Seedling Establishment: A Dimmer Switch-Regulated Process between Dark and Light Signaling[1][OPEN]

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By being exquisitely sensitive to their light surroundings, plants are able to continuously adjust their growth to optimize fitness. Darkness is an important cue for plants and a time when they actively grow and develop through regulation of the appropriate gene networks and biochemical changes. Although plants might not possess "dark receptors," inactive photoreceptors facilitate activation and inhibition of dark-specific processes, and thus darkness itself might be considered a signal triggering a myriad of responses. In this *Update*, we review the effects of dark and light signaling during seedling establishment. We describe the features of seedlings germinated in the dark and their switch in development upon emerging into the light. We examine how aboveground growth is regulated by the duration of dark/light cycles and how circadian clock signaling is integrated. Finally, we discuss some of the challenges faced by young seedlings during their establishment, such as variations in temperature or in light quality and quantity. Although mentioned briefly, we do not cover in detail the contribution of sugars or temperature to seedling establishment in response to dark and light signals; we refer readers to excellent recent reviews (Franklin et al., 2014; Legris et al., 2017; Seluzicki et al., 2017). The emerging view is that of seedling establishment regulated as a dimmer-type switch where relative amounts of dark and light signaling dynamically optimize plant development to the surrounding light environment.

SEEDLING ESTABLISHMENT IS FIRST HETEROTROPHIC AND FUELED BY SEED RESERVES

The process of seedling establishment starts with seed germination, when the newly emerging seedling grows heterotrophically on seed reserves, and it is completed when the seedling has gained photosynthetic competence and becomes autotrophic. It is one of the most critical and vulnerable processes in the life of a plant, and it often represents a challenge after emerging from the protected environment of the seed. Until the seedling reaches photoautotrophy, post-germinative seedling development is fueled on seed storage reserves. These nutrient reserves are deposited in the seed during seed maturation in the mother plant, and consist of oil, storage protein, and/or carbohydrates (usually starch), depending on the plant species. Reserves can remain intact as insoluble compounds in desiccated seeds for extended periods of time. The predominant storage tissue in some plant species, such as the oilseed castor bean (*Ricinus communis*), is the endosperm, whereas in others with a greatly reduced endosperm, it is the embryo (Eastmond and Graham, 2001). Upon seed germination, reserves are mobilized into soluble metabolites to fuel growth and achieve establishment before seed nutrients are depleted. The efficiency of reserve mobilization is associated with seedling vigor, a key determinant of seedling establishment and crop yield in the field (Finch-Savage and Bassel, 2016).

ADVANCES

- Dark and light signaling are interconnected and balanced during seedling emergence and day/night cycles.
- Photoreceptor-regulated transcription factors like PIFs and HY5 regulate seedling establishment through the regulation of 20% of the transcriptome in Arabidopsis.
- Cross-talk and integration between endogenous and light signaling pathways are necessary to optimize seedling establishment.
- Chloroplast-to-nucleus retrograde signaling impacts seedling establishment in high light conditions to protect from photo damage.
- Organ-specific and long-distance traveling signals are emerging as sophisticated regulatory mechanisms in the life of plants.

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BOX 1. Perceiving and Signaling Dark and Light: Receptors and Primary Regulators

The relative amount of light and dark modulates the flow of information signaled through a variety of wavelength-specific photoreceptors to their downstream signaling partners. UVR8 perceives Ultra Violet B light (UVB; 280-315 nm), phototropins (PHOT), cryptochromes (CRYs) and zeitlupe (ZTL) account for UV-A, blue, and green light (±315–550 nm) perception, and phytochromes (phyA-E) are sensitive for red (R) and far-red (FR) light (±600–750 nm). These photoreceptors regulate similar and distinct developmental transitions or adaptations in response to changing light environments (Galvão and Fankhauser, 2015). Seedling photomorphogenesis and establishment are mainly under control of phyB and phyA, and blue-light-activated CRY1 and CRY2. Active phys form nuclear photobodies mediated by HEMERA (HMR) or tandem zinc knuckle/plus3 (TZP) to centralize destabilization and transcription of photomorphogenesis-inhibiting proteins (Chen et al., 2010; Kaiserli et al., 2015; Huang et al., 2016b). The bHLH PHYTOCHROME INTERACTING FACTORS (PIFs) are transcription factors inhibited by light-activated phys and CRYs that repress photomorphogenesis and regulate many phytohormone pathways (Leivar and Monte, 2014; Ni et al., 2014; Pedmale et al., 2016; Dong et al., 2017; Ni et al., 2017; reviewed in this focus issue by Pham et al., 2017). DELLA proteins create another inhibition level by preventing PIF promotor binding in the light (de Lucas et al., 2008; Feng et al., 2008). Supporting the key-role of PIFs during seedling establishment, the *pif-quadruple* mutant (*pifq*; *pif1pif3pif4pif5*) is photomorphogenic in darkness and shorter in photoperiodic growth conditions (Bae and Choi, 2008; Leivar et al., 2008; Fig. 4).

Partially synergistically with PIFs act the central inhibitors of light signaling CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1) and DE-ETIOLATED1 (DET1; Dong et al., 2014; Xu et al., 2014). COP1 is a ubiquitin E3 ligase, which targets the photomorphogenesis-promoting transcription factors ELONGATED HYPOCOTYL 5 (HY5), HY5-HOMOLOGUE (HYH), and LONG HYPOCOTYL IN FAR RED (HFR1) in darkness (Osterlund et al., 2000; Yang et al., 2005). COP1 acts in a complex with SUPPRESSOR OF PHYA (SPA) proteins (Hoecker, 2017). Active phys and CRYs disassociate SPAs from COP1, releasing the suppressed proteins and causing export of COP1 from the nucleus (Pacin et al., 2014). DET1 is part of the CDD complex, together with COP10 and DAMAGED-DNA BINDING PROTEIN 1 (DDB1), which interacts with the CUL4 E3 ligase machinery. The CUL4-CDD complex suppresses photomorphogenesis by enhancing the COP1-SPA-mediated inhibition of HY5 and by stabilizing PIFs in the dark (Osterlund et al., 2000; Dong et al., 2014).

Lipid in the form of triacylglycerol (TAG) is the main seed reserve in many plant species, such as Arabidopsis (*Arabidopsis thaliana*) or the oilcrops soybean (*Glycine max*), sunflower (*Helianthus annuus*), rapeseed (*Brassica napus*), safflower (*Carthamus tinctorius*), and maize (*Zea mays*; Graham, 2008). In Arabidopsis, about 90% of the reserves (TAGs and protein) are stored in the cotyledons and the rest in the endosperm (Penfield et al., 2004). Through gluconeogenesis, plants make sugars from lipid and protein stores to fuel seedling establishment. In fact, Arabidopsis lipid reserve mobilization is critical for seedling establishment (Kelly et al., 2011). Whereas oils in the cotyledons fuel their transformation into photosynthetic organs, oils in the endosperm fuel hypocotyl growth in the dark. In several plant species, such as Arabidopsis, rapeseed, cucumber (*Cucumis sativus*), and sunflower, lipid reserve mobilization is enhanced by light (Theimer and Rosnitschek, 1978; Davies et al., 1981; Sadeghipour and Bhatla, 2003; Leivar et al., 2009). In others species, like mustard (*Sinapis alba*) or tomato (*Solanum lycopersicum*), light appears not to regulate oil mobilization but the activity of two key enzymes of the glyoxylate cycle (isocitrate lyase and malate synthase) involved in the synthesis of Glc from the acetate generated in fatty acid β-oxidation (Bajracharya and Schopfer, 1979; Eckstein et al., 2016). The lipases sugar dependent 1 (SDP1) and SDP1-like (SDP1L) account for 95% of postgerminative TAG degradation in Arabidopsis, given that a double mutant *sdp1sdp1l* is unable to break down any storage oil (Eastmond, 2006; Kelly et al., 2011). However, it is still not clear whether the light-enhanced oil mobilization during seedling establishment involves increased levels or activity of these lipases.

OUT OF THE DARK AND INTO THE LIGHT: SWITCHING THE BALANCE FROM DARK TO LIGHT SIGNALING INDUCES AUTOTROPHIC PHOTOMORPHOGENESIS

When buried under the soil directly after germination, a seedling's mission is to grow toward the light as soon as possible. This is facilitated by rapid elongation of the embryonic stem, the hypocotyl, accompanied by a hook in its most apical part to protect the shoot apical meristem. During this so-called skotomorphogenic growth, cotyledons and roots remain underdeveloped. Reaching the soil surface and the light, the young seedling has to establish a photoautotrophic lifestyle. The light is perceived by several classes of photoreceptors, which induce a signaling cascade toward photomorphogenic

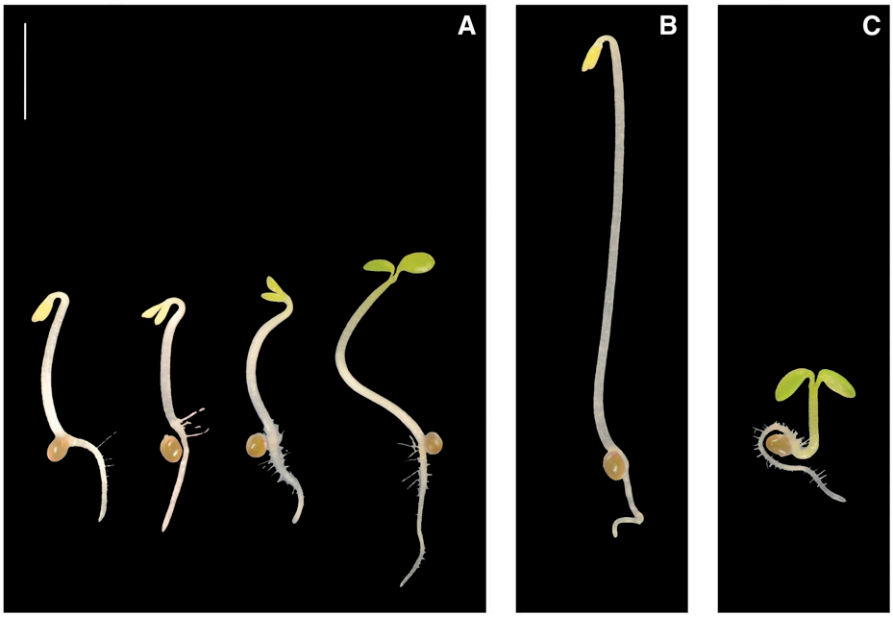


Figure 1. Arabidopsis seedling establishment after the switch from dark to light. Representative pictures of 2-d-old dark-grown seedlings (A) exposed to, left to right, 0 h, 2 h, 6 h, or 24 h of low light (approximately 5 μmol m^{-2} s^{-1} photosynthetically active radiation), and 3-d-old dark-grown (B) and light-grown (C) seedlings. Scale bar = 2 mm.

development (Box 1; Galvão and Fankhauser, 2015; Chen et al., 2010; Kaiserli et al., 2015; Huang et al., 2016b; Leivar and Monte, 2014; Ni et al., 2014; Pedmale et al., 2016; Dong et al., 2017; Ni et al., 2017; Pham et al., 2017; Bae and Choi, 2008; Leivar et al., 2008; Hoecker, 2017; Osterlund et al., 2000; Dong et al., 2014) that leads to extreme, organ-specific developmental changes that require local promotion (cotyledons, roots) and inhibition (hypocotyl) of growth (Fig. 1). Seedling photomorphogenesis is mostly studied in the model species Arabidopsis but is common among a wide variety of plant species. In the field, successful crop seedling establishment is essential for plant growth and yield (Finch-Savage and Bassel, 2016). Most diploid species experience photomorphogenic changes similar to Arabidopsis (see the examples of tomato and quinoa [*Chenopodium quinoa*] in Fig. 2), while dark-grown monocots typically elongate the coleoptile to protect the first true leaf in the dark and then stop elongation upon exposure to light (example of sorghum [*Sorghum bicolor*] in Fig. 2). In the next section, we highlight the plant organs that undergo the most striking developmental switch when an Arabidopsis seedling grows out of the dark and into the light: the apical hook, the cotyledons, the hypocotyl, and the root.

THE APICAL HOOK

Soon after germination, darkness triggers asymmetrical cell expansion and division at the apical part of the hypocotyl, which results in bending. Expansion of the inner (concave) cells is inhibited, while division in the outer (convex) cells is promoted (Silk and Erickson, 1978; Raz and Koornneef, 2001), which forms an apical hook bending up to 180 degrees (Fig. 3A). This asymmetrical cell expansion is caused by an auxin maximum in the concave part of the hook, created by auxin influx and outflux carriers (AUXIN1 [AUX1] and LIKE-AUX1, and PIN-FORMED [PIN] proteins, respectively) in the epidermal cells of the young hypocotyl (Box 2; Žádníková et al., 2010, 2016; Farquharson, 2017). In darkness, PHYTOCHROME INTERACTING FACTORs (PIFs; Box 1; reviewed in this Focus Issue by Pham et al., 2018) enhance auxin synthesis and signaling, and the synthesis of two other important hormones in hook formation and maintenance, ethylene (ET) and gibberellic acid (GA; Box 2; for review, see Mazzella et al., 2014). ET signaling via transcription factors ETHYLENE INSENSITIVE3

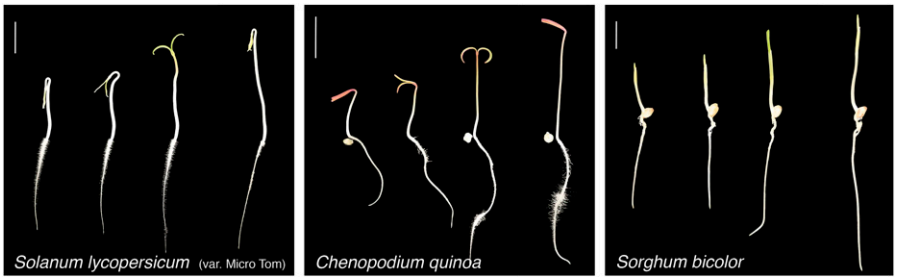


Figure 2. Photomorphogenesis among crop species. Representative pictures of tomato, quinoa, and sorghum seedlings grown for 2 d in the dark exposed to, from left to right, 0 h, 6 h, or 24 h of low light (approximately 5 μmol m^{-2} s^{-1} photosynthetically active radiation), and 3 d in the dark. Scale bars = 1 cm.

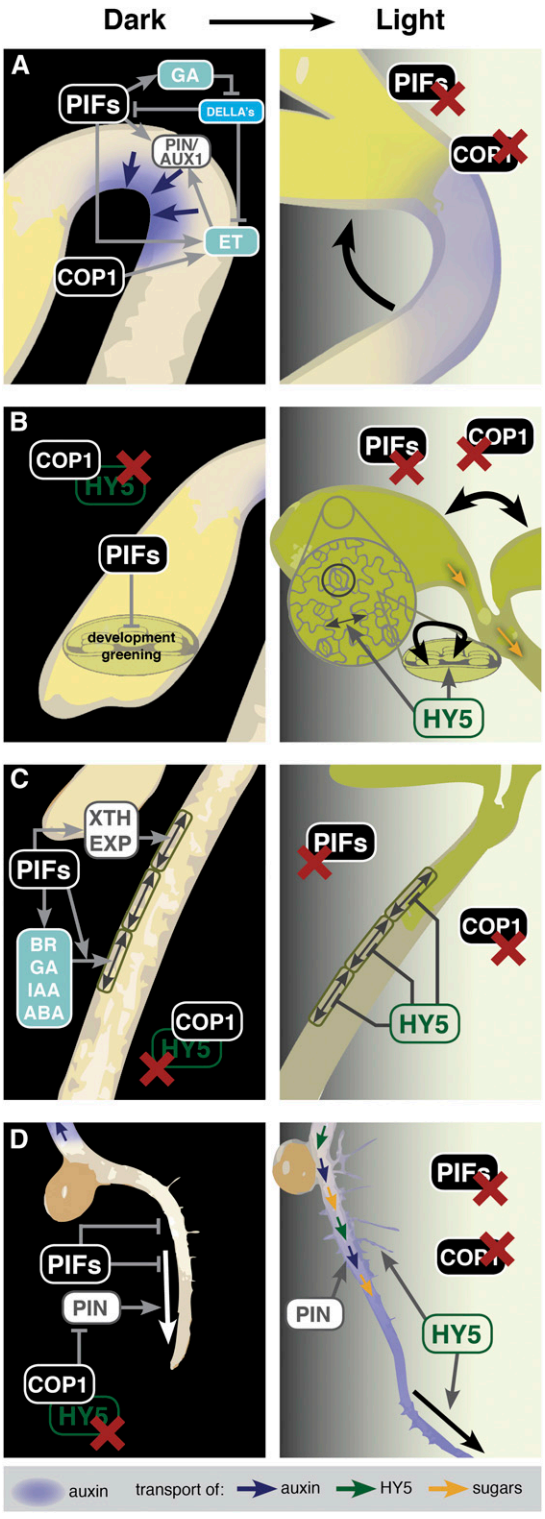


Figure 3. Dark and light signaling induce organ-specific developmental traits in Arabidopsis seedlings. Simplified representation of the traits that accompany development in the dark (left) and upon first light signaling (right). For each organ (apical hook, A; cotyledons, B; hypocotyl, C; and root, D), the most important regulatory factors are shown. Schematic seedling cartoons are modified from the pictures in Figure 1.

(EIN3) and EIN3-LIKE1 (EIL1) induces local PIN gene expression in the epidermis and auxin transport (Žádníková et al., 2016). Accordingly, exogenous treatment with ET causes exaggerated hooks in Arabidopsis (Gallego-Bartolomé et al., 2011). GA appears essential for hook formation as the inhibitor of DELLA proteins, which, in the absence of GA, inhibit both PIFs and EIN3/EIL1 (Box 2; de Lucas et al., 2008; Feng et al., 2008; Gallego-Bartolomé et al., 2011; An et al., 2012). As a consequence, the constitutive DELLA-expressing mutant *gai-1* is unable to form a hook in the dark, and *della* loss-of-function mutants have exaggerated hooks (Gallego-Bartolomé et al., 2011). Although continuous dark periods will slowly cause opening of the apical hook (Raz and Ecker, 1999), this process is significantly enhanced by a light signal (Fig. 1). Light activates phytochromes (phys) and cryptochromes (CRYs), which directly target and degrade PIFs, as well as EIN3 (Box 1; Shi et al., 2016). This causes a rapid loss of GA, ET signaling, and the directional auxin gradient, which enhances cell expansion in the concave part of the hook, followed by opening (Fig. 3A).

THE COTYLEDONS

While in the dark, cotyledons have little to no function and remain closed. Once in the light, cotyledons have to undergo important developmental changes to allow for efficient photosynthesis to fuel autotrophic growth (Fig. 3B).

Separation and Expansion

Dark-grown seedlings have relatively small epidermal pavement cells, which results in small cotyledon areas (Wei et al., 1994). ELONGATED HYPOCOTYL5 (HY5)-mediated cotyledon cell division and expansion are suppressed in darkness by PIFs and COP1 (Stoynova-Bakalova et al., 2004; Xu et al., 2014). Light releases the suppression of HY5 (Box 1) and, thus, allows cotyledon expansion (Josse et al., 2011).

Stomata Development

Light induces stomata development to allow for gas exchange between the plant and the environment. Stomata are epidermal pores, formed by two guard cells with thick elastic walls that resist the high turgor pressure generated during opening. In Arabidopsis, stomatal development is characterized by a series of epidermal cell divisions. In the cotyledons, a subset of protodermal cells can become a meristemoid mother cell committed to the stomatal pathway. The meristemoid mother cell divides asymmetrically to give rise to a small meristemoid (M) and a large sister cell. The M can undergo two further asymmetrical divisions to increase the number of total epidermal cells

BOX 2. Hormonal Regulation of Seedling Photomorphogenesis

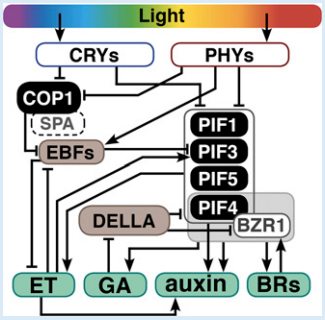
Auxin, brassinosteroids (BRs), gibberellic acid (GA), and ethylene (ET) are key regulators of photomorphogenesis and are under tight control of dark/light signaling components like PIFs, COP1 and HY5 (Box 1; Lau and Deng, 2010; Leivar and Monte, 2014; de Lucas and Prat, 2014; Chaiwanon et al., 2016; de Wit et al., 2016a).

Auxin locally induces growth and can be transported from the shoot towards the hypocotyl and roots. PIFs induce auxin synthesis (Hornitschek et al., 2012; Pfeiffer et al., 2014) and downstream signaling factors (*AUXIN RESPONSE FACTORS* [*ARFs*], *INDOLEACETIC ACID-INDUCIBLE* [*AUX/IAA*] and *SMALL AUXIN UPREGULATED* [*SAUR*] genes), while auxin influx (AUXIN1 [AUX1] and LIKE-AUX1 [LAX]) and efflux PIN-FORMED [PIN] proteins account for polar auxin transport. In dark-grown seedlings, PIN4 and PIN7 create the auxin gradient that causes the apical hook (Fig. 3; Žádníková et al., 2016). Dark-active COP1 suppresses *PIN1* transcription in the shoot and PIN1/2 polar localization in roots, resulting in low auxin levels in the root system (Fig. 3; Sassi et al., 2012).

BRs are essential for skotomorphogenic growth, proven by the *cop*-like phenotype of *DE-ETIOLATED2* (*DET2*) deficient mutants impaired in BR synthesis (Li et al., 1996). BR does not accumulate in darkness (Symons et al., 2002), but PIF4 function greatly depends on dimerization with the BR-stabilized BRASSINAZOLE-RESISTANT 1 (BZR1). The PIF4-BZR1 module induces auxin signaling, and BR and GA synthesis (Oh et al., 2012; Oh et al., 2014; Shahnejat-Bushehri et al., 2016). In light, BZR1 interacts with HY5, which subsequently makes BRs regulators of photomorphogenis (Li and He, 2016).

In darkness, PIF induction of **GA** synthesis activates the GIBBERELLIN INSENSITIVE DWARF 1 (GID1) receptor, which subsequently targets DELLA proteins for degradation. DELLA proteins act, in the absence of GA, as repressors of PIFs and BZR1 (Feng et al., 2008; de Lucas et al., 2008; Shahnejat-Bushehri et al., 2016).

ET is induced by PIFs and accumulates when seedlings experience pressure by a soil column. ET and COP1 destabilize the F-BOX proteins EIN3 BINDING FACTOR 1 and 2 (EBF1 and 2), suppressors of ETHYLENE INSENSITIVE 3 (EIN3). In darkness, ET induces the triple response (thick hypocotyl, exaggerated hook, short root; Guzman and Ecker, 1990), which strengthens the seedling and protects the meristem during soil outgrowth. In return, EIN3 induces PIF3 expression (Zhong et al., 2012). In light, phyB stimulates EBF1/2 mediated EIN3 and PIF3 degradation, and ET signaling is inhibited (Jeong et al., 2016; Shi et al., 2016; Dong et al., 2017).



Box 2 Figure. Simplified schematic representation of hormone functions downstream of dark/light signaling components.

or differentiate into a guard mother cell. The guard mother cell then gives rise to two guard cells that form the stoma. The larger sister cell can become a pavement cell or undergo additional asymmetric spacing divisions to generate satellite Ms away from the existing stoma (the "one-cell spacing rule"; Pillitteri and Torii, 2012; Wengier and Bergmann, 2012). Regardless of light conditions, Ms are generated during the first 2 d of seedling establishment. In darkness, their development is then arrested (Wei et al., 1994) by the active COP1-SPA complex (Kang et al., 2009). Guard cell differentiation is completed in both the hypocotyl and the expanding cotyledons (Wei et al., 1994), mediated by CRYs, phyA, and phyB, with phyB having a dominant role in white light. The COP1-SPA interaction is inhibited (Box 1), and PIF4 fine-tunes stomatal development in response to light quantity (Casson et al., 2009). The consecutive steps in stomata differentiation are regulated by three bHLH transcription factors (MUTE, SPEECHLESS, and FAMA) downstream of a MAP kinase signaling cascade regulated by light quantity (for review, see Lau and Bergmann, 2012).

Chloroplast Development and Pigment Biosynthesis

In higher plants, all cells contain plastids derived from embryonic proplastids. In darkness, seedling proplastids develop into etioplasts, which contain a prolamellar body that incorporates lipids and NADPH-dependent protochlorophyllide oxidoreductase (POR). Upon exposure to light, the prolamellar body disperses, thylakoid membranes form coinciding with greening due to chlorophyll biosynthesis, and a fully functional chloroplast develops. In light, proplastids in subepidermal meristematic cells differentiate into green chloroplasts in the cotyledons (for review, see Jarvis and López-Juez, 2013). In linear monocot leaves, a gradient of chloroplast differentiation can be observed in detail from the base of the leaf near the meristem where

young cells contain proplastids to the older cells toward the tip that contain differentiated chloroplasts (Li et al., 2010; Majeran et al., 2010). Based on these observations, three different chloroplast developmental phases have been defined: a heterotrophic phase of cellular proliferation and growth; a transition phase of chloroplast biogenesis where proteins such as the plastid translation apparatus and plastid enzymes accumulate; and a maturation phase of photosynthetic protein accumulation and photosynthetic activity. Similar phases take place during dicot leaf development, although their spatial distribution is not as distinct (López-Juez et al., 2008; Charuvi et al., 2012; Dubreuil et al., 2018). During biogenesis, the photosynthetic pigments chlorophyll and carotenoid are synthesized through activation of the NADPH-dependent POR that converts protochlorophyllide into chlorophyll, and the PSY central carotenoid biosynthesis gene (Toledo-Ortiz et al., 2010). Excessive accumulation of the chlorophyll precursor protochlorophyllide in the dark can result in photooxidative damage (Reinbothe et al., 1996), which is minimized by the photoprotective role of carotenoids during photosynthetic apparatus assembly (Niyogi, 1999; Walter and Strack, 2011).

Dark/light signaling pathways are tightly associated with chloroplast biogenesis. During the heterotrophic phase in darkness, PIF1 and PIF3 are negative regulators of chloroplast development, particularly of tetrapyrrole biosynthesis genes (Huq et al., 2004; Stephenson et al., 2009), and transcriptionally suppress together with EIN3 (which is stabilized by soil pressure-enhanced ET production; see Box 2; Lau and Deng, 2010; Leivar and Monte, 2014; de Lucas and Prat, 2014; Chaiwanon et al., 2016; de Wit et al., 2016a; Hornitschek et al., 2012; Pfeiffer et al., 2014; Žádníková et al., 2016; Li et al., 1996; Symons et al., 2002; Oh et al., 2012; Oh et al., 2014; Shahnejat-Bushehri et al., 2016; Li and He, 2016; Feng et al., 2008; de Lucas et al., 2008; Guzman and Ecker, 1990; Zhong et al., 2012; Jeong et al., 2016; Shi et al., 2016; Dong et al., 2017) chloroplast development genes (Liu et al., 2017). Among these are the transcription factors *GOLDEN2-LIKE1* (*GLK1*) and *GLK2*, which are necessary for chloroplast development (Fitter et al., 2002; Oh and Montgomery, 2014), and target genes involved in chlorophyll biosynthesis, light harvesting, and electron transport (Waters et al., 2009). HY5, in contrast, promotes chloroplast development during the light transition and early maturation phases (Lee et al., 2007). The PIF-HY5 regulatory module is essential to tightly regulate chloroplast development and involves antagonistic activities of PIFs and HY5 as negative and positive regulators, respectively, through direct binding to G-boxes of common targets (Chen et al., 2013; Toledo-Ortiz et al., 2014). Its relative activity is dynamically sensitive to dark, low light, or higher light through modulation of PIF and HY5 abundance (Chen et al., 2013; Toledo-Ortiz et al., 2014). Molecular evidence indicates that PIF and HY5 coexist and can form bHLH/bZIP heterodimers. In the dark, PIF1/PIF3 are abundant, whereas HY5 and its homolog HYH are unstable (Box 1), and thus the module activity is essentially repressive. In low light, HY5/HYH are stabilized (Box 1) and form heterodimers with PIF1/PIF3, which might function as inactive forms. Under higher light conditions, PIF1/PIF3 are almost completely degraded and HY5/HYH become more prevalent, activating transcription of common PIF-HY5 module targets (Chen et al., 2013). PIF-HY5 prevent protochlorophyllide overaccumulation, control ROS signaling pathway, and regulate pigment accumulation through directly binding to G-box motifs in the promoters of POR genes, ROS-responsive genes, and PSY and other central carotenoid and chlorophyll pathway genes (Toledo-Ortiz et al., 2010; Chen et al., 2013; Toledo-Ortiz et al., 2014).

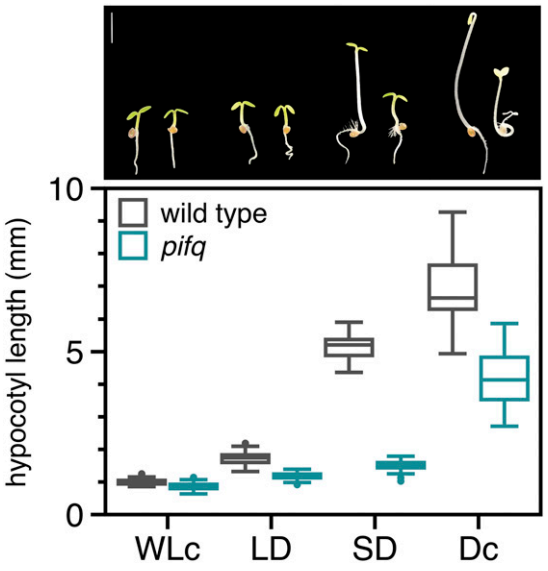


Figure 4. Night length strongly affects photomorphogenesis in Arabidopsis seedlings. Hypocotyl length (mm) of 3-d-old Arabidopsis wild-type (Columbia-0) and *pifq* (*pif1-1 pif3-3 pif4-2 pif5-3*; Leivar et al., 2008) seedlings, grown in continuous white light (WLc), long days (LD; 16 h light/8 h dark), SDs (8 h light/16 h dark), or continuous dark (Dc). Above the graph are pictures of representative seedlings in the same order. All were grown in continuous temperature (22°C) and a light intensity of approximately 5 μmol m^{-2} s^{-1} photosynthetically active radiation. Scale bar = 2 mm.

Fully developed chloroplasts are essential for the fixation of energy from sunlight, and in turn function as light signaling structures with great impact on photomorphogenesis through close coordination between the nucleus and chloroplast genomes. In Arabidopsis, chloroplast retrograde signals from the chloroplast to the nucleus are able to optimize photosynthetic capacity and growth, prevent photodamage in high light environments, and fine-tune circadian-regulated processes by releasing light-specific signals (Strand and Hernandez-Verdeja, 2018; Waters et al., 2009; Martín et al., 2016a; Dubreuil et al., 2018; Box 3).

THE HYPOCOTYL

To quickly reach for the light, the elongated hypocotyl of dark-germinated seedlings is the most remarkable phenotype. The Arabidopsis hypocotyl is an intensively studied model in seedling etiolation and de-etiolation. The hypocotyl consists of a set number of 20 cells, and thus elongation mainly depends on cell expansion rather than divisions (Wei et al., 1994; Gendreau et al., 1997) and requires the uptake of water to maintain turgor pressure (Ishikawa et al., 2013; Chaumont and Tyerman, 2014). To facilitate cell expansion, the cell wall of the epidermal cells gains flexibility, which appears to be independent of cell wall synthesis, and is regulated by specialized proteins such as expansins and XYLOGLUCAN ENDOTRANSGLUCOSYLASE /HYDROLASEs (XTHs; Ivakov et al., 2017). In dark conditions, PIFs directly induce the expression of the genes encoding for these proteins (Leivar et al., 2009), and integrate the strong influence of several hormones such as auxin, brassinosteroids (BRs), GA, and ET in hypocotyl elongation (Box 2; for review, see Leivar and Monte, 2014; de Wit et al., 2016a; Fig. 3C). Auxin accumulates in the cotyledons and is actively transported toward the hypocotyl, where PIN proteins locate it to the epidermal cells (Box 2). Auxin acidifies the cell wall, which favors expansin and XTH-mediated elongation, and enhances expression of the genes encoding for these proteins (Rayle and Cleland, 1992; Paque et al., 2014). The dwarf phenotype of dark-grown BR-deficient mutants (e.g. *de-etiolated2*) pointed out the important role of these steroid hormones in hypocotyl elongation during skotomorphogenesis (Chory et al., 1991; Li et al., 1996). Recently, it became clear that the main function of BRs during elongation (in response to darkness, shade, and high temperatures) is indirect via the binding of BR-stabilized protein BZR1 to PIF4 (Box 2; Oh et al., 2012). PIFs and BZR1 induce GA synthesis, which indirectly enhances hypocotyl growth by inhibition of the repressing DELLA proteins (Box 2). In darkness, under mechanical pressure created by soil, ET accumulates and inhibits hypocotyl growth, to strengthen the hypocotyl (Box 2; Yu and Huang, 2017). As an additional level of signaling, elongating cell walls release fragments that trigger a forward loop and enhance skotomorphogenesis in the hypocotyl and cotyledons (Sinclair et al., 2017).

Upon light exposure, hypocotyl elongation is quickly inhibited. Light-activated photoreceptors cause PIF degradation and COP1 inactivation, which brings down hormone levels and releases growth-suppressing proteins such as HY5 (Boxes 1 and 2). Phys are found plant-wide in different organs and tissues, but can play different roles in different cell layers. A recent study shows how epidermal phyB is completely responsible for light-induced germination and hypocotyl growth arrest in red (R) light (Kim et al., 2016). Not much is known about the role of other hypocotyl cell layers in growth (arrest) during seedling establishment. Nevertheless, another recent study supports the cell type-specific functions in Arabidopsis hypocotyls. Trichoblasts form hair-like structures and acquire nutrients from the external environment, while the neighboring atrichoblasts provide shortcut routes for these nutrients to be unloaded and moved up the stem (Jackson et al., 2017).

THE ROOTS

When a seed germinates underground, reaching the light seems top priority, and this goes at the cost of root development. To regulate this shoot-over-root trade-off, root development in dark-grown seedlings is actively repressed. Auxin availability in the roots is strongly limited. The suppression of PIN gene expression in the hypocotyl and the localization of PIN proteins into the vacuole, both COP1-dependent, inhibit polar auxin transport and, thus, root growth (Box 2; Sassi et al., 2012; Fig. 3D). Even though the roots will remain in close-to-dark conditions throughout the plant life cycle, light perception by the shoot dramatically affects root development (Lee et al., 2017; van Gelderen et al., 2018). When the shoot experiences light, COP1 is mobilized out of the nucleus, and this releases the suppression of the PIN proteins and activates polar auxin transport. Like many other aspects of seedling establishment in the light, root development greatly depends on HY5. The role for HY5 in Arabidopsis root development has been known for a long time, as HY5-deficient mutants show defects in root hair development, gravitropism, lateral root outgrowth, and elongation (Oyama et al., 1997; Sibout et al., 2006). The HY5 protein is, as was discovered recently, translocated via the phloem toward the root, with root-specific *HY5* and *HYH* transcription, and promoted root development as a consequence (Chen et al., 2016; Zhang et al., 2017; Fig. 3D). In addition to HY5 being a traveling molecule, another recent study showed that its stability and transcription are induced by stem-piped light that locally activates PHYB molecules in the Arabidopsis roots (Lee et al., 2016). Besides auxin and HY5, sugar molecules travel from the light-exposed cotyledons, which started photosynthesis, to the roots and enhance root elongation (Kircher and Schopfer, 2012; Fig. 3D). By quickly enhancing root elongation and lateral root outgrowth upon seedling establishment, the young photoautotrophic plant can start the uptake of water and nutrients such as nitrate to fuel growth (Chen et al., 2016).

SEEDLING ESTABLISHMENT IN ALTERNATING LIGHT/DARK CYCLES

Upon seedling exposure to sunlight after germination, establishment proceeds under light/dark

BOX 3. Chloroplast-to-Nucleus Retrograde Signaling

The chloroplast genome, or plastome, carries fewer than 100 protein-coding genes. The majority of chloroplast proteins (~2000–3000) are encoded by the nucleus and are imported into the chloroplast following synthesis in the cytosol. This nucleus-to-chloroplast signaling is termed anterograde signaling. Chloroplasts are well known as the organelles where photosynthesis is performed, but they are also dynamic signaling compartments that function as intracellular and environmental sensors. They can communicate with the nucleus through a process termed retrograde signaling (RS) to regulate expression according to chloroplast status. In developing chloroplasts, RS coordinates photosystem assembly and maintenance with the other processes required for chloroplasts biogenesis (biogenic RS). Once mature, chloroplasts communicate with the nucleus to maintain homeostasis in the prevailing environment (operational RS; Chi et al., 2013; Jarvis and Lopez-Juez, 2013; Norén et al., 2016).

During chloroplast development, use of lincomycin or norflurazon to inhibit plastid translation or carotenoid biosynthesis, respectively, leads to photobleaching and repression of photosynthesis-associated nuclear genes (*PhANGs*), such as those from the chlorophyll-binding LHCb gene family. *genomes uncoupled* (*gun*) mutants exhibit *PhANG* derepression in response to norflurazon and have helped elucidate components of biogenic signaling, such as heme, tetrapyrroles, and GUN1 (Koussevitzky et al., 2007). Other key components include chloroplast-localized PLASTID REDOX INSENSITIVE2 (PRIN2) and plastid-encoded RNA polymerase (PEP; Kindgren et al., 2012), and nucleus-localized ABI4 and GLKs (Koussevitzky et al., 2007; Kakizaki et al., 2009; Waters et al., 2009).

On the basis of the phenotypes of plants with disrupted plastid functionality, RS has been shown to impact normal light-regulated development. Whereas light at moderate levels acts through the phy sensory-photoreceptor system to induce photomorphogenic development, light at excessive levels is sensed by the plastid and represses photomorphogenesis through a GUN1-mediated RS mechanism independent of PIF mediation (Ruckle and Larkin, 2009; Martín et al., 2016a).

cycles of variable duration and light intensity depending on the latitude and time of the year. This section reviews our current knowledge on how seedling growth in these conditions integrates light and dark signals with the circadian clock, which is synchronized and oscillates strongly after light exposure (Salomé et al., 2008).

In photoperiodic conditions, growth is dark-dependent and promoted by accumulation of the PIFs, similar to etiolated growth. Noteworthy, acceleration of hypocotyl elongation in photoperiodic conditions is not linear as a function of the duration of the dark period but instead is a short day (SD)-specific event. Up to approximately 12 h of darkness, Arabidopsis hypocotyls are as short as if they were in constant light, and then elongation increases with longer nights (Niwa et al., 2009; Fig. 4). Mutants in the central clock component *CCA1ox* or *prr5prr7prr9* exhibit a nearly linear growth pattern in increasing night lengths (Niwa et al., 2009), indicating that the circadian clock inhibits growth in photoperiodic conditions. Whereas hypocotyl growth in the dark can be considered clock independent, seedling establishment in light/dark cycles requires the integration of clock and dark/light signaling to regulate elongation, cotyledon development and greening.

Regulation of hypocotyl elongation in light/dark cycles offers an example of the intricate combined action of dark, light, and clock signaling. In SDs, PIF proteins control rhythmic growth by collectively promoting increased elongation rates in the predawn hours when they are most abundant. As a consequence, *pifq* seedlings are shorter than the wild type in SDs, a difference that is less apparent in long days, when nights are too short to allow for strong PIF accumulation (Fig. 4). PIF accumulation and activity are regulated at several levels. First, *PIF4* and *PIF5* transcripts in SDs rise at midday through the night, with a peak at dawn (Nozue et al., 2007). This oscillation is imposed by the evening complex (EC) formed by ELF3, ELF4, and LUX (Nusinow et al., 2011), and by TOC1, PRR5, and PRR7 (Yamashino et al., 2003; Niwa et al., 2009) that repress *PIF4* and *PIF5* expression during the day and early night. *PIF7* transcript levels oscillate as well, suggesting clock regulation (Kidokoro et al., 2009; Lee and Thomashow, 2012). In contrast, *PIF1* and *PIF3* transcription is maintained at a low and constant level during the diurnal cycle (Soy et al., 2012, 2014). Second, as a consequence of phy activity, PIF protein abundance in SDs oscillates diurnally with low PIF levels during the light hours and progressive accumulation during the dark to peak at dawn (Nozue et al., 2007; Soy et al., 2012; Yamashino et al., 2013). During the first night hours, phyB Pfr persists and inhibits PIF accumulation while slowly dark reverting to inactive Pr (Sweere et al., 2001; Rausenberger et al., 2010; Medzihradszky et al., 2013). The photoactivated phyB Pfr forms dynamic nuclear photobodies together with Hemera (HMR) to induce

rapid phosphorylation of PIFs, leading to their degradation (Kircher et al., 2002; Chen et al., 2010; Van Buskirk et al., 2014). phyB also is found in tandem zinc knuckle/plus3-dependent photobodies that also contain members of the EC (Kaiserli et al., 2015; Huang et al., 2016a, 2016b) but apparently not in HMR, which could indicate the existence of specialized phyB-containing photobodies that might regulate PIF accumulation or transcription separately. As a result of phy-imposed action, PIF1, PIF3, PIF4, and PIF5 abundance oscillates in SDs to peak at dawn and induce growth-related genes (Nozue et al., 2007, 2011; Nomoto et al., 2012; Soy et al., 2012, 2014; Yamashino et al., 2013). Last, the growth-promoting activity of PIFs, as they progressively accumulate during postdusk darkness, is directly inhibited by PIF-interacting clock components to prevent detrimental early growth. The transcriptional activator activity of PIFs is directly repressed by TOC1 during postdusk, when TOC1 is most abundant in the circadian cycle (Soy et al., 2016; Zhu et al., 2016). In addition, DNA binding of at least PIF4 is inhibited by ELF3 in an EC-independent manner (Nieto et al., 2015). Thus, whereas the dark promotes accumulation of the PIFs, the integration and convergence with the circadian clock limit the timing of maximum responsiveness to dawn (Allen et al., 2006). This permissive gating involves phasing of downstream effector transcript abundance (Covington et al., 2008; Michael et al., 2008; Martín et al., 2016b) and calculation of the rate of starch breakdown to ensure lasting energy to fuel growth at dawn (Graf et al., 2010).

OUTSTANDING QUESTIONS

- Is cell-specificity of key factors like PIFs, HY5, or hormones a regulatory mechanism in photomorphogenesis? Can they move to and / or accumulate in different cell types to coordinate rapid and local cellular responses to light?
- How does below-optimal seedling establishment affect growth and (crop) yield in later stages of plant development?
- How do environmental factors perceived underground before light exposure, such as temperature, soil minerals and water availability, affect seedling establishment?
- What are the composition and dynamics of dark and light-sensitive regulatory protein complexes?
- How are the relative amounts of dark and light signaling translated into transcriptional and biochemical responses?
- How is chloroplast retrograde signaling integrated with dark, light, and circadian clock signals to regulate development?

ABOVEGROUND CHALLENGES DELAY SEEDLING ESTABLISHMENT

Even though germination is in a lot of plant species properly timed by external (humidity, temperature, light) and internal (circadian rhythmic) cues, the aboveground environment often appears suboptimal for a young, establishing seedling. A combination of stresses will inhibit or postpone photomorphogenic development during the dark-to-light transition or in diurnal conditions. In this section, we will review the most studied external factors (excessive light levels, light quality, neighbor detection, and high temperatures) that, to more or less extent, inhibit the photomorphogenic phenotype to protect the seedling and escape harmful situations.

Light Intensity

Coming from a (close to) dark environment underground, the first light seen by the de-etiolating seedling can cause problems. Excessive light levels are detrimental for plants and cause damage to the photosystem, resulting in ROS accumulation. Phys, CRYs, PHOTs, and UVR8 selectively monitor for changes in light quality and small changes in fluence rate. Nevertheless, photoreceptor activation saturates, and is insensitive for extremely high, possibly damaging light intensity. As mentioned above, the chloroplasts can sense and process information about the light intensity (see also Box 3; Chi et al., 2013; Jarvis and Lopez-Juez, 2013; Noren et al., 2016; Koussevitzky et al., 2007; Kindgren et al., 2012; Kakizaki et al., 2009; Waters et al., 2009; Ruckle and Larkin, 2009; Martín et al., 2016a). In high light levels, RS inhibits the transcription of photomorphogenic genes involved in photosynthesis and development. As a consequence, young seedlings that are shifted from darkness to a high light environment have long hypocotyls and keep their cotyledons closed, to protect them and the shoot apical meristem from the damaging light levels. Major players in the high light-mediated RS are the plastid-localized PRR protein GENOMES UNCOUPLED1 and ABI4 (Koussevitzky et al., 2007; Martín et al., 2016a; Xu et al., 2016).

Light Quality and Neighbor-Induced Competition

Above the ground, seedlings often are not alone. The presence of neighboring plants can threaten light availability and, thus, photosynthesis rates. To prevent being completely shaded, most seedlings of sun-loving plants will partly inhibit photomorphogenesis. The shade avoidance syndrome (SAS) triggers hypocotyl elongation, despite the availability of light, and helps the plant reach the top of the canopy. This response is

triggered by the low ratio between R and far-red (FR) light, caused by the preferential absorption of R and reflection of FR light by green tissues, and is enhanced when additional blue (B) light depletion occurs during more severe shading (Filiault and Maloof, 2012; Kohnen et al., 2016; de Wit et al., 2016b). The low R:FR light signal inactivates PhyB, and thus will keep the main PIFs acting in SAS (PIF4, PIF5, and PIF7) active (Lorrain et al., 2008; Li et al., 2012) and the production of growth-promoting hormones such as auxin, BR, GA, and ET high (Li et al., 2012; Bou-Torrent et al., 2014). In young seedlings, the SAS consists of a delay of some aspects of photomorphogenesis (hypocotyl growth arrest, cotyledon expansion, root development, pigment accumulation), and promotes cotyledon petiole elongation and upward cotyledon positioning (for review, see Ballaré and Pierik, 2017; Fiorucci and Fankhauser, 2017). In dense canopies, the emission of all kinds of volatile compounds increases, and they accumulate due to reduced airflow (Kegge et al., 2013). The most important signaling volatile is ET, which in the light enhances elongation growth enabling seedlings to reach the top of the canopy. ET enhances PIF3 expression, and via similar regulatory pathways as shade perception, synthesis and signaling of the growth-promoting hormones auxin, GA, and BR (Zhong et al., 2012; Das et al., 2016). Interestingly, although some aspects of photomorphogenesis are clearly suppressed by ET (hook unfolding and cotyledon expansion; see above), others strongly depend on the light availability (hypocotyl elongation: suppressed in darkness but induced in light; Pierik et al., 2006). Another stress-full light signal is UV-B radiation, which can cause DNA damage. Interestingly, in low quantities, UV-B radiation perceived by the UVR8 receptor strongly enhances photomorphogenesis. It is, most probably, used by plants as a signal for reaching the sunlight and suppresses the elongated response of seedlings grown in shade (Hayes et al., 2014), via inhibition of COP1-mediated HY5 and HYH suppression (Favory et al., 2009; Rizzini et al., 2011; Christie et al., 2012).

High Temperatures

With temperatures rising due to global climate change, heat is a more and more relevant stress for plants. Small changes in temperature, sensed by PhyB and phototropins (Jung et al., 2016; Legris et al., 2016; Fujii et al., 2017), partly inhibit photomorphogenesis in young seedlings. This so-called thermomorphogenic response includes elongated hypocotyls and epinastic cotyledons, and serves to enhance cooling of the young leaves and thus warmth adaptation (for review, see van Zanten et al., 2014; Quint et al., 2016). The key factor in this warmth-mediated arrest on de-etiolation is PIF4. The inactivation of phys by high temperatures stabilizes the protein (Jung et al., 2016; Legris et al., 2016), but also triggers COP1-mediated degradation of HY5, which releases the suppression of PIF4 expression (Delker et al., 2014). High temperature-stabilized PIF4 will continue to keep auxin synthesis high and hypocotyl elongation going, despite the light availability (Franklin et al., 2011). The direct effect of other climate-related stresses such as drought and humidity on seedling photomorphogenesis are less well understood. Nevertheless, it is well-known that these contrasting stresses strongly affect the synthesis of the phytohormone abscisic acid (Christmann et al., 2007; Okamoto et al., 2009; Bauer et al., 2013), which in turn interferes with light-induced development (Pierik and Testerink, 2014).

CONCLUSION

Plants have evolved sophisticated photoperception mechanisms to interpret their environmental conditions and optimally coordinate and adjust their growth to thrive as sessile organisms. Here, we have reviewed how the relative dark and light signaling flux impacts several processes during seedling establishment, with a focus on the growth programs in the dark, upon first exposure to light, and in diurnal conditions where dark and light alternate. Because seedlings are exquisitely sensitive to and actively respond to darkness and different light intensities, we propose that seedling establishment is a dimmer-type switch-regulated process between dark and light signals. This allows plants to dynamically respond to the relative amounts of dark and light signaling to optimize development. Research efforts over the last decades have contributed to impressive progress in our understanding of seedling establishment, especially in Arabidopsis. As the scientific community in the field makes new discoveries, new exciting questions will arise and challenges still will be many. We have summarized a few important questions for future research in the Outstanding Questions box. We believe novel emerging and enhanced technologies for high-throughput organ, tissue, and single-cell -omics, cell-cell, macromolecule-, and organelle-level research (Nito et al., 2015), together with cross-disciplinary approaches, will inspire and advance our tasks ahead.

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