Coordinated Shoot and Root Responses to Light Signaling in Arabidopsis

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ABSTRACT

Light is one of the most important environmental signals and regulates many biological processes in plants. Studies on light-regulated development have mainly focused on aspects of shoot growth, such as de- etiolation, cotyledon opening, inhibition of hypocotyl elongation, flowering, and anthocyanin accumulation. However, recent studies have demonstrated that light is also involved in regulating root growth and development in Arabidopsis. In this review, we summarize the progress in understanding how shoots and roots coordinate their responses to light through different light-signaling components and pathways, including the COP1 (CONSTITUTIVELY PHOTOMORPHOGENIC 1), HY5 (ELONGATED HYPOCOTYL 5), and MYB73/MYB77 (MYB DOMAIN PROTEIN 73/77) pathways.

Key words: light signal transduction, root growth and development, Arabidopsis

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INTRODUCTION

Light not only provides energy for photosynthesis but also acts as an important signal that regulates plant growth and development. Light plays an essential role throughout the whole life cycle of plants, including seed germination, photomorphogenesis, flowering initiation, and other processes. Sunlight contains different wavelengths of light, including UV, blue, red, and far-red light; plants have evolved multiple photoreceptors to sense these different types of light. For instance, Arabidopsis possesses the ultraviolet B (UV-B) photoreceptor UVR8 (Rizzini et al., 2011), blue-light-sensing cryptochromes (CRYs) (Lin, 2002), phototropins (PHOTs) (Briggs and Christie, 2002), and ZTL (ZEITLUPE)/FKF (FLAVIN-BINDING, KELCH REPEAT, F BOX 1)/LK2 (LOV KELCH PROTEIN2) (Demarsy and Fankhauser, 2009), and red/far-red light phytochrome (PHY) photoreceptors (Quail, 2002). Most photoreceptors consist of an apoprotein bound to a chromophore; the chromophores absorb photons and activate the photoreceptors in response to light (Johnson et al., 1994; Deng and Quail, 1999; Sharrock and Clack, 2002; Yu et al., 2009; Kami et al., 2010; Wang et al., 2016; Liu et al., 2017). In the UVR8 protein, by contrast, several tryptophan residues absorb photons in response to UV-B light, facilitating dissociation of the homodimer to monomers (Kaiserl and Jenkins, 2007; Rizzini et al., 2011; Christie et al., 2012; Wu et al., 2012).

A fundamental mechanism of photoreceptor-mediated light signal transduction is direct interaction between photoreceptors and their target proteins in a light-dependent or light-independent manner. Many other components in addition to photoreceptors play essential roles in light responses, such as COP1 (CONSTITUTIVELY PHOTOMORPHOGENIC 1), HY5 (ELONGATED HYPOCOTYL 5), CIBs (CRYPTOCHROME INTERACING BASIC HELIX LOOP HELIXs), and PIFs (PHYTOCHROME-INTERACTING FACTORS) (Al-Sady et al., 2008; Liu et al., 2008a, 2008b, 2013a, 2013b; Lorrain et al., 2009; Debrieux et al., 2013; Ni et al., 2014; Ma et al., 2016; Pedmale et al., 2016; Park et al., 2018). Our understanding of how light signaling regulates shoot growth and development has increased greatly over many years of study. Notably, light also modulates root growth and developmental processes, such as primary root elongation, lateral root emergence and elongation, and negative phototropic responses. Indeed, PHYs are expressed in roots, where they mediate primary root development, jasmonic acid response, and gravitropism (Costigan et al., 2011). In addition, CRYs and PHOTs mediate blue-light-regulated primary root growth and phototropism (Briggs and Christie, 2002). ROOT UV-B SENSITIVE 1 (RUS1) and RUS2 were identified from a genetic screen for mutants whose primary root was hyposensitive to very low-fluence-rate UV-B. They play critical roles in UV-B-regulated root growth (Tong et al., 2008; Leasure et al., 2009). Lee et al. (2016) recently reported that light is channeled to the roots through the stem, activating PHY red light photoreceptors. Several studies have shown that COP1
and HY5 play important roles in root and shoot growth and demonstrated how light and photoreceptors regulate root and shoot growth via COP1 and HY5. Very recently, it was reported that the UV-B photoreceptor UVR8 directly interacts with MYB transcriptional factors MYB73/MYB77 (MYB DOMAIN PROTEIN 73/77) to regulate auxin responses and lateral root growth. In this review, we summarize current knowledge of how shoots and roots coordinate their responses to light signaling in Arabidopsis.

**COP1-MEDIATED LIGHT SIGNALING REGULATES SHOOT AND ROOT GROWTH**

COP1, an E3 ubiquitin ligase, is one of the most important light-signaling components regulating plant growth and development. COP1 is composed of an N-terminal RING (Really Interesting New Gene) domain, a central CC (coiled-coil) domain, and a C-terminal WD40 repeat domain (Deng et al., 1992). In darkness, COP1 interacts with SPAs (SUPPRESSOR OF PHYAs) and other components of E3 ubiquitin ligase complexes to polyubiquitinize positive regulators of light signaling, prompting their degradation by the 26S proteasome (Huang et al., 2014; Menon et al., 2016). The substrates of COP1/SPA E3 ligase are mainly transcription factors, including HY5 and its homolog HYH (HY5 HOMOLOG), which inhibit hypocotyl elongation and induce seedling de-etiolation (Osterlund et al., 2000; Lau and Deng, 2012), HFR1 (LONG HYPOCOTYL IN FAR RED), which plays a role in shade avoidance (Jang et al., 2005; Yang et al., 2005a, 2005b; Rolauffs et al., 2012), and CO (CONSTANS), which is a key transcription factor regulating photoperiodic flowering (Laubinger et al., 2006; Jang et al., 2008; Liu et al., 2008a, 2008b). However, under light conditions, some photoreceptors interact directly with COP1/SPA to inhibit degradation of HY5, HFR1, and CO (Hoecker, 2017; Yin and Ulm, 2017; Podolec and Ulm, 2018), promoting photomorphogenesis, shade avoidance, and flowering.

COP1-mediated light signaling not only regulates shoot growth but also plays an essential role in root growth and development. In 2012, Sassi et al. (2012) showed that COP1-mediated light signaling induces PIN1 (PIN-FORMED 1) transcription in shoots to regulate shoot-to-root polar auxin transport, and meanwhile regulates the intracellular distribution of PIN1 and PIN2 in roots to influence growth and development. PINs, which are auxin efflux carriers, show polar localization on the plasma membrane and are responsible for the polar transport of auxin (Benková et al., 2003; Friml et al., 2003; Wisniewska et al., 2006). Etiolated seedlings display shorter primary roots compared with light-grown seedlings (Sassi et al., 2012). The targeting of PIN1 and PIN2 to the root-cell plasma membrane is decreased in darkness (Bhalerao et al., 2002; Salisbury et al., 2007; Sassi et al., 2012), and expression of PIN1 is dramatically increased under light. Further studies showed that in darkness, the cop1 mutant has a longer primary root and much higher PIN1 expression in shoots than the wild type, implying that COP1 regulates PIN1 transcription in shoots and polar auxin transport in response to light. The cop1 mutant also shows greater PIN1 and PIN2 localization on the root-cell plasma membrane than the wild type under darkness (Sassi et al., 2012). Taken together, these findings suggest that light coordinates shoot and root growth through different COP1-mediated pathways (Figure 1A).

**LIGHT REGULATES SHOOT-TO-ROOT TRANSPORT OF HY5 TO COORDINATE SHOOT AND ROOT GROWTH**

HY5 was originally defined as a positive regulator of photomorphogenesis because of the light insensitivity of hy5 mutants (Koornneef et al., 1980; Ang and Deng, 1994). Further studies showed that HY5 is a member of the bZIP (basic leucine zipper) family of transcription factors. Many light-responsive genes contain light-response elements (LREs) such as the G-box, GT1 motif, and GAGA motif. HY5 directly binds to most of these LREs to regulate expression of light-responsive genes (Tobin and Kehoe, 1994; Terzaghi and Cashmore, 1995; Millar and Kay, 1996; Chattopadhyay et al., 1998), thus regulating photomorphogenesis in Arabidopsis. HY5 regulates photomorphogenesis downstream of the PHY, CRY, and UVR8 photoreceptors (Koornneef et al., 1980; Oyama et al., 1997; Ang et al., 1998; Oravecz et al., 2006; Yang et al., 2018).

In addition to regulating shoot growth, HY5 is also involved in the regulation of root growth and development in Arabidopsis (Chen et al., 2016; Sakuraba et al., 2018; van Gelderen et al., 2018). In 2016, Chen et al. observed that etiolated seedlings had longer hypocotyls but shorter primary roots compared with light-grown seedlings. When only the shoot was covered, seedlings showed the same shorter root phenotype as dark-grown seedlings, but if only the root was covered, the root phenotype was the same as that of light-grown seedlings. This suggests that shoot-to-root signaling mediates the regulation of root growth and development by light. In their experiment, Chen et al. (2016) found that light regulates root growth by regulating root NO3 influx, and that this process depends on HY5. HY5 regulates NO3 uptake in roots in two ways. On the one hand, shoot illumination promotes shoot-to-root translocation of HY5, where it activates HY5 expression; root HY5 then induces expression of the NO3 transporter NRT2.1 to regulate NO3 uptake and root growth. On the other hand, HY5 regulates C (carbon) levels by affecting carbohydrate photosynthate metabolism and shoot-root transport, which regulate NRT2.1 expression and NO3 uptake, so as to maintain a homeostatic balance of C and N (nitrogen) metabolism and coordinate shoot and root growth and development (Chen et al., 2016). HY5 also mediates the modulation of lateral root emergence by far-red light (van Gelderen et al., 2018). In 2018, van Gelderen et al. observed that supplementing white light with far-red light reduces lateral root density; HY5 is involved in the regulation of this process because hy5 mutants display the same phenotype with or without far-red light treatment. Moreover, HY5 accumulates in lateral root primordia (LRP) and the cortex above LRP under far-red light irradiation. By contrast, the expression of the PIN3 and LAX3 (LIKE AUX1 3) auxin transporters is decreased in cortex cells overlaying LRP. Further studies revealed that HY5 inhibits the expression of ARF19 (AUXIN RESPONSE FACTOR 19), PIN3, and LAX3. These results indicate that HY5 regulates lateral root emergence by affecting auxin signaling (van Gelderen et al., 2018). HY5-mediated light signaling not only regulates shoot growth but also influences root development by regulating...
NO$_3^-$ uptake, the balance of C/N, and the expression of the auxin transporters PIN3 and LAX3 to coordinate shoot and root growth in _Arabidopsis_ (Figure 1B).

**MYB73/MYB77-MEDIATED UV-B SIGNALING COORDINATES SHOOT AND ROOT GROWTH**

Two R2R3-MYB family transcription factors, MYB73/MYB77, were recently found to directly interact with the UV-B photoreceptor UVR8 to modulate shoot and root growth under UV-B light in _Arabidopsis_ (Yang et al., 2019). UV-B is a part of sunlight that is involved in not only the regulation of shoot photomorphogenesis but also root growth and development, DNA damage, UV-B stress, and other processes. RUS1 and RUS2 were identified in a forward genetics screen and play critical roles in UV-B photomorphogenetic responses, including root growth (Tong et al., 2008; Leasure et al., 2009). The hormone auxin is fundamental to plant growth and development (Weijers and Wagner, 2016; Leyser, 2018) and plays an essential role in lateral root development. UV-B stabilizes inhibitors of PIF4, including the DELLA and HFR1 (LONG HYPOCOTYL IN FAR RED) proteins, affecting auxin biosynthesis (Hayes et al., 2014, 2017). UV-B regulation of auxin also occurs at the level of redistribution via transport, influx, or efflux (Wargent et al., 2009; Ge et al., 2010; Yu et al., 2013). Furthermore, UV-B detected by UVR8 antagonizes auxin-responsive genes involved in regulating shade avoidance and bending toward UV-B (Hayes et al., 2014; Vandenbussche et al., 2014). UV-B treatment inhibits initiation and elongation of lateral roots of seedlings grown on plates and in soil in a UVR8-dependent manner. GUS (β-glucuronidase) staining assays showed that UV-B and UVR8 repress the expression of the auxin-signaling marker gene _DR5p::GUS_ in leaves, LRP, and lateral root tips, indicating that UVR8-mediated UV-B signaling regulates auxin signaling and lateral root growth and development (Yang et al., 2019). High concentrations of auxin repress the growth of main roots and lateral roots while promoting the generation of lateral roots in the wild type (Shin et al., 2007). However, UV-B-activated UVR8 inhibits root responses to high concentrations of auxin; interestingly, even when roots are covered with foil and a black box to reduce light signals, similar to natural soil conditions, UV-B still inhibits the effects of high auxin concentrations in the wild type (Shin et al., 2007). Grafting experiments revealed that UV-B treatment represses the effects of high auxin concentrations in wild-type roots regardless of whether they are grafted to wild-type or _uvr8_ mutant shoots, while _uvr8_ mutant roots grafted with wild-type shoots respond to high auxin concentrations in the same manner as those grafted with _uvr8_ mutant shoots, implying that root UVR8 autonomously regulates auxin responses and lateral root growth. Transcriptome analysis revealed that UV-B inhibits auxin-responsive gene expression in a UVR8-dependent manner.

The MYB transcription factor MYB77 interacts with ARFs to modulate auxin signal transduction and lateral root growth.
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A recent study showed that UVR8 physically interacts with MYB73/MYB77 in a UV-B-dependent manner to repress their DNA-binding activity and the expression of their target genes, thus modulating auxin signaling and lateral root development (Yang et al., 2019). The myb73 myb77 double mutant is less sensitive to high concentrations of auxin and shows much lower expression of auxin-responsive genes under UV-B treatment than the wild type, whereas the myb73 myb77 uvr8 triple mutant partially complements the increased lateral root and long hypocotyl phenotype of the uvr8 mutant under UV-B conditions. Consistent with this, expression levels of auxin-signaling genes are lower in the myb73 myb77 uvr8 mutant than in uvr8 under UV-B. Further analysis indicated that UV-B-activated UVR8 interacts with MYB73/MYB77 in both shoots and roots, inhibiting their DNA-binding activity to regulate auxin-responsive gene expression and coordinate shoot and root growth under UV-B conditions (Figure 1C) (Yang et al., 2019).

OTHER PATHWAYS

Many genes mediate light signaling and regulate shoot growth, including CIBs, PIFs, and CO (Liu et al., 2008a, 2008b, 2013a, 2013b; Ma et al., 2016; Pedmale et al., 2016). Light also coordinates the growth and development of shoots and roots through many other pathways, such as the blue-light photoreceptor PHOT1, which modulates the intracellular distribution of auxin transporters PIN2 and PIN3 to regulate root negative phototropic responses in Arabidopsis (Wan et al., 2012; Zhang et al., 2013). CRY1 and CRY2 also regulate root growth, with opposite functions (Canamero et al., 2006). PIFs have vital roles in light signaling, directly binding the promoters of auxin biosynthesis genes to regulate auxin biosynthesis and plant growth. Therefore, light may regulate auxin biosynthesis and plant growth by regulating PIFs. PHY red/far-red light photoreceptors and CRY blue-light photoreceptors directly interact with PIFs, and the UV-B photoreceptor UVR8 regulates the protein stability and transcriptional activity of PIFs to influence their functions and auxin biosynthesis, thus regulating hypocotyl elongation and shade avoidance (Ni et al., 2014; Hayes et al., 2014, 2017; Ma et al., 2016; Pedmale et al., 2016; Park et al., 2018). None of these studies describe root phenotypes; however, auxin plays an essential role in both shoot and root growth, and it is not difficult to infer that light, through regulating auxin biosynthesis, regulates shoot and root growth. Few studies have found that light plays an important role in cytokinin (CK) biosynthesis and metabolism, which regulates shoot and root growth and development (Zdarska et al., 2015). It has been shown that red/far-red treatment and phytochrome influence the CK levels in Nicotiana plumaginifolia and Scots pine (Pinus silvestris L.) (Qamaruddin and Tillberg, 1989; Kraepiel et al., 1995). The CO-FLOWERING LOCUS T (FT) module is critical for regulation of photoperiodic flowering. Potato CO and FT homologs are reported to be involved in tuber (underground storage organ) formation (Navarro et al., 2011; Abelenda et al., 2016). Light also regulates nodulation in Rhizobium leguminosarum through an LOV-histidine kinase photoreceptor, indicating that light controls plant root nodulation and nitrogen fixation (Bonomi et al., 2012).

Concluding Remarks and Perspectives

As one of the most important environmental factors, light is not only involved in regulation of shoot growth but also influences root growth and development. In this review, we summarized the progress in understanding how shoots and roots coordinate their responses to light signaling. Firstly, light-activated photoreceptors regulate COP1 to stabilize some proteins (such as HY5 and CO) and regulate morphogenesis, flowering, and other processes. In addition, COP1-mediated light signaling modulates expression of the auxin transporter PIN1 as well as the intracellular distribution of PIN1 and PIN2, thus regulating primary root elongation. Secondly, light-activated photoreceptors regulate HY5 expression and HY5 protein accumulation in shoots to regulate shoot growth. At the same time, HY5 moves from shoots to roots where it activates root HY5 expression to regulate NRT2.1 expression and NO3− uptake and modulate the balance of C/N. HY5 also regulates the expression of the auxin transporters PIN3 and LAX3 to coordinate shoot and root growth. Thirdly, the UV-B photoreceptor UVR8 directly interacts with MYB73 and MYB77 in a UV-B-dependent manner, inhibiting their DNA-binding activity to repress auxin-responsive gene expression and regulate hypocotyl elongation and lateral root growth. Meanwhile, many other pathways are also involved in mediating light-regulated root and shoot growth and development.

In addition to indirectly modulating root growth by regulating shoot growth, light is also directly involved in the regulation of root growth. However, the critical but very difficult question remains of how light signaling is activated in roots. It has been reported that light might pass through the stem to activate the red photoreceptor PHYB and regulate root growth (Lee et al., 2016), but it is still unknown whether light could pass through the stem to the root in seedlings or young plants, or whether other photoreceptors could be activated by stem-pipped light. In addition light can pass through very thin soil to regulate seed emergence (Shi et al., 2016). However, how does light regulate root development in deep soil? Is it possible that other light-signaling components besides HY5, such as the photoreceptors, could be activated by light in shoots and then move from shoots to roots to coordinate shoot and root growth? Alternatively, do any proteins move from roots to shoots to coordinate shoot and root growth? COP1 regulates the intracellular distribution of PIN1/2 and the UVR8–MYB73/MYB77 complex regulates auxin signaling and lateral root growth in a root-autonomous way (Sassi et al., 2012; Yang et al., 2019), implying that light signaling might be activated in roots; however, the mechanisms are still unknown. Shoots and roots need to coordinate their growth responses to allow better growth of the whole plant. Therefore, further investigations of these questions are required to fully understand how light coordinates the development and growth of shoots and roots.

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REFERENCES
Abelenda, J.A., Cruz-Oro, E., Franco-Zorrilla, J.M., and Prat, S. (2016). Potato StCONSTANS-like1 suppresses storage organ formation by directly activating the FT-like StSP5G repressor. Curr. Biol. 26:872–881.

Al-Sady, B., Kikis, E.A., Monte, E., and Quail, P.H. (2008). Mechanistic duality of transcription factor function in phytochrome signaling. Proc. Natl. Acad. Sci. U S A 105:2232–2237.

Ang, L.H., and Deng, X.W. (1994). Regulatory hierarchy of photomorphogenic loci: allele-specific and light-dependent interaction between the HY5 and COP1 loci. Plant Cell 6:613–628.

Ang, L.H., Chattopadhyay, S., Wei, N., Oyama, T., Okada, K., Batschauer, A., and Deng, X.W. (1998). Molecular interaction between COP1 and HY5 defines a regulatory switch for light control of Arabidopsis development. Mol. Cell 1:213–222.

Briggs, W.R., and Christie, J.M. (2002). Phototropins 1 and 2: versatile plant blue-light receptors. Trends Plant Sci. 7:204–210.

Benková, E., Michniewicz, M., Sauer, M., Teichmann, T., Seifertová, D., Jurgens, G., and Friml, J. (2003). Local, efflux-dependent auxin gradients as a common module for plant organ formation. Cell 115:591–602.

Bhalerao, R.P., Eklund, G., and Franklin, K.A. (2003). Signalling in light-controlled plant development. Semin. Cell. Dev. Biol. 14:121–129.

Chattopadhyay, S., Ang, L.H., Puente, P., Deng, X.W., and Wei, N. (2008). COP1/SPA proteins regulate photoperiodic flowering and interact with the floral inducer CONSTANS to regulate its stability. Development 133:3213–3222.

Christie, J.M., Arvai, A.S., Baxter, K.J., Heilmann, M., Pratt, A.J., O’Hara, A., Kelly, S.M., Hothorn, M., Smith, B.O., Hitomi, K., et al. (2012). Plant UVR8 photoreceptor senses UV-B by tryptophan-mediated disruption of cross-dimer salt bridges. Science 335:1492–1496.

Costigan, S.E., Warnasooriya, S.N., Humphries, B.A., and Montgomery, B.L. (2011). Root-localized phytochrome chromophore synthesis is required for photoregulation of root elongation and impacts root sensitivity to jasmonic acid in Arabidopsis. Plant Physiol. 157:1136–1150.

Demarsy, E., and Fankhauser, C. (2000). Higher plants use LOV to perceive blue light. Curr. Opin. Plant Biol. 12:69–74.

Deng, X.W., Matsui, M., Wei, N., Wagner, D., Chu, A.M., Feldmann, K.A., and Quail, P.H. (1992). COP1, an Arabidopsis regulatory gene, encodes a protein with both a zinc-binding motif and a G beta beta gamma domain. Cell 71:791–801.

Deng, X.W., and Quail, P.H. (1999). Signalling in light-controlled development. Semin. Cell. Dev. Biol. 10:121–129.

Demarsy, E., and Fankhauser, C. (2009). Conditional involvement of constitutive photomorphogenic1 in the degradation of phytochrome A. Plant Physiol. 161:2136–2145.

Demarsy, E., and Fankhauser, C. (2009). Higher plants use LOV to perceive blue light. Curr. Opin. Plant Biol. 12:69–74.

Deng, X.W., Matsui, M., Wei, N., Wagner, D., Chu, A.M., Feldmann, K.A., and Quail, P.H. (1992). COP1, an Arabidopsis regulatory gene, encodes a protein with both a zinc-binding motif and a G beta beta gamma domain. Cell 71:791–801.

Deng, X.W., and Quail, P.H. (1999). Signalling in light-controlled development. Semin. Cell. Dev. Biol. 10:121–129.

Friml, J., Vieten, A., Sauer, M., Weijers, D., Schwarz, H., Hamann, T., Offringa, R., and Jurgens, G. (2003). Efflux-dependent auxin gradients establish the apical-basal axis of Arabidopsis. Nature 426:147–153.

Ge, L., Peer, W., Robert, S., Swarup, R., Ye, S., Prigge, M., Cohen, J.D., Friml, J., Murphy, A., Tang, D., et al. (2010). Arabidopsis ROOT UVB SENSITIVE2/WEAK AUXIN RESPONSE1 is required for polar auxin transport. Plant Cell 22:1749–1761.

Hayes, S., Velanis, C.N., Jenkins, G.I., and Franklin, K.A. (2014). UV-B detected by the UVR8 photoreceptor antagonizes auxin signaling and plant shade avoidance. Proc. Natl. Acad. Sci. U S A 111:11894–11899.

Hayes, S., Sharma, A., Fraser, D.P., Trevisan, M., Cragg-Barber, C.K., Tavridou, E., Fankhauser, C., Jenkins, G.I., and Franklin, K.A. (2017). UV-B perceived by the UVR8 photoreceptor inhibits plant thermomorphogenesis. Curr. Biol. 27:120–127.

Hoecker, U. (2017). The activities of the E3 ubiquitin ligase COP1/SPA, a key repressor in light signaling. Curr. Opin. Plant Biol. 37:63–69.

Huang, X., Ouyang, X., and Deng, X.W. (2014). Beyond repression of photomorphogenesis: role switching of COP/DET/FUS in light signaling. Curr. Opin. Plant Biol. 21C:96–103.

Jang, I.C., Yang, J.Y., Seo, H.S., and Chua, N.H. (2005). HFR1 is targeted by COP1 E3 ligase for post-translational proteolysis during phytochrome A signalling. Genes Dev. 19:593–602.

Jang, S., Marchal, V., Panigrahi, K.C., Wenkel, S., Poppe, W., Deng, X.W., Valverde, F., and Coupland, G. (2008). Arabidopsis COP1 shapes the temporal pattern of CO accumulation conferring a photoperiodic flowering response. EMBO J. 27:1277–1288.

Johnson, E., Bradley, M., Harberd, N.P., and Whitelam, G.C. (1994). Photoreponses of light-grown phyA mutants of Arabidopsis. Plant Physiol. 105:141–149.

Kam, C., Lorrain, S., Hornitschek, P., and Fankhauser, C. (2010). Light-regulated plant growth and development. Curr. Top. Dev. Biol. 91:29–66.

Kaiserli, E., and Jenkins, G.I. (2007). UV-B promotes rapid nuclear translocation of the Arabidopsis UV-B-specific signaling component UVR8 and activates its function in the nucleus. Plant Cell 19:2662–2673.

Koornneef, M., Rolffeb, E., and Spruitab, C.J.P. (1980). Genetic control of light-inhibited hypocotyl elongation in Arabidopsis thaliana. Z. Pflanzenphysiol. 100:147–160.

Kraepiel, Y., Marree, K., Sotta, B., Caboche, M., and Migniac, E. (1995). In vitro morphogenic characteristics of phytochrome mutants in Nicotiana plumbaginifolia are modified and correlated to high indole-3-acetic acid levels. Planta 197:142–146.

Laubinger, S., Marchal, V., Le Gourrierec, J., Wenkel, S., Adrian, J., Jang, S., Kulajta, C., Braun, H., Coupland, G., and Hoecker, U. (2006). Arabidopsis SPA proteins regulate photoperiodic flowering and interact with the floral inducer CONSTANS to regulate its stability. Development 133:3213–3222.
Plant Communications

Lau, O.S., and Deng, X.W. (2012). The photomorphogenic repressors COP1 and DET1: 20 years later. Trends Plant Sci. 17:584–593.

Leasure, C.D., Tong, H., Yuen, G., Hou, X., Sun, X., and He, Z.H. (2009). ROOT UV-B SENSITIVE2 acts with ROOT UV-B SENSITIVE1 in a root ultraviolet B-sensing pathway. Plant Physiol. 150:1902–1915.

Lee, H.J., Ha, J.H., Kim, S.G., Choi, H.K., Kim, Z.H., Han, Y.J., Kim, J.I., Oh, Y., Fragoso, V., Shin, K., et al. (2016). Stem-piped light activates phytochrome B to trigger light responses in Arabidopsis thaliana roots. Sci. Signal. 9ra106.

Leyser, O. (2018). Auxin signaling. Plant Physiol. 176:465–479.

Lin, C. (2002). Blue light receptors and signal transduction. Plant Cell. 2002S:S207–S225.

Liu, H., Yu, X., Li, K., Kleijnot, J., Yang, H., Lisiero, D., and Lin, C. (2008a). Photoreexcited CRY2 interacts with CIB1 to regulate transcription and floral initiation in Arabidopsis. Science 322:1535–1539.

Liu, L.J., Zhang, Y.C., Li, Q.H., Sang, Y., Mao, J., Lian, H.L., Wang, L., and Yang, H.Q. (2008b). COP1-mediated ubiquitination of CONSTANS is implicated in cryptochrome regulation of flowering in Arabidopsis. Plant Cell 20:292–306.

Liu, H., Wang, Q., Liu, Y., Zhao, X., ImaiZumi, T., Somers, D.E., Tobin, E.M., and Lin, C. (2013a). Arabidopsis CRY2 and ZTL mediate blue-light regulation of the transcription factor CIB1 by distinct mechanisms. Proc. Natl. Acad. Sci. U S A 110:17582–17587.

Liu, Y., Li, X., Li, K., Liu, H., and Lin, C. (2013b). Multiple bHLH proteins form heterodimers to mediate CRY2-dependent regulation of flowering-time in Arabidopsis. PLoS Genet. 9:e1003861.

Liu, Q., Wang, Q., Deng, W., Wang, X., Piao, M., Cai, D., Li, Y., Barshop, W.D., Yu, X., Zhou, T., et al. (2017). Molecular basis for blue-light-dependent phosphorylation of Arabidopsis cryptochrome 2. Nat. Commun. 8:15234.

Lorrain, S., Trevisan, M., Pradervand, S., and Fankhauser, C. (2009). Phytochrome interacting factors 4 and 5 redundantly limit seedling temperature-mediated hypocotyl elongation in response to blue light. Proc. Natl. Acad. Sci. U S A 113:224–229.

Menon, C., Sheerin, D.J., and Hilbrunner, A. (2016). SPA proteins: SPAning the gap between visible light and gene expression. Planta 244:297–312.

Millar, A.J., and Kay, S.A. (1996). Integration of circadian and phototransduction pathways in the network controlling CAB gene transcription in Arabidopsis. Proc. Natl. Acad. Sci. U S A 93:15491–15496.

Navarro, C., Abelenda, J.A., Cruz-Oró, E., Cuéllar, C.A., Tamaki, S., Silva, J., Shimamoto, K., and Prat, S. (2011). Control of flowering and storage organ formation in potato by FLOWERING LOCUS T. Nature 478:119–122.

Ni, W., Xu, S.L., Tepperman, J.M., Stanley, D.J., Maltby, D.A., Gross, J.D., Burlingame, A.L., Wang, Z.Y., and Quail, P.H. (2014). A mutually assured destruction mechanism attenuates light signaling in Arabidopsis. Science 344:1160–1164.

Oravecz, A., Baumann, A., Máté, Z., Brzezinska, A., Molinier, J., Oakeley, E.J., Adám, E., Schafer, E., Nagy, F., and Um, R. (2006). CONSTITUTIVELY PHOTOMORPHOGENIC1 is required for the UV-B response in Arabidopsis. Plant Cell 18:1975–1990.

Osterlund, M.T., Hardtke, C.S., Wei, N., and Deng, X.W. (2000). Targeted destabilization of HYS during light-regulated development of Arabidopsis. Nature 405:462–466.

Oyama, T., Shimura, Y., and Okada, K. (1997). The Arabidopsis HY5 gene encodes a bZIP protein that regulates stimulus-induced development of root and hypocotyl. Genes Dev. 11:2983–2995.

Park, E., Kim, Y., and Choi, G. (2018). Phytochrome B requires PIF degradation and sequestration to induce light responses across a wide range of light conditions. Plant Cell 30:1277–1292.

Pedmale, U.V., Huang, S.C., Zander, M., Cole, B.J., Hetzel, J., Ljung, K., Reis, P.A.B., Sridive, P., Nito, K., Nery, J.R., et al. (2016). Cryptochromes interact directly with PIFs to control plant growth in limiting blue light. Cell 164:233–245.

Podolec, R., and Ulm, R. (2018). Photoreceptor-mediated regulation of the COP1/SPA E3 ubiquitin ligase. Curr. Opin. Plant Biol. 45:18–25.

Qamaruddin, M., and Tillberg, E. (1989). Rapid effects of red light on the isopentenyladenosine content in Scots pine seeds. Plant Physiol. 91:5–8.

Quail, P.H. (2002). Phytochrome photosensory signalling networks. Nat. Rev. Mol. Cell Biol. 3:85–93.

Rizzini, L., Favory, J.J., Cloix, C., Faggionato, D., O’Hara, A., Kaiserli, E., Baumeister, R., Schaefe, E., Nagy, F., Jenkins, G.J., et al. (2011). Perception of UV-B by the Arabidopsis UVR8 protein. Science 332:103–106.

Rolauffs, S., Fackendahl, P., Sahm, J., Fiene, G., and Hoecker, U. (2012). Arabidopsis COP1 and SPA genes are essential for plant elongation but not for acceleration of flowering time in response to a low red light to far-red light ratio. Plant Physiol. 160:2015–2027.

Sakuraba, Y., Kanno, S., Mabuchi, A., Monda, K., Iba, K., and Yanagisawa, S. (2018). A phytochrome-B-mediated regulatory mechanism of phosphorus acquisition. Nat. Plants 4:1089–1101.

Saleski, F.J., Hall, A., Grierson, C.S., and Halliday, K.J. (2007). Phytochrome coordinates Arabidopsis shoot and root development. Plant J. 50:429–438.

Sassi, M., Lu, Y., Zhang, Y., Wang, J., Dhoukshes, P., Biloiu, I., Dai, M., Li, J., Gong, X., Jaillais, Y., et al. (2012). COP1 mediates the coordination of root and shoot growth by light through modulation of PIN1 and PIN2-dependent auxin transport in Arabidopsis. Development 139:3402–3412.

Sharrock, R.A., and Clack, T. (2002). Patterns of expression and normalized levels of the five Arabidopsis phytochromes. Plant Physiol. 130:442–456.

Shi, H., Liu, R., Xue, C., Shen, X., Wei, N., Deng, X.W., and Zhong, S. (2016). Seedlings transduce the depth and mechanical pressure of covering soil using COP1 and ethylene to regulate EBF1/EBF2 for soil emergence. Curr. Biol. 26:139–149.

Shin, R., Burch, A.Y., Huppert, K.A., Tiwari, S.B., Murphy, A.S., Quail, P.H., E., Baumeister, R., Schachtman, D.P., Cashmore, A.R. (1995). Light-regulated degradation and sequestration of UVR8 to mediate bending towards UV-B in Arabidopsis. Nature 377:445–474.

Terzaghi, W.B., and Cashmore, A.R. (1995). Light-regulated transcription. Annu. Rev. Plant Physiol. Plant Mol. Biol. 46:445–474.

Tobin, E.M., and Kehoe, D.M. (1994). Phytochrome-regulated gene expression. Semin. Cell Biol. 5:335–346.

Tong, H., Leasure, C.D., Hou, X., Yuen, G., Briggs, W., and He, Z.H. (2008). Role of root UV-B sensing in Arabidopsis early seedling development. Proc. Natl. Acad. Sci. U S A 105:21039–21044.

Van den Bussche, F., Tilbrook, K., Fiero, A.C., Marchal, K., Poelman, D., Van Der Straeten, D., and Ulm, R. (2014). Photoreceptor-mediated bending towards UV-B in Arabidopsis. Mol. Plant 7:1041–1052.

van Gelderen, K., Kang, C., Paalman, R., Keuskamp, D., Hayes, S., and Pierik, R. (2018). Far-red light detection in the shoot regulates lateral
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root development through the HY5 transcription factor. Plant Cell 30:101–116.

Yang, Y., Liang, T., Zhang, L., Shao, K., Gu, X., Shang, R., Shi, N., Li, X., Zhang, P., and Liu, H. (2018). UVR8 interacts with WRKY36 to regulate HY5 transcription and hypocotyl elongation in Arabidopsis. Nat. Plants 4:98–107.

Yang, Y., Zhang, L., Chen, P., Liang, T., Li, X., and Liu, H. (2019). UVR8 interacts with MYB73/MYB77 in a UV-B dependent manner to regulate auxin responses and lateral root development. EMBO J. https://doi.org/10.15252/embj.2019101928.

Yin, R., and Ulm, R. (2017). How plants cope with UV-B: from perception to response. Curr. Opin. Plant Biol. 37:42–48.

Yu, H., Karampelias, M., Robert, S., Peer, W.A., Swarup, R., Ye, S., Ge, L., Cohen, J., Murphy, A., Friml, J., et al. (2013). ROOT ULTRAVIOLET B-SENSITIVE1/weak auxin response3 is essential for polar auxin transport in Arabidopsis. Plant Physiol. 162:965–976.

Zdarska, M., Dobisová, T., Geloňová, Z., Pernisová, M., Dabravolski, S., and Hejátko, J. (2015). Illuminating light, cytokinin, and ethylene signalling crosstalk in plant development. J. Exp. Bot. 66:4913–4931.

Zhang, K.X., Xu, H.H., Yuan, T.T., Zhang, L., and Lu, Y.T. (2013). Blue-light-induced PIN3 polarization for root negative phototropic response in Arabidopsis. Plant J. 76:308–321.

Zhao, Y., Xing, L., Wang, X., et al. (2014). The ABA receptor PYL8 promotes lateral root growth by enhancing MYB77-dependent transcription of auxin-responsive genes. Sci. Signal. 3ra53.