Light Signaling, Root Development, and Plasticity[1][OPEN]

Kasper van Gelderen,[2] Chiakai Kang,[2] and Ronald Pierik[3]

Plant Ecophysiology, Utrecht University, 3584 CH Utrecht, The Netherlands

ORCID IDs: 0000-0001-7809-2812 (K.v.G.); 0000-0002-5580-2380 (C.K.); 0000-0002-5320-6817 (R.P.).

Light is the energy source for plants as it drives photosynthesis to produce sugars. Given the obvious fact that light mostly occurs above ground and not in the soil, most interactions of plants with light have been studied in shoot parts of the plant. Research over more than a century has yielded tremendous insights into how light not only drives photosynthesis but also acts as an environmental cue that informs plants about their environment. Light quality and duration, for example, drive major developmental changes such as photomorphogenesis, photoperiodic induction of flowering, phototropism, and shade avoidance (see, for example, the following recent reviews: Wu, 2014; Fankhauser and Christie, 2015; Xu et al., 2015; Ballaré and Pierik, 2017). The picture that has emerged is that plants have very detailed light signaling mechanisms, with photoreceptors dedicated to different wavelengths in the light spectrum and interactions between these photoreceptors themselves and their downstream signal transduction pathways.

Studies have accumulated over the past 15 years, and intensified in recent years, showing pronounced effects of light on root physiology and development. Although some effects of light availability on root growth will be the simple consequence of differential sugar availability to the roots due to photosynthesis in the shoot, there is substantial evidence for more sophisticated signaling impacts of different aspects of the light environment.

In this *Update*, we will briefly review the core light signaling mechanisms, their impact on root development and plasticity, and the functional implications of these aboveground-belowground interactions.

LIGHT SIGNALING

Different wavelengths of light are associated with various functions in plant development, and plants have a range of photoreceptors to detect these wavelengths. UV-B RESISTANCE LOCUS8 (UVR8) is sensitive to UV-B light, cryptochromes (CRYs) and phototropins (PHOTs) detect UV-A and blue light, and phytochromes (PHYs) sense red (R) and far-red (FR) light. Photoreceptors occur all over the plant body, and although they are most abundant in the shoot, they are also expressed in the roots (Fig. 1). Photoreceptors share downstream signaling hubs, notably the CONSTITUTIVE PHOTOMORPHOGENESIS1 (COP1)/SUPPRESSOR OF PHYTOCHROME A (SPA) complex and PHYTOCHROME INTERACTING FACTORs (PIFs), which will be discussed first, followed by the properties of each photoreceptor group.

Shared Signaling Hubs

COP1-SPA-HY5

COP1 functions as a ubiquitin E3 ligase that targets proteins required for photomorphogenesis for degradation, such as the bZIP transcription factor ELONGATED HYPOCOTYL5 (HY5; Osterlund et al., 2000; Saijo et al., 2003) and HY5-HOMOLOG (HYH; Holm et al., 2002). Especially, HY5 is a key regulator in

ADVANCES

- New modes of information transfer between the shoot and root stems have been identified, including light piping and the light-sensitive transcription factor HY5.
- Light signaling interacts with root-environment interactions, including nutrient acquisition and gravitropism.
- A vertical agar plate system for Arabidopsis growth, D-root, was developed to keep roots in darkness, while the shoot experiences light. This system has allowed probing direct and indirect light effects on root system architecture.

[1] This work was supported by the Netherlands Organisation for Scientific Research (open competition grant 823.01.013 to R.P., K.v.G.) and the Ministry of Education, Taiwan (Scholarship of Government Sponsorship for Overseas Study, admission no. 0991167-2-UK-004, to C.K.).

[2] These authors contributed equally to the article.

[3] Address correspondence to r.pierik@uu.nl.

K.v.G., C.K., and R.P. wrote the article and composed the figures.

[OPEN] Articles can be viewed without a subscription.

www.plantphysiol.org/cgi/doi/10.1104/pp.17.01079

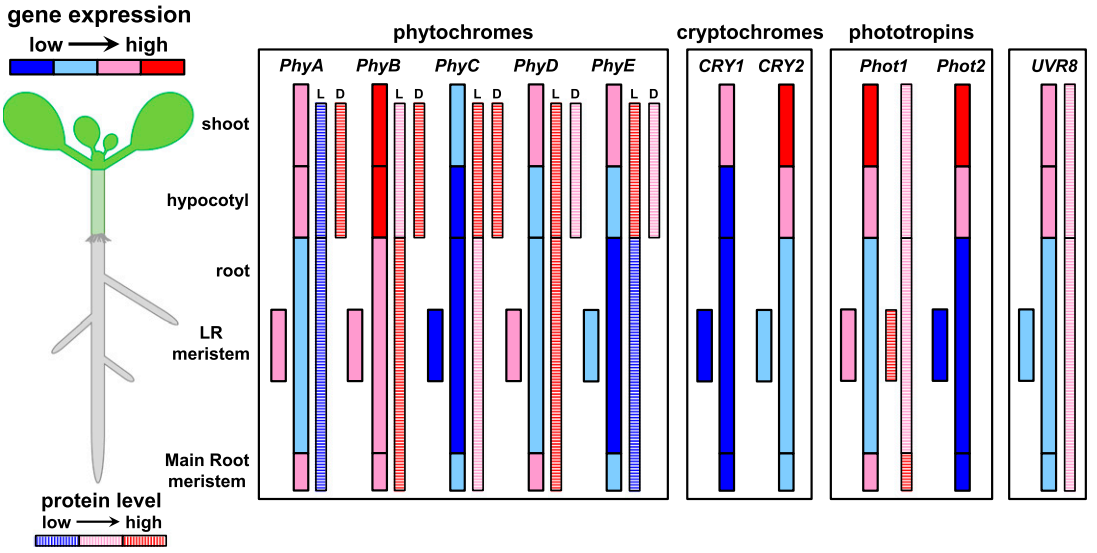

Figure 1. Relative amounts of photoreceptors in Arabidopsis tissues. The graph displays the relative expression of photoreceptors across seedling tissues. Both gene expression and protein (when data are available) abundance are shown. The box that groups classes of receptors indicates that intensities within can be compared. In the PHY box, "L" stands for protein levels in light and "D" for protein levels in the dark. Source data: for all, BAR eFP browser (http://bar.utoronto.ca/efp/cgi-bin/efpWeb.cgi), PHYs (Somers and Quail, 1995; Goosey et al., 1997; Tóth et al., 2001; Sharrock and Clack, 2002; Salisbury et al., 2007), PHOTs (Sakamoto and Briggs, 2002; Moni et al., 2015), CRYs (Tóth et al., 2001), and UVR8 (Rizzini et al., 2011).

photomorphogenesis, and it serves as the center of a transcriptional network hub of hormone and light signaling (Gangappa and Botto, 2016). Besides HY5, COP1 also targets factors like the MYB transcription factor LONG AFTER FAR-RED LIGHT1 (Seo et al., 2003), the basic helix-loop-helix protein LONG HYPOCOTYL IN FAR-RED1 (Duek et al., 2004), and even phytochrome A (phyA) and phyB photoreceptors (Seo et al., 2004; Jang et al., 2010). COP1 activity relies on physical interaction with SPAs in the COP1/SPA complex. The CRY photoreceptors CRY1 and CRY2, upon blue light activation, can bind to SPAs, and this results in reduced COP1-SPA interaction, leading to stabilization of COP1 targets (Lian et al., 2011; Liu et al., 2011; Zuo et al., 2011). Comparable interaction mechanisms exist between PHYs and SPAs (Zheng et al., 2013; Sheerin et al., 2015), and UVR8 and SPAs (Favory et al., 2009; Huang et al., 2013). Another mechanism that controls COP1 activity is its light-based nuclear exclusion that affects HY5 degradation (von Arnim and Deng, 1994; Pacín et al., 2014). COP1 and HY5 are well-known regulators of the transition from skoto- to photomorphogenesis; for a detailed overview, we refer to Huang et al. (2014).

PIFs

PIFs are a group of basic helix-loop-helix transcription factors that mediate various physiological responses, such as seed germination, seedling photomorphogenesis, shade avoidance, and shoot architectural responses to elevated temperature (Koini et al., 2009; Chen and Chory, 2011; Hornitschek et al., 2012; Jeong and Choi, 2013; Xu et al., 2015). PIFs are regulated by light, temperature, and the circadian clock, and these cues can lead to PIF degradation by concerted action of the PHYs and the E3-ligase Light-Response Bric-a-Brack/Tramtrack/Broad (Leivar and Monte, 2014; Ni et al., 2014; Jung et al., 2016; Legris et al., 2016). The PHY and CRY photoreceptors can physically interact with specific sets of PIF proteins and thereby regulate PIF phosphorylation. The phosphorylation status of PIFs subsequently determines their activity and in most instances their stability (Paik et al., 2017). ChIP-seq studies on PIFs have identified a very broad range of target genes, including those associated with cell wall modifications, auxin biology and several other transcription factors. This broad range of targets combined with the multitude of signals that impact on PIF stability makes PIF proteins a signaling hub to integrate environmental conditions (Leivar and Monte, 2014; Paik et al., 2017).

Photoreceptors

UVR8

The effect of UV-B radiation on plant growth is dual. High fluence UV-B exposure causes photodamage, but low fluence UV-B contributes to photomorphogenesis and increases the resistance to herbivorous insects

and pathogens (Ballaré et al., 2012; Galvão and Fankhauser, 2015). UV-B (280–315 nm) is perceived by UVR8, which uses a structure based on tryptophans and a complex salt bridge network. Upon sensing UV-B light, the salt bridges are disrupted, inducing dimer dissociation into UVR8 monomers and initiating signal transduction (Christie et al., 2012). The UV-B-induced responses include hypocotyl growth inhibition, altered leaf morphogenesis, stomatal closure, and compound synthesis associated with the prevention and repair of UV damage (Binkert et al., 2014; Galvão and Fankhauser, 2015). UVR8 regulates UV-B responses by negatively affecting COP1 function through the UVR8-SPA interaction (Osterlund et al., 2000; Favory et al., 2009; Huang et al., 2013; Hayes et al., 2014). Formation of UVR8-SPA leads to inhibition of COP1 function, and this results in stabilization of, among others, HY5 and HYH, thereby inducing genes downstream associated with UV-B signaling (Osterlund et al., 2000; Rizzini et al., 2011; Hayes et al., 2014).

CRYs

Blue light (320–500 nm) is used for photosynthesis and also serves as a signal for shade, photoperiodism, and directional light. Blue light sensing is performed by three groups of light receptors: CRYs, PHOTs, and other LOV domain-containing receptors such as ZEITLUPE (ZTL). CRYs are blue light receptors found in a broad range of organisms, including bacteria, fungi, animals, and plants. Three CRYs are encoded in the Arabidopsis (*Arabidopsis thaliana*) genome: *CRY1*, *CRY2*, and *CRY3*. *CRY1* and *CRY2* act redundantly in promoting flower induction, sensing blue light as input to circadian clock, and stomatal opening in Arabidopsis (Li and Yang, 2007; Galvão and Fankhauser, 2015; Mo et al., 2015). Both CRY1 and CRY2 regulate primary root elongation, but CRY1 promotes primary root elongation in blue light, whereas CRY2 has the opposite effect (Canamero et al., 2006). Mainly, *CRY2* is expressed in Arabidopsis roots (Fig. 1), and CRY1 and CRY2 inhibit root growth via modulation of free auxin levels and polar auxin transport (Mo et al., 2015). The biological function of CRY3 is yet unclear (Song et al., 2006; Klar et al., 2007; Mo et al., 2015). CRYs are nuclear flavoproteins, composed of two domains, an N-terminal photolyase-related region and a C-terminal domain of varying size. The photolyase-related region binds the chromophore FAD and serves as the light-sensing part. Upon absorbing blue/UV-A light, CRY is phosphorylated and can interact with other protein partners, such as COP1, SPAs, and PIFs (Lian et al., 2011; Liu et al., 2011; Zuo et al., 2011; de Wit et al., 2016; Pedmale et al., 2016).

PHOTs

PHOTs are blue light receptors that mediate phototropism, chloroplast movement, and stomatal opening in Arabidopsis (Briggs and Christie, 2002). There are two PHOTs identified in Arabidopsis, phot1 and phot2, with similar function and structure. Besides their function in the shoot, *phot1* is also expressed in the roots, regulating root bending (Wan et al., 2012; Zhang et al., 2013). In contrast to other photoreceptors, which are present in the nucleus or cytoplasm, PHOTs are located in the plasma membrane (Sakamoto and Briggs, 2002). When phot1 is activated by blue light, it phosphorylates PHYTOCHROME KINASE SUBSTRATE4 (PKS4), and interacts with NON-PHOTOTROPIC HYPOCOTYL3 (NPH3) to form a phot1-PKS-NPH3 protein complex (Pedmale and Liscum, 2007; Demarsy et al., 2012). This modulates auxin transport and thus underlies plant phototropism (Fankhauser and Christie, 2015). PHOTs have N-terminal FMN chromophore-binding light oxygen voltage (LOV1 and LOV2) domains for light absorption and a C-terminal AGC-type Ser/Thr protein kinase signaling domain (Briggs and Christie, 2002).

The ZTL, FLAVIN-BINDING, KELCH REPEAT, F-BOX, and LOV KELCH PROTEIN2 are blue light photoreceptors involved in circadian clock and photoperiodic flowering regulation, with a structure similar to PHOTs but with only one LOV domain followed by an F-box and six Kelch repeats (Galvão and Fankhauser, 2015).

PHYs

PHYs are photoreceptors sensing R and FR light that occur in plants as well as in fungi and prokaryotes (Burgie and Vierstra, 2014). Plants use R/FR light signaling through phytochromes to regulate germination, de-etiolation, stomatal development, flowering transition, senescence, and shade avoidance (Franklin and Quail, 2010). Five PHYs are identified in Arabidopsis, phyA through phyE. PHYs use the N-terminal covalently linked phytochromobilin to sense light and the C terminus to transmit the light signal. PHYs undergo reversible conformation changes: The inactive Pr form absorbs R light (max = 660 nm) that leads to its photoconversion into the active Pfr form that can then absorb FR light (max = 730 nm) to be inactivated. Upon activation, Pfr translocates from the cytosol to the nucleus, where it interacts with PIFs, modulating their activity (Chen and Chory, 2011; Leivar and Quail, 2011; Xu et al., 2015). PhyA, PhyB, PhyD, and PhyE are expressed in the root, while PhyC expression in the root is hardly detectable (Fig. 1). *Phyb* mutants have been shown to produce fewer lateral roots (Salisbury et al., 2007), and *Phyb* and *Phya* single and double mutants have reduced root elongation compared with the wild type (Correll and Kiss, 2005; Silva-Navas et al., 2015). Recently, PhyB has been identified to act as a temperature sensor (Jung et al., 2016; Legris et al., 2016), which is interesting since heat stress is known to lead to increased main root growth (Hanzawa et al., 2013). If this occurs through PhyB signaling has yet to be resolved, but since high temperatures destabilize PhyB and *PhyB* mutants have reduced root lengths, this may not be likely.

BOX 1. Root Development

Plant roots take up water and nutrients that are essential for plant growth. The Arabidopsis root grows from a set of stem cells at the root tip governed by the organizing cells of the quiescent center (QC), four cells that can be traced back to the triangular embryo development stage (Scheres et al., 1994). Around the QC, stem cells divide to form all the layers of the Arabidopsis root, which are from outer to inner: the root cap, epidermis, cortex, endodermis, pericycle, and vasculature, including the xylem and phloem (Petricka et al., 2012). In the meristem zone above the QC, stem cells divide and are not yet differentiated, while at roughly 0.2 mm above the QC the cells differentiate and elongate. It is at the boundary of these two zones where the lateral roots are primed in the xylem pole pericycle layer through an auxin signal (De Smet et al., 2007). Lateral roots develop and emerge at a later time by anticlinal and periclinal divisions of the primed xylem pole pericycle cells (De Rybel et al., 2010), after which the growing lateral root primordium actively modifies the overlaying endodermis, cortex, and epidermis tissue to emerge (Péret et al., 2013; Vermeer et al., 2014).

The plant hormone auxin is necessary for all aspects of root development. In the root tip, there is a high concentration of auxin that is achieved by the active transport of auxin towards the tip and QC (Blilou et al., 2005) and local auxin biosynthesis in the root stem cells (Stepanova et al., 2008). The auxin in the root tip drives the expression of PLETHORA transcription factors, which regulate differentiation via a degradation-based PLETHORA gradient (Galinha et al., 2007; Mähönen et al., 2014). In lateral root development, auxin is similarly important and facilitates the first divisions of the primordium, followed by the development through cell division and the emergence through the overlaying tissue (Lavenus et al., 2013). Cytokinin acts antagonistically to auxin, and together these two plant hormones determine root patterning. Briefly, auxin induces cell division, while cytokinin promotes differentiation (Dello Ioio et al., 2007, 2008).

IMPACT OF DIRECT LIGHT SIGNALING ON ROOT DEVELOPMENT AND PLASTICITY

Root Development in Dark Versus Light

Root development (Box 1) starts at embryogenesis (Scheres et al., 1994), and all root layers are continuously formed from stem cells at the tip (Petricka et al., 2012) that are maintained by a constant auxin flow (Blilou et al., 2005; Galinha et al., 2007; Stepanova et al., 2008; Mähönen et al., 2014) while cytokinin promotes differentiation of these root layers (Dello Ioio et al., 2007, 2008). Lateral roots form after embryogenesis and are primed in the differentiation zone of the meristem (De Smet et al., 2007; De Rybel et al., 2010). Subsequently, they emerge through the outer layers of the main root (Lavenus et al., 2013) upon modification of these layers (Péret et al., 2013; Vermeer et al., 2014). In total darkness, the Arabidopsis seedling elongates its hypocotyl in an attempt to penetrate the soil, but its root stays very small (Fig. 2). Roots of dark-grown seedlings are much shorter and have a much thinner diameter than those of light-grown seedlings (Laxmi et al., 2008; Dyachok et al., 2011). When etiolated seedlings are exposed to light, they inhibit hypocotyl elongation, develop their cotyledons, and start to photosynthesize (Wu, 2014). Cotyledon-derived sugars are essential for the start of root growth, and when young seedlings are decapitated, root growth is slowed dramatically, also when grown in the light (Kircher and Schopfer, 2012). Besides Suc, the basipetal flow of auxin is necessary to facilitate root growth in seedlings (Bhalerao et al., 2002), and in the dark this basipetal auxin transport is very low due to the depletion of PIN-FORMED (PIN) auxin efflux carriers from the plasma membrane (Laxmi et al., 2008; Sassi et al., 2012). Light induces root growth by providing sugars and auxin to the young root, and specifically R and blue light exhibit a positive effect on root elongation when compared with darkness

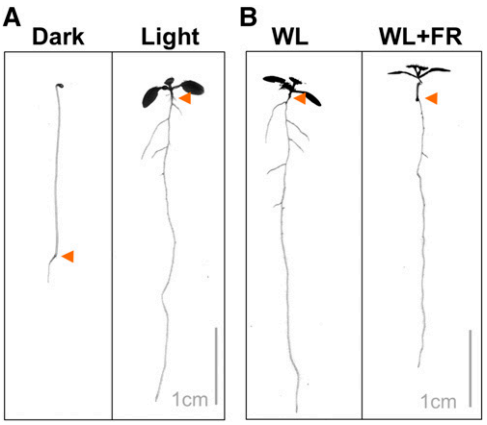

Figure 2. Root growth is affected by light quantity and quality. A, Eight-day-old seedlings grown on half-strength Murashige and Skoog medium in darkness and white light (WL; 140 μM m^{-2} s^{-1} photosynthetically active radiation). B, Eight-day-old seedling grown in white light (140 μM m^{-2} s^{-1}) or white light plus FR (WL+FR; R:FR 0.1). The arrowheads point to the root-shoot junctions.

(Sweere, 2001; Canamero et al., 2006; Costigan et al., 2011; Fig. 2). However, the addition of Suc to the agar medium can sometimes reverse this effect (Correll and Kiss, 2005). Supplementation of white light with FR light reduces root growth compared with normal white light (Salisbury et al., 2007; Fig. 2), and UVB has a strong inhibiting effect on root growth, either when supplied to the whole seedling or only the root (Tong et al., 2008; Leasure et al., 2009; Silva-Navas et al., 2015).

Many experiments addressing root development have been performed in the presence of light on the whole seedling since root development is typically studied in vertical agar plate setups with transparent medium. In field conditions, the top part of the root system will grow in minimal light and the lower part will even develop in darkness, while the shoot can be exposed to various different light conditions (Smith, 1982). Several solutions to these undesirable lab conditions have been postulated, including dark agar plugs (Sassi et al., 2012), black-colored vertical plates (Xu et al., 2013), and the D-Root system consisting of plate inserts plus cover slips (Silva-Navas et al., 2015). In the D-Root system, seedlings grow on medium in vertical square plates, but an insert at the root-shoot junction and an external cover slip prevent light exposure of the roots, whereas the shoot is exposed to the ambient light conditions. Compared with plants with roots grown in fully exposed light conditions, plants with roots in darkness have increased main root length and lateral root number, while root hair length decreased. When dark-grown roots were exposed to light for a duration longer than 8 h, their growth rate and root meristem size declined (Silva-Navas et al., 2016). Interestingly, shielding roots from light decreased the sensitivity of the main root to the plant hormones abscisic acid, brassinolide, and 6-benzyladenine, while the sensitivity to indole-3-acetic acid was increased (Silva-Navas et al., 2015). Interestingly, dark-exposed roots were less sensitive to salt and low nitrogen conditions compared with light-exposed roots (Silva-Navas et al., 2015). These data show that direct perception of light by the root is physiologically relevant in Arabidopsis seedlings.

Light Affects Root Developmental Plasticity

The root system can change the direction of growth in response to stimuli such as gravity (Morita, 2010) or light (Kutschera and Briggs, 2012). The movement of the root away from light sources, or root negative phototropism, is dependent upon blue light perception by PHOTs (Wan et al., 2012). Contrary to the negative response to blue light, a positive growth response of the root to R light has also been observed (Kiss et al., 2001), but this response is weak and can only be observed in the absence of gravity sensing (Ruppel et al., 2001; Kiss et al., 2003). Downstream of light perception, root phototropism impinges on elements involved in root gravitropism (Kiss et al., 2003; Kutschera and Briggs, 2012).

Root Negative Phototropism

Root negative phototropism is induced by blue and white light, and the photoreceptors involved are mainly phot1 and phot2, with minor roles for phyA and cry1/cry2 (Boccalandro et al., 2008; Wan et al., 2012; Silva-Navas et al., 2016). NPH3, a target of phot1 and phot2 involved in hypocotyl phototropism, also is an important player in root negative phototropism (Wan et al., 2012). Downstream of directional light perception, polar auxin transport directs auxin away from the illuminated side. This auxin transport gradient requires rootward plasma membrane localization of the auxin efflux carrier PIN1 in the stele, lateral relocalization of PIN3 in the columella, and rootward relocalization of PIN2 in the epidermis (Wan et al., 2012; Zhang et al., 2013, 2014). The relocalization of PIN2 and PIN3 is dependent upon the recycling and targeted degradation (vacuolar targeting) of these PIN carriers from one side of the membrane to the other (Wan et al., 2012; Zhang et al., 2013). The initial perception of gravitropism and phototropism is different, but the downstream signaling events of negative phototropism are very similar to those found in root gravitropism, involving comparable PIN protein and auxin transport dynamics (Friml et al., 2002; Abas et al., 2006; Baster et al., 2013). Most root phototropism experiments have been performed under conditions where the whole seedling was directionally illuminated. When roots that had been grown in the dark were stimulated by a one-sided white light stimulus while the shoot still remained in the dark, the negative phototropism persisted and an important role for flavonols was uncovered in the regulation of this response (Silva-Navas et al., 2016). White light, together with cytokinins, stimulates the accumulation of flavonols on the lighted side of the root, which

induces cell elongation and stimulates PIN1 plasma membrane abundance (Buer and Muday, 2004; Silva-Navas et al., 2016).

Interaction of Light and Gravitropism

As mentioned above, both root negative phototropism and gravitropism rely on polar auxin transport. Light influences the direction of polar auxin transport by controlling the plasma membrane abundance of PIN proteins (Laxmi et al., 2008; Sassi et al., 2012; Wan et al., 2012; Zhang et al., 2013, 2014). An interesting example of how light interacts with the gravitropic output is the U-turn that an inverted maize (*Zea mays*) seedling root makes when growing in a glass tube exposed to light (Burbach et al., 2012; Suzuki et al., 2016). When these seedlings are inverted in the dark, they do not show this strong gravitropic response (U-turn), indicating that light can increase gravitropism. In accordance with this, Arabidopsis root slanting (on agar plates) and the root gravitropic response are reduced in the D-Root system where roots are kept in darkness (Silva-Navas et al., 2015). Light stimulates the gravitropic response through the increase of flavonol biosynthesis, which increases root auxin levels (Buer and Muday, 2004; Silva-Navas et al., 2016). Interestingly, FR light enrichment of Arabidopsis seedlings grown fully in the light leads to reduced activity of the auxin reporter pDR5::GUS (Salisbury et al., 2007), showing how light quality can markedly change root auxin homeostasis. Another way that light signaling influences auxin transport in the root is by controlling the removal of PIN proteins from the plasma membrane via the process of vacuolar degradation. Since PINs are transmembrane proteins, their degradation occurs through vacuolar targeting and subsequent degradation of multivesicular bodies containing PINs (Korbei and Luschnig, 2013). This vacuolar degradation of PINs is an important process in changing PIN polarity and is essential for the regulation of gravitropism (Baster et al., 2013). PIN2-GFP vacuolar targeting is controlled by the COP1/CSN complex in a light-dependent manner (Laxmi et al., 2008; Sassi et al., 2012). When a seedling is incubated in darkness for several hours, PIN2-GFP is targeted toward the vacuole (Kleine-Vehn et al., 2008), but this does not occur when only the seedling shoot is given a light treatment, or in the *cop1-6* mutant (Sassi et al., 2012), showing how (COP1-mediated) light signaling in the shoot can affect root development.

ABOVEGROUND LIGHT REGULATES ROOT DEVELOPMENT: MECHANISMS AND CONSEQUENCES

As mentioned above, it is critical to research the effects of light signaling on root developmental plasticity under conditions where roots are not directly exposed to the light environment as they are typically shielded from by the soil under natural conditions. Indeed, root systems develop differently between dark and light conditions of the roots themselves. Since plants constantly coordinate growth and development of root and shoot in response to their highly dynamic environment, they do need to translate important information about their light environment to the root system. This is of particular importance under dense planting conditions, such as in most agricultural fields, where both above- and belowground competition for resources occurs (Pierik et al., 2013; Gundel et al., 2014). Below ground, plants compete for water and nutrients, whereas above ground they struggle for light. Belowground competition is size-symmetric, which means that resource acquisition is proportional to the size of the root system of a given individual in a dense stand. Competition for light is size-asymmetric: A plant that is only slightly taller than its neighbors can put its leaves above those neighbors, thereby severely limiting their total access to light while itself not being affected at all by its neighbors (Weiner, 1985; Weiner and Thomas, 1986). Above ground, plants maximize their competitive performance against neighbors by activating the so-called shade avoidance response (Box 2). Briefly, FR light reflected by neighbor plants inactivates the PHY photoreceptors, and this relieves their repression of PIF4, PIF5, and PIF7. PIFs then accumulate, induce auxin biosynthesis and transport, and auxin subsequently induces elongation of hypocotyls, stems, and petioles as well as upward leaf movement (Lorrain et al., 2008; Keuskamp et al., 2010; Casal, 2013; Gommers et al., 2013; Kohnen et al., 2016; de Wit et al., 2016; Ballaré and Pierik, 2017; Michaud et al., 2017; Pantazopoulou et al., 2017). In this section, we briefly review the currently established mechanisms of light signal information transfer from the shoot to the root, followed by a discussion on its functional importance under dense planting conditions and plant competition.

Mechanisms of Light Signal Information Transfer from Shoot to Root

Stem-Piped Light

Stem-piped light refers to the light transmitted through the internal tissues of the plants from the shoot to the root. This manner of light transmission through the interiors of the plant has been described for woody and herbaceous species. Light piping is wavelength specific, and long wavelengths such as FR and near infrared light are transmitted relatively well, while shorter wavelengths such as blue and green light are less effectively transmitted (Sun et al., 2003, 2005). Stem-piped light can activate root-expressed phyB, which on its turn regulates HY5 in the Arabidopsis root (Lee et al., 2016). HY5 is involved in root growth in response to light, modulating, for example, root gravitropism and nitrogen uptake (Cluis et al., 2004; Lee et al., 2007; Huang et al., 2015; Chen et al., 2016). Therefore, stem-piped light might communicate information about the aboveground light environment to the root (Fig. 3).

BOX 2. Shade Avoidance

When shade-intolerant plants are surrounded by neighbors, they typically engage in direct competition by inducing the "shade avoidance syndrome" (see fig.). Shade avoidance responses include elongation of stems and petioles, upward leaf movement (hyponasty), enhanced apical dominance (reduced branching), and early flowering (Gommers et al., 2013; Ballaré and Pierik, 2017). These responses help plants to escape from shade caused by neighboring leaves and enable access to direct sunlight. Shade avoidance responses are adaptive, but may come at the costs of the economic yield of crops or at the cost of pathogen and herbivore resistance (Ballaré et al., 2012; Ballaré, 2014), and therefore are not always desirable in agricultural systems. Shade avoidance is induced by the sensing of light signals: First, due to the reflection of far-red (FR) light of neighboring leaves, which lowers the R:FR ratio, and second, by the depletion of blue (B) light when light limitation through canopy shading occurs (Casal, 2013; Ballaré and Pierik, 2017). The low R:FR ratio is perceived by phytochromes, which are subsequently inactivated and leading to PIF stabilization, as described in the main text. Mainly PIF4, PIF5, and PIF7 are involved in the shade avoidance response, and their stabilization and transcriptional responses lead to auxin accumulation, induction of cell wall-remodeling genes, and subsequent cell elongation, ultimately resulting in hypocotyl and petiole elongation and hyponastic leaf movement (Lorrain et al., 2008; Keuskamp et al., 2010; Kohnen et al., 2016; Michaud et al., 2017; Pantazopoulou et al., 2017). Low B is perceived by the cryptochromes and their signaling pathway is partly converged with phytochromes during shade avoidance by acting on PIFs (Pedmale et al., 2016) and on the degradation of the negative regulator of shade avoidance HFR1 (Keuskamp et al., 2011; de Wit et al., 2016). The combination of low B and low R:FR represents the actual canopy shade, and the shoot elongation response to this signal combination is stronger than the response to low R:FR alone (de Wit et al., 2016), indicating that plants adjust shade avoidance responses to signal intensity.

BOX 2 , Figure A. Shade avoidance induced by low R:FR. Carrot (*Daucus carota*) plants grown in white light (WL; left) and WL+FR (right). Plants were grown in WL or WL+FR for 8 weeks. PAR was ~120 µmol m^{-2} s^{-1}, and the FR ratio was 1.8 (WL and 0.2 (WL+FR). Scale bar = 1 cm.

However, the light transmission goes down to 1% when conduction distances increase to 3 cm in herbaceous plants (Sun et al., 2005), which suggests that this mechanism might play a relatively modest role in mature planting systems.

Mobile (Signaling) Chemicals

Although various components are transported from the shoot to the root, only a few of them have been directly linked to light signaling in the shoot. These include sugars derived from photosynthesis and transported

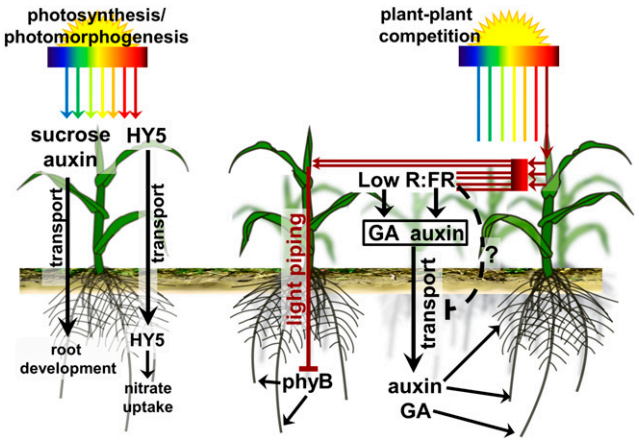

Figure 3. The aboveground regulation of root development in dense vegetation involves photosynthesis, light piping, hormones, and mobile factors. The primary effect of light is to enable photosynthesis, which leads to the production of sugars (sucrose) that enable the root to grow. Photomorphogenic development is associated with the production of auxins in the shoot, which are transported rootward and enable root development. HY5 is stabilized in the shoot during photomorphogenesis and is transported rootward, where it regulates nitrate uptake and root development. Light is used as a cue to detect neighboring plant competition via sensing of the R:FR ratio. Plant tissues reflect FR, which lowers the nearby R:FR ratio, leading to shade avoidance responses mediated by, among others, auxin and GA. These hormones can be transported rootward, where they affect root development. There also are indications that shade avoidance responses, in a negative feedback mechanism, decrease the amount of rootward auxin transport. FR light itself also can be transmitted directly through woody, vascular tissues from the shoot to the root, where it can affect root-localized PHYs. Plant vector drawing: Lobet (2017).

through the phloem, plant hormones, and HY5. These will be briefly discussed below.

Sugars. Once a seed is germinated, it first invests energy in hypocotyl growth. Upon penetrating the soil and perceiving light, photomorphogenesis is initiated and the seedling acquires the ability to conduct photosynthesis, followed by root growth (Kircher and Schopfer, 2012). It was shown in Arabidopsis seedlings that blocking photosynthesis inhibits root growth, just like in darkness, and that adding Suc to the growth medium can rescue root growth. Interestingly, Suc addition could not induce additional root growth in photosynthesis positive seedlings (Kircher and Schopfer, 2012). These data confirm that Suc is needed for root growth and development, and indicate that Suc can serve as a long-distance signal from the shoot to inform the root system about light availability above ground (Fig. 3).

Auxin. Young shoot tissues are the main source of the plant hormone auxin that is then transported to the root system, where it regulates root development, including lateral root formation (Reed et al., 1998; Bhalerao et al., 2002; Fig. 3). Interestingly, light signaling affects auxin biosynthesis and transport, implicating this hormone as a potential integrator of light signaling and root development. PHY inactivation in low R:FR light triggers auxin biosynthesis in the shoot (Hornitschek et al., 2012), which is then transported laterally through the hypocotyl during low R:FR conditions by PIN3 as well as PIN4 and PIN7 (Keuskamp et al., 2010; Kohnen et al., 2016) and rootward by PIN1 and PIN2 in response to light (Sassi et al., 2012). In darkness, the expression of PIN1 is largely reduced, thus reducing auxin delivery to the root system (Sassi et al., 2012).

Gibberellic Acid. The plant hormone gibberellic acid (GA) mediates various growth and developmental processes, such as seed germination, cell elongation, and reproductive development (Hedden and Sponsel, 2015). Low R:FR induces GA biosynthesis, at least partly through elevated expression of *GA20OX* genes (Hisamatsu et al., 2005). GAs are diterpenoid tetracyclic carboxylic acids, but only a few are biological active, such as GA_1 and GA_4 (Hedden and Thomas, 2012). Interestingly, biologically inactive GA_{12} has been identified as a long-distance growth signal that is transported from the shoot to the root. Here, GA_{12} is converted into active form by GA20ox and GA3ox enzymes and subsequently promotes root growth in Arabidopsis (Regnault et al., 2015; Fig. 3). It is yet unknown if low R:FR-induced production of bioactive GAs in the shoot affects downward GA_{12} transport.

HY5. The transcription factor HY5 is a key integrator of photomorphogenesis and is involved in light, hormone, and stress signaling (Cluis et al., 2004; Lee et al., 2007; Gangappa and Botto, 2016). HY5 was recently shown to be transported upon light activation from the shoot to the root (Chen et al., 2016). In the root system, HY5 activates its own expression and that of HYH, creating a positive feedback loop after shoot-to-root transport of HY5 (Zhang et al., 2017). HY5 and HYH modulate lateral root development and lateral root gravitropism (Oyama et al., 1997; Sibout et al., 2006). Interestingly, R:FR ratios influence the expression and stability of HY5, and this transcription factor is, therefore, together with auxin and gibberellin, a candidate regulator of root developmental adjustments to shoot-sensed R:FR light ratios, which indicate the presence of neighboring competitors.

Functional Implications in Dense Vegetation

R:FR light conditions above ground are a reliable cue for the presence of competing neighbors and effectively trigger shade avoidance (Box 2). Interestingly, if the R:FR ratio signals neighbor proximity, it would also signal the likely presence of neighbors below ground competing for water and nutrients (Gundel et al., 2014). Competition experiments in Arabidopsis have shown that root biomass decreases when plants are competing in dense stands and that there is a separate transcriptomic regulation in the root versus the shoot (Masclaux et al., 2012). In controlled growth on medium, seedlings experiencing a low R:FR ratio have a lower lateral root number and main root length (Salisbury et al., 2007). However, as argued previously, in soil conditions the roots are not

OUTSTANDING QUESTIONS

- Do plants use light cues associated with density in vegetation to adjust root development, architecture, and nutrient acquisition physiology to neighbors?
- Do root responses to soil (stress) conditions affect aboveground (architectural) responses to light signals?
- Which mobile signals control root system architecture upon photoreceptor activation by different wavebands in the shoot, and through which tissue(s) do these factors travel towards the root system?
- Is there strong genetic variation for light (quality and quantity) effects on root development, or are these broadly occurring responses throughout the higher plant kingdom?

directly exposed to low R:FR light, and the shoot might thus relay information about nearby competitors to the root system either by direct piping or through secondary mobile messengers.

An important question that remains is what are the functional implications of light signal transmission from the shoot to the root? One clear functional example is that HY5 can stimulate nitrate uptake via NRT2;1 and will do so upon light-activation in the shoot (Chen et al., 2016; Fig. 3). This will help keep the carbon and nitrogen acquisition in tune. In accordance with these findings, direct shading in different phases of the growth period of field-grown maize was shown to suppress root mass, length, and absorptive area, suggesting reduced nutrient and/or water uptake rates (Gao et al., 2017). In addition to true shade, a reduced R:FR light ratio also affects root growth in different species (Kasperbauer and Hunt, 1992, 1994; Salisbury et al., 2007). The effects of reduced R:FR ratios on lateral root formation (Salisbury et al., 2007) may go at the expense of nutrient uptake rates, and might reflect a resource prioritization strategy at the whole plant level, ensuring that resources are invested to consolidate light capture in a growing vegetation with increasing competition for light. It is presently unknown if the root architecture responses to low R:FR affect nutrient acquisition at all, but the resulting reduced root length would suggest so. Nevertheless, much more detailed research into nutrient and water uptake rates of plants under high and low R:FR conditions is needed to assess the precise functional implications of shoot-to-root communication of the aboveground light climate.

Alternatively, plants may also sense neighbors below ground through, for example, nutrient depletion zones and chemical exudates. It is unknown if these cues are transferred to the shoot to prepare for upcoming competition or to adjust shoot responses to light cues from neighbors. Finally, abiotic stresses, for example, drought, occur primarily in the belowground environment and may interact with aboveground light responses. Although little is known about interactions between abiotic stresses and shade responses of the shoot, there is ample information about the interaction of biotic stress and neighbor detection through light cues. The emerging picture is that shade avoidance responses and PHY signaling dominate plant defenses against pathogenic microorganisms and insects (de Wit et al., 2013; Ballaré, 2014), thus prioritizing light interception. It will be interesting to study if, next to biotic stresses, responses against abiotic stresses are suppressed to accommodate shade avoidance responses at high plant density.

CONCLUDING REMARKS

Plants have a variety of photoreceptors that control many different aspects of plant life, including root development. Recently, several novel mechanisms have been discovered that allow plants to relay information from the shoot and its environment to the root system. These include direct light transmission, hormones, and mobile proteins. Although research into these different mechanisms will continue to identify novel mechanisms, it is also crucial to establish the functional implications of this information transfer. It is therefore pertinent that ecologists, agronomists, and plant scientists join forces to unravel both the mechanisms and functional implications of shoot-root communication induced by light cues from the environment.

Received August 1, 2017; accepted September 19, 2017; published September 22, 2017.

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