

Review

## From seed to seed: the role of photoreceptors in *Arabidopsis* development

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### Abstract

As sessile organisms, plants have evolved a multitude of developmental responses to cope with the ever-changing environmental conditions that challenge the plant throughout its life cycle. Of the many environmental cues that regulate plant development, light is probably the most important. From determining the developmental pattern of the emerging seedling, to influencing the organization of organelles to best maximize energy available for photosynthesis, light has dramatic effects on development during all stages of plant life. In plants, three classes of photoreceptors that mediate light perception have been characterized at the molecular level. The phytochromes recognize light in the red portion of the spectrum, while cryptochromes and phototropins perceive blue and UVA light. In this review, we discuss the different aspects of development that are regulated by these photoreceptors in the model plant species *Arabidopsis thaliana* and how the phytochromes, cryptochromes, and phototropins bring about changes in development seen in the growing plant.

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### Plant photoreceptors

Unlike animals, plants are unable to move away from an unfavorable environmental stimulus. To cope with this sessile lifestyle, plants have evolved an extraordinary degree of developmental plasticity to optimize their growth and reproduction in response to changing environmental conditions. Of all the environmental cues that challenge the developing plant, light is probably the most important. Light acts not only as a primary source of energy through photosynthesis, but also provides the developing plant with means of sensing its environment. Plants have evolved complex methods of sensing the quality, quantity, direction, and duration of light and interpreting these signals to produce the appropriate physiological and developmental response (Möller et al., 2002; Montgomery and Lagarias, 2002). To monitor the light environment, plants have evolved a series of photoreceptors, characterized by the wavelength of light that they perceive (Fig. 1). Red/Far-red

light (600–750 nm) is perceived by the phytochrome family of photoreceptors, Blue/UVA (320–500 nm) through the cryptochromes and phototropins, and UVB (282–320 nm) through an, at present, uncharacterized photoreceptor (Kendrick and Kronenberg, 1994; Briggs and Huala, 1999; Briggs and Christie, 2002).

### *Phytochromes*

Phytochromes, which are by the far the most studied of all the plant photoreceptors, were initially purified on the basis of being responsible for the reversible control of night-break of short day flowering plants by red and far-red light. Borthwick et al. (1952) showed that red light stimulates germination of lettuce seeds, and that this induction can be inhibited by a subsequent exposure to far-red light. In fact, the lettuce seeds can be sequentially exposed to red and far-red light with the germination response being determined by the final light-treatment. This physiological response allowed the purification of the photoreceptor responsible, later termed phytochrome (“plant-color”). Phytochrome (which is found in plants as a soluble homodimer) consists of an apoprotein (of approx. 120

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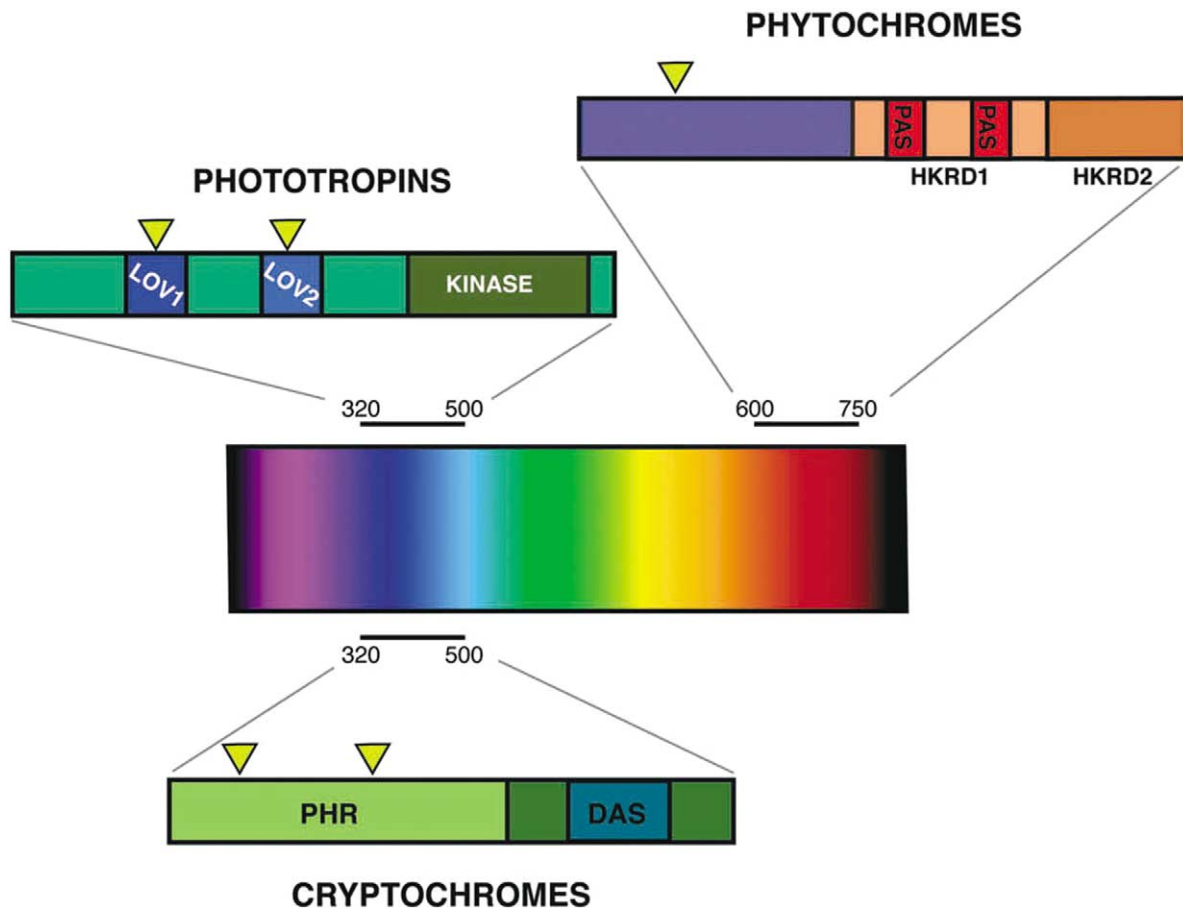


Fig. 1. The plant photoreceptors. Three classes of photoreceptors have been characterized from plants at the molecular level. (A) Phytochromes perceive red and far-red light of between 600 and 750 nm. The phytochrome apoprotein contains two histidine kinase related domains (HKRD1 and HKRD2) at the carboxyl terminus and two Per-Amt-Sim domains (PAS) within the HKRD1 domain that have been shown to function as protein–protein interaction domains and small ligand response modules. (B) Cryptochromes perceive blue and UVA light (320–500 nm); at the amino terminus is a photolyase related domain (PHR), and at the carboxyl terminus is DQXVP-acidic-STATES (DAS) motif. (C) Phototropins also perceive blue and UVA light (320–500 nm). The phototropin apoprotein contains 2 chromophore binding domains (LOV1 and LOV2) as well as a Kinase domain at the carboxyl terminus. Yellow triangles represent the chromophore attachment sites in each of the photoreceptors.

kDa) covalently attached to a linear tetrapyrrole chromophore. In vivo phytochrome exists in two photoreversible forms. In dark-grown plants, phytochrome exists in the red light absorbing (Pr) form, on exposure to red light Pr is converted to the far-red light absorbing form, Pfr. Pfr is generally considered to be the biologically active form of phytochrome, and can be converted back to the inactive Pr form by exposure to red light (Quail, 1997). The change between Pr and Pfr is associated with both a conformational change in structure as well as corresponding changes in the absorption maxima from 666 nm (Pr) to 730 nm (Pfr) (Quail, 1997). It should be noted that there is some evidence which suggests that Pr has some biological activity, and that the switch between Pr and Pfr (rather than Pr or Pfr) can act as a short-lived signal (Reed, 1999; Shinomura et al., 2000)

Phytochromes can be classified into two groups based on their stability. Type I (light-labile) phytochrome degrades rapidly on exposure to red or white light, while type II (light-stable) phytochrome does not (Clough and Vierstra,

1997). In the model plant species *Arabidopsis thaliana*, there are five distinct phytochrome apoprotein genes, *PHYA–E*, that have distinct but overlapping functions (Sharrock and Quail, 1989). *phyA* is a type I phytochrome, while *phyB–E* are all type II (Quail, 1997). Recent evidence suggests that phytochrome may have evolved from a bilin-sensor protein in the bacterial progenitor that gave rise to the photosynthetic organelles (chloroplasts) in plant cells (Montgomery and Lagarias, 2002).

The modes of action of phytochrome have been classified into four groups. Very low fluence responses (VLFR) are saturated at very low levels of active phytochrome (Pfr) after light pulses or constant irradiation. Low fluence responses (LFR), which are typified by the red/far red reversibility response, involve low light intensities. Two further high irradiance responses have also been described, one to red light (red HIR) and one to far-red light (far-red HIR). HIRs are characterized by a dependence on the intensity of light (fluence rate) used in the experiment and by the ob-

servation that continuous irradiation can only be replaced by very frequent pulses of light (Nagy and Schäfer, 2002).

### *Cryptochrome*

It has long been known that plants show biological responses to blue light (Cashmore et al., 1999; Lin, 2002). However, despite having been given a name many years before their characterization, cryptochromes (Gressell, 1977), it was not until 1993 that the first sequence of a blue-light receptor, Cryptochrome1 (CRY1), was published (Ahmad and Cashmore, 1993). Analysis shows that *Arabidopsis* contains two cryptochrome genes *CRY1* and *CRY2* showing strong homology to each other and to bacterial DNA photolyase genes (Ahmad and Cashmore, 1993; Lin et al., 1998). DNA photolyases are flavoproteins found in microbes that catalyze blue/UVA-dependent repair of DNA damage (Sancar, 2000; Lin, 2002). All photolyases contain a flavin adenine dinucleotide (FAD) chromophore and have either deazaflavin or pterin as a light-harvesting chromophore (Sancar, 1994). Despite not showing any detectable photolyase activity, *cry1* contains an FAD and a pterin (methenyltetrahydrofolate, MTHF) chromophore (Lin et al., 1995; Malhotra et al., 1995). Cryptochromes also contain a C-terminal extension not found in DNA photolyases. Although the exact role of this extension is not clear, its importance is demonstrated by the observation that several of the *cry* alleles contain mutations in this region (Ahmad and Cashmore, 1993).

### *Phototropin*

Phototropins are the most recently characterized group of plant photoreceptors. (Briggs and Christie, 2002). A blue-light-activated phosphorylation activity in the plasmamembrane was first reported by Gallagher et al. (1988), the further characterization of which showed a strong correlation with blue-light-mediated phototropism (Short and Briggs, 1994). It was the observation that an *Arabidopsis* mutant, *JK224*, with a defective phototropic response also lacked light-activated photophosphorylation that provided the first genetic link between blue-light-mediated phototropism and photophosphorylation (Reymond et al., 1992). The molecular characterization of another *Arabidopsis* mutant with a defective phototropic response, *nph1*, led to the identification of phototropin1 (Huala et al., 1997). Phototropin1 (Phot1) is a 996-residue protein that has 2 LOV domains (for light, oxygen, and voltage-regulated proteins) at the amino terminus and a classic serine/threonine kinase domain at the carboxy terminus (Huala et al., 1997). When recombinant Phot1 is expressed in *Escherichia coli* and insect cells, it binds flavin mononucleotide (FMN) through the LOV domains in a noncovalent manner and can undergo

blue-light-dependent autophosphorylation (Christie et al., 1998, 1999). A second *Arabidopsis* phototropin gene, *Phot2*, has also been isolated on the basis of sequence similarity to *Phot1* (Jarillo et al., 1998). Like *Phot1*, *Phot2* has two LOV domains, binds FMN, and exhibits photochemical activity similar to that observed with *Phot1* (Sakai et al., 2001).

### **Photoreceptor-regulated development in *Arabidopsis***

Much of our understanding of the role of photoreceptors in plant development has come from research on the model plant species *Arabidopsis thaliana*. Analysis of mutants with altered functionality of one or more of the photoreceptor genes have allowed researchers to identify which photoreceptors control a particular aspect of light-regulated development. Of course, in many of the developmental responses described below, light is not the only factor controlling the growth. The final growth pattern is in fact a product of the interaction between many different environmental stimuli and intrinsic developmental programs. The limits of *Arabidopsis* as a model species for light-regulated development must also be recognized. This is particularly true for the regulation of flowering time where what happens in *Arabidopsis*, an ephemeral long-day flowering species, may not be the case in species with a completely different flowering strategy (Mouradov et al., 2002). Despite these caveats, most of our current understanding of plant photoreceptors has come from the investigation of light-regulated development in *Arabidopsis*.

### *Germination*

The seed is an important stage in the life cycle of a higher plant. In unfavorable environmental conditions, the seed is able to remain dormant in a dry state for extended periods, only germinating when those unfavorable conditions no longer exist (Bentsink and Koornneef, 2002). In *Arabidopsis*, the germination of dormant seeds is controlled by factors such as light, temperature, and time of storage in the dried state (Koornneef and Karssen, 1994). As with many species, the light-dependent germination of *Arabidopsis* seed is mediated entirely by phytochrome (Casal and Sánchez, 1998). Analysis of mutants that lack phyA (*phyA*) or phyB (*phyB*) has shown the importance of these phytochromes in the regulation of germination. In *Arabidopsis*, red/far-red reversible (LFR) germination is largely mediated through phyB. Germination is also induced by low quantities of red or far-red light (VLFR) or continuous far-red light (far-red HIR) all mediated through phyA (Casal and Sánchez, 1998). The involvement of another phytochrome in germination was also suggested by the observation that *phyAphyB* double mutants still show some R/FR reversible germination (Poppe and Schäfer, 1997). Recent experiments

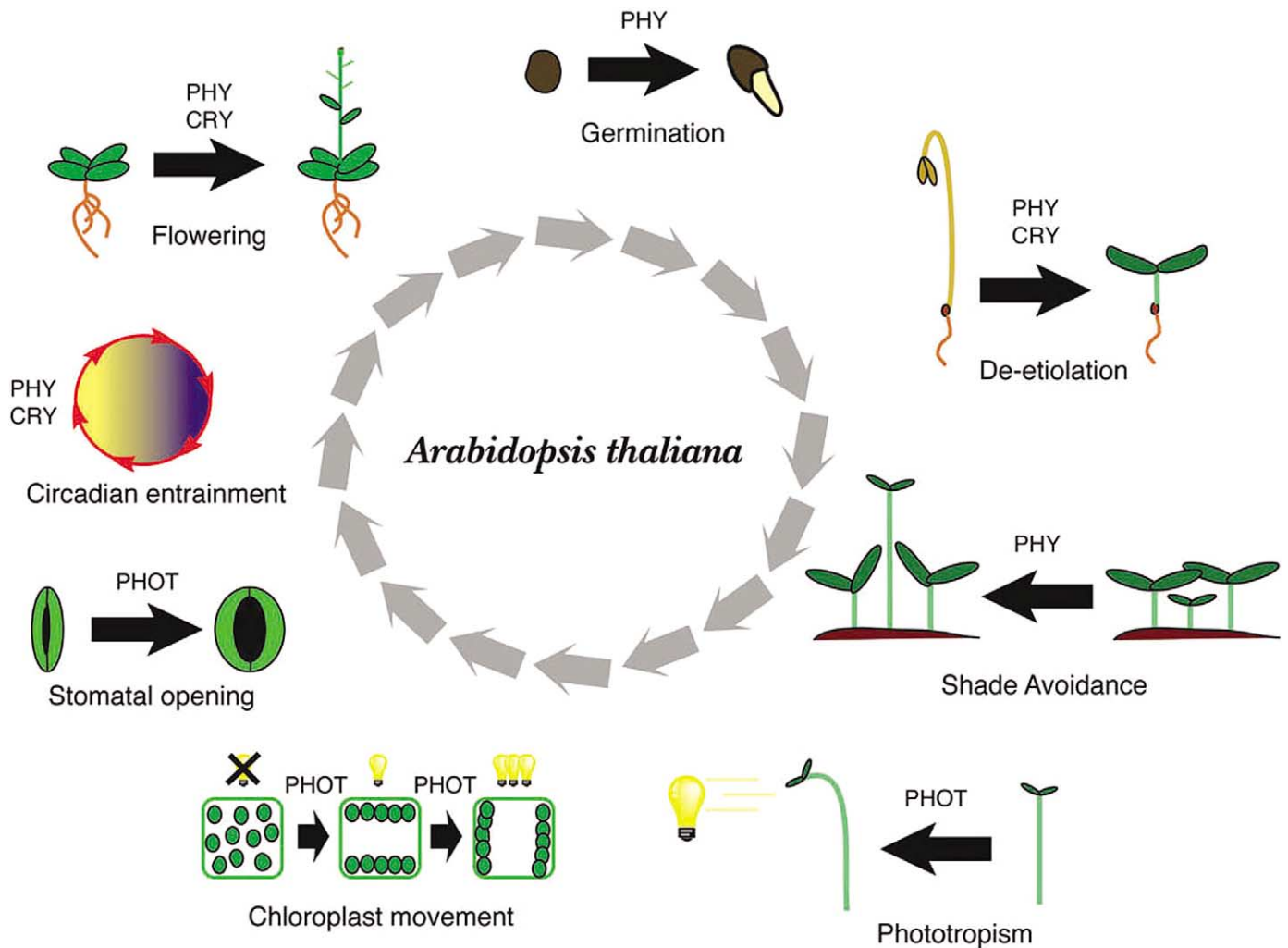


Fig. 2. Light-regulated development in the model plant species *Arabidopsis thaliana*. Light affects the development of *Arabidopsis* throughout its life cycle. Multiple aspects of development are regulated the photoreceptors phytochromes (PHY), cryptochromes (CRY), or phototropins (PHOT) acting alone or in combination with each other.

using *phyC*, *phyD*, and *phyE* mutants have demonstrated a role for *phyE* in seed germination (Hennig et al., 2002).

#### Photomorphogenesis (de-etiolation)

One of the most extensively studied stages of *Arabidopsis* development is the period between seed germination and the formation of the first true leaves (Quail, 2002). After seed germination, *Arabidopsis* seedlings follow one of two developmental patterns. In darkness, seedlings follow skotomorphogenic (or etiolated) development having long stems (hypocotyls) and closed, unexpanded leaves (cotyledons) protected by an apical hook (Fig. 2). In contrast, growth in the light results in photomorphogenic (or de-etiolated) development characterized by short hypocotyls and open expanded cotyledons that are capable of photosynthesis. In the natural environment, the switch between etiolated and de-etiolated development allows the buried seed to emerge through soil, reach light, and switch to a

developmental pattern optimal for photosynthesis (Frankhauser and Chory, 1997). The regulation of de-etiolation involves a complex interplay of both phytochromes and cryptochromes (Nemhauser and Chory, 2002; Wang and Deng, 2002; Fig. 3). In general, under low intensities of light, development is primarily under the control of PHYA. As the seedling reaches light, *phyA* (as a type I phytochrome) is degraded and control through *phyB* and the cryptochromes becomes dominant (Frankhauser and Chory, 1997; Nemhauser and Chory, 2002; Wang and Deng, 2002). Under experimental conditions, *phyA* perceives continuous far-red light, *phyB* perceives red light, while both *cry1* and *cry2* function in the perception of blue light during de-etiolation (Ahmad and Cashmore, 1993; Lin et al., 1998; Quail, 2002). Many other factors also impinge on the response to light of *Arabidopsis* during early development. Such other factors include circadian regulation and regulation by growth hormones such as auxin, cytokinins, brassi-

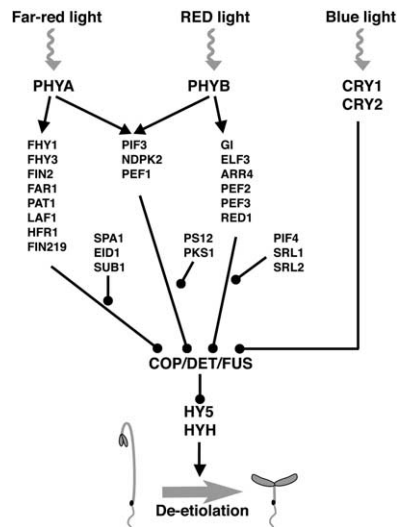


Fig. 3. Simplified model of the genetic interactions regulating de-etiolation in *Arabidopsis* seedlings. PHYA and PHYB have both separate and shared signaling intermediates, with the COP/DET/FUS loci acting as an integration point between the phytochrome and cryptochrome signaling pathways. Arrowheads indicate positive interaction; closed circles indicate a repressive effect.

nosteroids, abscisic acid, and ethylene (recently reviewed in Nemhauser and Chory, 2002).

### Shade avoidance

In the natural environment, plants are in constant competition with their neighbors, and as with other resources, plants grown in close proximity to each other will compete for light. Two options are open to a plant trying to grow under a canopy of overhanging vegetation: live with the shade (shade tolerance) or get out of the way (shade avoidance). Flowering plants have evolved some remarkable mechanisms to avoid shade, which have probably contributed to their evolutionary success (Smith and Whitelam, 1997). One of the most dramatic shade avoidance responses is the stimulation of elongation growth, often associated with reduced leaf development, increased apical dominance, and a reduction in branching. At the more extreme end of the shade avoidance syndrome is inhibition of seed germination, the acceleration of flowering, truncated fruit development, and reduced seed set (Smith and Whitelam, 1997; Morelli and Ruberti, 2002). Shade avoidance is mediated by the phytochrome family of photoreceptors through the sensing of the ratio between red and far-red light (R/FR). As light passes through, or is reflected by, an overhanging leaf there is selective absorption of red light by the photosynthetic pigments, resulting in light that contains a high proportion of far-red light. The R/FR ratio therefore provides a unique quantifiable signal of the competitive threat from neighboring plants (Botto and Smith, 2002). *Arabidopsis* seedlings are capable of sensing very small changes in

R/FR, which can act as an early warning system for a potential shade threat. Under laboratory conditions, seedlings given a single pulse of far-red light before entering the night phase of growth will show stem elongation, a response called the end-of-day (EOD) far-red response (Cassal et al., 1997). *Arabidopsis* mutants that lack functional phyB show constitutive shade avoidance responses, such as elongated stems, accelerated flowering, and increased apical dominance under high R/FR (Smith and Whitelam, 1997). However, the observation that these *phyB* mutants still show some shade avoidance responses under low R/FR light suggested the involvement of other phytochromes. Subsequent analysis of *phyBphyD* and *phyBphyE* double mutants of *Arabidopsis* demonstrates the importance of phyB, phyD, and phyE in the regulation of shade avoidance (Devlin et al., 1998, 1999).

### Phototropism

Phototropism, the directional curvature of plant organs in response to light, was one of the first aspects of light-regulated plant development to be studied. It was Charles Darwin who first demonstrated that phototropic movement could be eliminated if blue light was removed from the light source by using a solution of potassium dichromate as a crude filter (Darwin, 1881). Although many plant organs appear to show phototropic responses, the vast majority of experimental data concerns the positive phototropism (growth toward light) of stems or the negative phototropism (growth away from light) of primary roots (Liscum, 2002). Although the function of negative phototropism in primary roots is not clear, it is thought that the positive phototropic response of stems is an evolutionary adaptation to maximize photosynthesis during both early development and following the formation of gaps during growth under dense canopies (Iino, 1990; Ballare, 1999). Positive phototropic curvature toward a unidirectional light source results from increased growth of cells on the “shaded” side of the stem and a corresponding decrease in growth in cells facing the light source. In the case of negative phototropism, the opposite is true, with shaded cells decreasing and lit cells increasing growth, thus causing the root to bend away from the light. In both positive and negative phototropism, gradients of responsiveness to the plant hormone auxin produce the differential rates of growth seen on either side of the illuminated organ (Liscum, 2002). In *Arabidopsis*, phototropism is mediated entirely by blue light through the phototropins Phot1 and Phot2 (Sakai et al., 2001). Analysis of *Arabidopsis* mutants that lack Phot1 and Phot2 suggests that, while Phot1 functions under all intensities, Phot2 seems only to function under high-intensity blue light (Jarrillo et al., 1998). Recently, it has been suggested that, although phototropins control blue-light mediated phototropism in etiolated plants, phytochromes may play some role in regulating phototropism in de-etiolated plants (Liscum, 2002). It has been well established that the spectral proper-

ties of phytochrome allow it to function as a blue light sensor (Whitelam et al., 1993). However, experimental evidence argues against phytochrome being a primary blue light sensor, and it is proposed that phytochrome acts as a modulator of phototropin-mediated responses (Liscum, 2002).

#### *Chloroplast movement and stomatal opening*

Chloroplasts are the organelles within plant cells in which photosynthesis takes place. It is thought that chloroplasts are derived from once free-living Cyanobacteria that were incorporated into the ancestral plant cell (Martin and Herrmann, 1998). Under low light conditions, chloroplasts accumulate on the upper surface of the palisade mesophyll cells to maximize photosynthesis. While under strong light conditions, chloroplasts line up perpendicular to the direction of the light source to minimize photo damage caused by excess light (Briggs and Christie, 2002; Kasahara et al., 2002; Fig. 2). It has been known for some time that treatment with blue light is sufficient to bring about chloroplast relocation (Kagawa and Wada, 2002). Screens by two groups for *Arabidopsis* mutants that were defective in chloroplast relocation both identified *Phot2* as a photoreceptor responsible (Jarillo et al., 2001; Kagawa et al., 2001). It was initially thought that *Phot2* was the major photoreceptor for chloroplast relocation as *phot1* mutants show only partial loss of chloroplast accumulation and no change in chloroplast avoidance in high light (Briggs and Christie, 2002). However, subsequent analysis showed that *phot1/phot2* double mutants show a much more severe phenotype than single mutants alone, since chloroplasts show neither accumulation in low light or avoidance in response to high intensities of blue light (Sakai et al., 2001; Kasahara et al., 2002).

Stomata are small pores in the leaf and stem that regulate gas exchange. Stomata are surrounded by a pair of guard cells, the swelling and shrinking of which regulates the stomatal aperture. It has been known since the late 1970s that there is a blue light-regulated component to stomatal opening (Briggs and Christie, 2002). Like chloroplast relocation, the phototropin family of photoreceptors regulates blue light-induced opening of stomata. While *phot1* and *phot2* single mutants show only small changes in blue light-induced stomatal opening, this response is completely absent in a *phot1phot2* double mutant (Kinoshita et al., 2001). Thus, both phototropins show redundancy in regulating blue light-mediated chloroplast relocation and stomatal opening, with *Phot1* and *Phot2* showing some differences in their sensitivity to light intensity.

#### *Day length perception and the circadian clock*

The perception of day length, or photoperiod, allows organisms to adjust their development in anticipation of annual seasonal changes (Yanovsky and Kay, 2002). The

perception of day length in plants is mediated through the interaction of light-regulation pathways with circadian rhythms. When carefully tested, all organisms so far examined show rhythms in metabolism, physiological processes, and behavior in response to the day/night cycle (Devlin, 2002). These rhythms are not just responses to the environment, as they will persist in the absence of any environmental cues, suggesting the presence of an internal oscillator (Millar and Kay, 1991). However, the circadian clock is not completely isolated from environmental stimuli and must be reset or “entrained” to allow it to be synchronized with the day/night cycle. In plants, light is a very important signal in synchronizing the circadian clock (Devlin, 2002). It has been demonstrated in *Arabidopsis* that both phytochromes and cryptochromes contribute input into the clock. Under high light intensities of blue and red light, *cry1* and *phyB*, respectively, are most active in the entrainment of the circadian clock (Somers et al., 1998). In contrast, only under low light intensities are small effects on clock entrainment seen in *phyA* and *cry2* mutants (Somers et al., 1998).

In plants, the perception of day length is an important signal in the control of flowering. It is thought that flowering is induced in long day species, or repressed in short day species, when a light signal coincides with a sensitive phase of the circadian clock (Roden et al., 2002). *Arabidopsis* is a facultative long-day plant, which flowers earlier under long days but will eventually flower even under short days. In fact, under laboratory conditions, *Arabidopsis* will flower after just a single long day (Mouradov et al., 2002). Interestingly, despite *phyA* and *cry2* having only small effects on circadian clock entrainment, mutations in both these genes have marked effects on the photoperiodic control of flowering (Johnson et al., 1994; Guo et al., 1998). Therefore, *phyA* and *cry2* do not affect flowering-time responses by influencing clock entrainment, but by modulating other aspects of the flowering response (Samach and Coupland, 2000).

#### **Downstream signaling components**

Much of the current research into light-regulated plant development focuses on the signaling events downstream of photoreceptors, with the majority of our understanding coming from the examination of de-etiolation in *Arabidopsis* seedlings (Quail, 2002). Recent studies have shown that the developmental changes seen during de-etiolation result from a change in expression of approximately 30% of genes in the *Arabidopsis* genome (Ma et al., 2001; Tepperman et al., 2001). Such studies have demonstrated that, although each photoreceptor perceives distinct light cues, all the photoreceptors act to control the expression of a common fraction of the genome (Ma et al., 2001). The identification of mutants defective in different aspects of de-etiolation has identified many components of the signaling pathways

downstream of photoreceptors (for recent reviews, see Lin, 2002; Quail, 2002; Möller et al., 2002; Wang and Deng, 2002). Fig. 3 shows a current model for how some of these downstream signaling components interact.

Among the genes shown to be important for de-etiolation are the essential COP/DET/FUS genes that are necessary for the repression of photomorphogenesis in darkness (Wang and Deng, 2002). One of these genes, *COP1*, functions as a light-inactivatable repressor of photomorphogenesis (von Arnim and Deng, 1994). COP1 shows nuclear enrichment in darkness but not in light and has been shown to interact with transcription factors such as HY5 and HYH that act as positive regulators of photomorphogenesis (Oyama et al., 1997; Ang et al., 1998; Holm et al., 2002). It has been shown that, in darkness COP1, acting alone or with other proteins, interacts with HY5 in the nucleus, resulting in its degradation (Osterlund et al., 2000). A model has been proposed in which COP1 acts as an E3 ubiquitin ligase, targeting proteins such as HY5 and HYH for degradation (Osterlund et al., 2000; Holm et al., 2002). This is consistent with the recent finding that the genome expression profile of a dark-grown COP1 mutant mimics that of seedlings grown in the light (Ma et al., 2002). It is interesting to note that a direct interaction between COP1 and CRY1 has been demonstrated, which is primarily responsible for cryptochrome-mediated blue light regulation of photomorphogenesis (Wang et al., 2001). Six of the other *COP/DET/FUS* loci define an eight-subunit complex, the COP9 signalosome (CSN) (Serino et al., 1999). The CSN is widely conserved in multicellular organisms and shows one-to-one subunit homology with the lid subcomplex of the 26S proteasome (Schwechheimer and Deng, 2001). This homology and the observation that the CSN interacts with the SCF<sup>TIR1</sup> E3 ubiquitin ligase and is required for the degradation of a SCF<sup>TIR1</sup> target protein also suggests a role for the CSN in ubiquitin-dependent proteolysis (Schwechheimer et al., 2001). Recently, it has been shown that the protein DET1 is part of a protein complex and interacts with the DNA binding proteins DDB1 and histone H2B, suggesting a role for chromatin remodeling in the regulation of gene expression during photomorphogenesis (Benvenuto et al., 2002; Schroder et al., 2002).

One of the most interesting observations for phytochrome signaling is the discovery that phytochromes can change their nucleocytoplasmic partitioning and interact directly with transcription factors such as PIF3 (Kircher et al., 1999; Ni et al., 1998; Nagy and Schaefer, 2002). Light and the circadian clock differentially regulate the partitioning of the five *Arabidopsis* phytochromes and there is correlation between the subnuclear localization of the phytochrome and its activity (Kircher et al., 2002). This raises the intriguing possibility that phytochromes can regulate gene expression directly by interacting with transcription factors, rather than acting through a signaling cascade.

### What's next for light-regulated development?

There are still many gaps in our understanding of how photoreceptors regulate development processes. Although we have a good understanding of the identity of photoreceptors involved in light control of the various development processes and some understanding of the downstream signaling (Fig. 3), much of the signaling process still needs to be defined. Many signaling components have been identified, but their function at the molecular level remains unclear. The list of plant developmental processes regulated by photoreceptors is also by no means complete. For example, very little information exists about the role of light in very early developmental processes, such as embryogenesis and seed maturation.

It seems, in *Arabidopsis* seedling development at least, phytochromes and cryptochromes ultimately regulate the same genes, thus indicating considerable signal integration at some point during downstream signaling. Central to this integration are the COP/DET/FUS proteins, which have hypothesized roles in proteolysis and chromatin remodeling. Just how these functions are regulated, and how they relate to each other, remains to be elucidated. The regulation of import and export of proteins from the nucleus is also an important question in understanding photoreceptor-regulated development. Not only does the phytochrome family of photoreceptors show changes in nuclear localization, but the downstream regulator COP1 also shows differential light-regulated nucleocytoplasmic partitioning. Determining how these changes in protein localization are achieved is central to the understanding of phytochrome signaling and downstream integration.

Another aspect of phytochrome biology that needs to be investigated is the possibility that the cytosolic forms of phytochrome have some function. The subcellular localization of phytochromes was for a long-time a very contentious issue. Early experimental data suggested that phytochrome was mainly cytosolic with a small proportion being bound to the plasma membrane (reviewed in Moller et al., 2002). It was the use of phytochrome fused to reporter genes such as GUS ( $\beta$ -glucuronidase) and GFP that finally established the presence of phytochromes in the nucleus. However, questions still remain about the role of cytosolic phytochrome, and in particular the phytochrome associated with the plasma membrane.

The study of plant photoreceptors has a long history. Experiments performed over 120 years ago first determined that different wavelengths of light could elicit different growth responses in plants. With the advent of modern molecular biology, the genes encoding these plant photoreceptors have been identified and cloned. In the future, new advances in genomics and proteomics should help us to understand how light signals perceived by the different photoreceptors are integrated with each other and with other environmental and developmental cues, to bring about changes in plant development.

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