

## Review

## Multiple Routes of Light Signaling during Root Photomorphogenesis

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Plants dynamically adjust their architecture to optimize growth and performance under fluctuating light environments, a process termed photomorphogenesis. A variety of photomorphogenic responses have been studied extensively in the shoots, where diverse photoreceptors and signaling molecules have been functionally characterized. Notably, accumulating evidence demonstrates that the underground roots also undergo photomorphogenesis, raising the question of how roots perceive and respond to aboveground light. Recent findings indicate that root photomorphogenesis is mediated by multiple signaling routes, including shoot-to-root transmission of mobile signaling molecules, direct sensing of light by the roots, and light channeling through the plant body. In this review we discuss recent advances in how light signals are transmitted to the roots to trigger photomorphogenic responses.

## Illuminating Root Photomorphogenesis

Light, in addition to its role as a primary energy source for photosynthesis, acts as a crucial environmental signal that profoundly influences various growth and developmental processes in plants. Prominent morphological and architectural changes occur when developing seedlings are exposed to light. In the darkness of the soil, hypocotyls elongate, cotyledons remain closed, and leaf greening is arrested [1,2], a suite of traits referred to as **skotomorphogenesis** (see Glossary). When skotomorphogenic seedlings are exposed to light as they emerge from the soil, they undergo a series of **photomorphogenic** responses, including deceleration of hypocotyl elongation, cotyledon opening, and leaf greening [3]. These morphogenic traits contribute to **photoautotrophic** growth and protect young seedlings from photo-oxidative damage [4].

Perception of light signals by photoreceptors initiates the photomorphogenic process. Plants possess multiple photoreceptors to efficiently perceive particular ranges of light wavelengths, such as far-red, red, blue, and UV light [5]. Phytochromes are red and far-red light-sensing photoreceptors that undergo reversible protein conformational changes induced by the red to far-red ratio [6]. Cryptochromes, phototropins, and ZEITLUPE proteins are blue light-sensing photoreceptors that regulate hypocotyl growth, **phototropism**, and photoperiodic flowering, respectively, but with some overlapping functions [7–11]. Plants also are able to perceive UV-B light as a photomorphogenic cue using the UV-B resistance 8 (UVR8) photoreceptor [12,13].

Photomorphogenesis is widely studied in shoots, where leaves are regarded as the major organ for light perception [14,15]. Notably, recent accumulating evidence demonstrates that the roots also experience dramatic changes in morphology and development in response to light, such

## Trends

Although the roots are embedded in the soil, they undergo photomorphogenesis when the shoots are exposed to light. There are three major routes of light signaling from the shoots to the roots: transmission of mobile signaling messengers, direct sensing of light by the roots, and light channeling through the plant body.

Phytohormones, photosynthetic compounds, mobile proteins, and RNA molecules are translocated from the shoots to the roots for balanced root/shoot growth and development.

Photoreceptors expressed in the roots directly perceive soil-penetrating light to regulate root growth, development, and tropic responses mostly via auxin and cytokinin signaling.

Recent breakthroughs identify a distinct route of light signaling during root photomorphogenesis in which the red and far-red light-sensing photoreceptor, phyB, perceives stem-piped light to trigger morphogenic responses in the roots.

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as primary root elongation, lateral root formation, negative phototropism, **gravitropism**, **root nodule** formation, nitrate uptake, **tuberization**, and greening [16–22]. Accordingly, plants lacking functional photoreceptors exhibit defects in root architecture as well as in shoot morphology [18,23]. This indicates that, while the roots are mostly embedded in the soil under natural conditions, they are able to directly or indirectly perceive light signals to trigger photomorphogenic responses. Therefore, mechanistic and photochemical studies of how roots perceive aboveground light information will enable a comprehensive understanding of the molecular events underlying root photomorphogenesis. In this review, recent advances in understanding root photomorphogenesis are highlighted with emphasis on the spatial organization of light perception and transmission of signaling messengers. Physiological roles of the root-perceived light signals are also discussed in terms of plant growth and environmental adaptation. In-depth discussion on root photomorphogenesis is particularly important because most studies on root growth and development have been performed using plants grown on culture media in the light.

## Transduction of Light Signals by Mobile Signaling Molecules

### Mobile Phytochemicals

Light directly or indirectly influences virtually all metabolic and physiological processes and morphological modifications occurring in both shoots and roots. Shoots clearly perceive aboveground light more efficiently than do roots that are buried in the soil. Therefore, it is not surprising that plants utilize mobile **phytochemicals** produced in the shoots to modulate root morphology and function.

The plant hormone **auxin** is an iconic long-distance signaling molecule that dramatically influences root growth and development by means of its polar transport [24]. The PIN-FORMED (PIN) transporters are responsible for auxin flow, and their localization in the plasma membranes directs the polar transport of auxin [25]. The light-induced auxin transport to the roots is associated with the CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) E3 ubiquitin ligase that functions as a master photomorphogenic repressor by degrading target proteins involved in light responses [26]. In darkness, COP1 mediates the transcriptional repression of the *PIN1* gene in the shoots, possibly by targeting the photomorphogenic inducer ELONGATED HYPOCOTYL 5 (HY5) [27]. In the light, COP1 function is suppressed [28], triggering the PIN1-mediated auxin flow to the roots.

The shoot-derived auxin induces the translocation of PIN transporters to the plasma membranes in root cells. When *Arabidopsis thaliana* seedlings are grown in darkness, the elongation of the primary root is arrested because most PIN1 and PIN2 transporters are localized to the vacuoles in the root cells [29]. However, when shoots are exposed to light, PIN transporters are relocalized to the plasma membranes of the root cells to trigger polar auxin transport, linking shoot-to-root auxin transport with light-induced primary root elongation.

**Jasmonic acid** (JA) is another phytohormone that links light perception in the shoots with root morphogenesis. *Lotus japonicus* phytochrome B (*phyB*)-deficient plants exhibit a reduction in root nodule formation [19]. The expression of JA-responsive genes is impaired in *phyB* mutants, and exogenous application of JA rescues the formation of defective root nodules in the mutants [19]. Of particular interest is that root nodule formation is regulated by shoot *phyB*, but not by root *phyB*, revealing that the photo-activated shoot *phyB* enhances JA signaling toward root photomorphogenesis.

Photosynthetic products are also potential candidates for the shoot-to-root mobile signaling messengers. It is known that photosynthetic metabolites play a role in modulating the function of the circadian clock in the roots [30]. The root circadian clock regulates lateral root emergence

## Glossary

**Auxin:** a class of plant growth hormones that regulate diverse cellular responses such as cell expansion, division, and differentiation.

**Cytokinins:** a class of plant hormones that regulate diverse cellular responses including cell division, shoot initiation, and embryonic development.

**Gravitropism:** a growth behavior of plants in response to gravity. While the roots grow toward gravity, the shoots grow against gravity.

**Jasmonic acid:** an organic compound synthesized in some plants that regulates growth and developmental processes as well as plant responses to biotic and abiotic stresses.

**Photoautotroph:** an organism, typically a plant, that obtains energy from sunlight to synthesize organic materials for their nourishment.

**Photomorphogenesis:** light-induced developmental and morphological processes of plants, which are represented by leaf greening, decelerated stem elongation, and cotyledon opening.

**Phototropism:** a growth behavior of plants in response to unidirectional light. While the shoots bend toward the unilateral light, the roots bend away from the light source.

**Phytochemicals:** naturally occurring chemicals produced in plants; these include inorganic and organic chemical compounds.

**Root nodule:** a specific organ formed in plant roots as a result of an association with symbiotic nitrogen-fixing bacteria. In the nodule, bacteria convert nitrogen gas into ammonia, and this is used by plants as a nitrogen source.

**Skotomorphogenesis:** developmental and morphological processes of plants, such as elongated hypocotyls and etiolated leaves, that take place in darkness.

**Tuberization:** a developmental process that induces differentiation of the stolon into tuber. The tuber is a storage organ that is present in several plant species including potato.

in arabidopsis [31]. Notably, the shoot circadian clock modulates the circadian rhythms in the roots through a hierarchical multi-oscillator network [32]. These observations suggest that the shoot-to-root transport of photosynthesis-related signals contributes to the synchronization of clock functions in the roots and shoots, a result consistent with the observation that the function of the root clock is disrupted by exogenous applications of sugars [30].

#### Mobile Proteins and RNA Molecules

Mobile signaling proteins and RNA molecules are known to mediate the transduction of shoot-to-root light signals in various plant species. The HY5 transcription factor is a pivotal photomorphogenic inducer [27] which is degraded by COP1-mediated ubiquitination pathways in darkness [33]. Light stabilizes the HY5 protein by suppressing COP1 activity, thereby enhancing photosynthetic capacity and sucrose translocation to sink organs in the shoots [34].

Interestingly, the photo-activated HY5 protein moves from the shoots through the phloem to the roots, where shoot-derived HY5 induces transcription of the *HY5* gene [20]. The shoot-derived HY5 transcription factor also promotes nitrate uptake in the roots by directly activating the *NITRATE TRANSPORTER 2.1* gene in the roots. It is apparent that shoot-to-root mobilization of HY5 facilitates nutrient balance by simultaneously controlling carbon assimilation in the shoots and nitrate uptake in the roots.

In tomato (*Solanum lycopersicum*), a shoot-derived protein regulates auxin responses in the roots [35]. The tomato *Cyclophilin 1* (*Cyp1*) gene encodes a peptidyl-prolyl *cis/trans* isomerase that functions in auxin signaling by degrading auxin signaling mediators, AUX/indole acetic acid (IAA). Tomato *diageotropica* mutants harboring a *cyp1* mutation exhibit defects in root morphogenesis, such as secondary root growth and lateral root formation [35]. Notably, the shoot Cyp1 protein moves through the phloem to the roots, and this process is accelerated in response to increasing light intensity. These observations indicate that the light intensity-dependent shoot-to-root translocation of the Cyp1 protein links the aboveground light perception with auxin-mediated root morphogenesis.

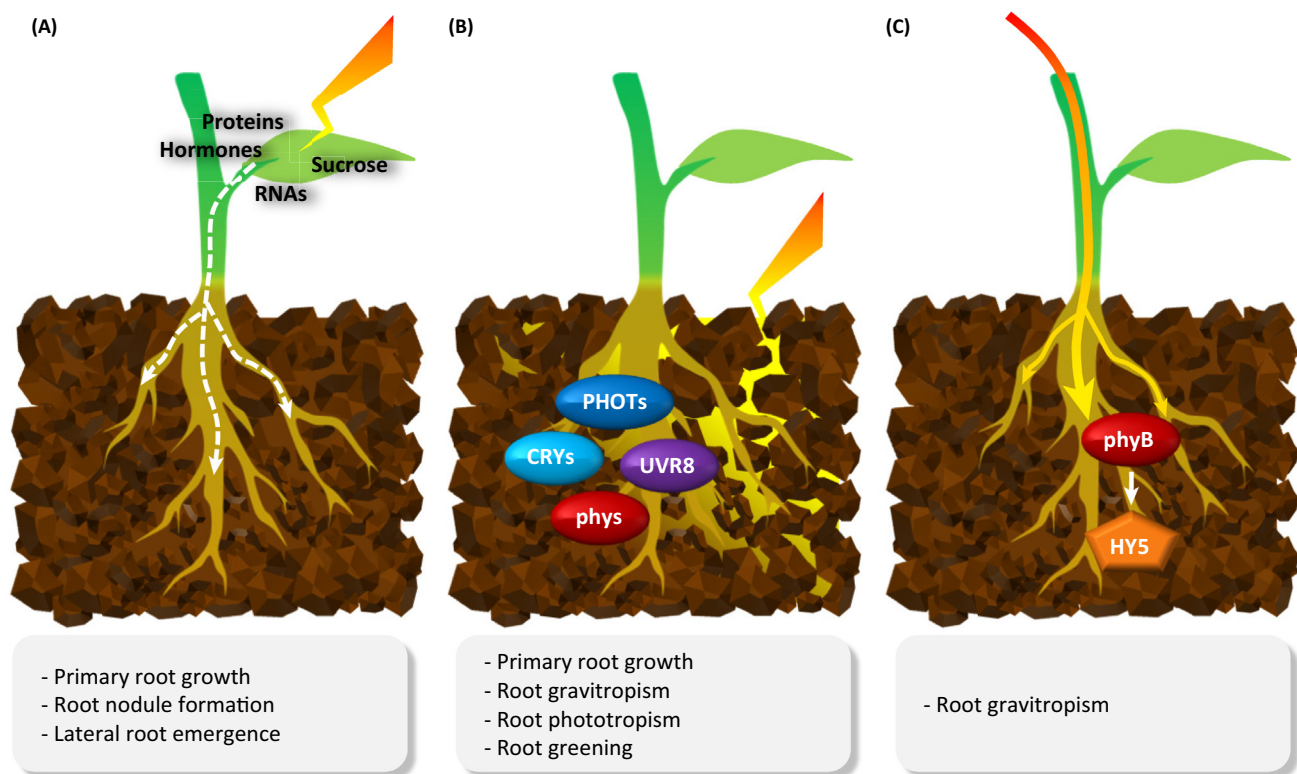
In potato (*Solanum tuberosum*), aboveground light affects the tuberization process that occurs in the underground stolons, a distinct type of stems. While stolons are not roots, it is worth describing them because mobile light-signaling molecules from the shoots affect the underground organ [36]. It is known that SELF-PRUNING 6A (SP6A), an arabidopsis FLOWERING LOCUS T (FT)-like protein, acts as a mobile light-signaling molecule in the tuberization process [36]. FT is a well-known mobile protein that induces flowering initiation, thus termed florigen [37]. Similarly, potato SP6A protein is often called tuberigen [36]. SP6A-mediated tuberization is affected by daylength changes. While long-day conditions inhibit tuberization, short-day conditions promote it [34,36,38], suggesting that under short days the activated SP6A proteins are translocated from the shoots to the underground stolon tips [36,38,39].

Shoot-to-stolon signaling plays an important role in the potato tuberization process in which the potato BEL1-like transcription factor BEL5 is key [40]. The expression of the *BEL5* gene is induced in shoots under short days [41]. Notably, *BEL5* mRNA molecules produced in the phloem cells of the shoots migrate to the tips of stolons, where BEL5 proteins are produced. BEL5 and its interacting partner POTATO HOMEODOMAIN BOX1 suppress the production of gibberellic acid to adjust the orientation of cell growth to induce tuberization in the stolon tips [41]. Hence, it is thought that potato stolons perceive light information via mobile RNA molecules to promote tuber formation.

Because plants are sessile organisms, shoot-to-root transmission of mobile light signaling molecules is crucial for balanced root/shoot growth and development [20] (Figure 1A, Key

## Key Figure

## Routes of Light Signal Transduction Mediating Root Photomorphogenesis



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Figure 1. For a Figure360 author presentation of Figure 1, see <http://dx.doi.org/10.1016/j.tplants.2017.06.009#mmc1>.

(A) Shoot-to-root transmission of mobile signaling messengers. In response to light, various molecules and metabolites, such as phytohormones, sucrose, RNAs, and proteins, are produced in the shoots and mobilized to the roots, where they trigger photomorphogenic responses including primary root growth, root nodule formation, and lateral root emergence. (B) Direct sensing of light by the roots. Aboveground light can penetrate at least several millimeters into the soil under natural conditions. Some plant species develop aerial roots in tropical areas. Under these circumstances, the roots are exposed to light. Root photoreceptors, such as phytochromes (phys), cryptochromes (CRYs), phototropins (PHOTs), and ultraviolet-B resistance 8 (UVR8), directly perceive light to trigger root photomorphogenesis, including primary root growth, root greening, and tropic responses. (C) Light channeling through the plant body to the roots. Aboveground light is conducted through the plant body, possibly via the vascular tissues, to the roots. The photoactivated root PhyB and its downstream regulator HY5 modulates root gravitropism.

Figure), which in turn is important in optimizing productivity and adaptation to fluctuating light conditions [35,41].

### Direct Sensing of Light by the Roots

Photoreceptor genes are expressed at a significant level in the roots [42]. Numerous studies, including those using direct illumination of the roots and grafting of root-specific photoreceptor-deficient plants [19,29,42], indicate that root photoreceptors are functional in sensing the aboveground light.

Several plant species in tropical areas develop aerial roots to avoid oxygen deprivation caused by flooding of the roots [43–46]. The photoreceptors in these aerial roots are able to perceive light [22,47]. Meanwhile, light can penetrate at least several millimeters into the soil, depending on soil type and water content, and thus roots growing in a loose soil consisting of larger particles or in dry soil are exposed to ambient light [48], further indicating that root photoreceptors are able to perceive light signals under natural conditions.

Both shoot and root photomorphogenesis are largely disrupted in the absence of phytochromobilin, a chromophore molecule that absorbs light to trigger conformational changes in the phytochrome photoreceptors [49–51]. Consequently, arabidopsis *hy2* mutants with defects in phytochromobilin biosynthesis exhibit an elongated primary root in the light [47]. Notably, root-specific inactivation of phytochromobilin biosynthesis induces primary root elongation [47], revealing that it is the root phytochromes, not the stem phytochromes, that suppress primary root elongation. Studies on the effects of light on root growth using phytochrome-deficient mutants show similar results. While exposure of dark-grown roots of wild-type seedlings to red light inhibits primary root elongation, such an inhibitory effect does not occur in the seedlings of *phyA*-, *B*-, or *D*-deficient mutants [18], supporting the notion that root phytochromes suppress the elongation of primary roots.

Phytochromes also play a role in the regulation of root gravitropism by light [18]. The *phyB* mutants and *phyAB* double mutants exhibit disturbed root gravitropism under red light conditions [18], consistent with the hypothesis that these phytochromes mediate the effects of light on root gravitropic responses.

Blue light affects growth, greening, and phototropic responses of roots. Under blue light conditions, the primary root phenotypes of cryptochrome 1 (*CRY1*)- and *CRY2*-deficient mutants differ dramatically. While *cry1* mutants exhibit short primary roots, the primary roots of *cry2* mutants are longer than those of wild-type plants [23]. However, the cryptochrome-mediated regulation of root growth could be indirect in that the application of auxin transport inhibitors abolishes the altered primary root phenotypes of the *cry* mutants [23]. *CRY1*, together with *phyA* and *phyB*, is also involved in blue light-induced root greening [22]. Chloroplast development and chlorophyll biosynthesis, which are triggered by prolonged exposure of the roots to blue light, are markedly reduced in the roots of *cry1* and *phyAB* mutants [22].

The root-localized phototropin 1 (*PHOT1*) plays a major role in the negative phototropic responses of roots. In *PHOT1*-deficient mutants, negative phototropism of the roots is largely disrupted [52,53]. It is known that blue light-activated *PHOT1* induces the localization of the auxin efflux carrier *PIN2* to the plasma membrane of root cells [52]. The *PIN2*-mediated auxin gradient then triggers localized cell elongation in the roots, resulting in negative phototropism [52]. *PHOT1* also plays a role in the primary root growth [54]. It has been proposed that blue light-activated *PHOT1* promotes downward root growth from the soil surface under drought conditions, indicating that *PHOT1*-mediated root growth enhances adaptive root responses to drought stress [54].

Notably, blue light responses of the roots are mediated by phytohormones, including **cytokinins** and auxins. Cytokinins are known to promote the production of flavonols in the illuminated side of the roots during negative phototropism [17]. Flavonols promote cell differentiation to help the roots to grow rapidly away from blue light. Cytokinins are also involved in blue light-mediated root greening [22,55]. When the roots are exposed to blue light, cytokinins promote the accumulation of *HY5* and *GOLDEN 2-LIKE 2* (*GLK2*) transcription factors, leading to root greening. Notably, the roles of cytokinins are antagonistically regulated by auxin during root greening. Shoot-derived auxin suppresses the accumulation of *HY5* and *GLK2* in the blue

light-illuminated roots [55]. It is likely that signaling crosstalk between cytokinins and auxin modulates the blue light responses of the roots.

Plant roots also perceive UVB in the wavelength range of 280–320 nm. While high fluence rates of UVB cause damage to plant cells, plants perceive low fluence rates of UVB as a signal for photomorphogenesis [56–58]. Recently, it has been reported that arabidopsis roots exhibit negative phototropism in response to low fluence rates of UVB [56]. Unilateral illumination of UVB to the roots triggers auxin accumulation in the shaded side. As a result, the roots bend away from UVB because auxin inhibits cell elongation in the roots [20,56,59]. It has been proposed that polar auxin transport during root phototropism is mediated by UVB-induced endocytic vesicle recycling [56].

ROOT UV-B SENSITIVE 1 (RUS1) and RUS2 have been identified as root-specific proteins that eliminate UVB-induced growth suppression in the roots [60,61]. Accordingly, in *rus1* and *rus2* mutants root growth and development are disrupted under UVB conditions. However, it is currently unclear which photoreceptor(s) is responsible for the RUS-mediated regulation of root growth [61]. In arabidopsis, UVB is perceived by the UVR8 UVB receptor [12,62]. While UVR8-deficient mutants do not exhibit any alterations in root growth under low fluences of UVB, UVR8-overexpressing plants exhibit a reduction in primary root growth and lateral root development under the identical light conditions, and this may result from increased levels of flavonoids that modulate auxin transport [62].

It is now apparent that root photoreceptors are able to perceive the aboveground light to regulate root growth and developmental processes and tropic responses (Figure 1B), and that these photomorphogenic responses are at least in part mediated by auxin and cytokinins. An important inference from these results is that root phenotypes of plants grown on media where the roots are exposed to light should be interpreted with caution [63].

### Light Channeling to the Roots

It has long been suggested that light might be transmitted through the stems, possibly via the vascular tissues, to the roots [64,65]. Indeed, previous studies indicate that light is transmitted through the stems and roots in various plant species, including oat, mung bean, corn, and many other herbaceous and woody plants [64,65]. However, how the stem-piped light is perceived by the roots, and whether the root-sensed light influences root morphogenesis, remained elusive until recently.

A recent optical study demonstrates that light is transmitted through the stems to the roots, and that the stem-piped light activates root phyB in arabidopsis [42]. The photo-activated root phyB is localized in the nucleus and induces transcription and protein stabilization of the HY5 transcription factor [27]. That the photo-activated molecular events in the root cells are triggered by stem-piped light is clear because they still occur when light transmission through soil particles is completely blocked. Moreover, the light responses disappear in roots lacking functional phyB, confirming that stem-piped light triggers light responses in the roots (Figure 1C).

Root phyB and its downstream signaling mediators, such as HY5, are known to regulate root gravitropism [18,42]. Under red light conditions, the roots of arabidopsis phyB-deficient mutants exhibit disturbed gravitropic responses [18]. It is known that HY5 overproduction induces root gravitropism even in darkness [42], showing that stem-piped light triggers root gravitropic responses by activating root phyB, which in turn activates HY5. While it is known that the HY5 protein moves from shoots to roots [20], it is currently unclear whether this shoot-derived HY5 plays a role in inducing root gravitropism.

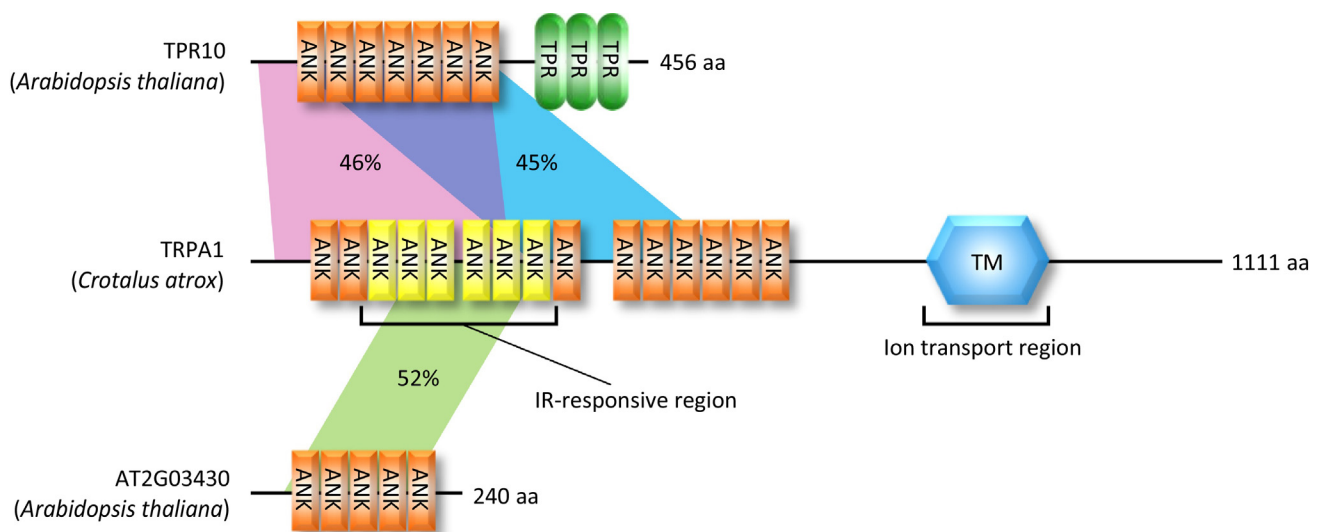
Light is transmitted through plant body to the roots in herbaceous and woody plants [64,65]. The wavelength of the transmitted light ranges from green to IR, with longer wavelengths being transmitted more efficiently [42,64,65]. On the basis of the optical properties of water that efficiently guides light transmission, it is likely that the vascular bundles serve as the primary routes for light channeling to the roots. It has been reported that phytochromes and cryptochromes located in the vascular tissues play a crucial role in plant development [14,66]. It will be interesting to investigate whether stem-piped light also activates the photoreceptors located in the vascular bundles.

### Spectral Properties of Stem-Piped Light

In arabidopsis, the stem-piped light has a distinct spectral pattern: light in a wavelength range of far-red (710–850 nm) to near-IR (850–1000 nm) is efficiently transmitted through the stems [42]. In addition, the transmission efficiency is related with wavelengths: the intensity of near-IR wavelengths is at least fivefold higher than that of far-red wavelengths in the stem-piped light.

While it is clear that root phyB perceives stem-piped light to activate HY5 in the roots, it is unknown whether near-IR light channeled through the stems influences root morphology and physiology. One possibility would be that the Pfr forms of phytochromes sense near-IR light, as has been proven in some diatom species [67]. Because the spectrum of sunlight includes IR light wavelengths longer than 1000 nm, it is likely that IR light would also be efficiently transmitted to the roots. If this is the case, distinct root photoreceptors other than phyB would be more likely to sense IR light to trigger light responses in the roots. IR is frequently considered as thermal radiation in living organisms [68]. Therefore, it is possible that the roots might monitor changes in aboveground temperatures by sensing IR light.

While the pathways underlying near-IR or IR light responses remain unknown in plants, the physiological roles of IR light perception have been characterized at the molecular level in



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**Figure 2. Amino Acid Sequence Analysis of Rattlesnake TRPA1 Homologs in Arabidopsis.** The amino acid sequence of rattlesnake TRPA1 was used as a bait for BLAST analysis against arabidopsis protein sequences deposited in NCBI databases. Arabidopsis TPR10 has a sequence similarity of ~45% to the N-terminal region of the rattlesnake TRPA1 protein, which is known to sense IR light. The arabidopsis AT2G03439 protein has a higher sequence similarity of 52% to the IR light-sensing region of TRPA1. Protein domains were analyzed using the SMART program (<http://smart.embl-heidelberg.de>). The two arabidopsis homologs of TRPA1 have not yet been functionally characterized. Abbreviations: ANK, ankyrin repeat domain; arabidopsis, *Arabidopsis thaliana*; TM, transmembrane domain; TPR, tetratricopeptide repeat domain.

animals. In snakes, including vipers, pythons, and boas, IR light is perceived at the pit organs located on their face [68,69]. The IR-sensing receptors are known to play a role in the recognition of prey movement and in thermoregulation of body temperature [70]. Upon sensing IR light, the IR receptors are thermally activated to evoke currents in sensory neurons to transmit temperature signals to the brain [68].

The transient receptor potential A1 (TRPA1) ion channel acts as an IR light receptor in snakes [68]. TRPA1 proteins are widely conserved in various animal species. Human, mouse, fruit fly, and *Caenorhabditis elegans* have homologs of the snake TRPA1 proteins, and these exhibit different sensitivities to cold, heat, and chemical stimuli in different animals [69,71–73]. The N-terminal ankyrin repeat domains of the TRPA1 proteins are essential for sensing IR light [69].

Sequence comparisons of the snake TRPA1 proteins with arabidopsis proteins in public databases reveals that the N-terminal ankyrin repeat domain of arabidopsis tetratricopeptide repeat 10 protein (TPR10, AT3G04710) shares a sequence similarity of 46% with the IR light-sensing domain of TRPA1 proteins (Figure 2). Sequence analysis using the IR light-sensing domains of TRPA1 as bait shows that the arabidopsis ankyrin repeat family protein AT2G03430 shares 52% sequence similarity with TRPA1. Expression analysis of these genes *in silico* predicts that the *TPR10* and *AT2G03430* genes are expressed primarily in the procambium and vasculature of the roots, respectively. It will be interesting to evaluate if the TPR10 and AT2G03430 proteins are involved in sensing near-IR or IR light in the roots.

### Concluding Remarks and Future Perspectives

In plants, there are three major routes of light signal transduction to the roots: transmission of mobile signaling messengers, direct sensing of light by the roots, and light channeling through plant body (Figure 1). Most studies on light responses of the roots have been performed either by direct illumination of the roots or by molecular characterization of mobile signaling messengers. Systematic studies on the modes and mechanisms of sensing stem-piped light by the roots have only recently been started. Further studies will be necessary to extend our understanding of the detailed molecular mechanisms by which the roots sense light information to induce root photomorphogenesis. In particular, the HY5 transcription factor acts as an integrator of diverse light-signaling events in the roots [20,27,33,34]. It will be of particular interest to identify downstream targets of HY5 in modulating root photomorphogenesis (see Outstanding Questions).

What is the physiological significance of root photomorphogenesis? Light is the sole energy source for photosynthesis in plants. Plants have evolved versatile adaptive mechanisms to optimize growth and architecture for efficient light harvesting under fluctuating environmental conditions. Shoot-derived light signals may contribute to the optimization of root growth and performance, such as nutrient uptake and lateral root formation, which should be balanced with those of the shoots for maximal photosynthesis. It is also probable that the roots monitor aboveground environments, such as diurnal and seasonal variations of light, and the presence of predators and neighbors, by sensing shoot-derived light signals. In this view, it is interesting that near-IR wavelengths, and perhaps IR wavelengths as well, are efficiently transmitted through the plant body to the roots. Further studies on plant responses to near-IR or IR light might open a new field in plant root biology. It is notable that the arabidopsis TPR10 and AT2G03430 proteins share high sequence similarities with the snake IR receptor TRPA1, and thus would be potential candidates for future research on root photomorphogenesis.

Root photomorphogenesis is a crucial trait in the cultivation of crop plants [74,75]. It is widely perceived that light regulates the growth and development of both the shoots and roots, and thus the light responses of roots would be potential targets for engineering the yield and quality

### Outstanding Questions

How are specific proteins and RNA molecules selected as shoot-to-root mobile signaling messengers?

Which plant tissue(s) is responsible for channeling light from the shoots to the roots? What are the photochemical properties of the vascular tissues?

Can plant roots differentiate between shoot-derived light signals and root-sensed light signals, and if so, how?

How do root photoreceptors modulate hormonal signaling during root photomorphogenesis?

Do plants perceive and respond to IR or near-IR light in the roots? Do plants possess specific IR or near-IR light-sensing photoreceptors?

Do light responses in the roots influence shoot morphogenesis and performance?



of crops [1, 16, 75]. Further understanding of how light triggers morphological and architectural changes at the molecular level in the roots would provide a means of developing genetically engineered crops with improved root productivity and performance.

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### Supplemental Information

Supplemental information associated with this article can be found online at <http://dx.doi.org/10.1016/j.tplants.2017.06.009>.

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