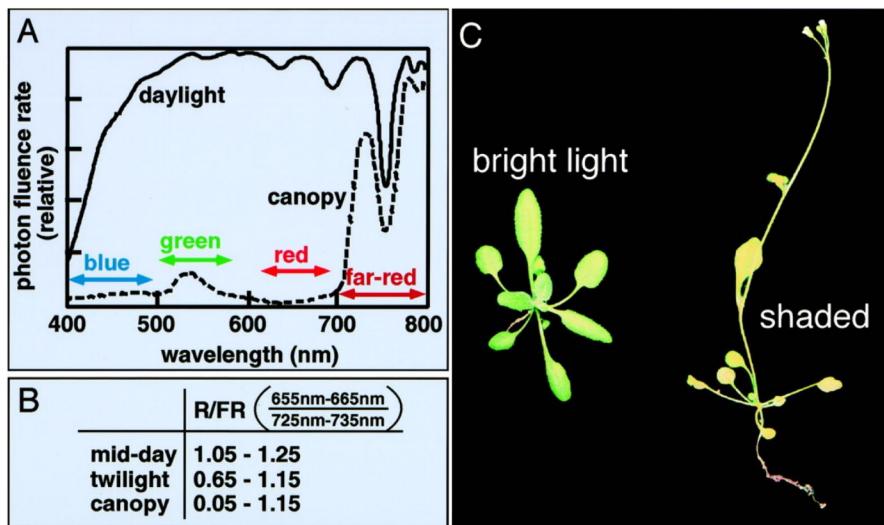


La qualité de la lumière comme indicateur du temps et de l'espace

Source: Neff, M. M., Fankhauser, C. & Chory, J. Light: an indicator of time and place. *Genes & Development* **14**, 257-271 (2000)



The ratio of R/FR light is a good indicator of time and place. (A) Light spectra of daylight and under a plant canopy. (B) R/FR ratios in different times and places.

Source: Martínez-García, J. F. et al. The Shade Avoidance Syndrome in Arabidopsis: The Antagonistic Role of Phytochrome A and B Differentiates Vegetation Proximity and Canopy Shade. *PLoS ONE* **9**, e109275 (2014)

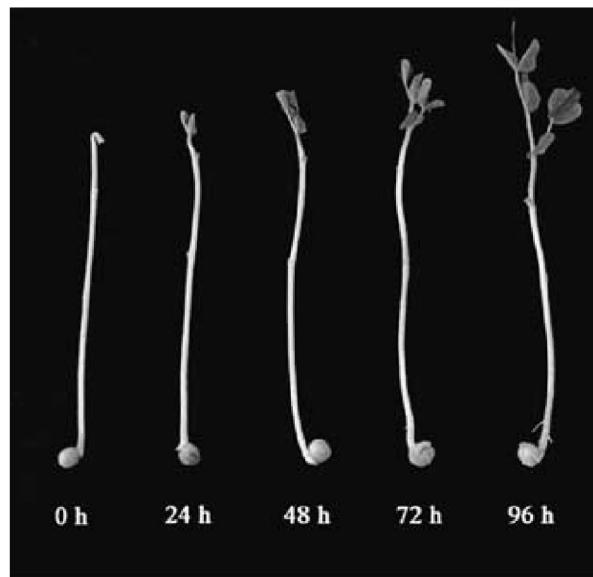
The shade avoidance syndrome (SAS) refers to a set of plant responses aimed at adapting plant growth and development to high plant density environments, like those found in forests, prairies or orchard communities. Two related but different situations can occur in these environments: plant proximity (without direct vegetative shading) and direct plant canopy shade [1]-[3]. Because vegetation preferentially reflects far-red (FR) light compared to other wavelengths, plant proximity generates a reduction in the red (R, about 600-700 nm) to far-red (FR, between 700-800 nm) ratio (R:FR) in the light impinging on neighbors. By contrast, under a plant

canopy, light from the visible region (called photosynthetically active radiation or PAR, between 400-700 nm) is strongly absorbed by the chlorophyll and carotenoid photosynthetic pigments whereas FR, which is poorly absorbed by the leaves, is transmitted through (or reflected from) vegetation. As a consequence, under direct plant canopy shade both the amount of PAR (light quantity) and R:FR (light quality) are greatly reduced, in the latter case mostly by the selective depletion of R light caused by the filtering of sunlight through the leaves [1], [2], [4]-[6].

Etiollement - dé-étiolement

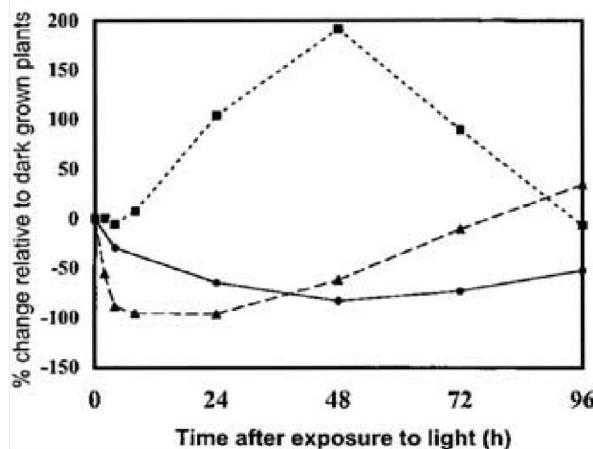
Source: Li, J., Li, G., Wang, H. & Wang Deng, X. Phytochrome Signaling Mechanisms. *The Arabidopsis Book / American Society of Plant Biologists* 9 (2011)

Dark-grown seedlings undergo skotomorphogenesis (etiolation) and are characterized by long hypocotyls, closed cotyledons and apical hooks, and development of the proplastids into etioplasts. Light-grown seedlings undergo photomorphogenesis (de-etiolation) and are characterized by short hypocotyls, open and expanded cotyledons, and development of the proplastids into green mature chloroplasts (McNellis and Deng, 1995).



Source: Symons, G. M. & Reid, J. B. Interactions Between Light and Plant Hormones During De-etiolation. *Journal of Plant Growth Regulation* 22, 3–14 (2003).

Light has a profound influence on virtually all aspects of plant growth and development, including seed germination, seedling development, morphology and physiology of the vegetative stage, the control of circadian rhythms and flowering (Kim and others 2002; Nemhauser and Chory 2002). The effect of light on plant growth and development is perhaps most obvious during the transition from a dark-grown (etiolated) to a light-grown (de-etiolated) morphology. Etiolated dicotyledonous seedlings exhibit a phenotype that includes a pronounced apical hook, elongated epicotyl/hypocotyl and undifferentiated chloroplast precursors (Chory and others 1996; Clouse 2001). Upon exposure to light, seedlings undergo a number of dramatic changes, including a significant reduction in the rate of elongation, opening of the apical hook, expansion of true leaves and the development of mature chloroplasts (Chory and others 1996; Clouse 2001; Figure 1).



Top: Morphological changes in WT pea seedlings during de-etiolation. All plants were grown for 7 days at 20°C in continuous darkness before being transferred to continuous W light at an intensity of 150 $\mu\text{mol.m}^{-2}\text{s}^{-1}$. Bottom: Percentage change in endogenous hormone levels in etiolated WT plants after exposure to light. All plants were grown for 7 days at 20°C in continuous darkness before being transferred into continuous W light at an intensity of 150 $\mu\text{mol.m}^{-2}\text{s}^{-1}$. Values represent the percentage change in hormone levels (relative to the ng/g FW levels in the dark-grown controls) at various timepoints (0, 2, 4, 8, 24, 48, 72, and 96 h) after exposure to light. Each value was calculated using the mean hormone levels, determined from three individual replicates, each containing either 5 or 6 plants. [Square] indicates the change in IAA levels, [circle] the change in ABA and [triangle] the change in GA1 at each time point.

While the perception of light through photoreceptors is well understood, the downstream components of light-signal transduction and the mechanisms by which light mediates phenotypic change are not clear (Fankhauser and Chory 1997; Fankhauser and Staiger 2002; Nemhauser and Chory 2002). However, many of the light-induced changes during de-etiolation, particularly the change in stem elongation, are also known to be regulated by plant hormones (Garcia-Martinez and Gil 2002). Thus the integration of light and hormone signalling pathways is also thought to be required for normal plant

development (Clouse 2001). Indeed, plant hormones are thought to act as transducers of the light signal by mediating the effects of light on plant growth and development (Nemhauser and Chory 2002). A number of plant hormones have been implicated in the regulation of morphological change during de-etiolation, including gibberellins (GA), indole-3-acetic acid (IAA), abscisic acid (ABA), cytokinins (CK), brassinosteroids (BRs) and ethylene (Chory and Li 1997; Garcia-Martinez and Gil 2002; Kraepiel and Miginiac 1997; Neff and others 2000; Tian and Reed 2001).

Gravitropisme: généralités

Source: Chen, R., Rosen, E. & Masson, P. H. Gravitropism in Higher Plants. *Plant Physiology* **120**, 343–350 (1999)

Since 1806, we have known that plant organs use gravity as a guide for growth (Knight, 1806). The gravity-directed growth process, called gravitropism, dictates upward shoot growth to ensure a proper positioning of the leaves for efficient photosynthesis and gas exchange. It also directs roots to grow downward in soil, where they can reach out to take up the water and mineral ions required for plant growth and development.

Gravitropism has an important impact on agriculture. It allows plants to compete for the limited resources available in their immediate environment and ensures that crop shoots resume upward growth after prostration by the action of wind and rain (Fig.1). Consequently, plants can keep their seeds away from soil moisture and pathogens and are more amenable to mechanical harvesting.

Source: Blancaflor, E. B. & Masson, P. H. Plant Gravitropism. Unraveling the Ups and Downs of a Complex Process. *Plant Physiology* **133**, 1677–1690 (2003)

In nature, plant organs can use a variety of environmental cues to guide their growth, including gravity, touch, light, gradients in temperature, humidity, ions, chemicals, and oxygen. In the example illustrated above, the stems of younger crops were able to perceive a change in their orientation within the gravity field. The corresponding information was then translated into a complex growth response called gravitropism that allowed them to straighten up and to eventually resume growth at a defined angle from the gravity vector, the gravitational set point angle (GSPA).

The GSPA associated with specific plant organs is a function of the identity of the species and organ under consideration, its developmental phase, the physiological status of the plant, and a variety of environmental

parameters to which the plant has been exposed. A plant organ is capable of detecting any deviation from its assigned GSPA and responds to the corresponding stimulus (gravitropic stimulus) by developing differential cellular elongation on opposite flanks, resulting in tip curvature and subsequent realignment with the GSPA (Firn and Digby, 1997).

Gravitropism has been observed and analyzed in a variety of plant organs, including roots, hypocotyls, and inflorescence stems of dicots; roots, coleoptiles, and pulvini of monocots; and rhizoids and protonemata of algae and moss. It also has been observed and studied in fungal fruiting bodies.

Photorécepteurs: généralités

Source: Li, J., Li, G., Wang, H. & Wang Deng, X. Phytochrome Signaling Mechanisms. *The Arabidopsis Book / American Society of Plant Biologists* 9 (2011).

As sessile organisms, plants have acquired a high degree of developmental plasticity to optimize their growth and reproduction in response to their ambient environment, such as light, temperature, humidity, and salinity. Plants utilize a wide range of sensory systems to perceive and transduce specific incoming environmental signals. Light is one of the key environmental signals that influences plant growth and development. In addition to being the primary energy source for plants, light also controls multiple developmental processes in the plant life cycle, including seed germination, seedling de-etiolation, leaf expansion, stem elongation, phototropism, stomata and chloroplast movement, shade avoidance, circadian rhythms, and flowering time (Deng and Quail, 1999; Wang and Deng, 2003; Jiao et al., 2007).

Plants can monitor almost all facets of light, such as direction, duration, quantity, and wavelength by using at least four major classes of photoreceptors: phytochromes (phys) primarily responsible for absorbing the red (R) and far-red (FR) wavelengths (600-750 nm), and three types of photoreceptors perceiving the blue (B)/ultraviolet-A (UV-A) region of the spectrum (320-500 nm): cryptochromes (crys), phototropins (photos), and three newly recognized LOV/F-box/Kelch-repeat proteins ZEITLUPE (ZTL), FLAVIN-BINDING KELCH REPEAT F-BOX (FKF), and LOV KELCH REPEAT PROTEIN 2 (LKP2). In addition, UV RESISTANCE LOCUS 8 (UVR8) was recently shown to be a UV-B (282-320 nm) photoreceptor (Rizzini et al., 2011). These photoreceptors perceive, interpret, and transduce light signals, via distinct intracellular signaling pathways, to modulate photoresponsive nuclear gene expression, and ultimately leading to adaptive changes at the cell and whole organism levels.

Phytochromes: propriétés et mode d'action (1/2)

Source: Neff, M. M., Fankhauser, C. & Chory, J. Light: an indicator of time and place. *Genes & Development* **14**, 257–271 (2000)

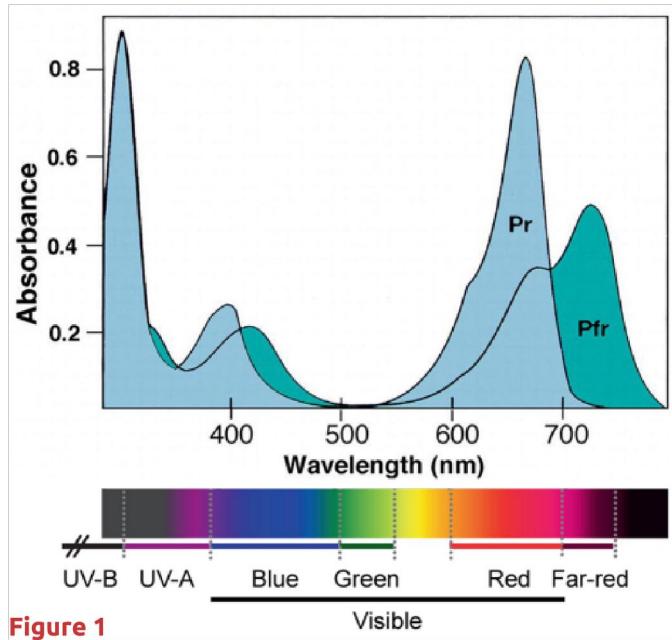


Figure 1

Phytochromes are photochromic proteins composed of a large protein (~125 kD) covalently attached to a linear tetrapyrrole chromophore. Phytochromes are synthesized in a red-light-absorbing form, Pr ($\lambda_{\text{max}} = 660 \text{ nm}$) which, upon exposure to red light, can be phototransformed into a far-red-light-absorbing form, Pfr ($\lambda_{\text{max}} = 730 \text{ nm}$). Upon exposure to far-red light, Pfr is photoconverted to Pr (Kendrick and Kronenberg 1994). Both Pfr and Pr that has been photocycled have been shown to induce developmental responses (Shinomura et al 2000). Thus, phytochrome acts as a light-controlled developmental switch. Phytochromes have been found in all taxa of lower and higher plants examined (Mathews and Sharrock 1997; Mathews and Donoghue 1999), as well as cyanobacteria (Hughes et al. 1997; Lamarter et al. 1997; Yeh and Lagarias 1997).

Phytochromes: propriétés et mode d'action (2/2)

Source: Neff, M. M., Fankhauser, C. & Chory, J. Light: an indicator of time and place. *Genes & Development* **14**, 257–271 (2000)

Phytochromes are soluble proteins and exist as homodimers. The molecular mass of the apoprotein monomer is approximately 125 kDa. Phytochrome apoproteins are synthesized in the cytosol, where they assemble autocatalytically with a linear tetrapyrrole chromophore, phytochromobilin (PΦB). The synthesis of PΦB is accomplished by a series of enzymatic reactions in the plastid that begins with 5-aminolevulinic acid (Figure 2A). The early steps in the PΦB pathway are shared with chlorophyll and heme biosynthesis. The committed step is the oxidative cleavage of heme by a ferredoxin-dependent heme oxygenase (HO) to form biliverdin IX (BV). BV is subsequently reduced to 3Z-PΦB by the enzyme PΦB synthase. Both 3Z-PΦB and its isomerized form 3E-PΦB can serve as functional precursors of the phytochrome chromophore. PΦB is then exported to the cytosol, where it binds to the newly synthesized apo-PHYs to form holo-PHYs (Terry, 1997; Figure 2A). The chromophore is attached via a thioether linkage to an invariant cysteine in a well-conserved domain among all phytochromes (see below).

The intrinsic photochemical activity of the chromophore prosthetic group allows phytochromes to convert between the two forms. Phytochromes are synthesized in the Pr form in dark-grown seedlings. It has been widely accepted that absorption of R light triggers a “Z” to “E” isomerization in the C15-C16 double bond between the C and D rings of the linear tetrapyrrole, resulting in the FR-absorbing Pfr form (Andel et al., 1996; Figure 2B). However, a recent NMR analysis showed that the A pyrrole ring around C4-C5 double bond rotates during photoconversion (Ulijasz et al., 2010). This discrepancy should be resolved in future studies. In addition, the Pr-to-Pfr transition is associated with rearrangement of the protein backbone (Figure 2B). The active Pfr form can be converted back to the inactive Pr form, either by a slow non-photoinduced reaction (dark reversion) or much faster upon absorption of FR light (Mancinelli, 1994; Quail, 1997a; Fankhauser, 2001; Figure 2B). This property allows phytochrome to function as a R/FR-dependent developmental switch.

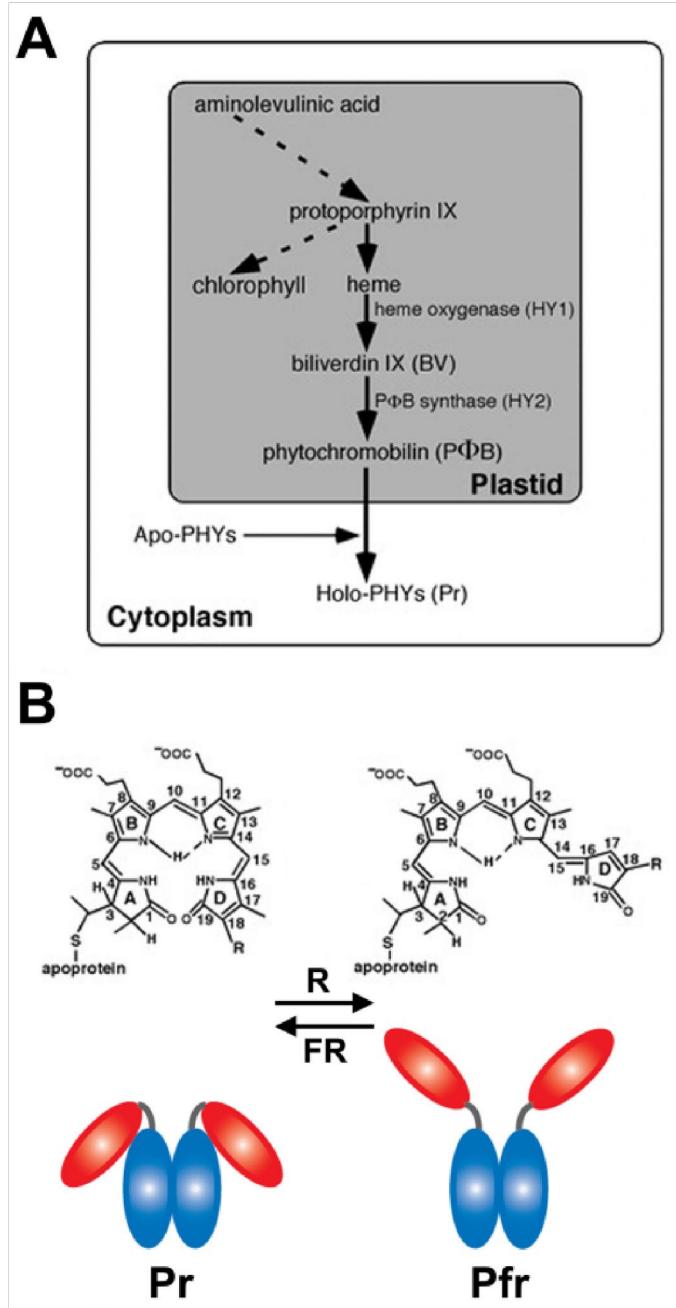


Figure 2

Phytochromes: mode d'action

Source: Li, J., Li, G., Wang, H. & Wang Deng, X. Phytochrome Signaling Mechanisms. *The Arabidopsis Book / American Society of Plant Biologists* 9 (2011).

The term phytochrome, meaning “plant color”, was originally coined to describe the proteinous pigment that controls photoperiod detection and floral induction of certain short-day plants (such as cocklebur and soybean) (Garner and Allard, 1920), and the reversible seed germination of lettuce (c.v. Grand Rapids) by R and FR light (Borthwick et al., 1952). R light promotes seed germination, whereas subsequent FR light treatment abolishes R light induction of seed germination. The germination response of lettuce seeds repeatedly treated with R/FR cycles is determined by the last light treatment. Thus R/FR photoreversibility is a characteristic feature of this response. In addition, the law of reciprocity applies to this response, i.e. the response is dependent on the total amount of photons received irrespective of the duration of light treatment.

Over the years, three action modes for phytochromes have been defined, i.e. low-fluence responses (LFRs), very-low-fluence responses (VLFRs) and high-irradiance responses (HIRs) (Table 1). The above-mentioned F/FR reversible response is characteristic of LFRs.(...)

Photoreversibility occurs because phytochromes exist as two distinct but photoreversible forms in vivo: the R light-absorbing form (Pr) and the FR light-absorbing form (Pfr). The Pr form absorbs maximally at 660 nm, whereas the Pfr form absorbs maximally at 730 nm (Quail, 1997a; Figure 1). The Pfr forms of phytochromes are generally considered to be the biologically active forms. It should be noted that in addition to their maximal absorptions of R and FR wavelengths, phytochromes also weakly absorb B light (Furuya and Song, 1994; Figure 1).

Table 1.
Diagnostic Features of Different Phytochrome Action Modes

Action Mode	Fluence Requirements
VLFR	0.1 $\mu\text{mol}/\text{m}^2$ - 1 $\mu\text{mol}/\text{m}^2$
LFR	1 - 1000 $\mu\text{mol}/\text{m}^2$
HIR	> 1000 $\mu\text{mol}/\text{m}^2$
VLFR: very-low-fluence response; LFR: low-fluence response; HIR: high-irradiance response.	

Phytochromes: aspects génétiques

Source: Li, J., Li, G., Wang, H. & Wang Deng, X. Phytochrome Signaling Mechanisms. *The Arabidopsis Book / American Society of Plant Biologists* 9 (2011).

In *Arabidopsis thaliana*, there are five phytochromes, designated phytochrome A (*phyA*) to *phyE*. They are encoded by five distinct members of the phytochrome gene family and are classified into two groups according to their stability in light (Sharrock and Quail, 1989). *phyA* is a type I (light labile) phytochrome, and *phyB* to *phyE* are all type II (light stable) phytochromes. *phyA* is most abundant in dark-grown seedlings, whereas its level drops rapidly upon exposure to R or white (W) light. In light-grown plants, *phyB* is the most abundant phytochrome, whereas *phyC*-*phyE* are less abundant (Clack et al., 1994; Hirschfeld et al., 1998; Sharrock and Clack, 2002).

Sequence analysis suggests that these phytochromes can be clustered into three subfamilies: *phyA/phyC*, *phyB/phyD*, and *phyE* (Figure 3). Analysis of reconstituted recombinant *phyA*, *phyB*, *phyC* and *phyE* proteins revealed that they have similar but not identical spectral properties (Kunkel et al., 1996; Remberg et al., 1998; Eichenberg et al., 2000). Orthologs of *Arabidopsis PHY* genes are present in most, if not all, higher plants (Clack et al., 1994; Sharrock and Quail, 1989; Mathews and Sharrock, 1997).

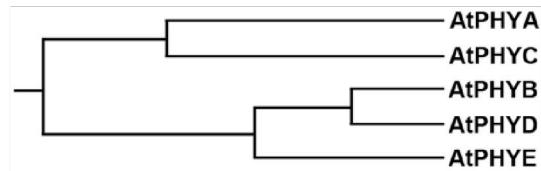


Figure 3

Cryptochromes & Phototropins

Source: Liu, H., Liu, B., Zhao, C., Pepper, M. & Lin, C. The action mechanisms of plant cryptochromes. *Trends in Plant Science* **16**, 684–691 (2011).

Cryptochromes (CRY) are photosensory receptors that regulate growth and development in plants and the circadian clock in plants and animals [1, 2]. Plant cryptochromes are best studied in Arabidopsis (*Arabidopsis thaliana*). The Arabidopsis genome encodes three cryptochrome genes, CRY1, CRY2, and CRY3. CRY1 and CRY2 act primarily in the nucleus [3, 4], whereas CRY3 probably functions in chloroplasts and mitochondria [5].

Source: Briggs, W. R. et al. The Phototropin Family of Photoreceptors. *The Plant Cell* **13**, 993–997 (2001).

The past decade has seen dramatic advances in our knowledge of plant photoreceptors and in our understanding of the signal transduction pathways that they activate (Briggs and Olney, 2001). A major part of these advances has been the identification and characterization of photoreceptors that respond to signals from the blue region of the electromagnetic spectrum. We now know that there are at least two classes of blue light photoreceptors: the cryptochromes and the phototropins.

Source: Christie, J. M. Phototropin Blue-Light Receptors. *Annual Review of Plant Biology* **58**, 21–45 (2007).

Since the isolation of the *Arabidopsis* PHOT1 gene in 1997, phototropins have been identified in ferns and mosses where their physiological functions appear to be conserved. *Arabidopsis* contains two phototropins, phot1 and phot2, that exhibit overlapping functions in addition to having unique physiological roles. Phototropins are light-activated serine/threonine protein kinases. Light sensing by the phototropins is mediated by a repeated motif at the N-terminal region of the protein known as the LOV domain. Photoexcitation of the LOV domain results in receptor autophosphorylation and an initiation of phototropin signaling.

Transduction de signaux par les hormones: historique

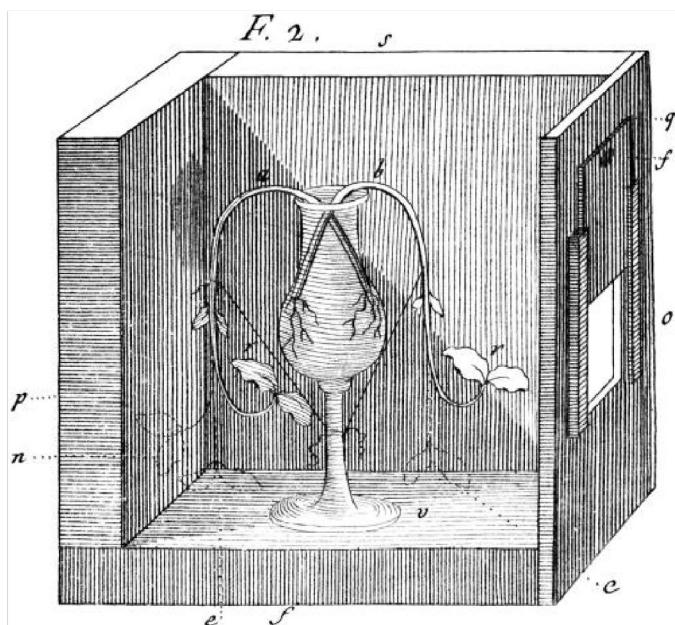
Source: Whippo, C. W. & Hangarter, R. P. Phototropism: Bending towards Enlightenment. *The Plant Cell* **18**, 1110–1119 (2006)

Two etiolated bean seedlings (a and b) oppositely placed in a vase (v) of water were tied downward (e). With the shutter (f) closed, each seedling reoriented upward toward the nearest wall (seedling a toward wall q and seedling b toward wall p). When the shutter was raised, both seedlings reoriented toward the opening (o). Reprinted from Bonnet (1779).

Charles Darwin (1809-1882) further explored the inductive nature and mechanistic connection between phototropism and gravitropism. He proposed that the back and forth circumnutation associated with plant growth could be directed by a stimulus such as light or gravity (Darwin, 1880). Although Darwin's circumnutation theory of tropism served to propose a common mechanism underlying gravitropism and phototropism, the most significant discovery from his studies of plant movements was his demonstration that the site of photoperception at the shoot tip and the location of curvature are separable. From his observations, Darwin was able to propose that a transmissible substance produced in the tip is responsible for inducing curvature in lower regions of the plant (Darwin, 1880). This insightful discovery eventually lead to the discovery of the first plant hormone, auxin.

Darwin's ideas were initially dismissed by other plant physiologists (reviewed in Heslop-Harrison, 1980). Nevertheless, evidence in favor of Darwin's transmissible substance began to accumulate when Rothert (1894) also showed that light sensitivity is greatest near the tip of maize coleoptiles. Subsequent results of Fitting (1907), Boysen-Jensen (1911), and Paal (1918) provided more direct evidence that a transmissible substance produced in the tip participates in the response. This research culminated in a model put forth independently by

Chodlony (1927) and Went (1926, 1928), which proposed that light-mediated lateral redistribution of a plant growth hormone to the shaded side of the seedling causes the differential growth associated with phototropic curvature. This growth substance was shortly identified from human urine by Kogl and Haagen-Smit (1931), who named the hormone auxin, derived from the Greek verb auxein, meaning "to grow."



Transduction de signaux par les hormones

Source: Jensen, P. J., Hangarter, R. P. & Estelle, M. Auxin Transport Is Required for Hypocotyl Elongation in Light-Grown but Not Dark-Grown *Arabidopsis*. *Plant Physiology* **116**, 455–462 (1998)

The development of a plant is influenced by a variety of environmental cues. Differences in light quantity and quality can lead to dramatically different growth forms. Light signals are perceived by a number of different photoreceptors, including the phytochromes and the blue light receptors. Developmental processes under the control of the phytochromes include stem elongation, hypocotyl hook unfolding, leaf expansion, seed germination, and flower initiation (for review, see von Arnim and Deng, 1996). Blue light receptors have been shown to be involved in phototropism, regulation of stem elongation, stomatal opening, and the initiation of chloroplast development (for review, see Senger and Schmidt, 1994).

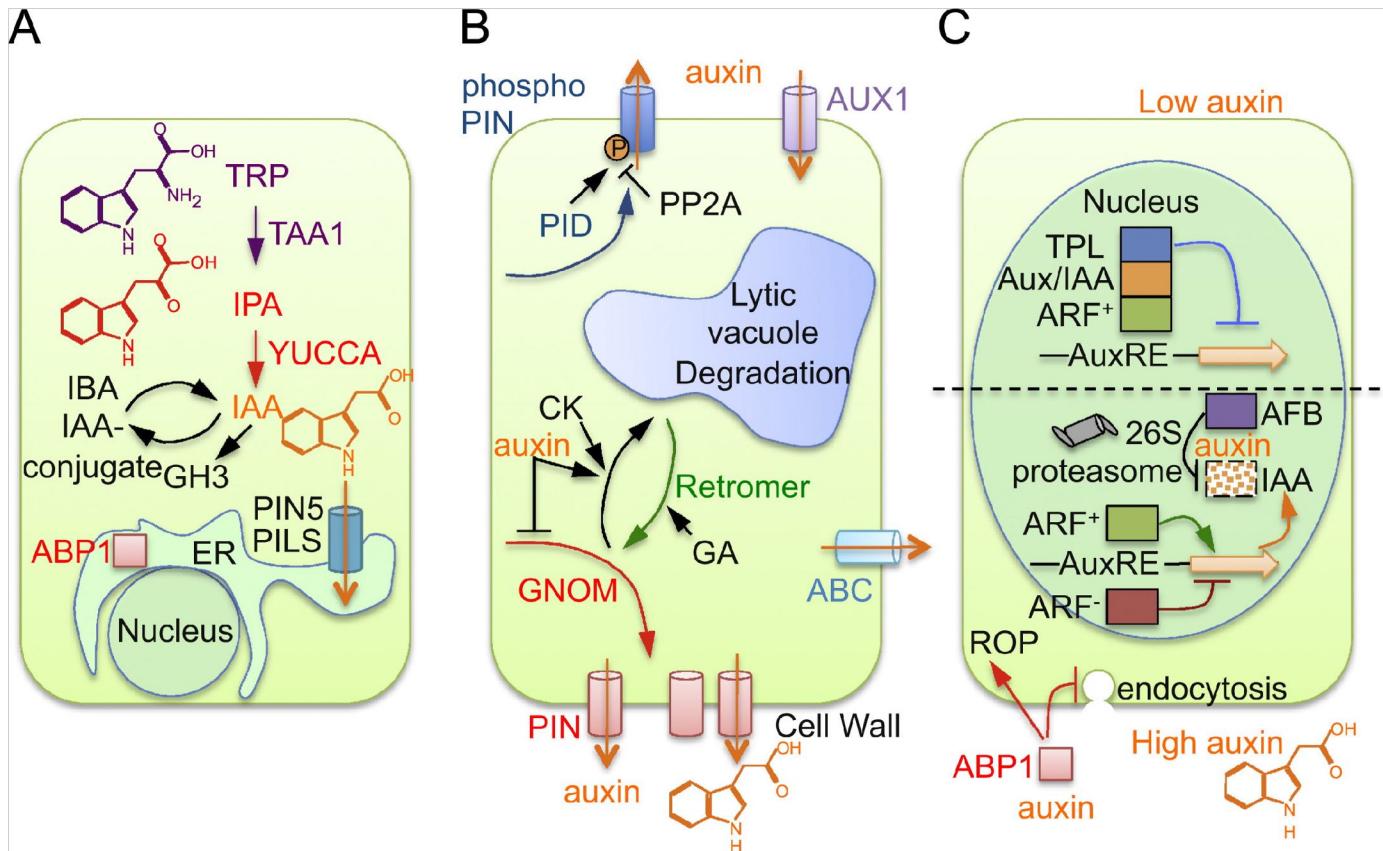
Many of the developmental processes that occur as a result of light signals are dependent, at least in part, on the action of phytohormones. For example, light has been shown to alter the levels of IAA (Bandurski et al., 1977; Jones et al., 1991; Behringer and Davies, 1992), GAs (Ross et al., 1992; Foster and Morgan, 1995), ABA (Weatherwax et al., 1996), cytokinins (Qamruddin and Tillberg, 1989; Kraepiel et al., 1995), and ethylene (Kathiresan et al., 1996, and refs. therein). Behringer and Davies (1992) proposed that phytochrome regulation of stem elongation is partly the result of changes in IAA levels. Phytochrome-deficient mutants of *Arabidopsis thaliana* require GAs to express the elongated phenotype of these plants (Peng and Harberd, 1997). Light regulation of BR levels or sensitivity clearly plays a central role in light-regulated development, because *Arabidopsis* mutants with defects in BR biosynthesis and response are severe dwarfs in both light and dark conditions (Clouse et al., 1996; Kauschmann et al., 1996; Li et al., 1996; Szerkes et al., 1996).

The phytohormone auxin is involved in diverse developmental processes, many of which depend on regulated auxin transport (Went and Thimann, 1937). For example, apical dominance is maintained by auxin produced in the apical meristem and transported basipetally to the target tissues, where it inhibits growth of lateral branches. In the case of tropic responses, lateral redistribution of auxin gives rise to differential growth rates, resulting in curvature of the growing organ. In addition, a gradient in auxin concentration from tip to base is believed to be responsible for differential elongation rates in different regions of shoots (Went and Thimann, 1937; Sanchez-Bravo et al., 1992).

The formation and maintenance of auxin gradients is thought to occur through the action of a specific polar auxin-transport system that requires active efflux of auxin through an auxin-anion uniport (Sabater and Rubery, 1987). Auxin efflux is inhibited by synthetic phytotropins such as NPA (Morgan, 1964; Katekar and Giesler, 1980; Jacobs and Rubery, 1988). The exact nature of this inhibition is not known, but NPA and other auxin-transport inhibitors bind to a single plasma-membrane protein (Lembi et al., 1971; Muday et al., 1993; Bernasconi et al., 1996). The endogenous auxin IAA does not compete with NPA for this binding site (Lomax et al., 1995). In the *tir3* mutant of *Arabidopsis*, reduced NPA binding is associated with defects in auxin-regulated growth processes, suggesting that the NPA-binding site is important for auxin transport (Ruegger et al., 1997).

Auxine: généralités et transporteurs (1/2)

Source: Finet, C. & Jaillais, Y. AUXOLOGY: When auxin meets plant evo-devo. *Developmental Biology* **369**, 19–31 (2012)



Schematic representation of auxin signaling: (A) biosynthesis and homeostasis, (B) polar auxin transport and (C) perception. GA, gibberellin; CK, cytokinin; auxRE, Auxin Response Element.

Auxine: généralités et transporteurs (2/2)

Source: Finet, C. & Jaillais, Y. AUXOLOGY: When auxin meets plant evo-devo. *Developmental Biology* **369**, 19–31 (2012)

Auxin pathway is controlled at many levels that include auxin biosynthesis, auxin metabolism, and auxin transport. Moreover, auxin was proposed to act as an integrator of the activities of multiple plant hormones, altogether suggesting a vast regulatory network of auxin during plant development (Jaillais and Chory, 2010).

[...]

Indole-3-acetic acid (IAA) is the most potent naturally occurring member of the auxin family. High IAA levels are detected in shoot and root meristematic tissues, in cotyledons, as well as in young leaves that have the highest biosynthetic capacity (Ljung et al., 2001). In mature leaves and roots, IAA remains present but in smaller amounts.

[...]

In plants, two distinct pathways are known to play a role in auxin transport: a passive distribution through vascular tissue and an active cell-to-cell polar transport. This polar auxin transport is fundamental for auxin distribution over both short and long distances. This transport occurs in a cell-to-cell manner and depends on specific influx and efflux carrier proteins that facilitate the uptake and release of auxin from/to the apoplast (Fig. 1B). Many auxin carriers are well characterized: the PIN-FORMED (PIN) proteins (Galweiler et al., 1998) and several proteins of the ABCB and ABCG transporter family (Cho et al., 2007, Geisler et al., 2005 and Ruzicka et al., 2010) are involved in auxin efflux from the cell and the AUX1/LIKE AUXIN PERMEASE (AUX1/LAX) proteins are involved in auxin influx (Bennett et al., 1996 and Swarup et al., 2001).

Among these carriers, PIN proteins have been proposed to be central rate-limiting components in polar auxin transport (Petrasek et al., 2006 and Wisniewska et al., 2006). A key characteristic of these proteins is their polar localization in the cell (Fig. 1B). This polar localization correlates with putative auxin fluxes in the

plants and are key to establish local auxin concentrations (Wisniewska et al., 2006). The processes behind the establishment and maintenance of PIN polarity at the cell level are extremely complex and rely on connections with the cell wall, the actin cytoskeleton, phosphoinositide and calcium signaling, slow diffusion in the plasma membrane as well as intracellular trafficking (Fig. 1B) (Dhonukshe et al., 2008a, Kleine-Vehn et al., 2011, Mravec et al., 2011 and Zhang et al., 2011). A determinant factor for PIN polarity is their endocytic trafficking. The current model proposes that PIN proteins are secreted in a non-polar manner and that their subsequent endocytosis and recycling establish their polar localization at the rootward pole of the cell (Dhonukshe et al., 2008b). This polar recycling is dependent on the endosomal protein GNOM (Geldner et al., 2003 and Kleine-Vehn et al., 2009). Phosphorylation of PINs by several kinases, including PINOID (PID), targets these auxin carriers to a GNOM-independent recycling pathway that target them to the shootward pole of the cell (Fig. 1B) (Kleine-Vehn et al., 2009). This action is antagonistically controlled by the regulatory subunit of protein phosphatase 2A (PP2A) (Fig. 1B) (Michniewicz et al., 2007).

Endocytosis and recycling also control the quantity of PIN protein at the plasma membrane by regulating the balance of protein that is recycled back to the plasma membrane or targeted to the lytic vacuole for degradation (Fig. 1B) (Abas et al., 2006, Jaillais et al., 2006 and Jaillais et al., 2007). The retromer, a conserved protein complex, is involved in this balance as it promotes the retrieval of PIN proteins from late endosomes and reroute them toward the plasma membrane (Fig. 1B) (Jaillais et al., 2007). Auxin itself plays a key role in this regulation as it can inhibit endocytosis at certain concentration or promotes PIN proteins degradation at others (Abas et al., 2006, Paciorek et al., 2005 and Robert et al., 2010).