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Title page

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Light-regulated plant growth and development

Running title: Photomorphogenesis in Arabidopsis

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Abstract

Plants are sessile and photo-autotrophic, their entire life cycle is thus strongly influenced by the ever-changing light environment. In order to sense and respond to those fluctuating conditions higher plants possess several families of photoreceptors that can monitor light from UV-B to the near infrared (far-red). The molecular nature of UV-B sensors remains unknown, red (R) and far-red (FR) light is sensed by the phytochromes (phyA-phyE in Arabidopsis) while 3 classes of UV-A/blue photoreceptors have been identified: the cryptochromes, phototropins and members of the Zeitlupe family (cry1, cry2, phot1, phot2, ZTL, FKF1 and LKP2 in Arabidopsis). Functional specicialization within photoreceptor families gave rise to members optimized for a wide range of light intensities. Genetic and photobiological studies performed in Arabidopsis have shown that these light sensors mediate numerous adaptive responses (e.g. phototropism and shade avoidance) and developmental transitions (e.g. germination and flowering). Some physiological responses are specifically triggered by a single photoreceptor but in many cases multiple light sensors ensure a coordinated response. Recent studies also provide examples of crosstalk between the responses of Arabidopsis to different external factors in particular between light, temperature and pathogens. Although the different photoreceptors are unrelated in structure in many cases they trigger similar signaling mechanisms including light-regulated protein-protein interactions or light-regulated stability of several transcription factors. The breath and complexity of this topic forced us to concentrate on specific aspects of photomorphogenesis and we point the readers to recent reviews for some aspects of light-mediated signaling (e.g. transition to flowering).

1. Multiple photoreceptors to sense a variety of light colors and intensities

Higher plants transform solar energy into chemical energy through the process of photosynthesis but also use light as an informational cue to control a multitude of physiological responses throughout their life cycle. Collectively these responses are known as photomorphogenesis (Kendrick and Kronenberg, 1994). Such responses can be reversible such as stomata opening or irreversible such as seed germination. The light quality (spectral composition), quantity, direction, and duration change depending on the season, latitude, (magnitude of day-length variable) and local condition (weather, position within plant communities). For instance, light under a plant canopy has a typical signature with a strong reduction of blue and red light absorbed by the photosynthetic pigments while levels of green and in particular far red (FR) light (near infra-red λ 700-750nm) remain relatively high (Figure 1A). To sense such a diversity of light conditions higher plants possess multiple light-sensors (Chen et al., 2004; Quail, 2002; Somers and Fujiwara, 2009). Plant photobiology has a long history with detailed descriptions of photomorphogenic responses dating back to the 19th century (e.g. (Sage, 1992; Whippo and Hangarter, 2006)). In the second half of the 20th century light-responses were analyzed in many plant species using primarily physiological, photobiological and biochemical approaches (Kendrick and Kronenberg, 1994). With the development of molecular genetics, Arabidopsis became the primary model to discover photoreceptors and signaling factors (Chen et al., 2004; Quail, 2002; Somers and Fujiwara, 2009). In this review, we will describe how the light environment shapes most aspects of the Arabidopsis life cycle and present recent progress in light-regulated development.

Four classes of photoreceptors have been identified in Arabidopsis. These photoreceptor families are present in all sampled higher plants although the number of members in each family is somewhat variable. Arabidopsis possesses five phytochromes (phyA-phyE) maximally absorbing red and FR light (Figure 1B) (Franklin and Quail, 2010; Rockwell et al., 2006). Three distinct classes of specific UV-A/blue light sensors are known: the cryptochromes (cry1, cry2), phototropins (phot1, phot2) and ZEITLUPEs (ZTL, FKF1, LKP2) (Figure 1B) (Christie, 2007; Demarsy and Fankhauser, 2009; Lin and Shalitin, 2003; Somers and Fujiwara, 2009). Cryptochromes that are related to DNA photolyases possess a third member in Arabidopsis known as cry3 (or cry-DASH). It is still unclear whether cry3 is a photosensory photoreceptor however it is involved in DNA repair mechanisms (Pokorny et al., 2008). Higher plants posses a UV-B receptor of unknown molecular nature with broad roles in photomorphogenesis (Figure 1B, table I) (Jenkins, 2009). Finally a number of green light responses in plants might be mediated by a yet to be identified photoreceptor (Folta and Maruhnich, 2007).

Photoreceptors are chromoproteins composed of an apo-protein bound to a variety of chromophores (Christie et al., 1998; Imaizumi et al., 2003; Lin et al., 1995; Rockwell et al., 2006). The characteristic absorption spectra are determined by the chemical character of the chromophore and apo-protein. The chromophores and a simplified scheme of the light reactions of plant photoreceptors are presented on Figure 2. Phytochromes are synthesized in their red light (λmax 670 nm) absorbing state known as Pr. Upon light absorption the chromophore isomerizes leading to a FR absorbing state (λmax 730 nm)

known as Pfr. This is due to the isomerization of a double bond between the C and D rings of the tetrapyrrol (Figure 2) (Rockwell et al., 2006). This traditional view has however been challenged by recent NMR data of the Pr and Pfr states of a bacterial phytochrome indicating that the primary light reaction is an isomerization between the A and B rings (Ulijasz et al., 2010). Whether this new finding is applicable to all phytochromes remains to be established. Phytochromes also possess a secondary absorption peak in the UV-A/blue (Rockwell et al., 2006). These spectral properties correlate with the action spectra of phytochrome-mediated responses showing maximal activity for red and FR light but also responses in the UV-A/blue range (Table I). Light-induced changes of the chromophore lead to structural changes of the protein initiating photoreceptor-mediated signal transduction (e.g. (Harper et al., 2003; Pfeifer et al., 2010)). For the phototropins this primary light reaction leads to activation of the protein kinase activity (Tokutomi et al., 2008). Light-regulated kinase activity has also been proposed for plant phytochromes and cryptochromes but the physiological relevance of those activities remains to be firmly established (Bouly et al., 2003; Shalitin et al., 2003; Shen et al., 2009; Yeh and Lagarias, 1998). In contrast the light-induced interaction between phytochromes in their Pfr form and transcription factors of the PIF (Phytochrome Interacting Family) class is an established output of phytochrome light activation (see below) (Castillon et al., 2007).

Although members of one photoreceptor family have similar absorption properties each of the best-characterized plant photoreceptor families is broadly speaking composed of members specialized for high and low light responses. This difference in activity can be

traced back to both changes of the biochemical properties of the photoreceptor and expression patterns (Christie, 2007; Demarsy and Fankhauser, 2009; Lin and Shalitin, 2003; Rockwell et al., 2006). For example, phyA, cry2 and phot1 function in low light while phyB-E, cry1 and phot2 are more specialized for high light responses (Lin et al., 1998; Sakai et al., 2001; Smith and Whitelam, 1990). This correlates with the high levels of phyA and phot1 in etiolated seedlings allowing them to perceive minute amounts of light as the seedling grows towards to upper layers of the soil (Christie, 2007; Rockwell et al., 2006). Moreover, phyA, cry2 and to lower extent phot1 are unstable and degraded soon after activation (Clough and Viestra, 1997; Sakamoto and Briggs, 2002; Shalitin et al., 2002). In contrast a photoreceptor like phot2 is transcriptionally induced by light which correlates with the need for this photoreceptor under high light (Christie, 2007). Finally there are differences in the photochemistry of the members of a given photoreceptor family. This has been extensively characterized for the phytochromes with phyA having much slower dark-reversion (thermal relaxation of the activated Pfr to the Pr ground state) (Rockwell et al., 2006). Similarly for the phototropins differences in LOV2 (Light, Oxygen, Voltage domain) photochemistry between phot1 and phot2 may also contribute to the functional specialization of those photoreceptors (Aihara et al., 2008).

The analysis of phytochrome evolution in the green lineage has shown that members of this gene family have diverged very early in the evolution of seed plants. The repertoire of phytochromes is somewhat species-specific with most having at least three types (phyA, phyB and phyC) and all seed plants sampled to date having a phyA and a phyB

(Mathews, 2006). The functions and molecular properties of phyA and phyB are quite distinct and it has been argued that phyA has evolved novel properties in order for seedlings to better cope with the higher density of large plants (table I) (Mathews, 2006; Rockwell et al., 2006). Indeed phyA has the ability to signal in FR-rich light conditions, which leads to a very low ratio of Pfr/Ptot (due to the overlapping spectra of Pfr and Pr even canopy light leads to some Pfr production). This ability of phyA allows seedling establishment (de-etiolation) under dense plant cover and is thus a competitive advantage for angiosperms which all posses a phyA (Mathews, 2006). Studies comparing Arabidopsis accessions have also demonstrated that the phytochromes are subject of natural variation that may enhance the fitness of those plants in diverse environments (Balasubramanian et al., 2006; Filiault et al., 2008; Samis et al., 2008). Thus, plants can responds to a wide range of distinct and variable light conditions and natural variation at the level of the photoreceptors participates to their adaptation to their environment.

2. Physiological responses mediated by plant photoreceptors

Photoreceptors modulate plant growth and development throughout their life cycle, moreover by monitoring the light environment they contribute to the timing of key developmental transitions such as seed germination and initiation of flowering (Figure 3). We have summarized this information on Table I, which lists the light-dependent physiological responses for which the photoreceptor has been determined. We will describe many of these responses quite briefly and would like to point the readers to more specific reviews in particular for photoperiodic induction of flowering (Imaizumi and

Kay, 2006; Kobayashi and Weigel, 2007; Turck et al., 2008). Traditionally light responses are subdivided depending on the amount of light needed and whether the response requires continuous irradiation or whether it is efficiently triggered by light pulses (Kendrick and Kronenberg, 1994). So-called very low fluence responses (VLFR) are initiated in response to as little as 100 pmol m^{-2}. Low fluence responses (LFR) occur in the range of 10 to 1000 μmol m^{-2} while high irradiance responses (HIR) require continuous light with a total fluence typically in excess to 10 mmol m^{-2}. This classification has been particularly useful to characterize different types of phytochrome-mediated responses (Rockwell et al., 2006; Shinomura et al., 1996; Shinomura et al., 2000). PhyA is the only phytochrome mediating both the VLFR and the FR-HIR (Shinomura et al., 1996; Shinomura et al., 2000). In addition all phytochromes are also capable of mediating the classical R/FR reversible LFR (Rockwell et al., 2006). The exact difference in signaling of the phytochromes under these different light conditions is not fully understood however a number of studies have indicated that phyA uses at least partially distinct signaling mechanisms when acting in the VLFR and FR-HIR (Casal et al., 2000; Kneissl et al., 2009; Lariguet et al., 2003; Staneloni et al., 2009)

Germination

In the seed the embryo is in a very protected environment while the young seedling is very vulnerable. Germination is thus under strong environmental control including effects of water, oxygen, temperature and light (Penfield and King, 2009). Seeds only become competent to respond to those environmental signals once they have broken dormancy

(Penfield and King, 2009). Among all photoreceptors the phytochromes play the most predominant role to promote germination under favorable light conditions and to prevent it when the light conditions are suboptimal as for example under a canopy (Franklin and Quail, 2010). In order to promote germination the phytochromes primarily act on gibberellin (GA) synthesis and signaling (Oh et al., 2007; Piskurewicz et al., 2009). The study of germination illustrates the distinct roles of phyA and phyB, with phyA acting as a broad-band sensor for low light and phyB controlling R/FR reversible induction of germination (Shinomura et al., 1996). In addition phyD and phyE have also been shown to promote germination (Dechaine et al., 2009; Hennig et al., 2002). It should be pointed out that the germination potential of seeds is conditioned by light-stable phytochrome that is transmitted in the dry seed in a Pfr/Ptot ratio depending on the growth conditions of the mother plant (Casal and Sánchez, 1998). In contrast phyA is only synthesized during seed imbibition (Casal and Sánchez, 1998; Shinomura et al., 1996). This may explain recent findings showing that the phytochromes in the mother plant also condition the germination potential of their seeds by modulating seed maturation and dormancy (Dechaine et al., 2009; Donohue et al., 2008; Heschel et al., 2007). Finally as discussed in a later section the predominance of a given phytochrome to control germination is modulated by temperature.

Young seedling development

Following germination the young seedling may encounter a variety of environments. The most extreme case is darkness and higher plants have evolved a strategy to survive for a

few days in this situation by living from their seed reserves (etiolated development). This developmental strategy is characterized by fast elongation of the hypocotyl growing against the gravity vector, the maintenance of an apical hook, inhibition of cotyledon expansion and inhibition of leaf initiation (Chen et al., 2004). This strategy maximizes the chances of the seedling to rapidly reach the soil surface where the process of de-etiolation will be initiated. Phytochromes and cryptochromes predominantly control the de-etiolation phase by inhibiting hypocotyl elongation, initiating chloroplast development, promoting cotyledon expansion and leaf initiation to enable the seedling to start its photosynthetic life (Chen et al., 2004). The predominant photoreceptor controlling de-etiolation depends on the light environment with phyA single-handedly mediating this response in FR light (as encountered under a canopy), while multiple phytochromes are involved in red light (with phyB playing a predominant role) and the cryptochromes with contributions from the phytochromes in blue light (Chen et al., 2004; Franklin and Quail, 2010; Lin and Shalitin, 2003; Quail, 2002). UV-B also mediates this developmental transition and does not require any of the known photoreceptors. This UV-B response critically depends on UVR8 (UV Resistance Locus 8), the ubiquitin E3 ligase COP1 (COnstitutively Photomorphogenic) and the transcription factor HY5 (elongated HYpocotyl 5) (Jenkins, 2009). The phototropins also play an important role during this phase of development because once emerging from the soil the seedling may have to direct its growth towards a more favorable place (with better light) (Christie, 2007). The phototropins mediate a fast but transient inhibition of hypocotyl elongation and later are crucial to guide growth towards a directional light cue (Christie, 2007; Folta and Spalding, 2001). Although directional growth depends on the phototropins, the

magnitude of this response is modulated by both the phytochromes and the cryptochromes (Nagashima et al., 2008). By modulating the hypocotyl growth rate and inhibiting the hypocotyl gravitropic response the later two classes of photoreceptors affect the phototropic potential of young seedlings (Iino, 2006; Lariguet and Fankhauser, 2004; Whippo and Hangarter, 2003; Whippo and Hangarter, 2004).

Vegetative development

Broadly speaking throughout vegetative development the different photoreceptors allow the optimization of photosynthesis according to the prevalent light conditions (table I). The shade avoidance response (SAR) is a good illustration of this concept (Franklin, 2008; Franklin and Quail, 2010; Vandenbussche et al., 2005). Shade from the vegetation has a distinct spectral signature (Figure 1), which has a strong influence on the phytochrome photoequilibrium due to alterations of the R:FR ratio (Franklin, 2008). Moreover the green:blue ratio is also modified, which is predicted to alter the proportion of the cryptochromes in their signaling state (Figures 1 and 2) (Banerjee et al., 2007; Bouly et al., 2007). A plant response related to shade avoidance is neighbor detection, which occurs in response to a decrease of the R:FR ratio due to the reflexion of FR light from neighboring plants but does not necessarily lead to a reduction of PAR (Photosynthetically Active Radiation) (Franklin, 2008). In shade-intolerant plants like Arabidopsis this reduction in the R:FR ratio has a number of striking effects on plant growth and development. The SAR is characterized by increased hypocotyl, stem and petiole elongation, a more erect leaf position, increased apical dominance and early

flowering (Franklin, 2008; Vandenbussche et al., 2005). As for the other light-responses discussed above, these morphological changes are accompanied by rapid and extensive alterations of the gene expression profile (Franklin, 2008; Vandenbussche et al., 2005). The light-stable phytochromes (phyB-phyE) with phyB playing a prevalent function repress the SAR in direct sunlight (Franklin, 2008; Franklin and Quail, 2010). In contrast phyA due to its ability to limit hypocotyl growth in FR light counteracts the activity of the other phytochromes. However the light-labile nature of phyA limits its role in de-etiolated plants (Franklin and Quail, 2010; Salter et al., 2003). A role for the cryptochromes in this adaptive response has also been demonstrated, this can be explained by the overall reduction of blue light and the low blue:green ratio under a canopy, which inhibits cryptochromes activity (Banerjee et al., 2007; Bouly et al., 2007; Vandenbussche et al., 2005; Yanovsky et al., 1995). Upward positioning of leaves which is typical of the SAR (leaf epinasty) is also triggered by low light environments and has been shown to depend on the combined action of phyA, phyB, cry1 and cry2 (Millenaar et al., 2009; Vandenbussche et al., 2005). This growth response, which presumably depends on asymmetric growth of the two sides of the petioles is also under the control of the phototropins (Inoue et al., 2008b). Interestingly the phototropins also ensure that leafs are flat which combined with their effect on leaf and stem positioning maximizes the photosynthetic potential in low light environments (Christie, 2007; Inoue et al., 2008b; Takemiya et al., 2005).

Controlled gas exchange by the stomata represents another physiological parameter that is directly related to photosynthetic capacity. A tight regulation of this activity is essential

to properly control CO_2 uptake, release of O_2, plant cooling and water loss depending on the external conditions (Casson and Hetherington, 2009). It has long been known that blue light promotes stomata opening. This response primarily depends on phot1 and phot2 with cry1 and cry2 playing a more limited role (Kinoshita et al., 2001; Mao et al., 2005). While the relatively weak effect of red light on stomata opening was regarded as a photosynthetic effect recent evidence suggests a role for the phytochromes in this response (Sharkey and Raschke, 1981; Wang et al., 2009). In addition to light's short-term effect on stomata opening several photoreceptors have also been shown to control the stomata index (ratio of guard cells over total cells). Both a decrease in irradiance and in the R:FR ratio typical of shading is perceived in mature leaves and will decrease the stomata index in the newly emerging leaves (Boccalandro et al., 2009; Casson et al., 2009; Lake et al., 2001). By analyzing stomatal pattern in monochromatic lights and in different mutant backgrounds it was shown that phyA, phyB and the cryptochromes are the principal regulators of stomata formation and pattern in FR, red and blue light respectively (Boccalandro et al., 2009; Casson et al., 2009; Kang et al., 2009). Interestingly this developmental response involves elements of light signaling that were initially identified in the context of seedling de-etiolation such as COP1 and PIF4 (Casson et al., 2009; Kang et al., 2009). However while *pif4* and *phyB* have opposite phenotypes during seedling de-etiolation in red light (see below), their stomata development phenotypes are similar suggesting a developmentally regulated mode of interaction of these two factors.

Also of great importance for the optimization of photosynthesis is a proper control of chloroplast positioning (Suetsugu and Wada, 2007). In low-light conditions the chloroplasts display an accumulation response towards the source of blue light presumably in order to maximize light capture. This response is controlled by phot1 and phot2 (Sakai et al., 2001). In contrast high light conditions that are typical of a sunny day trigger the phot2-mediated chloroplast avoidance response preventing photooxydative damage and allowing plant survival (Jarillo et al., 2001; Kagawa et al., 2001; Kasahara et al., 2002). As for other responses primarily controlled by the phototropins the phytochromes modulate the extent of the response (DeBlasio et al., 2003). Moreover both the phytochromes and the cryptochromes play a central role in the development of etioplasts into chloroplasts (Rockwell et al., 2006; Ruckle et al., 2007).

Transition to flowering

Both light and temperature influence the transition from vegetative to reproductive growth. The phytochromes, cryptochromes and members of the Zeitlupe family all contribute to this complex regulatory network, either by acting directly on key regulators of floral transition such as CONSTANS (CO) or by modulating the circadian clock which has a profound influence on photoperiodic flowering. A detailed description of daylength-regulated flowering is beyond the scope of this review, we recommend the following recent review articles (Imaizumi and Kay, 2006; Kobayashi and Weigel, 2007; Turck et al., 2008). Light quality and in particular shading also leads to accelerated flowering (Franklin, 2008; Vandenbussche et al., 2005). The early flowering in short days

of mutants such as *phyB* presumably reflects the constitutive shade avoidance phenotype of these plants (Franklin, 2008; Franklin and Quail, 2010). This specific aspect of the shade avoidance response requires PFT1 (Phytochrome and Flowering Time) a component of the Mediator complex that has global roles in transcriptional regulation by acting as an adaptor between transcription factors and RNA polymerase II (Backstrom et al., 2007; Cerdan and Chory, 2003). Interestingly PFT1 has also been implicated in disease resistance providing an example of the possible crosstalk between different environmental factors affecting plant development (Kidd et al., 2009) (see below).

3. Photomorphogenesis in a changing environment.

Phenotypes developed by plants in response to changes in light quality/quantity can also be observed in others situations. For instance, the shade-avoidance phenotype described above is similar to the phenotype of plants grown under high temperatures (28°C versus 22°C) or in flood conditions (Franklin, 2008; Franklin, 2009; Koini et al., 2009; Millenaar et al., 2005; Pierik et al., 2005; van Zanten et al., 2009; Vandenbussche et al., 2003). Taking the leaves away from the warm/submerged soil presumably optimizes plant fitness by preserving their "power supply" (leaves). More surprising was the identification of a gene controlling shade avoidance that encodes a TIR-NBS-LRR protein typically involved in plant-pathogen interaction (Faigon-Soverna et al., 2006). Altogether these data suggest that multiple signaling pathways may control the same "core-genetic program" to modulate plant growth according to the environmental cues. This could be achieved through independent and parallel signaling pathways or by using

shared signaling components. Several pieces of evidence suggest that common regulators of growth are used in a variety of conditions. For instance, the DELLA proteins that negatively regulates GA pathways are involved in repression of growth responses to shade, pathogen, salt stress or cold treatment (Achard et al., 2006; Achard et al., 2008a; Achard et al., 2008b; Navarro et al., 2008). Similarly PIF4 is involved in elongation-growth responses in a variety of light responses and also in response to increased temperatures (Huq and Quail, 2002; Koini et al., 2009; Lorrain et al., 2008; Lorrain et al., 2009; Stavang et al., 2009). The variety of conditions in which PIF4 modulates growth is paralleled by a great complexity of PIF4 regulation. The control of PIF4 activity includes interaction with the DELLAs and HFR1 (long Hyprocotyl in FR) to prevent it from binding to DNA, transcriptional regulation by the clock and temperature and proteolytic degradation upon interaction with the phytochromes (de Lucas et al., 2008; Feng et al., 2008; Hornitschek et al., 2009; Koini et al., 2009; Nozue et al., 2007; Stavang et al., 2009). Although PIF4 was identified as a light-signaling component it also acts independently of photoreceptor activity indicating that light-signaling components also work in other pathways (Leivar et al., 2008b; Koini et al., 2009). As a consequence, light sensing can influence responses induced by different stimuli and *vice-versa*. Examples of such interactions are presented in the following sections.

Light sensing and pathogen defense

Light is required to mount an efficient response to pathogens in Arabidopsis (Chandra-Shekara et al., 2006; Genoud et al., 2002; Griebel and Zeier, 2008; Roden and Ingle,

2009; Zeier et al., 2004). Especially, light is important during the first hours following the inoculation as dark-infected plants support more bacterial growth and mount less efficient defense mechanisms than light-infected plants (Griebel and Zeier, 2008). Interestingly the appearance of spontaneous necrotic lesions in the so-called “lesion-mimic mutants” is also light dependent (Brodersen et al., 2002; Dietrich et al., 1994; Lorrain et al., 2004; Lu et al., 2003; Mach et al., 2001). This may reflect the requirement of photosynthetic energy for an efficient resistance or a cross talk between chloroplast-derived molecules and defense mechanisms (Genoud et al., 2002). In few cases participation of the photoreceptors in the defense mechanisms was studied (Chandra-Shekara et al., 2006; Genoud et al., 2002; Griebel and Zeier, 2008; Wu and Yang, 2010). PhyA, phyB and cry1 are involved in the resistance response to *P.syringae pv. tomato* carrying the *AvrRpt2* gene while they do not seem to play any role in response to *P.syringae pv. maculicola* (*AvrRpm1*) or to Turnip crinkle virus except in the set up of the systemic acquired resistance (Chandra-Shekara et al., 2006; Genoud et al., 2002; Griebel and Zeier, 2008; Wu and Yang, 2010). This does not necessarily mean that light is differentially required in response to various pathogen but rather that different mechanisms are involved in response to different pathogen. In both cases, light seems to act through salicylic acid perception/signaling.

The response of plants to pathogens and unfavorable light conditions may also compete with each other. This situation is encountered when plants are grown close to each other, as in agriculture. Plants competing for light resources may at the same time face pathogens such as attack by herbivores. Carbon resources have to be reallocated either to

growth-responses to reach the light or to defense mechanisms against pathogens: this is the "plant dilemma" (Ballare, 2009; Roberts and Paul, 2006). Priority is given to shade avoidance as it has been shown that shade increases the leaf area eaten by herbivores/herbivores fitness or the leaf area infected by pathogens (Izaguirre et al., 2006; Moreno et al., 2009; Roberts and Paul, 2006). This is not a passive phenomenon due to the modified plant architecture under shade conditions. Indeed the response to pathogens is also reduced by shade in *sav3* although this mutant does not respond to low R:FR by elongation growth (Moreno et al., 2009). Shade conditions inhibit biosynthetic pathways linked to production of defense molecules such as phenolic compounds, a response that is phytochrome-dependant in tomato (Izaguirre et al., 2006; Moreno et al., 2009). One hypothesis is that low R:FR ratio reduces plant sensitivity to jasmonates (JA) (Moreno et al., 2009). These phytohormones are important for defense against herbivores but were also shown to inhibit cell division and elongation (Bari and Jones, 2009; Zhang and Turner, 2008). Thus by reducing JA action shade may weaken defense mechanisms but allow full growth of the plants (Moreno et al., 2009).

Cross-talk between light and temperature

Important development transitions such as germination and flowering need to be synchronized with the environment to maximize the chances of species survival. For instance, most Arabidopsis accessions are typical "winter annual" that germinate in the autumn, spend all the winter as rosette and flower in the spring. In addition to light, a cold period called vernalization is required to induce flowering. Furthermore, if light is

necessary to induce germination in fresh seeds, it is not sufficient: a cold and wet treatment called stratification is required to break seed dormancy. These mechanisms are believed to prevent seeds maturation and germination during the winter, a period that can be deleterious for the newly developing organisms. Phytochrome functions are well described in these mechanisms (Franklin, 2009; Franklin and Whitelam, 2004; Penfield, 2008; Samach and Wigge, 2005; Seo et al., 2009). Depending on the temperature, the different phytochromes perform different functions (Dechaine et al., 2009; Donohue et al., 2008; Donohue et al., 2007; Franklin, 2009; Halliday and Whitelam, 2003; Heschel et al., 2007). For instance, while phyB plays a major role in germination under a wide range of temperatures, phyE and phyA are particularly important at cooler and warmer temperatures respectively (Heschel et al., 2007). Phytochromes function is not limited to germination: they are also involved in the perception of the temperature and light environment of the maternal plant during seed maturation (Dechaine et al., 2009; Donohue et al., 2008; Donohue et al., 2007). Indeed seeds from plants that experienced a cool environment are heavier but germinate less efficiently than those maturated under a warm environment (Dechaine et al., 2009). PhyA prevents germination/favors dormancy when seeds are matured under a cold and shaded environment while phyB is important to promote germination under cold environments (Dechaine et al., 2009). Integration of light- and cold- induced pathways will thus allow plants to anticipate changes in their environment. Another good example is the freezing tolerance conferred to Arabidopsis by low R:FR ratio when plants are grown at 16°C (Franklin and Whitelam, 2007). This is associated with the fact that plants experience longer periods of low R:FR ratio as winter approaches. This tolerance is conferred by the increased expression at 16°C of *CBF*

(CRT/DRE binding Factors) and COR (Cold-regulated) genes in low R:FR as compared to high R:FR and depends on the inactivation of phyB and phyD (Franklin and Whitelam, 2007). As a consequence, phyD mutant grown in high R:FR at 16°C present a higher expression of *COR15a* gene as compared to the wild type, which is correlated with a higher freezing tolerance (Franklin and Whitelam, 2007).

The way phytochromes and temperature signaling-pathways interact is not well known yet. Temperature can influence phytochrome photoequilibrium, which may explain why the phytochromes have different roles depending on the temperature (Kristie and Fielding, 1994; Pons, 1986). The two signals can also share signaling components such as PIF4 (Koini et al., 2009; Stavang et al., 2009). Interestingly temperature changes lead to alterations of the nucleosome composition (Kumar and Wigge, 2010). Thus temperature changes can modify the expression of different signaling components such as PIF4 whose activity could further be modulated by the phytochromes. Interestingly different signaling pathways are involved in response to temperature: decreasing temperature can suppress the *phyB* early-flowering phenotype but not *phyB*-induced elongation responses (Halliday et al., 2003). This suggests a developmentally regulated cross-talk between light and temperature pathways.

4. Sites of perception and action of a light signal

Tissue-specific considerations

Photoreceptors are present in most if not all plant tissues (Goosey et al., 1997; Sakamoto and Briggs, 2002), however light-responses are tissue-specific as illustrated during seedling de-etiolation when light inhibits growth in the hypocotyl while promoting it in the cotyledons. Such organ-specific light responses can also be observed at the gene expression level (Lopez-Juez et al., 2008; Ma et al., 2005). This could reflect tissue and/or developmentally regulated expression of signaling components. Furthermore photoreceptors in one organ/tissue can influence responses in distant parts of the plant in a non-cell autonomous way. The best-known example of such systemic signal induced by light is "florigen" that is induced in the leaves and moves to apical meristem to regulate the formation of flowers (Kobayashi and Weigel, 2007; Turck et al., 2008). Other examples include irradiation of mature leaves by a low light, which leads to decreased stomatal index in newly emerging leaves that grow under a high irradiance (Lake et al., 2001). More recently using tissue-specific phytochrome inactivation, Warnasooriya *et al* showed that a FR light signal perceived by the cotyledons controls hypocotyl elongation (Warnasooriya and Montgomery, 2009). This complements the data of (Tanaka et al., 2002) where FR light irradiation of the cotyledons induced the specific expression of a reporter gene in the hypocotyl while irradiation of the hypocotyl did not (Tanaka et al., 2002). This indicates that systemic signals are rather prevalent in the control of plant responses to light. We recommend two recent reviews extensively covering this aspect of light signaling (Bou-Torrent et al., 2008; Montgomery, 2008).

Sites of action of the photoreceptors within the cells

The cellular site of action of several photoreceptors has received considerable attention over the past few years and been recently reviewed for the phytochromes (Chen, 2008; Fankhauser and Chen, 2008). The bulk of all phytochromes is cytoplasmic in their inactive Pr state. However light triggers rapid translocation of the activated phytochromes into the nucleus. Interestingly only phyA has the ability to enter the nucleus under light conditions triggering a very low Pfr/Ptot ratio correlating with the ability of phyA to trigger the FR-HIR and the VLFR (Fankhauser and Chen, 2008). This special property is enabled by a dedicated phyA nuclear import system depending on FHY1 and FHL, two related proteins that interact with the light-activated phyA (Genoud et al., 2008; Hiltbrunner et al., 2006; Pfeiffer et al., 2009; Rosler et al., 2007). In addition the transcription of those phyA importers depends on two transposase-derived transcription factors, which therefore indirectly control phyA nuclear accumulation (Lin et al., 2007). Two recent publications indicate that FHY1 and FHL may play additional functions in addition to regulating phyA nuclear import (Shen et al., 2009; Yang et al., 2009). The light-regulation of phyB nuclear import appears to depend on the unmasking of an NLS specifically in the light activated Pfr conformation (Chen, 2008; Chen et al., 2005). The phenotypic analysis of a variety of mutants (e.g. *fhy1fhl*) and transgenic lines expressing phyA or phyB fused to NES (Nuclear Export Signal) or NLS (Nuclear Localization Signal) sequences in phytochrome mutant backgrounds has determined that the major site of action of the phytochromes is the nucleus (Genoud et al., 2008; Huq et al., 2003; Matsushita et al., 2003; Rosler et al., 2007). This fits well with the rapid phytochrome-dependent effects on gene regulation and with their direct control of the activity of

transcription factors of the PIF family (see below) (Castillon et al., 2007; Leivar et al., 2009; Tepperman et al., 2006). However phyA in particular may also have roles in the cytoplasm (Rosler et al., 2007).

While for the phytochromes light-induced nuclear import is an important regulatory mechanism both cry1 and cry2 are already nuclear in dark-grown seedlings and blue light does not alter the localization of those photoreceptors (Wu and Spalding, 2007). Cry1 is found both in the nucleus and the cytoplasm contrasting with the exclusively nuclear localization of cry2 (Kleiner et al., 1999; Lin and Shalitin, 2003; Wu and Spalding, 2007). Complementation studies with GFP-cry1 fused either to an NES or an NLS were used to determine that the major site of cry1 action is the nucleus (Wu and Spalding, 2007). However this study highlighted that different subcellular pools of cry1 have different functions with, for example, cytoplasmic cry1 promoting cotyledon expansion in blue light (Wu and Spalding, 2007).

In contrast to the aforementioned photoreceptors the phototropins are primarily found at the plasmamembrane (Kong et al., 2006; Wan et al., 2008). However a fraction of both phot1 and phot2 leaves the plasmamembrane upon blue light perception. Phot1 relocalizes to the cytoplasm while phot2 is found on the Golgi (Kong et al., 2006; Wan et al., 2008). The significance of this light-induced relocalization remains poorly understood. Interestingly however phyA modulates the blue-light induced phot1 relocalization and it has been proposed that this activity explains phytochrome

enhancement of phototropism (Han et al., 2008). This model fits with the previously proposed role of phyA in the cytoplasm to promote phototropism (Rosler et al., 2007).

The subcellular localization and cellular cite of action of members of the Zeitlupe family (ZTL, FKF1 and LKP2) has been analyzed less extensively (Somers and Fujiwara, 2009). Nevertheless, the currently available data on FKF1 and ZTL reveals some interesting differences between these two related photoreceptors (Kim et al., 2007; Sawa et al., 2007). ZTL controls the stability of the central circadian clock component TOC1 (Timing Of CAB1 expression) and the related protein PRR5 (Pseudo Response Regulator) by interacting with those proteins in a time-of-day specific manner in the cytoplasm (Kiba et al., 2007; Kim et al., 2007). In contrast, FKF1 appears to be nuclear where this F-box protein controls the stability of a repressor of *CO* expression thereby contributing to daylength regulated flowering (Fornara et al., 2009; Sawa et al., 2007). The precise function of LKP2 is less well understood but its localization is also nuclear (Yasuhara et al., 2004).

5. Signal transduction

A large number of signaling components acting downstream of the photoreceptors has been identified. However in many cases the events leading from photoreceptor activation to the specific function of a given signaling component is poorly understood. We will thus not attempt an exhaustive coverage of photoreceptor-mediated signal transduction, but rather focus on specific facets of the better understood signaling events. The analysis

of these signaling pathways reveals a number of communalities such as the importance of light regulated protein-protein interaction, protein stability and kinase activity that are briefly reviewed below. Finally we will present the PIF branch of phytochrome signaling in more detail.

Light-regulated degradation, protein-protein interactions and kinase activity.

The importance of light-regulated protein abundance was revealed with the identification of COP1 a ubiquitin E3 ligase that is required to maintain the de-etiolation program in the dark (reviewed in (Jiao et al., 2007; Yi and Deng, 2005)). COP1 in conjunction with members of the SPA family control the abundance of several light signaling components including HY5, LAF1 (Long After FR light), HFR1, CO and phyA (Jang et al., 2008; Jiao et al., 2007; Zhu et al., 2008). This list includes numerous transcription factors that need to be maintained at low levels in the dark and accumulate in the light to mediate multiple aspects of photomorphogenesis (Figure 4). Both the phytochromes and the cryptochromes inhibit COP1 activity but the underlying mechanism is still not fully understood (reviewed in (Jiao et al., 2007)). The cryptochromes directly interact with COP1 both in the light and the dark and a yet to be identified light-induced event in the cryptochromes leads to the inhibition of COP1 (Wang et al., 2001; Yang et al., 2001). How the phytochrome limit COP1 activity remains an open question but it is worth pointing out that by inhibiting COP1 and leading to the degradation of several PIFs (see below) the phytochromes profoundly influence transcription factor composition in a light-dependent fashion (Figure 4) (Jiao et al., 2007). Importantly COP1 and HY5 also

play essential roles during UV-B signaling. These exciting new developments are beyond the scope of this review and we point the interested readers to these excellent recent publications (Favory et al., 2009; Jenkins, 2009). Thus with the exception of phototropin signaling all other plant photoreceptors described here mediate light responses at least in part by controlling the abundance of key regulators in a light dependent fashion. Interestingly NPH3 (Non Phototropic Hypocotyl 3) a central component of phototropin signaling codes for a BTB/POZ containing protein (Pedmale and Liscum, 2007). Such protein domains typically interact with cullin3 leading to the speculation that regulated proteolysis may also take centre stage during phototropin signaling.

Light regulated protein-protein interactions is also a recurrent theme in light signaling as exemplified by the interaction between phytochromes and the PIFs (see below) and during ZTL and FKF1 signaling (Somers and Fujiwara, 2009). A light-regulated interaction between photoactivated cry2 and the bHLH protein CIB1 (Cryptochrome Interacting BHLH) has also recently been described (Liu et al., 2008). This interaction requires the cryptochrome chromophore and blue light. CIB1 and related bHLHs play a role in cryptochrome-regulated flowering, however they do not regulate seedling de-etiolation (Liu et al., 2008). Although more work is needed to fully understand the consequences of this interaction and the role of CIB1 and its family members this work suggests an analogous signaling mechanism for the phytochromes and the cryptochromes as both photoreceptor families display light-regulated interactions with bHLH factors. UV-B signaling provides another striking example of light-regulated protein-protein

interactions with the discovery that the UV-B specific signaling component UVR8 interacts with COP1 in a UV-B dependent manner (Favory et al., 2009).

Light-regulated kinase activity has long been proposed as a primary signaling mechanism for the phytochromes, a hypothesis that received new impetus with the discovery that cyanobacterial phytochromes are light-regulated histidine kinases (Yeh et al., 1997). However, uncovering the significance of the reported protein kinase activity of plant phytochromes requires more work. Similarly plant cryptochromes have been reported to possess Ser/Thr kinase activity but the physiological relevance of this finding remains to be established (Bouly et al., 2003; Shalitin et al., 2003). One problem for both classes of photoreceptors is that these enzymes have no homology with the well-characterized Ser/Thr protein kinase family and thus the characterization of mutants specifically inhibiting protein kinase activity has not be performed. On the other hand the importance of the light-regulated protein kinase activity of the phototropins has strong experimental support (Christie, 2007; Tokutomi et al., 2008). Ironically while there are potential targets of the debated phytochrome kinase activity (e.g. PIF, FHY1) there is still no known target of the phototropins except the photoreceptor itself (Inoue et al., 2008a; Shen et al., 2009).

The PIF branch of phytochrome signaling

A lot of attention was focused on members of the PIF class of bHLH transcription factor since the discovery that PIF3, the founding member of this family, specifically interacts with the light activated Pfr form of phyB (Ni et al., 1999). This distinguishing feature

suggests a mechanism by which the phytochromes directly control light-regulated gene expression (Castillon et al., 2007; Monte et al., 2007). The PIFs are part of a 15-members clade of bHLHs, many of which have been shown to act in light-regulated morphogenesis (Castillon et al., 2007; Heim et al., 2003; Toledo-Ortiz et al., 2003). Some of them are known as PIFs or PILs (PIF3 Like). We will use the PIF nomenclature for all members of this group that interact with phyB (Khanna et al., 2004). This group comprises PIF1 (PIL5), PIF3, PIF4, PIF5 (PIL6), PIF6 (PIL2) and PIF7. Several other members of this group such as PIL1, HFR1 and SPT do not interact with the light-activated phytochrome but nevertheless play functions in phytochrome-mediated morphogenesis (Castillon et al., 2007; Khanna et al., 2004). Interestingly PIF orthologs were identified in rice suggesting a similar mode of phytochrome-regulated transcriptional regulation in monocots and dicots (*Oryza sativa*) (Nakamura et al., 2007).

Most members of this subfamily contain two characteristic domains: the Active Phytochrome Binding (APB) domain and the bHLH domain. The HLH domain allows the formation of homo-and heterodimers and the basic domain is responsible for DNA binding. PIF1, PIF3, PIF4, PIF5 and PIF7 were shown to bind to a specific cis-element the E-box (5'-CANNTG-3') and more precisely the G-box (5'-CACGTG-3') frequently found in light-regulated promoter sequences (Martinez-Garcia et al., 2000; Huq et al., 2004; Huq and Quail, 2002; Oh et al., 2007; Shen et al., 2007; Hornitschek et al., 2009). HFR1 has an atypical basic domain, lacking two conserved amino acids resulting in the incapacity to bind to the G-box sequence (Fairchild et al., 2000; Hornitschek et al., 2009). PIFs contain an amino-terminal located APB domain that is necessary and sufficient for

interaction with light-activated phyB (Khanna et al., 2004). In vitro interaction studies indicate that PIF3 and PIF1 have a higher affinity for phyB than other PIFs (Huq et al., 2004; Khanna et al., 2004). How the conformational change of phyB from Pr to Pfr leads to conformer specific interaction with the PIFs is not fully understood. A combination of homology modeling based on the structure of a prokaryotic phytochrome and the analysis of phyB point mutants indicates that several residues present on the so-called light-sensing knot are crucial to mediate this interaction (Kikis et al., 2009; Oka et al., 2008). This is noteworthy given that this corresponds to a region of phyB that is predicted to change its conformation upon light excitation. In addition PIF1 and PIF3 also bind to the Pfr conformer of phyA through the APA (Active Phytochrome A binding site) domain, which surprisingly is not well conserved between PIF1 and PIF3 (Al-Sady et al., 2006; Shen et al., 2008).

The activity of the PIFs is regulated at multiple levels most prominently via interaction with the light-activated phytochromes leading to phosphorylation and subsequent degradation of PIF1, PIF3, PIF4 and PIF5 (Al-Sady et al., 2006; Bauer et al., 2004; de Lucas et al., 2008; Lorrain et al., 2008; Park et al., 2004; Shen et al., 2005; Shen et al., 2007). For PIF1, PIF3 and PIF5 rapid light-induced ubiquitylation has been reported suggesting a common mechanism for the regulated abundance of all those PIFs (Al-Sady et al., 2006; Shen et al., 2008; Shen et al., 2007). This results in a relatively high level of those proteins in the dark and a rapid decline in their abundance in light with a high R:FR ratio (typical of sunlight). In addition and correlating with phyA interaction assays PIF1 and PIF3 levels also significantly decline in FR light while the levels of PIF4 and PIF5

remain much higher under such light conditions (Bauer et al., 2004; Lorrain et al., 2009; Shen et al., 2008). PIF7 represents an exception because despite its ability to interact with phyB, PIF7 protein levels are not light regulated (Leivar et al., 2008a). The activity of several PIFs is also inhibited by dimerization with transcriptional regulators leading to the formation of non-DNA-binding heteromers (de Lucas et al., 2008; Feng et al., 2008; Hornitschek et al., 2009). PIF3 and PIF4 heterodimerize with members of the DELLA family leading to a crosstalk between hormone and light regulated growth (Alabadi et al., 2008; de Lucas et al., 2008; Feng et al., 2008). The activity of PIF4 and PIF5 is inhibited by HFR1, which accumulates to high levels in low R:FR conditions typical of shade (Hornitschek et al., 2009; Sessa et al., 2005). The regulation of HFR1 levels results from the combination of transcript upregulation in FR-rich environments and light-regulated COP1-mediated protein stability (Figure 4) (Fairchild et al., 2000; Hornitschek et al., 2009; Sessa et al., 2005). Finally, transcriptional regulation of *PIF4* and *PIF5* represents an additional level of regulation that determines when these factors promote elongation growth. Both genes are expressed under circadian control, in addition *PIF4* levels are strongly temperature-dependent (Koini et al., 2009; Nozue et al., 2007; Stavang et al., 2009).

Members of the PIF family play both specific and overlapping roles in the control of a variety of phytochrome responses. For instance germination is primarily controlled by PIF1 with SPT and PIF6 having a much more limited role for this response (Oh et al., 2004; Penfield et al., 2009; Penfield et al., 2005; Shin et al., 2009). Remarkably none of the 2031 genes that are regulated by a germination-inducing red light treatment in wild-

type seeds are light-regulated in a *pif1* mutant demonstrating large-scale effect of PIF1 in the control of seed germination (Oh et al., 2009). The picture emerging from these studies is that PIF1 is an inhibitor of seed germination that directly acts on ABA and GA the two principal hormones regulating seed germination (Oh et al., 2009; Piskurewicz et al., 2009). By triggering the degradation of PIF1 the light-activated phytochromes release this break and promote germination.

In contrast to the specific role of PIF1 in the control of seed germination at least 4 PIFs control the morphology of etiolated seedlings in a partially redundant manner (Leivar et al., 2008b; Leivar et al., 2009; Shin et al., 2009). An etiolated quadruple *pif1pif3pif4pif5* mutant displays numerous features of light grown seedlings including morphology and the global gene expression pattern (Leivar et al., 2008b; Leivar et al., 2009; Shin et al., 2009). In etiolated seedlings the PIFs play a particularly important function by controlling chlorophyll biosynthesis with PIF1, PIF3 and PIF5 being most important for this response (Huq et al., 2004; Shin et al., 2009; Stephenson et al., 2009). Thus the PIFs are required for the etiolated mode of seedling development and the phytochromes promote de-etiolation (at least in part) by leading to their inactivation.

The analysis of *pif* mutants during seedling development in red and FR leads to similar conclusions. It should however be pointed out that the interpretation of the results obtained in red light is somewhat complicated by the finding that PIFs regulate the abundance of phyB which is the primary photoreceptor controlling de-etiolation in red light (Leivar et al., 2008a). phyB levels are increased in *pif* loss-of-function mutants

while they are reduced in PIF-overexpressing plants correlating with enhanced de-etiolation in *pif* mutants and inhibited light responses in PIF over-expressers (Huq and Quail, 2002; Leivar et al., 2008a). The mechanism by which the PIFs control phyB abundance remains unclear but as for the light-regulated PIF degradation it requires interaction between the transcription factor and the photoreceptor (Al-Sady et al., 2008). In contrast in FR light PIF1, PIF4 and PIF5 also negatively regulate the de-etiolation response but without affecting the levels of phyA, which controls this light response (Lorrain et al., 2009; Oh et al., 2004). Moreover PIF4 and PIF5 also promote elongation growth in more mature plants during the shade avoidance response (Hornitschek et al., 2009; Lorrain et al., 2008). Phenotypic analysis and gene expression studies show that PIF4 and PIF5 regulate a subset of SAR and more studies are needed to understand the relationship between the PIFs and other regulators of the SAR (Hornitschek et al., 2009; Lorrain et al., 2008; Roig-Villanova et al., 2007; Sorin et al., 2009; Tao et al., 2008).

Outlook

Despite considerable progress during the last decades on the elucidation of molecular events underlying photomorphogenesis there are still a large number of unresolved issues. What is the molecular nature of the elusive UV-B receptor and are there really green light sensors in higher plants? Although extremely sophisticated biophysical approaches have been applied to analyze plant photoreceptors our biochemical understanding of the events triggered by activation of these light sensors remains in its infancy (with the possible exception of the PIF branch of phytochrome signaling). The application of more biochemical and biophysical approaches should allow us to better

address questions such as: How do both the phytochromes and cryptochromes inhibit COP1 in a light dependent fashion? Which phototoreceptors are really light-regulated kinases and what are their substrates? Photoreceptor-induced signaling mechanisms influence numerous aspects of plant development, however in most cases we do not understand at the molecular level how the photoreceptors modulate development. Significant progress on these important issues require the combined approaches of developmental and photo-biologists. In many cases phenotypes of relevant mutants will have to be analyzed with greater temporal and spatial resolution in order to understand the sequence of events and order of action of molecular players underlying a light response. A final fascinating avenue of research is to examine how all this knowledge gathered in Arabidopsis grown in the laboratory can be used to understand plant adaptation to their local environment.

Figure legends

Figure 1. The spectral photon irradiance of natural light environments and effective spectrum of photoreceptors.

(A) All of spectra were measured by spectroradiometer (LI-1800; Li-Cor, Lincoln, NE) in Nara, Japan (May 2003,15:00, fine weather). Unfiltered sunlight (Sunlight), the shadow of building (Shadow), sunlight transmitted through a green *Pueraria lobata* leaf and light brown *Pueraria lobata* leaf (Autumnal leaf). (B) Effective spectrum of photoreceptors for activation and inactivation.

Figure 2. Primary light reactions in the different classes of plant photoreceptors

Arabidopsis has five phytochrome-encoding genes (*PHYA-E*), three cryptochrome genes (*CRY1-3*), two phototropin genes (*PHOT1* and *PHOT2*) and three Zeitlupe family genes (*ZTL*, *FKF1*, *LKP2*). The protein domain organization of the different photoreceptors is schematized with the position of chromophore attachment marked with an arrowhead. Phytochromes have an N-terminal extension of unknown fold (NT) followed by a PAS (Per, ARNT, Sim) domain, a GAF (cGMP phosphodiesterase/adenyl cyclase/FhlA) domain that binds the chromophore, a PHY domain (related to PAS domains) and a C-terminus that is composed of two PAS domains and a histidine kinase related domain (HKRD). Cryptochromes have a photolyase homology region (PHR) and a C-terminus of unknown structure (CT). Phototropins are composed of two LOV (Light, Oxygen, Voltage) domains in their N-terminus (LOV1 and LOV2) and a Ser/Thr protein kinase domain (KD). Members of the ZTL family have an N-terminal LOV domain, an F-box

and KELCH repeats. Phytochromes have phytochromobilin (PΦB) as a chromophore that is covalently bound to an invariant Cys residue in a GAF domain and photoreversibly switches between the Pr and the Pfr conformers upon isomerization of a double bond between the A and B rings of the tetrapyrrol. Cryptochromes have two chromophores; flavin adenine nucleotide (FAD) and a pterin acting as an antenna pigment. The light reactions from FAD to flavin adenine dinucleotide ($FADH^{-}$) or neutral radical form of FADH (FADH*) are depicted on the figure (adapted from (Bouly et al., 2007)). Phototropins use flavin mononucleotide (FMN) as a chromophore. In darkness, each of the LOV domains non-covalently binds to FMN. After absorbing UV-A/blue light, an invariant Cys in the LOV domain covalently binds to FMN. This activated state rapidly return to the dark state. Zeitlupe family light-sensors also have a LOV photosensory domain. In contrast to the phototropins this LOV domains remains in the light-activated state for a long time (hours).

Figure 3. Photomorphogenesis in Arabidopsis.

After germination, the seedling undergoes etiolated development in darkness or develops as a photosynthetically active seedling in the light. As the etiolated seedling emerges from the soil it will undergo de-etiolation. Light affects growth and development throughout life cycle of plants.

Figure 4. Phytochromes modulate the activity of multiple transcription factors.

In the dark the phytochromes are present in the cytoplasm in their ground Pr state. COP1 in association with SPA proteins leads to the degradation of multiple transcription factors

including HY5 and HFR1. Multiple PIF proteins remain stable and contribute to the etiolated form of development of the seedling. Upon light perception the phytochromes in their Pfr conformation translocate into the nucleus where they lead to the inactivation of COP1 and the degradation of several PIFs. In addition to degradation the PIFs are also inactivated by dimerization with HFR1 and the DELLAs. The primary mechanism leading to PIF inactivation depends on the light condition with dimerization with HFR1 playing an important role in FR-rich light because under these conditions the PIFs are relatively stable and HFR1 accumulates to high levels. The abundance of DELLA proteins is also regulated by the environment with for example higher levels of GA in the etiolated seedlings leading to more DELLA degradation.

Table I. Photoreceptor-dependent responses in Arabidopsis.

Summary of the photomorphogenic responses with the identified photoreceptor triggering these reactions. The type of light treatments leading to these responses is indicated. P stands for Pulse with Very low corresponding to a fluence of $10^{-6} \sim 10^{-2}$ μmol m^{-2}, Low to $10^{-2} \sim 10^{3}$ μmol m^{-2} and High to $>10^{3}$ μmol m^{-2}. C stands for continuous light with Low corresponding to a fluence rate of $10^{-2} \sim 10^{1}$ μmol m^{-2} s^{-1} and High to $>10^{1}$ μmol m^{-2} s^{-1}. Wc = Continuous white light, LD = long days (16h white light / 8h dark), SD = short days (8h white light / 16h dark), EOD = End Of Day treatment which is done with FR light and leads to inactivation of the phytochromes. *Publication showing action spectra in Arabidopsis. ** Multiple narrowband monochromatic lights between 320-780 nm were used for this experiment.

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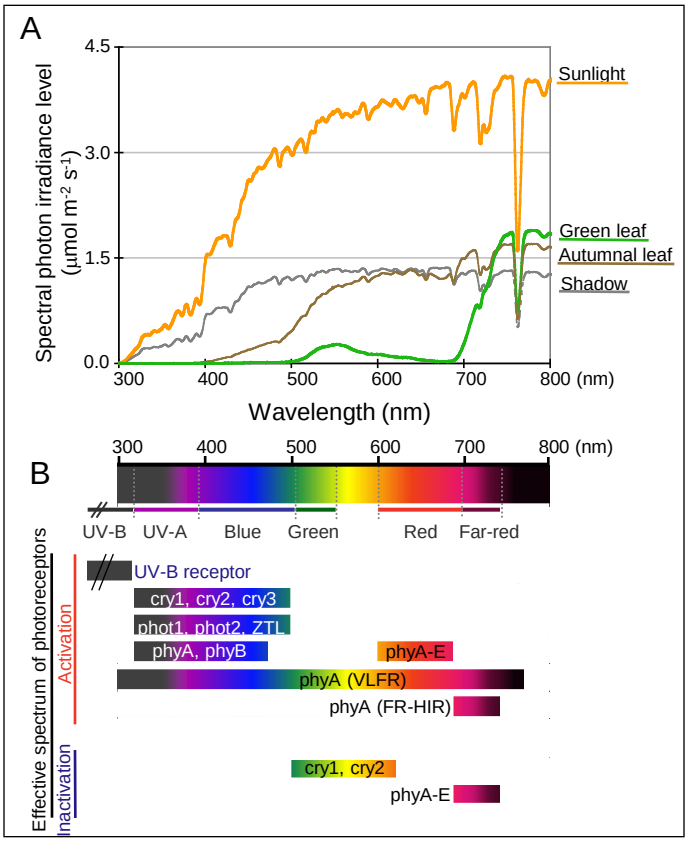

A
Spectral photon irradiance level (μmol m-2 s-1)
4.5
3.0
1.5
0.0
300
400
500
600
700
800 (nm)
Wavelength (nm)
Sunlight
Green leaf
Autumnal leaf
Shadow
B
UV-B
UV-A
Blue
Green
Red
Far-red
Effective spectrum of photoreceptors
Activation
Inactivation
UV-B receptor
cry1, cry2, cry3
phot1, phot2, ZTL
phyA, phyB
phyA-E
phyA (VLFR)
phyA (FR-HIR)
cry1, cry2
phyA-E

Figure 1

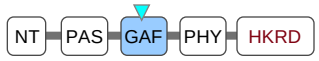
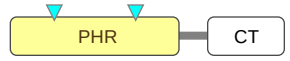
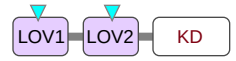
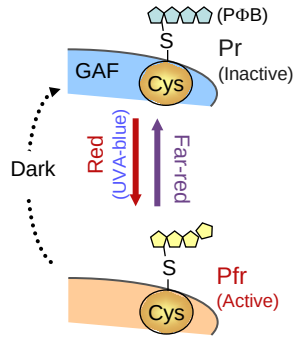
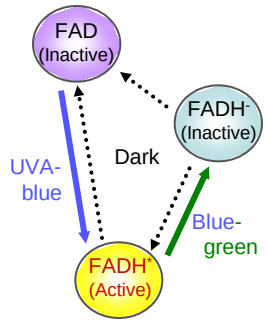
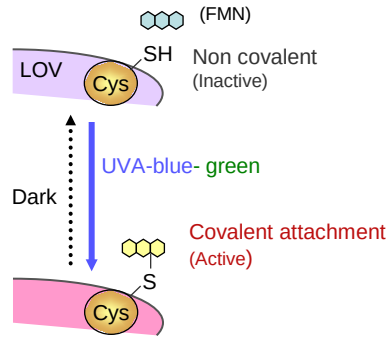
	Phytochrome (phy)	Cryptochrome (cry)	Phototropin (phot)	Zeitlupe (ZTL)
Gene family in *Arabidopsis*	*PHYA, B, C, D, E*	*CRY1, 2, 3*	*PHOT1, 2*	*ZTL, FKF1, LKP2*
Domain structure				
Chromophore	Phytochromobilin (PΦB)	Flavin adenine nucleotide (FAD), Flavin adenine dinucleotide (FADH), FADH*(neutral radical), Pterin	Flavin mononucleotide (FMN)	FMN (not confirmed)
Photoreversibility				

Figure 2

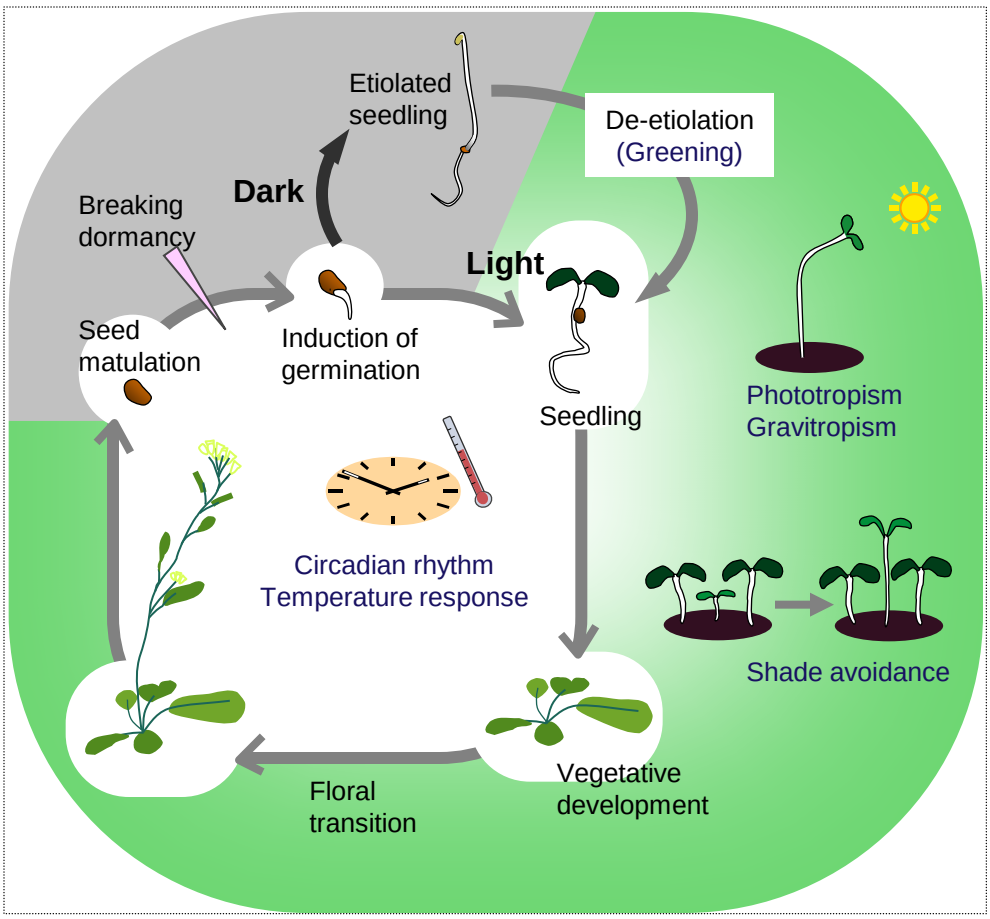

Etiolated
seedling
De-etiolation
(Greening)
Dark
Breaking
dormancy
Light
Seed
matulation
Induction of
germination
Seedling
Phototropism
Gravitropism
Circadian rhythm
Temperature response
Shade avoidance
Floral
transition
Vegetative
development

Figure 3

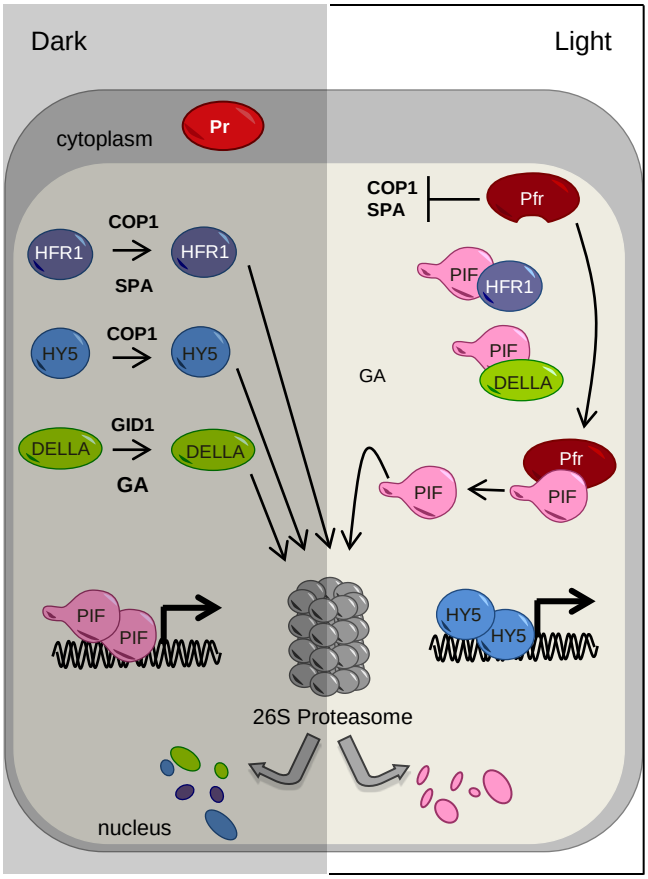

Dark
Light
cytoplasm
Pr
COP1
SPA
Pfr
HFR1
HFR1
SPA
PIF
HFR1
COP1
HY5
HY5
PIF
DELLA
GA
GID1
DELLA
DELLA
GA
Pfr
PIF
PIF
PIF
PIF
HY5
HY5
26S Proteasome
nucleus

Figure 4