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Published in final edited form as:

Title: Phototropism: at the crossroads of light-signaling pathways.

Authors: Goyal A, Szarzynska B, Fankhauser C

Journal: Trends in plant science

Year: 2013 Jul

Volume: 18

Issue: 7

Pages: 393-401

DOI: 10.1016/j.tplants.2013.03.002

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Trends in Plant Science

Phototropism: at the crossroads of light signaling pathways

--Manuscript Draft--

Manuscript Number:	PLANTS-D-12-00224R1
Article Type:	Review
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Abstract:	Phototropism enables plants to orient growth towards the direction of the light and thereby maximizes photosynthesis in low-light environments. In angiosperms, blue-light photoreceptors called phototropins are primarily involved in sensing the direction of light. Phytochromes and cryptochromes (sensing red/far-red and blue light, respectively) also modulate asymmetric hypocotyl growth leading to phototropism. Interactions between different light-signaling pathways regulating phototropism exist in cryptogams and angiosperms. In this review, we focus on the molecular mechanisms underlying the co-action between photosensory systems in the regulation of hypocotyl phototropism in <i>Arabidopsis thaliana</i> . I KEPT THE OLD ABSTRACT HERE BUT MODIFIED IT IN THE PAPER

1 **Phototropism: at the crossroads of light signaling pathways**

2

3

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13

14 **Phototropism enables plants to orient growth towards the direction of the light**
15 **and thereby maximizes photosynthesis in low-light environments. In**
16 **angiosperms, blue-light photoreceptors called phototropins are primarily**
17 **involved in sensing the direction of light. Phytochromes and cryptochromes**
18 **(sensing red/far-red and blue light, respectively) also modulate asymmetric**
19 **hypocotyl growth leading to phototropism. Interactions between different light-**
20 **signaling pathways regulating phototropism exist in cryptogams and**
21 **angiosperms. In this review, we focus on the molecular mechanisms underlying**
22 **the co-action between photosensory systems in the regulation of hypocotyl**
23 **phototropism in *Arabidopsis thaliana*. Recent studies have shown that**
24 **phytochromes and cryptochromes enhance phototropism by controlling the**
25 **expression of important regulators of phototropin signaling. In addition,**

1 **phytochromes may also regulate growth towards the light via direct interaction**
2 **with the phototropins.**

3

4 **Phototropism: plant strategy for effective growth**

5 When seeds germinate in darkness (buried in the ground), shoot growth orientation is
6 determined by gravity to allow seedlings to emerge from the soil. Upon reaching the
7 soil surface they use blue light to determine growth orientation. This response, termed
8 positive phototropism, optimizes light capture by the main photosynthetic organs
9 (leaves) and thereby has been proposed to maximize photosynthetic productivity and
10 growth [1,2]. Although phototropism is most frequently studied in etiolated seedlings,
11 phototropic growth is observed in different plant organs throughout their life cycle
12 (Box 1) (Figure 1).

13 Phototropism appeared early in the evolution of land plants and has been
14 described in numerous lineages, including mosses, ferns and angiosperms [3]. In
15 mosses and ferns, phototropism is triggered by both red and UV-A/blue light. In
16 flowering plants, the phototropic response is triggered primarily by blue light,
17 although red light has also been shown to enhance this process. The direction of blue
18 light is detected by UV-A/blue-light-sensing phototropins (phot) [4]. Efficient
19 phototropism also relies on light signaling mediated by the cryptochromes (cry) and
20 phytochromes [5]. Cryptochromes are blue/UV-A-absorbing photoreceptors
21 controlling circadian rhythms and plant developmental processes such as de-etiolation
22 (see Glossary) and induction of flowering [6]. Although phytochromes primarily
23 sense red/far-red light, they also absorb a significant amount of blue light [7].
24 Phytochromes control numerous facets of the plant life cycle, often in conjunction
25 with the cryptochromes [8]. Both photoreceptor families modulate phot-mediated

1 phototropism at several levels. Phytochromes and cryptochromes also influence
2 phototropism indirectly by inhibiting negative gravitropism of hypocotyls emerging in
3 the light [9]. In this review, we focus on links between different light-signaling
4 pathways regulating hypocotyl phototropism in *Arabidopsis* (*Arabidopsis thaliana*).
5 We also discuss the light signaling pathways underlying phototropism in mosses and
6 ferns to place this photoreceptor crosstalk in an evolutionary context.

7

8 **From light perception to the formation of an auxin gradient**

9 In a book published in 1880, Charles Darwin and his son Francis proposed that
10 phototropic curvature requires the transmission of a signal from the photoreceptive
11 coleoptile tip of a grass seedling to a spatially separated bending zone [10,11]. In
12 agreement with these early experiments, the top 2-mm of the maize (*Zea mays*)
13 coleoptile has been shown to be crucial for light sensing [12]. Phototropins and early
14 signaling components are highly expressed in the upper region of coleoptiles [12,13].
15 Light gradients have been measured in unilaterally irradiated coleoptiles [14]. In oat
16 (*Avena sativa*), phototropic stimulation leads to the establishment of the lateral phot
17 phosphorylation gradient, which may represent an early signal leading to coleoptile
18 bending [13]. In dicots, the site of light perception is less clearly established;
19 however, the hypocotyl tip has recently been proposed as the site of light perception
20 for phototropism in light-grown dicots [15]. In etiolated *Arabidopsis* seedlings, the
21 phot1 protein is rather broadly expressed, with a high level of expression within the
22 hypocotyl elongation zone and in the apical hook [16,17].

23 The signal triggering growth postulated by Darwin was later identified as the
24 plant hormone auxin [18]. Auxin is synthesized mainly in the shoot apex and young
25 leaves [19]. Upon unilateral irradiation, auxin is actively transported to more basal

1 parts of the plant stem and asymmetrically distributed across the hypocotyl. It is
2 generally accepted that the formation of a lateral auxin gradient ultimately results in
3 asymmetric growth [10]. Although such auxin gradients have never been directly
4 measured in *Arabidopsis*, there is genetic evidence to support this model. For
5 example, phototropism depends on the auxin-regulated transcriptional regulators
6 IAA19/MSG2 (INDOLE-3ACETIC ACID 19/MASSUGU2) and NPH4/ARF7
7 (NONPHOTOTROPIC HYPOCOTYL 4/AUXIN RESPONSE FACTOR 7) [20,21].
8 Moreover, auxin gradients have been detected in numerous species [4,10].

9

10 **Phototropins: sensors of directional blue light**

11 *Arabidopsis* possesses two phototropins (phot1 and phot2; see Glossary for
12 nomenclature of photoreceptors) that control a variety of physiological responses,
13 including phototropism, chloroplast positioning and opening of stomata [2].
14 Phototropins are light-activated AGC class serine/threonine protein kinases (cAMP-
15 dependent protein kinase, cGMP-dependent protein kinase G and phospholipid-
16 dependent protein kinase C family of kinases) [22]. The photoreceptive center of
17 phototropins consists of two LOV (light/oxygen/voltage-sensitive) domains (LOV1
18 and LOV2) on the amino-terminal portion of the photoreceptor. Despite the presence
19 of two LOV domains, light regulation of phototropin activity predominantly involves
20 LOV2 [2]. Each of the LOV domains non-covalently binds the cofactor flavin
21 mononucleotide (FMN). Upon blue-light irradiation, FMN forms an adduct with a
22 conserved cysteine residue within each LOV domain [2]. An α -helix known as J- α
23 connects the photosensory LOV2 domain to the carboxy-terminal Ser/Thr protein
24 kinase domain (KD) [23]. In the dark, LOV2 binds to the kinase domain, repressing
25 its catalytic activity [24]. Blue light leads to destructuring of the J- α helix and

1 dissociation of the LOV2–KD interaction, thereby activating phot protein kinase
2 activity [23,25]. Upon returning to darkness the phototropins undergo rapid
3 regeneration to the photosensitive state [25].

4 Blue-light excitation results in autophosphorylation of the photoreceptors
5 [26,27]; phosphorylation of some of those sites is essential to initiate phototropin-
6 mediated signaling [28,29]. Except for the photoreceptors themselves, only two phot
7 kinase targets, ABCB19 (ATP-BINDING CASSETTE B19) [15] and PKS4
8 (PHYTOCHROME KINASE SUBSTRATE 4) [30], are known. In both cases,
9 phosphorylation has been proposed to lead to substrate inactivation. It has also been
10 suggested that some of the high-light-induced phot phosphorylation sites play an
11 inhibitory role [26].

12 Phototropins are associated with the inner surface of the plasma membrane
13 [16,31] (Figure 1). This subcellular localization depends on a small part of the
14 extreme carboxyl terminus of the phototropins [32]. Upon blue-light irradiation, a
15 fraction of phot1 becomes released into the cytoplasm, whereas light-activation leads
16 to phot2 association with the Golgi apparatus [16,17,33]. The function of the light-
17 regulated internalization of phototropins is still uncertain. Phot1 internalization occurs
18 through the clathrin-mediated endocytic pathway, which depends on the kinase
19 activity of the photoreceptor and phosphorylation of Ser851 within its activation loop
20 [34]. Of particular interest in the context of the photoreceptor crosstalk regulating
21 phototropism is the finding that phytochrome A (phyA)-mediated red-light-sensing
22 inhibits blue-light-induced phot1 internalization [35] (discussed in detail in later
23 sections).

24

25 **Phototropin-interacting proteins and other phototropism signaling components**

1 Signaling pathway(s) leading from light perception by plants to asymmetric growth
2 involve many components and regulatory factors. In this review, we focus on the
3 function of proteins implicated in phototropism and involved in the crosstalk of
4 signaling pathways elicited by different photoreceptors (Table 1). Extensive reviews
5 on phototropin signaling have been published recently [4,36].

6 In *Arabidopsis*, members of two protein families: NRL (NPH3/RPT2-Like)
7 and PKS (PHYTOCHROME KINASE SUBSTRATE) are believed to be involved in
8 the early steps of phot-mediated signaling pathways inducing phototropism. NPH3
9 (NONPHOTOTROPIC HYPOCOTYL 3) [37,38], RPT2 (ROOT PHOTOTROPISM
10 2) [34,39], PKS1 [38,40,41], PKS2 [38] and PKS4 [30] are plasma membrane-
11 associated proteins that interact with phototropins.

12 NPH3 is essential for phototropism under a broad range of blue-light
13 intensities [37]. CP1 (COLEOPTILE PHOTOTROPISM 1), the ortholog of NPH3 in
14 rice (*Oryza sativa*), acts upstream of the formation of a lateral auxin gradient,
15 indicating that this protein has an early role in the pathway [42]. NRL family
16 members possess several protein–protein interaction domains, including a BTB
17 (broad complex, tramtrack, bric à brac) domain that is necessary for the interaction
18 between NPH3 and CULLIN3 (CUL3), a component of CULLIN3-based E3 ubiquitin
19 ligase complexes (CLR3) [43]. CLR3^{NPH3}-dependent mono/multi-ubiquitination was
20 proposed to result in clathrin-mediated phot1-relocalization into the cytoplasm, which
21 may regulate phototropism. In addition, CLR3^{NPH3} was suggested to control the
22 subcellular localization of phototropism signaling components, such as polar auxin
23 transporters [43].

24 The expression of the *RPT2* gene is enhanced by light, correlating with a role
25 for RPT2 specifically during high-light-induced phototropism [39,44]. Although the

1 biochemical function of RPT2 is unknown, based on sequence similarity with NPH3,
2 it can be hypothesized that this protein also acts as a CRL3 subunit. Another member
3 of the NRL protein family, NPY1 (NAKED PINS IN YUC MUTANT1, also known
4 as MAB4, MACCHI-BOU 4), functions together with the AGC kinase PID (PINOID)
5 to regulate localization of auxin transporters in organ formation and gravitropism
6 [45,46]. These results suggest that the NRL proteins together with AGC kinases play
7 a global role in regulating auxin transport in response to developmental and external
8 signals [22].

9 Phototropism also requires proteins belonging to the PKS family: PKS1,
10 PKS2 and PKS4 [40]. These proteins contain no domain of known biochemical
11 activity and their function in phototropism remains poorly understood, except that
12 they interact with the phototropins and NPH3 [38,40]. Expression of *PKS1* is rapidly
13 enhanced upon plant exposure to light [47], whereas abundance of *PKS4* mRNA is
14 down-regulated in response to light [48]. However, *PKS1* and *PKS4* share similarity
15 in terms of spatial pattern of expression, with high levels within the hypocotyl
16 elongation zone [47,48]. Recently, it has been shown that PKS4 is phosphorylated by
17 phot1 [30]. In the dark, PKS4 is present as a single isoform (PKS4D), whereas within
18 seconds of blue-light illumination, PKS4 is phosphorylated in a phot1-dependent
19 manner leading to the appearance of a second isoform (PKS4L) [30]. Although PKS4
20 is required for a full phototropic response, this recent study suggests that the PKS4L
21 negatively regulates phototropism [30,40]. Interestingly, the ratio of PKS4L and
22 PKS4D is controlled by both phot1 and the phytochromes (see below).

23 Formation of a lateral auxin gradient across the hypocotyl requires polar auxin
24 transporters (PAT), but how phototropin activation regulates auxin gradient formation
25 remains contentious [4,10,15,49,50]. Three PAT families have been implicated in

1 phototropism: the AUX1 (AUXIN RESISTANT 1) family, ABC transporters
2 (primarily ABCB19) and auxin efflux carriers of the PIN (PIN-FORMED) family (in
3 particular PIN1 and PIN3) [4]. The precise role that the members of these three
4 classes of PAT play in phototropism is beyond the scope of this review. Somewhat
5 surprisingly there are no reports of the PAT mutant strongly affecting phototropism,
6 and in most cases PAT mutants have phenotypes restricted to specific light conditions
7 [4,10,15,50].

8 Sensing the lateral auxin gradient to initiate phototropism involves both ABP1
9 (AUXIN BINDING PROTEIN 1) [51] and the TIR1/AFB (TRANSPORT
10 INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX) family of auxin receptors,
11 which regulate transcription by degrading Aux/IAA (AUXIN/INDOLE-3-ACETIC
12 ACID) proteins in an auxin-dependent manner [52,53]. MSG2/IAA19 is of particular
13 interest in the context of tropic growth responses because the dominant negative non-
14 degradable mutant shows reduced gravi- and phototropism [20]. IAA19 interacts with
15 and inhibits the activity of ARF7/NPH4, a transcription factor that regulates the
16 expression of genes required for asymmetric hypocotyl growth [20,21,54].

17

18 **Role of phytochromes in mediating phototropism in cryptogams**

19 Apart from blue light, unidirectional red light also induces positive phototropism in
20 the apical cells of the gametophyte in mosses and ferns. This phototropic growth in
21 red light is reversed by far-red light, hence mediated by phytochromes [3]. The
22 photoreceptor phy3 in the fern *Adiantum capillus-veneris* comprises a unique
23 combination of phytochrome and phototropin protein structures that controls
24 phototropism [55]. The amino terminus of the protein contains a phy photosensory
25 domain and the carboxyl terminus resembles full-length phototropin with functional

1 LOV domains, indicating that phy3 is a red and blue photoreceptor [55]. Expression
2 of phy3 in *Arabidopsis* rescues the phototropic defect of the *phot1-5 phot2-1* double
3 mutant and confers these plants with the ability to grow towards unidirectional red
4 light [56]. This experiment suggests the evolutionary conservation of the signaling
5 elements acting immediately downstream of the photoreceptor. These chimeric
6 receptors, known as neochromes, are only present in a subset of fern species
7 ('polypodiaceous' ferns) [55]. This dual color phototropism photoreceptor greatly
8 enhances the light sensitivity of *Adiantum*, thus potentially provides it with
9 physiological advantages under a dense canopy [55]. The filamentous green algae
10 *Mougeotia scalaris* also possesses two NEOCHROME-class photoreceptors (NEO1
11 and NEO2) that arose independently from fern neochrome [57]. No neochromes have
12 been identified in moss; however, *Physcomitrella patens* also grows towards red and
13 blue light and the phytochromes and phototropins interact physically [58]. These
14 examples argue in favor of evolutionarily conserved mechanisms connecting the two
15 classes of photoreceptors in the regulation of phototropism.

16

17 **Role of phytochromes and cryptochromes in the regulation of phototropism in** 18 **higher plants**

19 In angiosperms, phototropism is primarily induced by blue light, although in some
20 species red light induces a weak phototropic response that is also observed under
21 microgravity conditions in *Arabidopsis* [59]. Treating etiolated seedlings with red
22 light detected by the phytochromes enhances the magnitude of and accelerates blue-
23 light-induced phototropism [60-63]. Moreover, in response to continuous low-
24 intensity blue light (absence of red-light pretreatment), a *phyA* mutant shows strong
25 phototropic defects, a phenotype that is enhanced in the *phyA phyB* double mutant

1 [61,62,64-66]. However, phytochromes are not essential for phototropism because an
2 *Arabidopsis* mutant lacking all five phytochromes can still grow towards blue light
3 [67]. Under some light conditions the cryptochromes also become important for
4 efficient phototropism [68]. Finally, *phyA cry1 cry2* triple mutants and *phyA phyB*
5 *cry1 cry2* quadruple mutants show severe phototropic defects, indicating that the
6 combined activities of phytochromes and cryptochromes are required for robust
7 phototropism [5]. In the subsequent sections, we describe the molecular mechanisms
8 underlying phytochrome- and cryptochrome-mediated promotion of phototropism in
9 *Arabidopsis*.

10

11 **Regulation of gene expression by phytochromes and cryptochromes in response** 12 **to blue light**

13 Phytochromes and cryptochromes modulate phototropism through several direct and
14 indirect modes of action (Figure 2). How this occurs mechanistically is only starting
15 to emerge and it is important to begin by comparing the subcellular localization of
16 these photoreceptors (Figure 1). As discussed above, the phototropins localize at the
17 plasma membrane and are partially released into the cytosol upon blue-light
18 treatment. Phytochromes are primarily cytosolic in the dark and a fraction is imported
19 into the nucleus upon activation [8,69]. Cryptochromes are nuclear proteins although
20 a fraction of *cry1* is released into the cytosol upon light activation [70]. Importantly,
21 the primary site of action of both phytochromes and cryptochromes is the nucleus,
22 although they also act in the cytosol [70-73]. Both photoreceptor families are engaged
23 in the control of light-regulated gene expression [6,7]. Expression of the phototropism
24 signaling components *PKS1* and *RPT2* is strongly and rapidly (within one hour)
25 induced by blue light, a response that depends on *phyA* and the cryptochromes

1 [5,40,74]. Importantly, constitutive expression of *RPT2* partially complements the
2 *phyA cry1 cry2* triple mutant phototropic phenotype, demonstrating the importance of
3 the phy- and cry-mediated transcriptional response for efficient phototropism [5]. It
4 was initially proposed that phyA primarily acts in the cytosol to promote
5 phototropism [66]. This conclusion was based on the finding that a double mutant
6 strongly impaired in phyA nuclear import (*fhy1 fhl*) shows robust hypocotyl
7 phototropism, whereas in *phyA*, phototropic bending is reduced [66]. This issue was
8 re-evaluated by comparing the above-mentioned genotypes with seedlings expressing
9 a constitutively nuclear form of phyA, phytochrome A-nuclear localization signal
10 (phyA-NLS) [74]. Time-course analyses have shown that phototropism in the *fhy fhl*
11 double mutant is slow, whereas in phyA-NLS seedlings it is faster than in the wild
12 type [74]. This shows that nuclear phyA plays a primary role in controlling
13 phototropism. Moreover, it suggests that one mechanism by which a red-light
14 pretreatment accelerates phototropism is to induce phyA nuclear import and phyA-
15 regulated gene expression [74]. The greater phototropic response of the *fhy1 fhl*
16 double mutant compared with *phyA* could be due to at least two reasons. First, the
17 expression of phyA-regulated genes is still partially functional in the *fhy1 fhl* double
18 mutant, indicating that phyA nuclear signaling is not totally eliminated in this mutant
19 [74]. Second, phyA may play additional roles in the cytosol [66].

20

21 **Role of cytosolic phytochromes in mediating phototropism**

22 Cytosolic phyA modulates the light-induced relocalization of phot1. Indeed, a red-
23 light pretreatment inhibits the release of phot1 into the cytosol that occurs upon phot1
24 activation [35]. This red-light effect depends on phyA and is most efficient when it
25 occurs between 1 and 2 hours before turning on blue light. The functional significance

1 of phot1 relocation is not settled yet, but if one assumes that release of phot1 into
2 the cytosol is a desensitization mechanism, the phyA-mediated maintenance of phot1
3 at the plasma membrane would enhance phototropism [35]. How does phyA control
4 phot1 localization? It is possible that phyA-mediated gene expression leads to the
5 production of a component modulating phot1 subcellular localization given that a red-
6 light treatment is most effective when given 1–2 hours before phototropic stimulation.
7 Alternatively, the control of phot1 localization may involve direct contact between the
8 two classes of photoreceptors. The presence of hybrid phy–phot photoreceptors,
9 known as neochromes, in several species can be considered as an evolutionary
10 'Rosetta Stone', indicating the need for interaction between these two proteins [57,75].
11 This argument is supported by the interaction between phytochrome in its activated
12 state and phototropins at the plasma membrane in moss [58]. With the aid of a split
13 yellow fluorescent protein experiment, this study also demonstrated that *Arabidopsis*
14 phot1 and phyA bind to each other, suggesting that these photoreceptors also form a
15 complex in angiosperms [58].

16 The study of PKS4 phosphorylation provides another example of a potential
17 role for cytoplasmic phytochromes. Blue-light-activated phot1 phosphorylates PKS4
18 leading to the transient appearance of PKS4L (a light-specific phosphorylation state
19 of PKS4). PKS4L is rapidly dephosphorylated by type-2 phosphatases, a modification
20 that is enhanced by phytochromes [30]. Given that PKS4L has been proposed to
21 inhibit phototropism, phytochrome-enhanced dephosphorylation of PKS4L may
22 contribute to phototropism enhancement [30]. Whether phytochrome promotes this
23 modification of PKS4 directly in the cytosol or indirectly by controlling the
24 expression or translation of components regulating the phosphorylation state of PKS4

1 remains an open question [73]. In summary, it is likely that phytochromes enhance
2 phototropism by multiple mechanisms occurring in the nucleus and the cytosol.

3

4 **Phytochrome and cryptochromes regulate the formation and interpretation of** 5 **auxin gradients**

6 Light conditions modulate auxin transport and content in the hypocotyl. When
7 etiolated seedlings are irradiated with red and/or blue light, free IAA levels decline in
8 a phy- and cry-dependent manner [76]. In addition, in response to illumination,
9 phytochromes regulate basipetal auxin transport in the hypocotyl of *Arabidopsis* and
10 tomato [76,77]. Regulation of basipetal auxin transport is in part due to the
11 phytochrome-mediated inhibition of ABCB19 accumulation in light-grown
12 hypocotyls [76]. ABCB19 activity is also inhibited by phot1-mediated
13 phosphorylation, providing a striking example of photoreceptor co-action [15].
14 Inhibition of ABCB19 reduces basipetal auxin transport, leading to a higher auxin
15 concentration at the hypocotyl tip, which favors lateral redistribution and, thus,
16 asymmetric growth [15,76]. The expression of several members of the PIN family is
17 upregulated by light and the phytochromes contribute to this regulation in some
18 conditions [36,78]. This might contribute to phy-mediated enhancement of
19 phototropism, but this hypothesis requires further investigation.

20 Upon light perception, phytochromes also control the expression of genes
21 involved in auxin signaling [79]. Of particular interest in the context of phototropism
22 is *IAA19/MSG2*, which codes for an inhibitor of phototropism and is down-regulated
23 when etiolated seedlings are exposed to light [20,79]. The activation of phytochromes
24 may therefore not only regulate the formation of the auxin gradient but also the
25 transcriptional response induced by this gradient. Indeed, *IAA19* inhibits

1 NPH4/ARF7, which is required for tropic responses in hypocotyls, and the *nph4*
2 phenotype can be suppressed by a red-light treatment sensed by phyA [80].
3 Phytochrome-controlled gene expression might therefore modulate the formation of
4 the auxin gradient and its transcriptional readout.

5

6 **Promotion of phototropism by inhibition of gravitropism**

7 Phytochromes and cryptochromes both inhibit negative gravitropism in etiolated
8 seedlings emerging into the light [9,62,65,81,82]. Several studies have suggested that
9 by inhibiting gravitropism, phytochromes and cryptochromes promote phototropism
10 [9]. Indeed, *phot1* mutant hypocotyls are agravitropic in low blue light but gravitropic
11 in dark conditions. The former phenotype can be rescued by mutating phyA and/or
12 the cryptochromes indicating that phytochromes and cryptochromes inhibit negative
13 gravitropism in hypocotyls under light-grown conditions [65,82]. A crucial test for
14 this model is to perform phototropism experiments in microgravity conditions. A
15 recent experiment conducted in the International Space Station presents evidence for
16 enhanced phototropism under microgravity conditions; however, additional
17 experiments are needed to confirm this [83].

18 Although light plays the predominant role in determining hypocotyl growth
19 direction, light-grown seedlings must somehow integrate light and gravity to guide
20 growth. Recently, it has been reported that upon light activation, phytochromes lead
21 to the conversion of starch-filled gravity-sensing endodermal amyloplasts to other
22 plastids with chloroplastic features, thereby suppressing negative gravitropism [84].
23 Moreover, the crosstalk between gibberellic acid (GA) and IAA signaling pathways
24 also aids in coordinating the responses to light and gravity. Indeed, GA inhibits
25 gravitropism by controlling the expression of IAA genes, including *IAA19*. This GA-

1 mediated control of gravitropism was proposed to enhance the phototropic potential
2 [85]. Another study has proposed a more direct role for GA in phototropism
3 modulation by showing that phytochromes and cryptochromes control GA levels and
4 signaling, thereby tuning tropic growth [5]. Based on the available data we can
5 conclude that phytochromes and cryptochromes promote phototropism at different
6 levels, including inhibition of gravitropism.

7

8 **Outlook**

9 Despite the progress made in unraveling the molecular mechanisms underlying
10 photoreceptor crosstalk, we still lack sufficient spatial and temporal resolution of key
11 events leading to phototropism. The site of phot-mediated light perception in dicots
12 remains unclear. Moreover, it is unknown whether cryptochromes and phytochromes
13 act in the presumptive light-sensing hypocotyl apex and/or in the elongation zone
14 undergoing asymmetric growth. Such information is important to elucidate
15 photoreceptor crosstalk at the molecular level. Another important issue remains the
16 integration of gravitropic and phototropic signals, which ultimately control hypocotyl
17 growth direction. Finally, understanding the regulation of auxin fluxes by external
18 stimuli with cellular resolution is required to propose an integrated hypocotyl tropic
19 model.

20 Phytochrome modulation of phototropin-regulated processes has also been
21 reported for additional physiological responses that contribute to photosynthesis
22 optimization. Examples include the regulation of chloroplast position, stomata
23 opening and leaf flattening [38,86-90]. An important question for the future is
24 whether photoreceptor crosstalk mechanisms, discovered while studying
25 phototropism, also operate during other phototropin-regulated responses.

1

2 **Acknowledgments**

3 We thank Séverine Lorrain, Emilie Demarsy, Paolo Schumacher and Tobias Preuten
4 for helpful comments on the manuscript. We thank the University of Lausanne and
5 the Swiss National Science Foundation (Grant no. FNS 310030B_141181/1) for
6 funding.

7 **Conflict of interest: None declared**

8

9

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8

9 **Box 1. Roots, petioles and inflorescence stems exhibit phototropism**

10 Most phototropism experiments are performed with etiolated seedlings (which are
11 exposed to light for the first time). However, de-etiolated seedlings also exhibit
12 asymmetric growth in response to unilateral irradiation [15] (Figure 1). In addition,
13 leaf petioles and inflorescence stems also exhibit asymmetric growth upon unilateral
14 blue-light irradiation [91]. In hypocotyls, *phot1* has been shown to determine
15 phototropic response under a wide range of blue-light intensities (0.01–100.00 μmol
16 $\text{m}^{-2} \text{s}^{-1}$), whereas *phot2* induces hypocotyl bending when irradiated with high blue-
17 light fluence rates ($\geq 1 \mu\text{mol m}^{-2} \text{s}^{-1}$) [92]. Similarly, in stems, *phot1* plays a major
18 role in phototropic responses, whereas *phot2* acts redundantly under high light
19 conditions. However, the inflorescence stems show phototropic responsiveness to
20 blue light along their entire length and phototropic bending occurs slightly below the
21 unilaterally irradiated area. By contrast, in petioles, blue-light treatment applied from
22 the abaxial (lower) side, but not from the adaxial (upper) side of the leaf results in
23 petiole bending [91]. As far as we know, the impact of red light on the phototropism
24 of petioles and inflorescence stems has not been studied to date.

25 In contrast to aerial plant organs, many roots irradiated with unilateral blue
26 light show a negative phototropic response (away from the light source) [44,93]. This

1 mechanism, together with positive gravitropic and hydrotropic responses [94],
2 maintains roots embedded in soil and thereby facilitates efficient water and nutrient
3 supplies for plant growth [95]. Perception of the directional blue-light stimuli in roots
4 depends on phototropins [44]. Mutation in PHOT1 enhances randomization of root
5 growth orientation, which results in less-efficient soil penetration [95]. Roots do
6 exhibit positive phototropism when exposed to unilateral red light, although this
7 response is relatively weak compared with the effect of blue-light wavelengths. In
8 addition, red light absorbed by phytochrome photoreceptors modulates blue-light-
9 induced root phototropism because roots of the phyA mutants show reduced response
10 to unilateral blue light [96]. Analysis of *Arabidopsis* lines expressing functional
11 phytochromes in a tissue-specific manner demonstrated that perception of red light,
12 inducing root phototropism, occurs within this organ [97]. It remains to be tested
13 whether induction of blue-light-dependent negative phototropism in roots depends on
14 perception of blue-light wavelengths by root-localized phototropins [16].

15

1 **Glossary**

2 **De-etiolation:** a series of physiological and biochemical changes in seedlings
3 emerging into sunlight. It includes, among other processes, inhibition of hypocotyl
4 elongation, opening of the apical hook, and chloroplast maturation.

5 **Etiolation:** developmental program in dark-grown seedlings (includes long and thin
6 hypocotyl, small cotyledons, absence of chloroplasts).

7 **Mono- or multi-ubiquitination:** ligation of a single ubiquitin moiety to a single or
8 multiple lysine residues.

9 **Polyubiquitination:** ligation of polyubiquitin chains to one or more lysine residues.

10 **Nomenclature of photoreceptors:** apoproteins are designated by capital letters such
11 as PHOT1. Apoproteins bind light-harvesting chromophores, thereby forming the
12 holoproteins that are represented in lower case letters such as phot1.

13

Table 1. Key players in phototropism discussed in this review

Step	Factors	Refs
Perception of light signal	Primary role	
	phot1, phot2	[92]
	Secondary role	
	phyA	[64,65]
	cry1, cry2	[68]
Signal transduction	NPH3	[37]
	RPT2	[44]
	PKS1, PKS2, PKS4	[40]
Formation of lateral auxin gradient	AUX1	[98]
	PIN1	[99]
	PIN3	[49,100]
	PIN7	[50]
	PGP19/ABCB19/MDR1	[15,76,101]
	IAA19/MSG2	[20]
	ABP1	[51]
	MSG1/ARF7/NPH4	[21]
TIR1	[52]	

14
15
16
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Figure legends

1 **Figure 1.** Hypocotyls of (a) de-etiolated and (b) etiolated *Arabidopsis* seedlings (left)
2 and their bending in response to unidirectional blue light (right). Arrow indicates the
3 direction of incoming blue light. Localization of photoreceptors controlling
4 phototropism (c) in the dark, and (d) upon exposure to light. In the dark, phototropins
5 (depicted in blue) are localized at the plasma membrane. A fraction of blue-light-
6 activated phot1 is released into the cytoplasm, whereas phot2 associates with Golgi
7 apparatus. Cryptochromes (depicted in navy blue) are primarily nuclear but a fraction
8 of cry1 is released into the cytosol upon light perception [70]. Phytochromes
9 (depicted in red) in the inactive red-light-absorbing form of phytochromes (Pr) (in the
10 dark) are present in the cytoplasm. Light absorption leads to conformational changes
11 (to the active far-red-light-absorbing form of phytochrome) and relocation to the
12 nucleus.

13
14 **Figure 2.** Schematic representation of cross-talk between phot- and phy-mediated
15 signaling implicated in phototropism. (a) Molecular interactions and processes (I to
16 IV) involving phot1 and phytochromes in the regulation of phototropism. (I.) PKS1
17 interacts with phyA, phot1 and NPH3 at the plasma membrane. PKS1 might be a
18 molecular link between the two photoreceptors that may also directly interact at the
19 plasma membrane in flowering plants. NPH3 binds to CUL3-based SCF complexes
20 and is involved in ubiquitinylation of phot1. (II.) Phot1 and phytochromes are
21 involved in regulating PKS4 phosphorylation status. (III.) Phot1 inhibits ABCB19 via
22 its phosphorylation. (IV.) Phytochromes enhance the expression of genes involved in
23 phototropism, such as of *IAA19*, *PKS1* and *RPT2*. On other hand, phytochromes
24 down-regulate the levels of *ABCB19*. (b) Modulation of phototropism by phy-
25 mediated inhibition of gravity-sensing. (V.) In response to light, phytochromes are

1 involved in the conversion of the starch-filled gravity-sensing endodermal
2 amyloplasts to plastids with chloroplastic features. The consequent suppression of
3 negative hypocotyl gravitropism enhances phototropism. (VI.) Phytochromes might
4 be involved in the regulation of expression of genes involved in the conversion of
5 different forms of plastids.
6

Figure 1

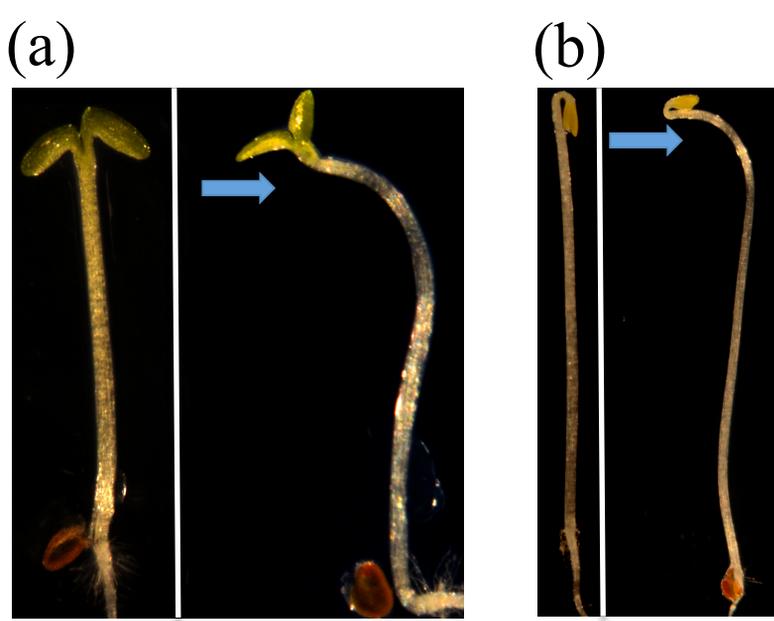
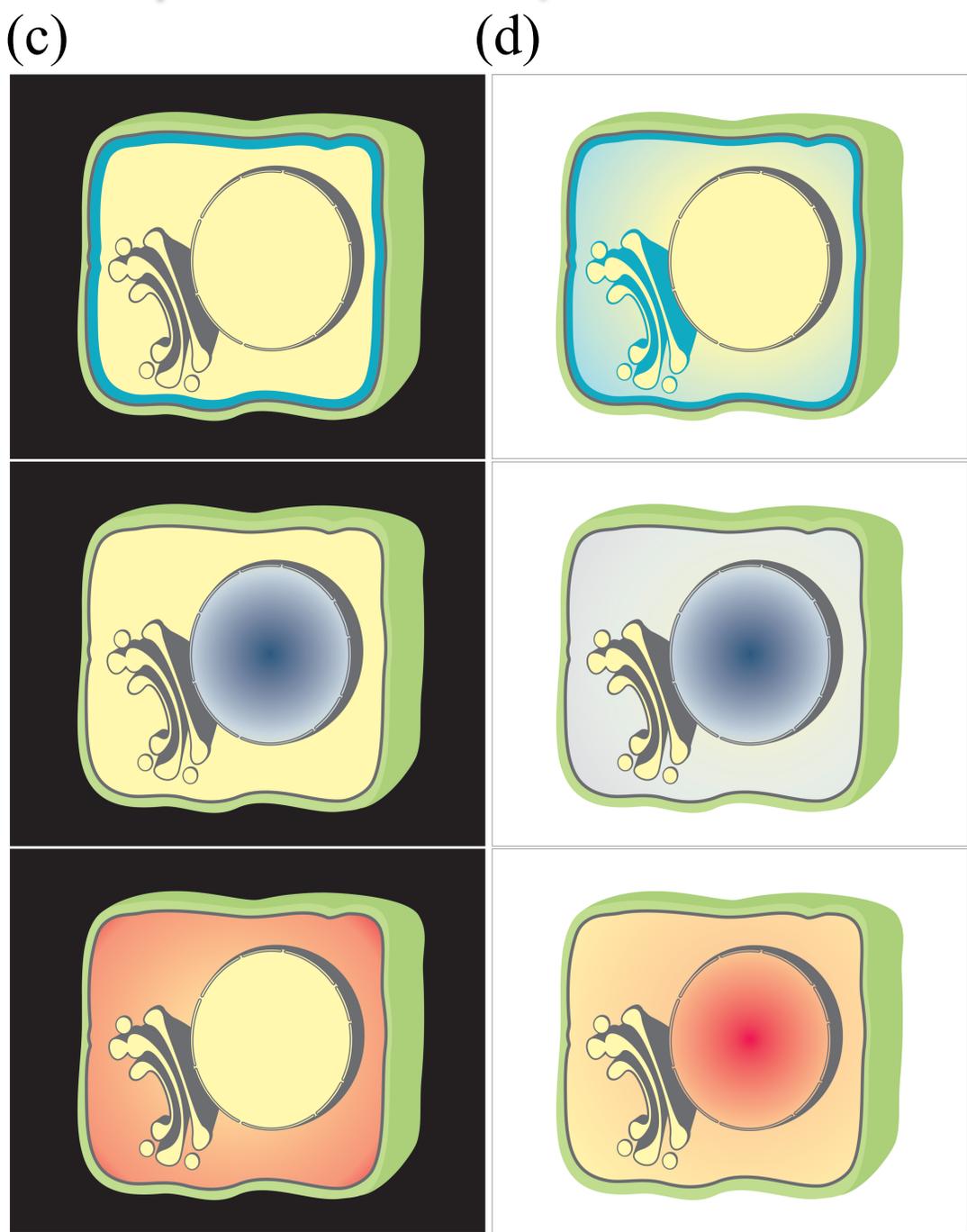


Figure 1.



■ Phototropins ■ Cryptochromes ■ Phytochromes

