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Title: Sensing the light environment in plants: Photoreceptors and early signaling steps.

Authors: Vinicius Costa Galvão & Christian Fankhauser

Affiliation:

Centre for Integrative Genomics, Faculty of Biology and Medicine, University of Lausanne, CH 1015 Lausanne, Switzerland. Phone: +41 21 692 3941.

Correspondence to: christian.fankhauser@unil.ch

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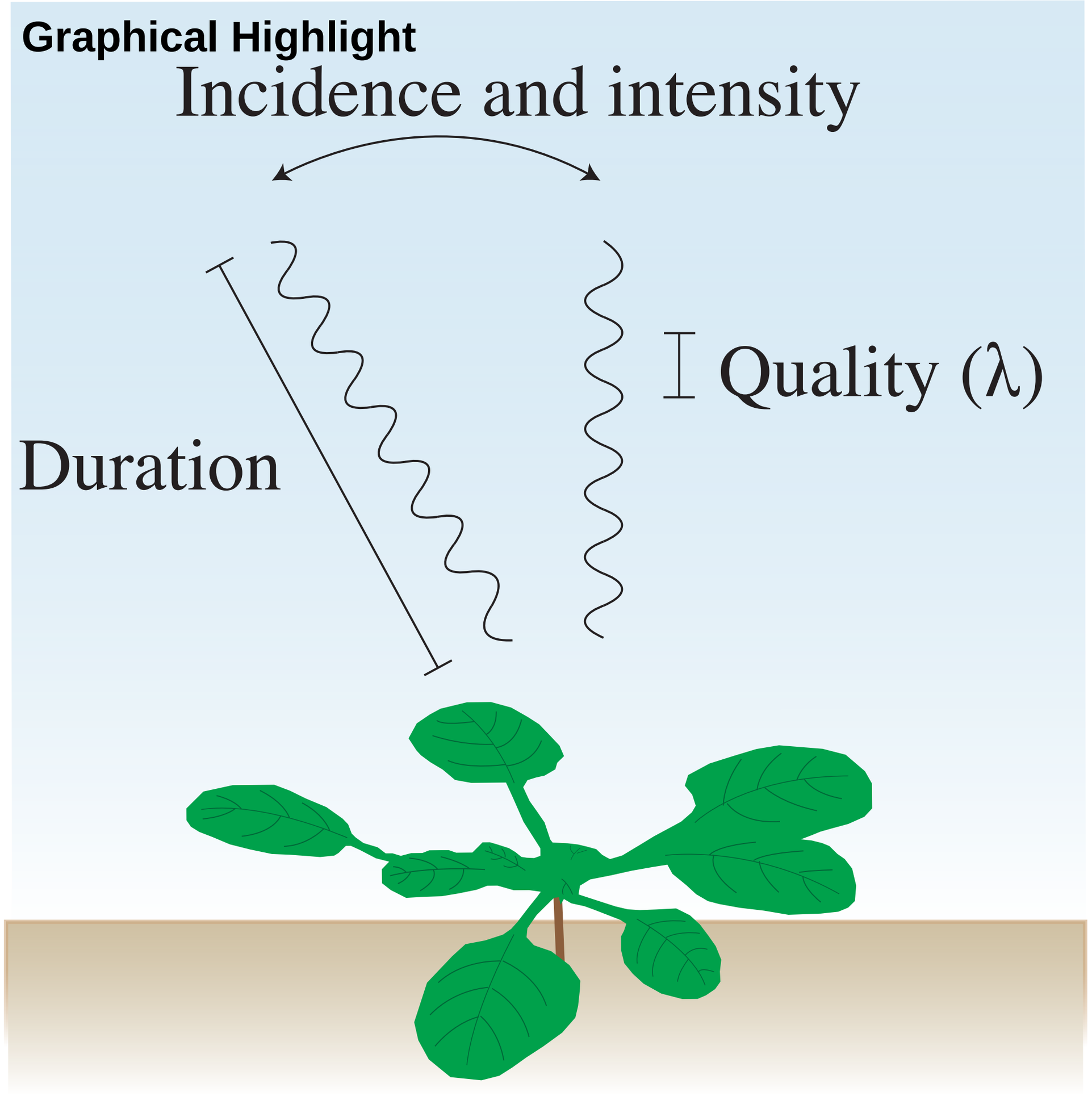
Graphical Highlight



Abstract

Plants must constantly adapt to a changing light environment in order to optimize energy conversion through the process of photosynthesis and to limit photodamage. In addition, plants use light cues for timing of key developmental transitions such as initiation of reproduction (transition to flowering). Plants are equipped with a battery of photoreceptors enabling them to sense a very broad light spectrum spanning from UV-B to far-red wavelength (280-750 nm). In this review we briefly describe the different families of plant photosensory receptors and the mechanisms by which they transduce environmental information to influence numerous aspects of plant growth and development throughout their life cycle.

Introduction

Sunlight is an environmental factor influencing behavior and physiology of most living organisms. Through the process of photosynthesis plants convert light energy into chemical energy stored as carbohydrates. Moreover, light has long been known to serve as a sensory cue to control, for example, plant movements (e.g. phototropism), reproduction and germination (Figure 1). In addition to irreversible developmental transitions (e.g. flowering and germination), adaptations to their light environment are also crucial for plant survival. In limiting light conditions leaf and chloroplast movement toward the light and phototropic bending optimize photosynthesis. In response to high light intensity and UV-B plants prevent photodamage by moving chloroplasts and the nucleus away from the light and by synthesizing photoprotectant pigments (Figure 1) [1-3].

Plants employ multiple photoreceptors to accurately detect and respond to dynamic changes of the spectral composition over a broad range of wavelength (UV-B to far-red), changes in light direction and duration (photoperiod). In contrast to animal photoreceptors, which are typically expressed in highly specialized organs, plant photoreceptors are present throughout the plant. Surprisingly, some plant photoreceptors are also present in roots [1]. In some cases the site of light perception coincides with the part of the plant responding to the light stimulus (e.g. chloroplast movement). However, there are many well-known examples where the site of the light response is distant from photoperception showing that in plants light triggers long-distance signals to mediate a response (e.g. floral transition) [1,4,5]. Finally, plants are sensitive to a broad range of light fluences ranging from seconds of a fluence rate corresponding to moonlight to hours of sunlight. The presence of both low-light and high-light specialists in several plant photoreceptor families explains this versatility [1,4]. In this

review, we will summarize the mechanisms of photoperception and early signaling events in response to red/far-red (R/FR) light (phytochromes), blue/UV-A light (cryptochromes, phototropins and 'Zeitlupes') and UV-B (UVR8) photoreceptors in higher plants. More extensive reviews on this topic can be found in the following [1,2,4-8].

Phytochromes

Phytochromes were first discovered in plants but these photosensory receptors are also present in some fungi and numerous prokaryotes [6] . In land plants these R/FR sensors (phyA-E in *Arabidopsis*) have partially overlapping but sometimes distinct functions throughout the plant life cycle including germination, de-etiolation (when a seedling emerges into the light and starts its photo-autotrophic life style), stomata development, flowering transition, senescence and shade avoidance (Figure 1a-c, 2a) [1,9-11].

Phytochromes are homo- or heterodimeric proteins consisting of a N-terminal photosensory region covalently binding a phytochromobilin tetrapyrrol chromophore (PϕB), and a C-terminal output region involved in dimerization and presumably contributing to relaying the light signal to downstream signaling events (Figure 2a) [6]. Phys are synthesized as a biologically inactive (Pr) form that converts to an active (Pfr) form following red light absorption. Pfr is rapidly converted back to the inactive Pr ground state following far-red light irradiation or slowly by thermal reversion. The recent crystal structures of bacterial and plant phytochrome photosensory modules provide long-awaited insights into the light-induced conformational changes initiated by chromophore isomerization [6,12].

Conformation-specific interaction between Pfr and several signaling elements is a key event in this pathway. This mode of action underlies translational control of specific mRNAs by Pfr, nuclear import of the light activated phytochromes and the control of light-regulated gene expression by transcriptional, post-transcriptional and post-translational mechanisms [11,13-17]. For instance, the interaction with Pfr leads to the inhibition of several PHYTOCHROME INTERACTING FACTORs (PIFs) transcriptional regulators, either by triggering their proteasome-mediated degradation or by leading to their phosphorylation [11]. Through poorly understood mechanisms Pfr also inhibits a ubiquitin E3 ligase complex comprising CONSTITUTIVE PHOTOMORPHOGENIC1 (COP1) and SUPPRESSOR OF PHYA (SPA) thereby enabling the stabilization of transcription factors required for light-grown development (e.g. ELONGATED HYPOCOTYL5 (HY5)) [17]. Nuclear reprogramming triggered by phytochrome activation also includes mechanisms that need further molecular

characterization such as regulated expression of non-coding RNAs, alternative splicing and repositioning of specific loci in the nucleus [18-21].

Several regulatory mechanisms prevent excessive signaling from the unusually long-lived phytochrome lit state (Pfr). These include rapid degradation of the highly light-labile photoactivated phyA [13]. Although much less dramatic, the levels of phyB also decline upon photoconversion. This degradation depends on the interaction between PIF3 and a ubiquitin E3 ligase component that leads to the simultaneous destruction of phyB and the bHLH factor [22]. In addition, light-regulated phosphorylation of phyB modulates thermal reversion of Pfr to Pr thereby also controlling the amount of active photoreceptor [23,24].

Cryptochromes

Cryptochromes are UV-A/blue photoreceptors ubiquitously found in bacteria, fungi, animals and plants sharing a common evolutionary ancestor with DNA photolyases. Despite their high similarity, cryptochromes do not use photons to repair damaged DNA but to convey light input sensed by a flavin adenine dinucleotide (FAD) chromophore to control different biological processes (Figure 1a-b, 2b) [4]. Arabidopsis has two cryptochromes, cry1 and cry2, with partially overlapping functions. Cry1 plays a predominant function during de-etiolation while the main role of cry2 is the photoperiodic control of flowering [1,4]. More recently, it was shown that cry1 controls seed dormancy and germination in barley [25] and cry2 regulates leaf senescence in soybean (Figure 1b) [26].

The primary light reactions leading to activation of cryptochromes have been quite controversial and will not be covered in detail (reviewed in [7]). Prior to blue light irradiation cryptochromes exist as homodimers most probably harboring a fully oxidized FAD chromophore within their N-terminal photolyases homology region (PHR) (Figure 2b). Blue light photoactivation initiates an electron transfer reaction involving conserved tryptophan residues and/or cellular metabolites triggering chromophore reduction to the “signaling state” [7,27]. Reduction of the chromophore leads to conformational modifications in both the PHR and the C-terminal region (CCT) enabling light-regulated interactions between the photoreceptor and signaling intermediates (Figure 2b). In particular, light-induced binding to SPA1 leads to cryptochrome-mediated inhibition of the COP1-SPA1 E3 ubiquitin ligase [28-30]. Consequently, HY5 and CONSTANS (CO) transcription factors accumulate to promote de-etiolation and flowering, respectively [28-30]. In a second mechanism, light-activated cry2 interacts with transcription factors CRY2-INTERACTING bHLH (CIB1, 2, 4, 5) and directly activates the transcription of FLOWERING LOCUS T (FT) to promote flowering [31]. In

soybean, photoactivated cry2 prevents binding of CIB1 to the promoter of genes regulating leaf senescence [26]. Hence, the interaction between photoactivated cry2 and CIB proteins leads to radically different regulatory outcomes depending on the situation. Upon photoactivation cry2 becomes extensively phosphorylated, leading to proteasome-mediated degradation [4,32]. Additionally, cryptochromes return to the inactive (oxidized FAD) conformer within minutes further attenuating signaling [7].

Phototropins

Phototropins (phot1 and phot2 in *Arabidopsis*) are blue light receptors present in the entire green lineage. Phototropins' primary structure can be divided into an N-terminal photosensory region and a C-terminal AGC-type Ser/Thr protein kinase domain (Figure 2c). Blue light is sensed by two flavin mononucleotide (FMN) chromophore-binding light oxygen voltage (LOV1 and LOV2) domains (Figure 2c) [8]. In contrast to other photoreceptors, which primarily act in the nucleus, phototropins are targeted to the plasma membrane. Blue light promotes the partial internalization of phot1 to the cytoplasm, whereas phot2 is targeted to the Golgi apparatus via its C-terminal domain [8]. The functional significance of the light-induced re-localization of these photoreceptors remains poorly understood [33].

Photoactivation induces the covalent binding of FMN to the LOV1/2 domains through a cysteinyl adduct, which in turn triggers conformational changes that liberate the kinase domain from the inhibitory action of the photosensory domain [8]. Light-activated phot1 and phot2 autophosphorylate residues located both in the sensory and kinase domains [34]. Phosphorylation of a pair of serines in their protein kinase activation loop is essential for all tested phototropin-mediated responses [35,36].

Following these common initial signaling events, the subsequent signaling steps differ depending on the physiological response [37-40]. In several cases this includes phototropin-induced phosphorylation of signaling components. For instance, the direct phosphorylation of the Ser/Thr kinase BLUE LIGHT SIGNALING 1 is essential for the subsequent signaling steps leading to stomata opening [37]. Moreover, phot kinase substrates have been identified that presumably control the establishment of a lateral auxin gradient leading to phototropism (Figure 1a,c) [38,39]. Phototropin signaling also include rapid light-induced modifications of both the actin and microtubule cytoskeleton, however how these events are triggered by phototropin activation remains poorly understood [8,40,41].

Zeitlupe family

Land plants contain an additional family of LOV UV-A/blue light photoreceptors comprising ZEITLUPE (ztl), FLAVIN-BINDING, KELCH REPEAT, F-BOX (fkf1) and LOV KELCH PROTEIN2 (lkp2) proteins (collectively referred to as Zeitlupes) [8]. In contrast to the phototropins, Zeitlupes contain a single FMN-binding LOV domain followed by an F-box and six Kelch repeats (Figure 2c) [5]. As suggested by their domain organization Zeitlupes form SCF E3 ubiquitin ligase complexes directly controlling light-mediated protein degradation [42-44]. In addition to the above mentioned domain organizations, photosensory LOV domains are also found associated with other output domains including DNA binding b-ZIP in aureochromes from photosynthetic stramenopile algae (reviewed in [8]). Therefore, LOV domains are versatile light absorption modules mediating different biochemical outputs.

Blue light induces the covalent binding of FMN to the fkf1 LOV domain (Figure 2c). However, in contrast to fast dark reversion observed in phototropins, the fkf1 signaling state is stable for days while for ztl adduct decay occurs within hours [5,45]. Light-regulated protein stability and interaction with GIGANTEA (GI), which regulates the activity and/or stability of this class of photoreceptors are additional regulatory mechanisms [5]. GI binding appears to alter the SCF^{ztl} activity thereby regulating the stability both proteins and SCF^{ztl} targets [42,46]. In contrast, the light-regulated GI-fkf1 interaction appears to enhance SCF^{fkf1} activity [43,47].

The protein-protein interaction and E3 ubiquitin ligase activity of Zeitlupes have a prominent role in the photoperiodic control of floral transition [5,43,47,48]. Through a complex interaction network, Zeitlupes and GI promote gene expression and protein stabilization of CO under inductive photoperiod, and the expression of the florigen gene *FT* in leaves [44,47,48]. Interestingly, fkf1 and GI also control the photoperiodic phase transition in the liverwort *Marchantia polymorpha* indicating early appearance of this role of Zeitlupes in the plant lineage [49]. Moreover, ztl and GI also control the circadian clock by regulating the stability of the clock proteins TIMING OF CAB EXPRESSION1 (TOC1) and PSEUDO RESPONSE REGULATOR5 (PRR5) [5,42].

UVR8

UV-B does not fuel photosynthesis but represents a threat to the integrity of plants. In order to acclimate to the harmful effects of UV-B plants use the UV RESISTANCE LOCUS8 (UVR8) photoreceptor to trigger large changes in gene expression leading morphological adaptations and the production of flavonols that act as UV-B protectant ‘sunscreen’ (Figure 2d) [2,50,51].

Moreover, UVR8 mediates phototropic bending, stomatal movement, and entraining of the circadian clock (Figure 1a-c) [52-54].

Rather than depending on a cofactor chromophore, UVR8 uses a triad of closely packed tryptophan residues (W233, W285 and W337) to perceive light (Figure 2d) [51,55,56]. UVR8 is present as an inactive homodimer that is converted to an active monomer after absorbing UV-B [51,55,56]. UV-B perception disrupts salt bridges flanking the tryptophan triad at the dimer interface leading to reversible monomerization independently of other factors [51,55-57]. The importance of the main chromophore tryptophan W285 was confirmed *in vivo* by expressing the constitutively monomeric W285A mutant in plants. These plants present constitutive photomorphogenesis and enhanced acclimation to UV-B, indicating that the structural changes leading to UVR8 monomerization represent the key event for its activation [57].

Following UV-B irradiation, active monomeric UVR8 is recycled to its homodimer ground state [2]. Although this reversion occurs with purified UVR8 *in vitro*, this back reaction is facilitated *in planta* through binding with the homologous proteins REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1/2 (RUP1 and RUP2) [58]. *RUP1* and *RUP2* gene expression is rapidly induced upon UV-B perception indicating that this represents a negative feedback mechanism [58]. Therefore, the reversible dynamic photocycle between active UVR8 monomeric and inactive homodimeric states enable plants to continuously measure and adapt to environmental UV-B levels.

Following monomerization UVR8 interacts with the E3 ubiquitin ligase COP1 in the nucleus [2,51] . This interaction with the UVR8 C-terminal region [2,59] leads to the expression and stabilization of the bZIP transcription factors HY5 and HY5 HOMOLOGUE (HYH), which directly bind to the promoter of several UV-B responsive genes [60]. Moreover, HY5 and HYH bind to the *HY5* promoter in a feed-forward mechanism enhancing downstream transcriptional events [60].

Conclusion

Important progress has been made over the past decades to identify the mode of action and early signaling steps initiated by plant photosensory receptors. There is no evidence for the presence of rhodopsin-based photoreceptors in land plants. Most plant photosensory receptors are not found in animals with the notable exception of cryptochromes that also have light-sensing functions in some invertebrates [4,7]. Signaling steps downstream of plant

photoreceptor activation do not appear to involve a G-protein coupled receptor process. However, several common themes emerge from the comparative study of plant photoreceptor signaling mechanisms (presented on Figure 3). Despite the noted differences between plant and animal photosensory mechanism, research in the plant field contributed to the development of optogenetic techniques, an application that is widely used in neurobiology. On the plant side much remains to be done to understand how the initial signaling events lead to the myriad of plant photomorphogenic responses. Beyond revealing new fascinating mechanisms enabling plant adaptation to a changing environment this will contribute to further improve and/or identify varieties with great value for agriculture.

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Figures Legend

Fig 1 – Photoreceptors regulate plants development and adaptation to the light environment. (a) Adaptive responses include phototropism and shade avoidance that maximize access to unfiltered sunlight in light-limiting conditions and the biosynthesis of photoprotective pigments in response to UV-B irradiation. (b) Developmental transitions throughout the life cycle of plants are regulated by photosensory receptors. These include: germination, de-etiolation, floral transition and senescence. (c) At the cellular level photoreceptors regulate the position of chloroplasts to maximize light capture in low light (small arrows) and minimize photodamage in high light (big arrows). They also control the development and opening of stomata, which represents a key regulatory mechanism controlling gas exchange (CO_2 uptake for photosynthesis, transpiration).

Fig 2 – Light absorption spectrum, chromophore structure and domain organization of plants photoreceptors. Phytochromes (a), cryptochromes (b), LOV proteins phototropins and ZTLs (c) and UVR8 (d). The acronyms for several protein domains were defined in the main text, the remaining ones are: HKRD, histidine kinase-related domain; PAS, Per-Arndt-Sim domain; GAF, cGMP phosphodiesterase/adenyl cyclase/Fh1A domain; F, F-box domain; β-propeller domains (B1- B7).

Fig 3 – Simplified model of plants photoreceptors activity. (a) Phytochromes and cryptochromes act both by direct interaction and control of transcription factors activity (PIF and CIB) and regulating COP1 E3 ubiquitin ligase activity. In the dark transcription factors exemplified by HY5 are degraded by the COP1/SPA E3 ligase, upon light activation COP1/SPA is inhibited leading to HY5-regulated transcription. (b) UVR8 interaction with COP1 promotes the accumulation of the transcription factor HY5, which is further increased after binding to its own promoter. (c) Light-activated ztls interact with GI stabilizing those photoreceptors and enabling them to act as E3 ligases to degrade transcriptional regulators (CDF and TOC1). In addition, light-activated fkf1 interacts with and stabilizes CO. (d) Blue

light-induced conformational changes activate phototropin kinase activity, leading to auto- and substrate phosphorylation. KD, Ser/Thr kinase domain.

Reference Highlights

*12. More than 50 years after its biochemical purification this paper reveals the first structure of a plant phytochrome photosensory domain in its dark (Pr) state. Taken together with several bacterial phytochrome structures (reviewed in 6) this work provides the foundation for structure-function studies to elucidate the initial phytochrome signaling steps.

**13. Angiosperms (flowering plants) possess multiple phytochromes including phyA, which has a distinct signaling mode enabling it to signal in light conditions that are very inefficient to trigger formation of the active Pfr conformer. Using a combination of modeling and experimentation this paper proposes a model explaining the spectral shift between the photoreceptor absorption spectrum and its action spectrum.

*15. FHY1 selectively interacts with light-activated phyA to transport it into the nucleus. This paper shows that an FHY1 homolog present in moss also controls nuclear entry of light-activated phytochromes revealing an ancient evolutionary history for light-regulated subcellular partitioning of the phytochromes.

*18. Spatial positioning of specific genes in the nucleus has been linked to cellular reprogramming in metazoans. This paper shows that upon light perception the phytochromes control nuclear positioning of light-regulated genes in *Arabidopsis*.

*19. In response to changes in the light environment phytochromes regulate the expression of hundreds of genes. This paper reveals that in addition phytochromes extensively regulate alternative splicing and identify an example where alternative splicing contributes to a photomorphogenic response.

*21. The advent of new sequencing techniques revealed the existence of large numbers of non-coding RNAs (ncRNA) in all eukaryotes, which for the most part remain without a known function. This paper identifies a ncRNA that regulates phytochrome signaling by modulating the expression of *PIF3* during photomorphogenesis. .

**22. A central regulatory step in phyB signaling is the conformer-specific interaction between PfrB and PIF3, which leads to phosphorylation of the transcription factor followed by co-degradation of PIF3 and phyB. This paper identifies a small family of BTB-POZ domain proteins that are part of a E3 ubiquitin ligase which interact with light-activated PIF3 and control the co-degradation of the light-activated photoreceptor and its early signaling intermediate PIF3.

**27. Plant cryptochrome activation has been linked to an electron transfer chain leading to

the photoreduction of the flavin chromophore. Three evolutionary conserved Trp residues were proposed to be central for this mechanism but *in vivo* studies have questioned their importance. This study shows that cellular metabolites including NADH, NADPH and ATP facilitate the electron transfer reaction resulting in the transition of flavin from the oxidized to the radical form, which is proposed to be the signaling state.

*28. Upon light activation phytochromes and cryptochrome inactivate the COP1-SPA E3 ubiquitin ligase through poorly understood mechanisms. These studies (28-30), identify a light-regulated interaction between the cryptochromes and SPA1. This light-regulated interaction is thought to alter the conformation and inactivate the COP1-SPA E3 ligase.

*29. See 28.

*30. See 28.

**37. The protein kinase activity of phototropins is essential for their function *in vivo* but very few substrates of this activity are known. This paper presents strong evidence to show that BLUS1 is a target of phototropin kinase activity, identifies a residue that is phosphorylated and shows that when this Ser is mutated into an Ala BLUS is inactive *in vivo* thereby indicating that phot-mediated phosphorylation of BLUS1 is essential for subsequent signaling events.

**41. In response to unilateral irradiation stem growth becomes asymmetric with the shaded side growing faster than the lit side leading to reorientation of growth towards the light source. This paper identifies rapid light-induced changes in the orientation of cortical microtubules that depend on phototropin activation. This light-induced cytoskeletal rearrangement may represent a very early event triggering asymmetric growth.

**48. Fkf1 plays a particularly important dual function to promote flowering in response to inductive long days. This work shows that fkf1 simultaneously promotes degradation of CO transcriptional repressors and stabilizes CO protein to promote flowering under inductive photoperiods.

*49. Orthologs of fkf1 and GI are already present in basal land plants known as liverwort. As in *Arabidopsis* both proteins interact with each other and are involved in day-length regulation of growth-phase transitions.

**55. This paper and 56 reveal the structure of the UVR8 photoreceptor, the mechanism of light sensing by closely spaced Trp residues and how the initial light reactions destabilize the UVR8 dimer leading to monomerization and hence activation of the photoreceptor.

**56. See 55

*58. Returning to the inactive state is a key regulatory step for all photoreceptors. In the case of UVR8 this process is greatly accelerated by the UV-B induced proteins RUP1 and RUP2. By promoting dimerization of UVR8, RUP1/2 disrupt the UVR8-COP1 signaling state.

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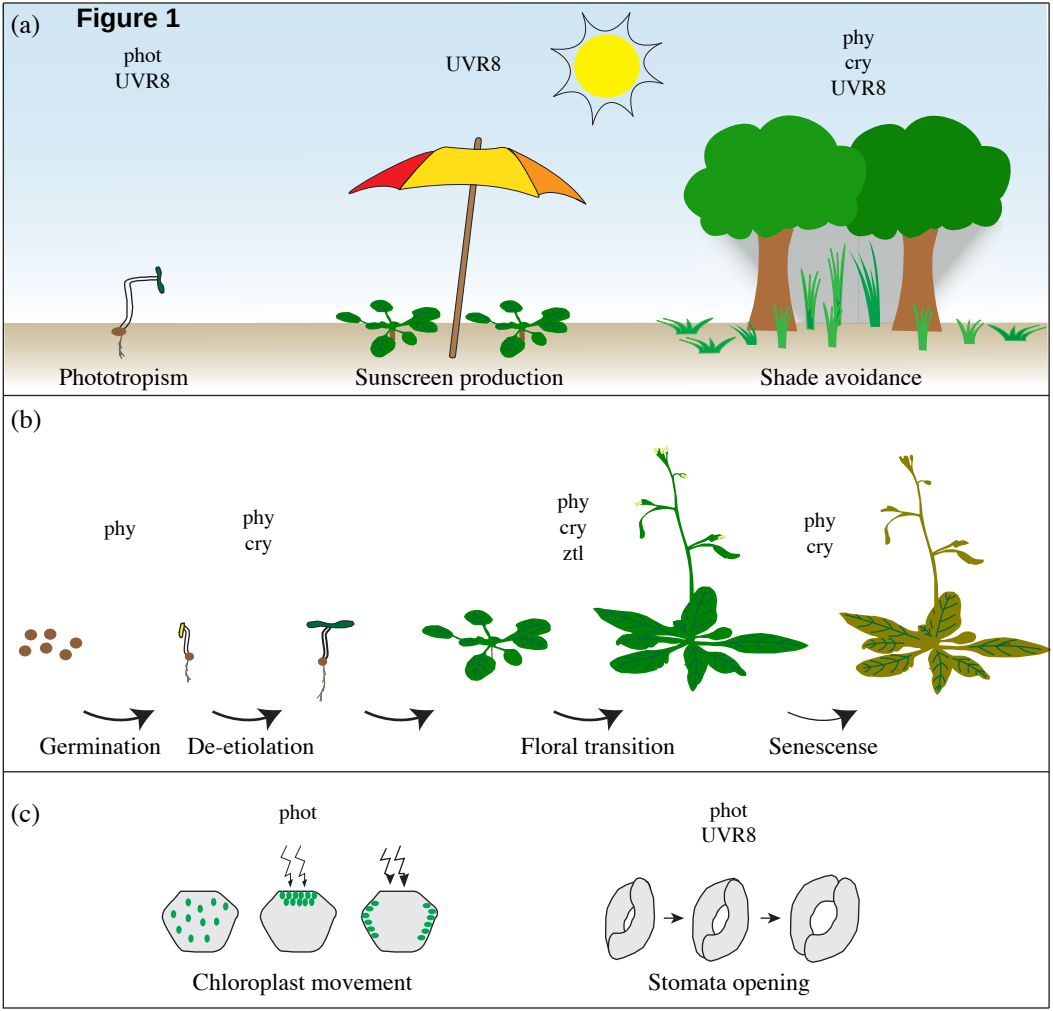
Figure 1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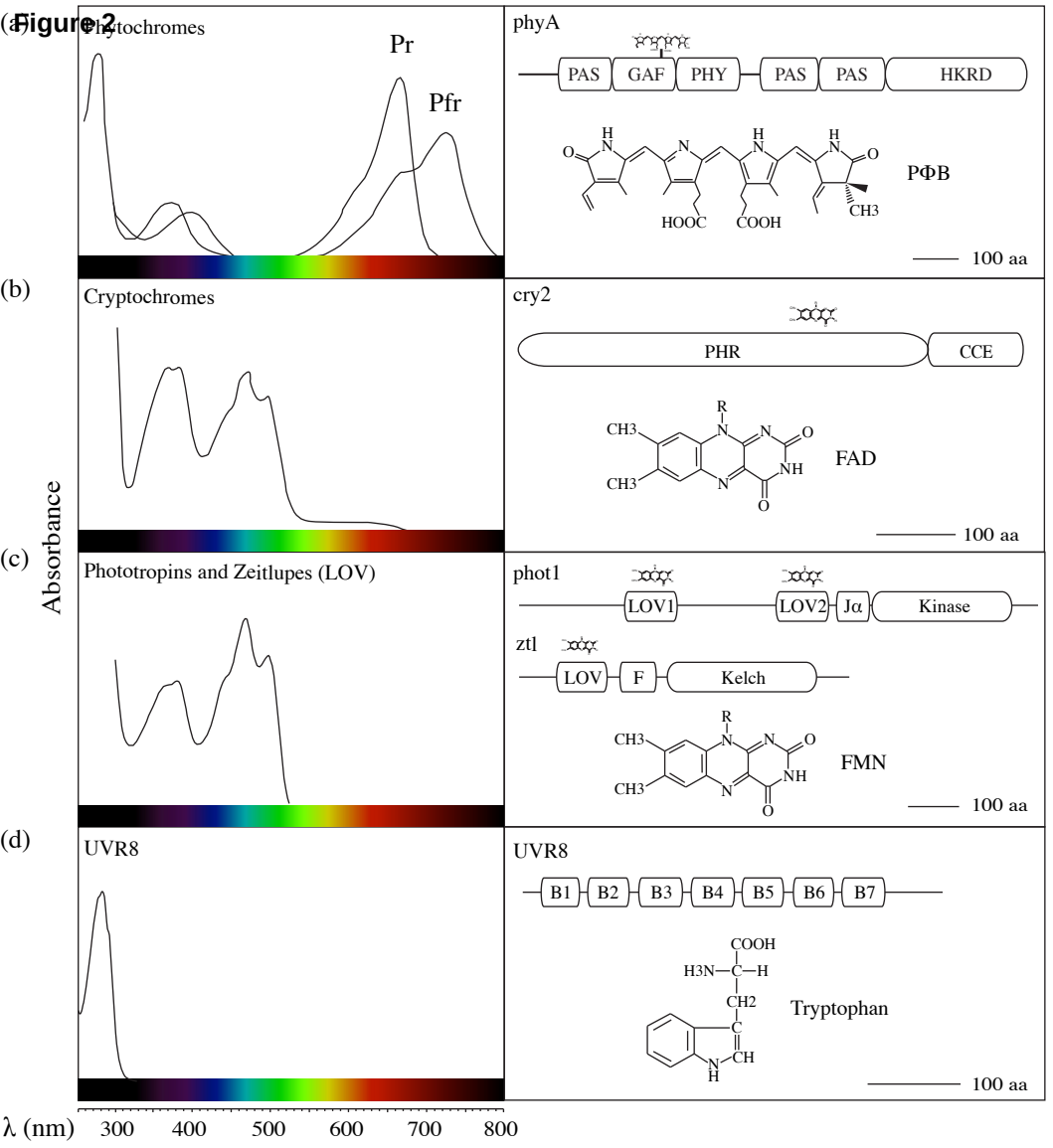
UVR8
UVR8
phy
cry
UVR8
Phototropism
Sunscreen production
Shade avoidance
(b)
phy
phy
cry
phy
cry
ztl
phy
cry
Germination
De-etiolation
Floral transition
Senescense
(c)
phot
phot
UVR8
Chloroplast movement
Stomata opening

Figure 2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PHR
CCE
FAD
100 aa
(c)
Phototropins and Zeitlupes (LOV)
phot1
LOV1
LOV2
Jα
Kinase
ztl
LOV
F
Kelch
FMN
100 aa
(d)
UVR8
UVR8
B1
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B5
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B7
Tryptophan
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λ (nm)
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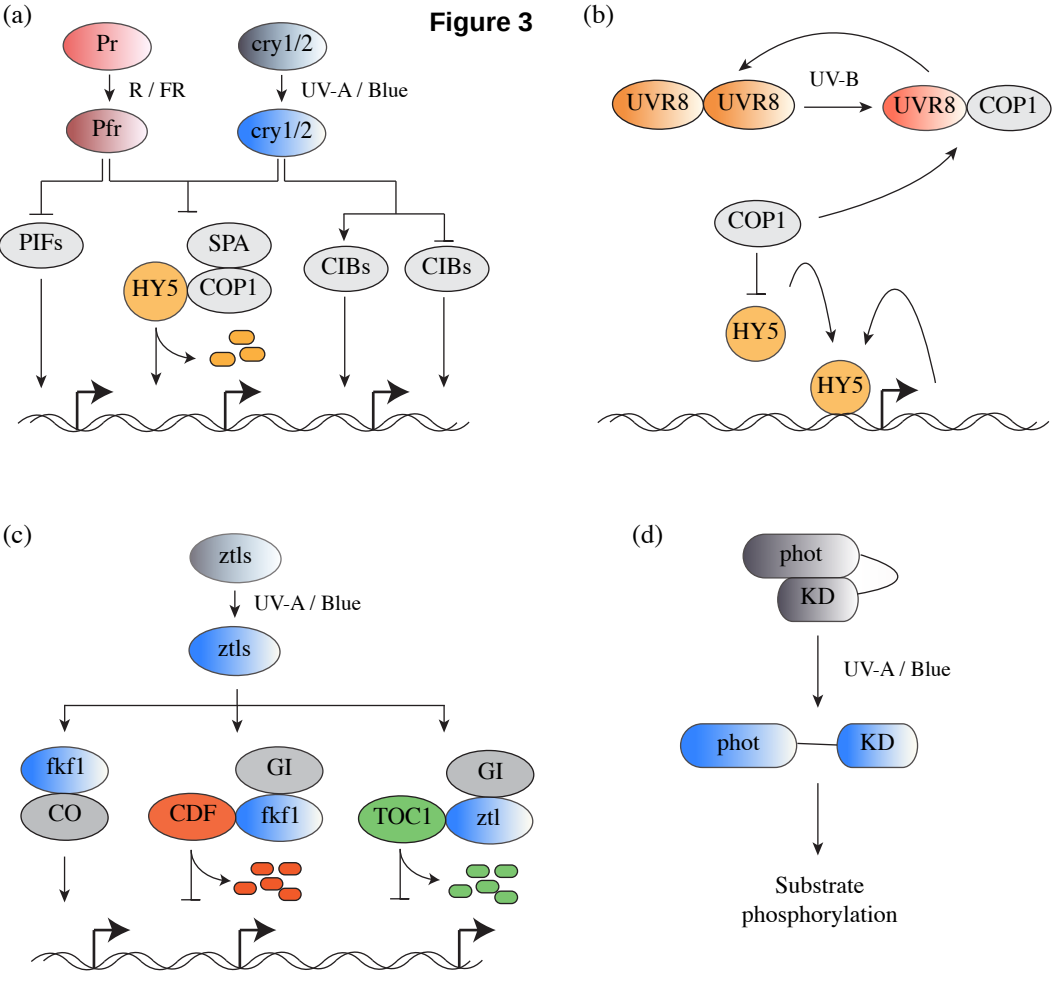
500
600
700
800

Figure 3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UV-A / Blue
Pfr
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PIFs
SPA
HY5
COP1
CIBs
CIBs
(b)
UV-B
UVR8
UVR8
UVR8
COP1
COP1
HY5
HY5
(c)
ztls
UV-A / Blue
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CO
GI
CDF
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GI
TOC1
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UV-A / Blue
phot
KD
Substrate
phosphorylation