cytosol. Recent exciting work has finally opened up the black box between phytochrome and gene expression. The most surprising finding is that in some cases phytochrome itself moves to the nucleus in a light-dependent manner.

Detection of this movement relied on the ability to fuse phytochrome to a visible marker, green fluorescent protein (GFP), that can be activated by light of an appropriate wavelength being shone on plant cells. A big advantage of GFP fusions is that they can be visualized in living cells, making it possible to follow dynamic processes within the cell under the microscope.

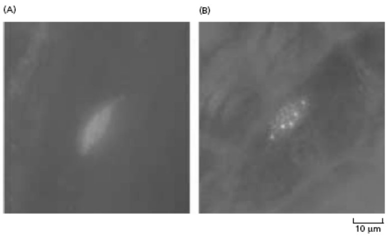


FIGURE 17.19 Nuclear localization of phy–GFP fusion proteins in epidermal cells of *Arabidopsis* hypocotyls. Transgenic *Arabidopsis* expressing phyA–GFP (left) or phyB–GFP (right) was observed under a fluorescence microscope. Only nuclei are visible. The plants were placed either under continuous far-red light (left) or white light (right) to induce the nuclear accumulation. The smaller bright green dots inside the nucleus are called "speckles." The significance of speckles is unknown. (From Yamaguchi et al. 1999, courtesy of A. Nagatani).

Both phyA–GFP and phyB–GFP show light-activated import into the nucleus (Figure 17.19) (Sakamoto and Nagatani 1996; Sharma 2001). The phyB fusion moves to the nucleus in the Pfr form only, and transport is slow, taking several hours for full mobilization. In contrast, phyA–GFP can move in the Pfr or the Pr form, provided that it has cycled through Pfr first. Movement of phyA–GFP is much more rapid than that of phyB–GFP, taking only about 15 minutes.

Most satisfying is the observation that phyB–GFP transport is promoted by red light and inhibited by far-red light, while transport of phyA–GFP is maximal under continuous far-red light. Furthermore, nuclear translocation of phyB is under circadian control, as would be expected, since phyB regulates the expression of clock-regulated genes. These light conditions are the ones known to be responsible for activation of phyA and phyB and would be consistent with their activity in the nucleus.

What happens when Pfr moves to the nucleus? Two nuclear proteins that interact with phytochrome have been identified to date, although there are probably additional targets. The first, ***p**hytochrome **i**nteracting **f**actor 3* (**PIF3**), reacts with the C-terminal end of phyA or phyB. However, it reacts preferentially with the full-length phyB protein in a light-dependent manner, and it is thought to be a functional primary reaction partner for this phytochrome.

Although its precise function is not yet known, PIF3 resembles transcription factors that bind to a particular element in plant promoters, the G-box motif, that confers light regulation to genes. It is also known that phyB in the Pfr form can form a complex with PIF3 bound to its target DNA. A picture is therefore emerging in which some phytochrome-regulated genes are activated directly by movement of phyB to the nucleus in the Pfr form. Once in the nucleus, phyB interacts with transcription factors such as PIF3. A model for the direct activation of gene expression by phyB in the nucleus is shown in Figure 17.20.

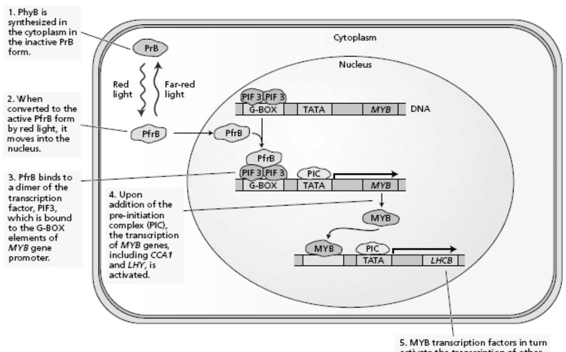
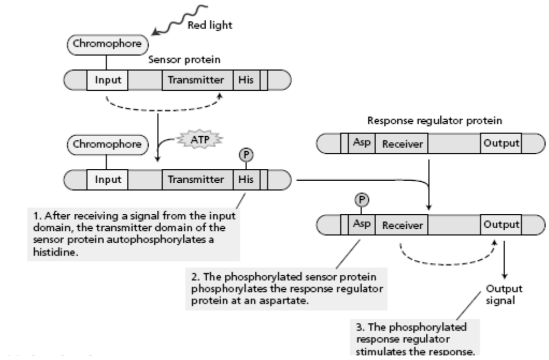


FIGURE 17.20 Direct regulation of gene expression by phyB transport to the nucleus. (After Quail 2000.)

Phosphorylation. The evidence for a potential role of phosphorylation in phytochrome action first came from red-light regulation of protein phosphorylation and phosphorylation-dependent binding of transcription factors to the promoters of phytochrome-regulated genes. Some highly purified preparations of phytochrome were also reported to have kinase activity.

Kinases are enzymes that have the capacity to transfer phosphate groups from ATP to amino acids such as serine or tyrosine, either on themselves or on other proteins. Kinases are often found in signal transduction pathways in which the addition or removal of phosphate groups regulates enzyme activity.

Phytochrome is now known to be a protein kinase. The evolutionary origin of phytochrome is very ancient, predating the appearance of eukaryotes. Bacterial phytochromes are light-dependent histidine kinases that function as **sensor proteins** that phosphorylate corresponding **response regulator** proteins (Figure 17.21A). (See also Chapter 14 on the web site and **Web Topic 17.11**)



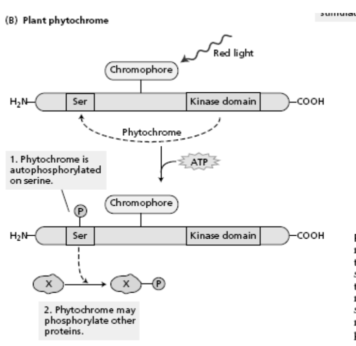
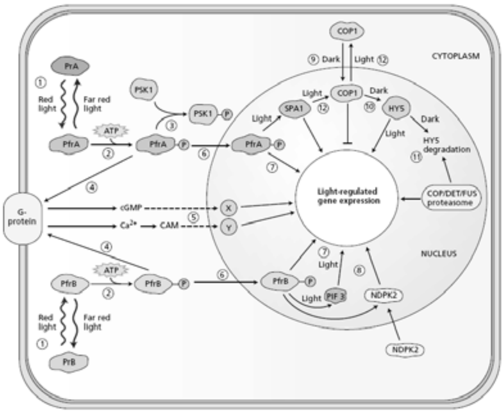


FIGURE 17.21 Phytochrome is an autophosphorylating protein kinase. (A) Bacterial phytochrome is an example of a two-component signaling system, in which phytochrome functions as a sensor protein that phosphorylates a response regulator (see Chapter 14 on the web site). (B) Plant phytochrome is an autophosphorylating serine/threonine kinase that may phosphorylate other proteins (X).

Phytochome Acts through Multiple Signal Transduction Pathways

Using biochemical approaches, researchers have shown that signaling involves several different mechanisms, including G-proteins, Ca^{2+}, and phosphorylation. We will consider the evidence for each of these in turn.



1. Red light converts PrA and PrB to their Pfr forms.
2. The Pfr forms of phyA and phyB phytochrome can autophosphorylate.
3. Activated PfrA phosphorylates phytochrome kinase substrate 1 (PKS1).
4. Activated PfrA and PfrB may interact with G-proteins.
5. cGMP, calmodulin (CAM), and calcium (Ca^{2+}) may activate transcription factors (X and Y).
6. Activated PfrA and PfrB enter the nucleus.
7. PfrA and PfrB may regulate transcription directly or through interaction with phytochrome interacting factor 3 (PIF3).
8. Nucleoside diphosphate kinase 2 (NDPK2) is activated by PfrB. 二磷酸核苷激酶
9. In the dark, COP1 enters the nucleus and suppresses light-regulated genes.
10. In the dark, COP1, an E3 ligase, ubiquitinates HY5.
11. In the dark, HY5 is degraded with the assistance of the COP/DET/FUS proteasome complex.
12. In the light, COP1 interacts directly with SPA1 and is exported to the cytoplasm.

FIGURE 17.22 Summary diagram of the known factors involved in phytochrome-regulated gene expression. It is likely that additional shared and phytochrome-specific pathways will be uncovered as more signaling intermediates are identified. (After Sharma 2001.)

7 蓝光—近紫外光反应

7．1 概念：由蓝光与近紫外光介导的形态建成反应。

7．2 例证：广泛存在于植物界，尤其是隐花植物。高等植物的向光性、下胚轴伸长的抑制、刺激气孔张开等是由蓝光与近紫外光调节(图)。

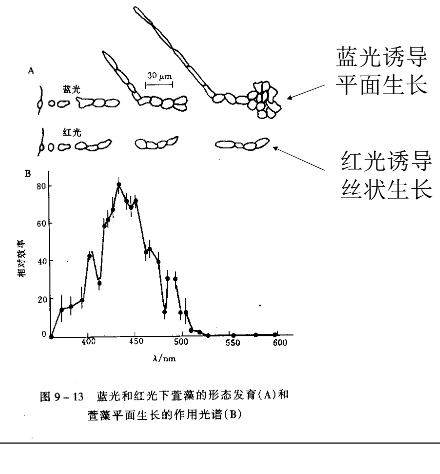


图 9－13 蓝光和红光下萱藻的形态发育(A)和萱藻平面生长的作用光谱(B)

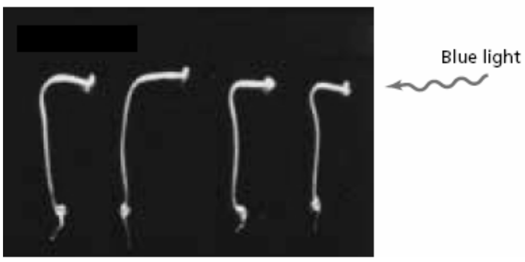


FIGURE 18.4 Phototropism in *Arabidopsis* seedlings. Unilateral light was applied from the right. (Courtesy of Dr. Eva Huala.)

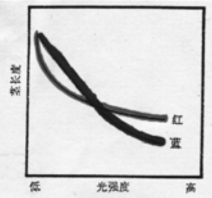


图 22 蓝光和红光对有些植物都抑制茎的伸长在低强度时，红光往往更有效，当强度较高时，蓝光变得更能抑制（引自 J. A. Lockhart 1963, *Adv. Frontiers Plant Sciences* 7: 1; 根据 G. Meijer, 1959, *Acta Botanica Neerlandica* 8: 189）.

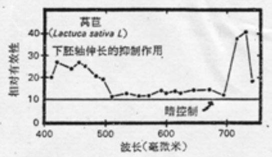


图 23 表示蓝光和远红光对莴苣下胚轴伸长抑制效应的一个作用光谱（根据 H. Mohr 和 M. Wehrung 1960, *Planta*, **55**: 438）.

7．3 作用光谱特征

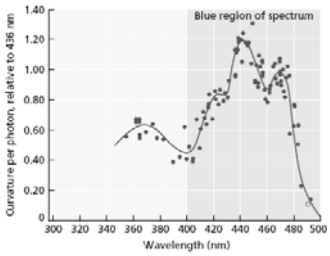


FIGURE 18.1 Action spectrum for blue light–stimulated phototropism in oat coleoptiles. An action spectrum shows the relationship between a biological response and the wavelengths of light absorbed. The "three-finger" pattern in the 400 to 500 nm region is characteristic of specific blue-light responses. (After Thimann and Curry 1960.)

在400-500nm的蓝光区有3个峰，呈“三指”状，在近紫外光区有1个峰(通常在370-380nm)，大于500 nm波长的光是无效的(图)。这也是判断隐花色素介导的蓝光—近紫外光反应的实验性标准。

7.4 蓝光受体研究进展

依据林晨涛（UC at Los angles）报告整理

●Cry2 acts as a blue light receptor mediating blue light inhibition of hypocotyl（下胚轴）elong-ation.

●Cry2 also acts as daylength sensor that controls photoperiodic flowering .

●Cry2 undergoes a blue light dependent protein phosphorylation.Nature(2002) .

● Cry2 phosphorylation is blue light specific. It is not phosphorylated in red light or far-red light. So phytochromes may not be the Cry 2 kinase.

●The kinetic analysis of Cry2 phosphorylation suggest:1. phosphorylated Cry2 may be degraded.2. phosphorylated Cry2 may be the active form.

●blue light induces a rapid degration of Cry2 protein,and this degration associate with its function.

●Cry1 also undergoes phosphorylation.

8 拟南芥(*Arabidopsis thaliana*)
—研究植物生理与分子生物学的模式植物

8.1 普通生物学特性

①生育期短。

②植株小，可在人工控制条件下大量种植，便于筛选突变体，排除因环境条件不同导致的形态变化。

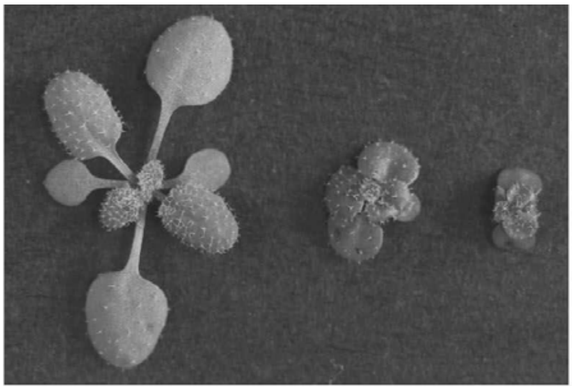
③典型的自花授粉植物，人工诱变后可以在子二代中直接筛选变异株的纯合子，另外每株种子量多，易于扩大变异株种子库。

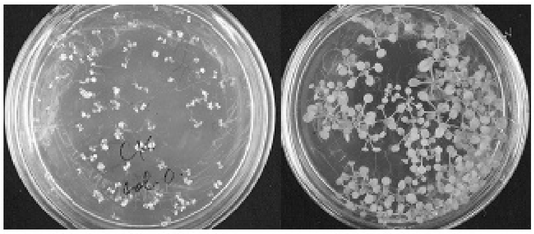
8.2 遗传学与分子生物学特性

① 80％的基因为单拷贝，容易获得突变体。

②单倍体5条染色体，2倍体为10条染色体。

③核基因组小，其单倍体基因组只有80000Kb左右，是第一个完成全序列测定的高等植物（2000），估计有27，000个基因。

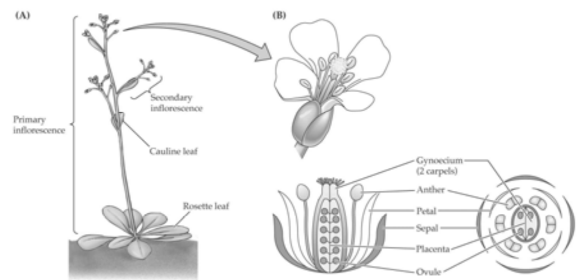




WT Transgene

图示 从T2代中筛选出的转基因拟南芥纯合体植株

Transgenic Arabidopsis plants of T_0 generation



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课堂练习

1．光形态建成是一种高能反应，它与光敏色素系统密切相关。 [ ]

【解析】 √。

2．促进莴苣种子萌发的光是( )

A．蓝光 B．绿光
C．红光 D．黄光

【解析】 C 。在探究植物测时问题的研究过程中， 美国Beltsville试验站的Borthwick & Hendricks以需光萌发的莴苣种子为材料进行试验。 1952年，发现红光促进莴苣种子发芽，而远红光逆转这个过程。

3．黑暗条件下生长的幼苗与正常光照条件下生长的幼苗相比，具有下列哪些特征？(多选)

A．根系更发达 B．胚轴伸长更显著
C．节间明显伸长 D．叶呈现黄白色

【解析】BCD。植物在黑暗中会表现出黄化现象：不能合成叶绿素，显现出类胡萝卜素的黄色；节间延长；根系、维管束和机械组织不发达等（ 见下图）。

黄化现象是植物对环境的一种适应。当种子或其他延存器官在无光的土层下萌发时，可使贮存量有限的有机营养物质最有效地用于胚轴或茎的伸长，保证幼苗出土见光。

很弱的光就能消除幼苗的黄化现象，恢复正常生长。人们常用遮光的方法生产黄化幼苗作为食品 ,如韭黄、蒜黄和豆芽等，因纤维素少而柔嫩可口。