Light and Hormone Interactions in the Seed-to-Seedling Transition

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Abstract

Plants exhibit sensitivity to dynamic or changing environments and respond to such fluctuations through short- and long-term adaptive responses. The transition from seed to established seedling is a critical phase of the plant life cycle. This brief, but highly important, phase is linked to species persistence and impacts long-term population dynamics. During the seed-to-seedling transition, key factors that modulate plant form and function are light, hormones, and integrated signaling at the light-hormone interface. During this stage of early plant development, germination, seedling development and the critical heterotrophic-to-autotrophic conversion, the latter of which includes chloroplast development and differentiation, are modulated by external light parameters and homeostasis of several plant hormones. Specific mechanisms used to mediate responses to light and/or hormones during the seed-to-seedling transition include the regulation of gene expression, protein dynamics, and metabolites (including sugars and reactive oxygen species). In this review, we highlight key mechanistic factors and components that are especially linked to integrating responses to light and hormones during germination and the post-germinative seed-to-seedling transition. These light-/hormone-dependent mechanisms have implications for short- and long-term dynamics and diversity of natural plant species and communities.

Keywords: heterotrophic-to-autotrophic conversion; hormones; light; photoreceptors; seed-to-seedling; seedling; signaling; cotyledon

1. Introduction

The seed-to-seedling transition is a critical stage of plant development. This transition has been described as a ‘bottleneck’ for species establishment that can ultimately drive the composition of plant populations (Poorter, 2007). This brief but profound transition from seed to established seedling is associated with the dynamics and/or diversity of natural communities and maintaining species diversity and persistence in natural environments (Muscarella et al., 2013). The seed-to-seedling transition comprises a transition from heterotrophic growth to autotrophic growth, characterized by organ development and maturation of the chloroplasts with the onset of photosynthesis, to promote the new life cycle of the plant. This process is regulated by light cues perceived by photoreceptors, hormone-mediated signaling and available nutrients. Newly germinated seedlings are capable of responding to short-term dynamic environmental conditions, including daily cycles of dark and light cues, fluctuating light conditions, other environmental oscillations, and long-term changes in natural environments, including climate change. Such adaptive responses are critical for these organisms to optimize growth, reproduction and survival. Responses to abiotic and biotic signals can include both short-term and long-term adaptations. Short-term responses can include activation of signaling pathways or stress responses; longer-term adaptations can include acclimatory physiological changes and survival strategies including colonization and competition advantages.

The focus of this review is on the interaction of light and hormone signaling pathways and responses in the seed-to-seedling transition and early seedling development, including the heterotrophic-to-autotrophic transition. We will address the role of photoreceptor- and hormone-dependent regulation of gene expression, protein homeostasis, plastid

differentiation/development, and associated impacts on facilitating the seed-to-seedling transition and seedling establishment, tuned to external cues. Such responses are critical for plants to adapt to dynamic environments and changing environmental cues in natural contexts, including those due to longer-term alterations. This latter association with long-term alterations may result in an expansion of the limitations of particular genotypes, or be evidence of links between phenotypic plasticity and evolutionary adaptation (Forsman, 2014).

1.1 Tuning gene expression during the seed-to-seedling transition. Tuning of the expression of many plant genes occurs in responses to light or hormone cues. Specific wavelengths of light or distinct hormones can modulate the expression of a significant portion of the plant genome – 20% or more of the plant genome has been estimated to be regulated by white light (Jiao et al., 2005); similar proportions of the genome (up to ~15%) may respond to various hormones (Nemhauser et al., 2006). Primary metabolism, which is supported by the reserves of the seed and upon seedling emergence is regulated by light (Farré and Weise, 2012), is also very important to a successful transition to seedling.

1.2. Light and the seed-to-seedling transition. The seed-to-seedling transition is characterized by the light-dependent etioplast-to-chloroplast transition and the onset of photosynthesis. Light is critical for establishing developmental and metabolic changes during this period, including seed germination, hypocotyl elongation, cotyledon and true leaf development, plastid development and greening, among others (Franklin and Quail, 2010; Kami et al., 2010). Distinct wavelengths of light are detected by multiple plant photoreceptors including the red/far-red responsive phytochromes (phy), blue/ultraviolet-A absorbing cryptochromes (cry) and phototropins (PHOT), and ultraviolet-B absorbing photoreceptors such as UVR8 (Franklin and Quail, 2010; Rizzini et al., 2011) [see Table 1]. However, known

photoreceptors cannot explain all light-dependent phenotypes, for example some responses to UV-B (Biever et al. 2014), UV or blue light (Warpeha et al., 2008), or green wavelengths (Zhang et al., 2011; reviewed in Wang and Folta, 2013).

Phytochromes regulate light-dependent seed germination (Arana et al., 2014; Botto et al., 1995; Botto et al., 1996; Hennig et al., 2002; Heschel et al., 2008; Heschel et al., 2007; Shinomura et al., 1994) and de-etiolation (Dehesh et al., 1993; Franklin et al., 2003; Hennig et al., 2001; Johnson et al., 1994; Monte et al., 2003; Nagatani et al., 1993; Parks and Quail, 1993; Parks and Spalding, 1999; Reed et al., 1994). Cryptochromes also contribute to the regulation of de-etiolation, primarily in response to blue light (Ahmad et al., 1998; Ahmad et al., 1995; Folta and Spalding, 2001). Blue-light receptive phototropins primarily drive directional growth of seedlings or phototropism (Folta and Spalding, 2001; Sakai et al., 2001). UV-B photoreceptors, including UVR8, contribute to phototropism and photomorphogenesis (Favory et al., 2009; Huang et al., 2014; Rizzini et al., 2011; Vandenbussche et al., 2014).

1.3. Hormones and the seed-to-seedling transition. Hormones are also critical for proper seed-to-seedling transition and may have both developmental roles and roles in the induction of protective responses against stresses (Kucera et al., 2005; Miransari and Smith, 2014). Specific hormones that play critical roles in this transition include abscisic acid (ABA), gibberellins (GAs), auxins (e.g., indole-3-acetic acid; IAA), ethylene, cytokinins and brassinosteroids (BR) [see Table 2]. ABA accumulates in seeds to promote dormancy and prevent premature germination (reviewed by Cutler et al., 2010; Sakata et al., 2014); whereas GA inhibits dormancy and promotes germination (Gupta and Chakrabarty, 2013; Peter and Stephen, 2012). The role of GA in these processes occurs in part through active antagonism of ABA activity (Cutler et al., 2010). Additionally, GAs function to promote the elongation of

stems and expansion of leaves (Gupta and Chakrabarty, 2013; Peter and Stephen, 2012). Auxins, the most common of which is IAA, promote cellular elongation and root initiation during seedling establishment (reviewed by Zhao, 2010), and phototropism (reviewed by Hohm et al., 2013). Ethylene promotes the release of dormancy and germination, in part through counteracting the effects of ABA on seeds similarly to GA (Corbineau et al., 2014; Kucera et al., 2005); ethylene also promotes growth and differentiation of shoots and roots in young seedlings (Corbineau et al., 2014). Cytokinins have a role in embryo development via the promotion of cell division and these molecules also promote root elongation (Perilli et al., 2010). The impact of cytokinins can be antagonistic to auxins for many responses (Kieber and Schaller, 2014; Schaller et al., 2015). BRs promote seed germination and seedling elongation (Clouse, 2011). It is clear, based on the antagonism by some hormones on the impact of others, that signals of the multiple hormone pathways can be integrated to impact apposite seed germination and seedling development.

1.4. Light and hormone interactions and the seed-to-seedling transition. Given some of the similar impacts of light and hormones on seedling establishment and development, it is not surprising that multiple plant hormone signaling pathways interface with or are modulated by light signaling pathways during the seed-to-seedling transition. The interaction of light and hormones specifically during de-etiolation has been previously reviewed (Alabadi and Blazquez, 2009; Arsovski et al., 2012; Halliday et al., 2009; Lau and Deng, 2010; Lin and Tang, 2014; Seo et al., 2009; Symons and Reid, 2003). Here, we highlight some examples of interactions between light and hormone signaling closely linked to the seed-to-seedling transition.

Interactions between the GA pathway and phytochromes that primarily impact the stages of seed germination and shoot growth have been established, including phytochrome-dependent

changes in GA metabolism and GA responsiveness and coordinated regulation of transcription factors (Achard et al., 2007; Arana et al., 2014; de Lucas et al., 2008; Feng et al., 2008; Kurepin et al., 2012; Oh et al., 2007; Oh et al., 2006; Toyomasu et al., 1998). Connections of cryptochrome 1 (cry1) to GA homeostasis and the regulation of hypocotyl growth have also been described (Folta et al., 2003; Zhao et al., 2007), as have cry1 connections to cytokinin signaling during the promotion of photomorphogenesis (Vandenbussche et al., 2007) and the regulation of auxin responsiveness (Folta et al., 2003). Blue-light-induced phototropic curvature of the shoot is mediated by the lateral transport of auxin (reviewed by Briggs, 2014), clearly an important process in the seed-to-seedling transition, when orientation to light is critical. Numerous interactions between phytochromes and auxin signaling during early development have been identified, including the light-dependent promotion of auxin homeostasis (Behringer and Davies, 1992; Behringer et al., 1992; Kurepin et al., 2012; Wu et al., 2010). IAA is transported from the developing leaves to the roots in a light-dependent manner in the early seedling stage, where IAA is required for lateral root formation (Bhalerao et al., 2002). Both phytochromes (Salisbury et al., 2007) and cryptochromes (Zeng et al., 2010) regulate auxin transport that impacts root development in early development. Additionally, PHOT impacts lateral root elongation through impacting auxin-related signal transduction (Moni et al., 2015). A regulation of ABA metabolism by phytochromes and phytochrome-dependent control of ABA-GA interactions that impact ABA- and/or GA-associated germination occurs (Sawada et al., 2008; Seo et al., 2006). Additionally, an interaction between phytochromes and ABA signaling that regulates transcription and impacts germination has been established (Joseph et al., 2014), and transcriptional repression that regulates light-, GA-, and ABA-responsive genes (Hsieh et al., 2012). BR and light antagonistically regulate de-etiolation (Luo et al., 2010). Also, distinct

interactions between light perception by phytochromes and modulation of BR homeostasis and signaling impact seedling development (Neff et al., 1999; Turk et al., 2003; Turk et al., 2005). Recently, an integration of GA, BR, and phytochrome pathways that is associated with coordinating growth through transcriptional regulation in response to light and hormone signals also was described (Bai et al., 2012).

In addition to visible and far-red light, UV wavelengths also interface with hormone responses. For example, UV-B photoreceptor UVR8 inhibits auxin biosynthesis and promotes GA catabolism, thereby inhibiting hypocotyl elongation (Hayes et al., 2014). UVR8-associated regulation of phototropic bending is correlated with a repression of auxin-responsive genes, indicating additional connections between UV-B and auxin signaling pathways (Vandenbussche et al., 2014).

1.5. Stress, hormones and the seed-to-seedling transition. During the seed-to-seedling transition, seedlings are especially sensitive to biotic and abiotic stresses. Seedlings are highly sensitive to potential photodamage/phototoxicity, primarily associated with excess light absorption (e.g., Barber and Andersson, 1992) resulting in the generation of potentially damaging reactive oxygen species (ROS) (Aarti et al., 2007; Alboresi et al., 2011; Durrant et al., 1990; Krieger-Liszkay, 2005). Accordingly, the induction of protective responses to mitigate potential light stress occurs during the seed-to-seedling transition and impacts seedling establishment (for review see Corbineau et al., 2014; El-Maarouf-Bouteau and Bailly, 2008). However, ROS may also serve as signaling molecules in seedlings. For example, the accumulation of ROS has been associated with breaking seed dormancy and promoting seed germination in *Arabidopsis* (Leymarie et al., 2011). ROS-associated promotion of germination and seedling development is linked to phytochromes (Chen et al., 2013; Lariguet et al., 2013)

and light signaling pathways (Busch and Montgomery, 2015). ROS also are associated with several hormones in impacting germination and seedling development. For example, ROS levels are increased by GA and repressed by ABA in the regulation of germination (Lariguet et al., 2013). ROS accumulation is also increased in the presence of ethylene (Corbineau et al., 2014; El-Maarouf-Bouteau et al., 2015). ROS are both induced by treatment with IAA (Joo et al., 2001; Joo et al., 2005; Peer et al., 2013; Schopfer, 2001; Schopfer and Liskay, 2006) and serve as a signal for auxin-mediated responses, including elongation growth (Liskay et al., 2004; Schopfer, 2001; Schopfer and Liskay, 2006) and gravitropism (Joo et al., 2001; Joo et al., 2005).

1.6 Responses to environmental cues during the seed-to-seedling transition and adaptation. Light cues perceived by photoreceptors and transduced via hormone-mediated signaling are essential for successful seedling establishment in natural contexts (Borevitz et al., 2002; Chen et al., 2008). Distinct Arabidopsis accessions have distinct quantitative trait loci (QTL) and expression level polymorphisms (ELPs) that underlie natural variations in light and hormone responses during seedling establishment (Borevitz et al., 2002; Delker et al., 2010; Yanovsky et al., 1997). Some of the natural variation related to light responses has been linked to photoreceptor variants naturally found in the environment (Botto et al., 2003; Maloof et al., 2001). Recently, an allele of a QTL for local adaptation of the timing of seed germination linked to ABA signaling has been described (Amiguet-Vercher et al., 2015). Such variation has been implicated in long-term plant adaptation responses in nature and in driving natural population diversity, range extension, and population dynamics (Alonso-Blanco et al., 2009; Delker and Quint, 2011; Mitchell-Olds, 2001; Remington and Purugganan, 2003; Weigel, 2012).

2. Mechanisms of the integration of light and hormone signaling in the seed-to-seedling transition

Mechanisms for integrating light and hormone signaling during the transition from seed to established seedling include regulation of some common factors. In cases where light and a specific hormone result in the same physiological responses, these signals can impinge upon a single factor or initiate a transcriptional cascade. Alternatively, light and hormones can have antagonistic effects on a single factor, thereby integrating divergent responses of these distinct cues.

Specific factors mediate the integration of light and hormone signaling during the seed-to-seedling transition, including a transcriptional regulator Imbibition-inducible 1 (IMB1) (Duque and Chua, 2003) and C2H2-type ZINC FINGER PROTEIN3 (ZFP3) (Joseph et al., 2014). Both IMB1 and ZFP3 have been shown to impact both ABA and phytochrome-dependent signaling linked to germination. Both phytochrome B (phyB) and cry1 activities also have been specifically associated with regulation of auxin efflux transporter ATP-BINDING CASSETTE B19 (ABCB19) that mediates auxin transport-associated regulation of hypocotyl growth (Wu et al., 2010). Additionally, PHOT1 directly interacts with ABCB19 to regulate phototropism (Christie et al., 2011). A GATA transcription factor, i.e., GATA2, functions in crosstalk between BR and light (Luo et al., 2010). Additional factors functioning in response to light and hormones include members of the Nuclear Factor Y (NF-Y) family, particularly the LEAFY COTYLEDON 1 (LEC1) and LEC1-LIKE members. LEC1 and LEC1-LIKE interact with ABA-response elements in seed-specific genes to impact embryogenesis and seed maturation (Yamamoto et al., 2009); however, these factors also regulate etiolation responses in seedlings, in part as integrators of light and hormone signaling during embryogenesis and post-germination

etiolation (Junker et al., 2012). LEC1 was also implicated in integrating responses to blue light and ABA (Warpeha et al., 2007), and ABA previously (Lapik and Kaufman, 2003), resulting from interaction with the protein Pirin1 (PRN1), a transcriptional cofactor protein. PRN1 also has been associated with responses to UV (Orozco-Nunnelly et al., 2014b) and biotic stress (Warpeha et al., 2013).

PRN1 is also associated with abiotic stress, including drought (Catala et al., 2007) and abiotic signaling, particularly white light- and UV-controlled orientation and growth (Orozco-Nunnelly et al., 2014b). The recent observation that multiple copies of hormone-regulated, abiotic-stress-associated, and light-responsive motifs are present in the *PRN1* promoter suggests that the PRN1 protein may also function in the integration of hormone and light responses (Orozco-Nunnelly et al., 2014a). PRN1 regulates quercetin levels in the young seedling, and the effects on quercetin are light dependent in the seed-to-seedling transition (Orozco-Nunnelly et al., 2014b). Quercetin is a flavonoid derived from phenylalanine, a potent antioxidant (Agati and Tattini, 2010) and UV-screening molecule (Rozema et al., 2002). Quercetin synthesis, like many flavonoids, is induced by light, most efficiently by UV and B (Kubasek et al., 1992), and accumulates in the cotyledonary node, hypocotyl/root transition and the elongation zone of the root in young *Arabidopsis* seedlings (Peer et al., 2001). In vivo evidence indicates that flavonols regulate auxin accumulation; studies of *transparent testa 4 (tt4)* mutant, which makes no flavonols, including kaempferol and quercetin, support a role for flavonoids in regulating auxin transport during seedling development (Brown et al., 2001; Buer and Muday, 2004; Murphy et al., 2000). Changes in light-induced auxin responses or metabolism may explain the overall PRN1-quercetin-caused seedling responses in light (Orozco-Nunnelly et al., 2014b) in the seed-to-seedling transition, as correct auxin transport is required for orientation and hypocotyl

elongation in light-grown, but not dark-grown seedlings (Jensen et al., 1998). Flavonols also induce changes in auxin transport, as demonstrated in *roll-2* (*repressor of lrx1*) mutant seedlings (Kuhn et al., 2011). When auxin transport was compared in flavonoid-deficient *tt4* and quercetin-deficient *tt7* (makes kaempferol but not quercetin) mutants, data indicated that derivatives of quercetin can inhibit basipetal auxin transport, elongation, and gravitropism (Lewis et al., 2011).

In this window of early seedling development, it is clear that photoreceptors have major regulatory, growth and development roles via interactions with hormone signaling pathways or hormone-mediated changes in metabolism or transport. These impacts affect germination and post-germinative processes in various tissues and temporal patterns. Ultimately, these light- and hormone-regulated processes influence the overall architecture and size of the seedling.

3. Regulation of gene expression

The role of modifications of gene expression, including transcription factor-mediated regulation of gene expression and chromatin remodeling or epigenetic modifications, in regulating the seed-to-seedling transition are recognized (Bouyer et al., 2011; Jia et al., 2014; van Zanten et al., 2014). Transcription factors bind promoter and/or enhancer segments of DNA to impact expression of genes (Phillips and Hoopes, 2008). A detailed list and mechanisms of transcriptional regulators known to function in light signaling and/or hormone signaling extend beyond the scope of this current review. Here, we specifically highlight gene expression-associated factors linked to integrated responses to light and hormones during the seed-to-seedling transition.

Histone deacetylases (HDACs) result in tighter wrapping of DNA on histones that represses gene expression (Jaenisch and Bird, 2003; Li et al., 2007). DNA methylases can

activate or repress gene transcription through histone methylation (Li et al., 2007), and other factors can impart epigenetic control over gene expression. There is both active repression of seedling development during the seed development and maturation stage (Jia et al., 2014; van Zanten et al., 2014), and the repression of seed maturation during the vegetative or seedling development stage (Jia et al., 2014). The role of epigenetic control in this process can involve, or be independent of, the roles of hormones ABA and GA (Bouyer et al., 2011; van Zanten et al., 2014). Furthermore, a role for histone deacetylation in inhibiting germination and coordinating the timing of the expression of some photosynthesis genes during the seed-to-seedling transition has been observed (van Zanten et al., 2014). Red light illumination acting through PhyB has been shown to promote seed germination through epigenetic transcriptional activation of genes encoding GA biosynthetic enzymes involving a histone demethylation process (Cho et al., 2012). Thus, light signaling, hormone signaling, and the interactions of light and hormone signals impact the seed-to-seedling transition through processes associated directly with the regulation of gene expression.

4. Regulation of protein abundance/turnover during the seed-to-seedling transition

Regulated protein degradation is implicated as a key factor in coordinating the seed-to-seedling transition. For example, the ubiquitin ligases, which ubiquitinate protein targets and thereby mark them for turnover, have been shown to impact this transition (Stone et al., 2006; Zhang et al., 2005). The KEEP ON GOING (KEG) E3 ligase has been associated with ABA-dependent regulation of germination and early seedling development (Stone et al., 2006). ABI3-interacting protein (AIP2) is responsible for targeting E3 ligase regulator ABI3 for degradation, which is associated with regulation of germination responses and vegetative seedling

development (Zhang et al., 2005). Specific components of the N-end rule pathway that is associated with targeting proteins for degradation also are associated with regulation of the seed-to-seedling transition, specifically ABA-dependent seed germination and seedling development (Holman et al., 2009).

Phytochromes and cryptochromes regulate protein turnover through impacting COP1, which is a RING-finger E3 ligase that negatively regulates photomorphogenesis (Liu et al., 2011; Sheerin et al., 2015; Zuo et al., 2011). Specifically, phytochromes and cryptochromes interact with SPA (SUPPRESSOR OF PHYA-105) proteins, which physically interact with COP1 and increase its E3 ligase function (Lian et al., 2011; Liu et al., 2011; Saijo et al., 2003; Seo et al., 2003; Sheerin et al., 2015; Zuo et al., 2011). Nuclear-localized phytochromes interact with PHYTOCHROME-INTERACTING FACTORS (PIFs), which also negatively regulate photomorphogenesis (de Lucas and Prat, 2014; Leivar and Quail, 2011). Interactions of PIFs with light-activated phytochromes result in targeting of the PIFs for degradation by the 26S proteasome (de Lucas and Prat, 2014). Notably, PIFs have been implicated in multiple studies in GA, BR, and auxin signaling; thus, these factors impact protein turnover and serve as integrators of light and hormone signaling [reviewed by (de Lucas and Prat, 2014)]. Light also regulates protein abundance in the plastids through light-regulated control of plastid translation (Marín-Navarro et al., 2007), a critical part of chloroplast development and function during seedling establishment.

5. Metabolism and the heterotrophic-to-autotrophic growth transition

During the transition of heterotrophic growth to photosynthesis-supported autotrophy, seed storage reserves are mobilized to provide energy to support growth and development during

seedling establishment. Seed reserves support light- and circadian-regulated primary metabolism to fuel the successful transition to seedling (Farré and Weise, 2012). Environmental and circadian regulation impact the source to sink relationships that are developing during the transition, with coordination of growth strongly altered by carbon availability in the form of sugars (Stitt and Zeeman, 2012). Like light, hormones also impact metabolism, particularly sugar metabolism, in the seed-to-seedling transition (Dekkers et al., 2008; Song et al., 2012; Yuan and Wysocka-Diller, 2006; Zhu et al., 2009). Sugars participate in hormone activity, but also may serve as signaling entities [reviewed in (Eveland and Jackson, 2012)]. Sugar impacts on the seed-to-seedling transition and subsequent development in seedlings also depend on the availability of other nutrients, including essential nutrients like phosphate, sulfate and nitrogen [reviewed in (Rolland et al., 2006)].

Several specific factors impacting the heterotrophic-to-autotrophic transition have been identified. The plastid triose phosphate isomerase (TPI) has been shown to have a critical role in the transition to autotrophic growth through impacting lipid metabolism (Chen and Thelen, 2010). A triacylglycerollipase also impacts oil breakdown during this transition (Eastmond, 2006).

Levels of the amino acid phenylalanine directly affect plant growth and development (Sullivan et al., 2014). Phenylalanine levels appear critical to proper chloroplast development and stress survival (Warpeha et al., 2008), in addition to proper responses to blue light (Warpeha et al., 2006) and UV responses in the seed-to-seedling transition. Its importance is underscored by the impact of B and UV in particular on the synthesis of flavonoids, a class of phenylpropanoids. Phenylalanine-derived molecules, including flavonoids (Agati and Tattini, 2010) and the simple phenolics (hydroxycinnamic acids and cinnamate esters, etc) (Burchard et

al., 2000; Landry et al., 1995; Sheahan, 1996) absorb in UV wavelengths, and many of these compounds are found in seeds (Lepiniec et al., 2006). Light induces flavonoid-biosynthetic enzymes sequentially in the temporal order of the biosynthetic pathway and in accordance to the developmental timing of germination and the seed-to-seedling transition, where maximal synthetic capacity peaks in 3-d-old seedlings grown in Wc (Kubasek et al., 1992). The germination process and responses to light within hours to days of germination require a reconfiguration of primary metabolites and secondary metabolism, involving many types of light-responsive metabolites in addition to flavonoids, described in a very detailed review (Chacón et al., 2013). Evolutionary studies in green plant lineages may further understanding of the importance of phenylpropanoids in the seed to seedling transition (Tohge et al., 2013).

The phenylpropanoids, alkaloids and terpenoids are capable of producing thousands of structures within a given genotype, and we are only beginning to uncover how discrete stimuli and changes in environmental stimuli received by the new seedling can enable a different outcome in individual chemical pathways due to the sensitivity to ecosystem parameters, including abiotic and biotic stimuli that impact the seed to seedling transition.

6. Light-dependent plastid development and heterotrophic-to-autotrophic conversion

A critical part of the transition to autotrophic growth is the establishment of functional chloroplasts. This establishment depends upon stoichiometric expression of plastid proteins encoded by both nuclear and plastid genome-located genes. Light has been long known to have a critical role in coordinating this process (Pogson and Albrecht, 2011). The involvement and general importance of photoreceptors in this process, including both phytochromes and cryptochromes, also has been described (Chun et al., 2001; Thum et al., 2001; Wellburn and

Wellburn, 1973) , and in some plant species, specific contributions of blue and red light have been quantified (eg. in *Cucumis*, Hogewoning et al., 2010). Development of plastids in both embryonic development and post-germination is still poorly understood, but involve many transcriptional and translation mechanisms, including plastid-specific elongation factor G (SCO1), required for embryonic survival and seedling plastid development and subsequent survival (Ruppel and Hangarter, 2007).

A limited number of factors that function downstream of the photoreceptors have been identified. These factors include PIFs, i.e., PIF1 and PIF3, which act as transcriptional regulators of light-dependent chloroplast development (Monte et al., 2004; Moon et al., 2008). Recently specific transcription factors, including nuclear-encoded, plastid-targeted sigma factors (SIG) and other known plastid development regulators such as golden-like kinases (GLK1 and GLK2), were shown to function downstream of phytochromes and cryptochromes (Mellenthin et al., 2014; Oh and Montgomery, 2013; Oh and Montgomery, 2014; Oh et al., 2013; Onda et al., 2008). Photoreceptor-dependent regulation of these factors is likely critical for directly regulating stoichiometric expression of nuclear and plastid-encoded components of key photosynthetic and other plastid protein complexes. Such coordination is required for light-dependent development of chloroplasts during seedling development and needed for proper autotrophic growth. SIG2 has a role in light-dependent cotyledon, root and hypocotyl development (Oh and Montgomery, 2013). In *Arabidopsis*, the redifferentiation of eoplasts, i.e., degenerate plastids present in mature seeds, and the chloroplast greening process are still poorly understood, but involve the protein SEEDLING PLASTID DEVELOPMENT 1 (SPD1) (Ruppel et al., 2011). A number of these above-described factors also directly impact other aspects of

seedling establishment, where there is still much to investigate regarding the development of fully functioning chloroplasts from dormant seed.

Light-dependent flavonoids localize to chloroplasts in a range of plants (Saunders and McClure, 1976). Phenylpropanoid production in the young seedling includes flavonoids in chloroplasts, where they may act as scavengers of the ROS created in the photosynthetic process (reviewed in Agati et al. 2012). Localization of PRN1, which cleaves the UV-induced flavonoid quercetin, includes the developing plastid in young seedlings (Orozco-Nunnelly et al., 2014b). Thus, flavonoids might have an important function in the protection of the developing plastid from solar UV (Orozco-Nunnelly et al., 2014b).

Chloroplast development during seedling establishment is also impacted by factors associated with hormone signaling. Cytokinins have been shown to stimulate expression of photosynthesis-related genes (Binns, 1994; Kravtsov et al., 2011; Schmölling et al., 1997) and chloroplast development (Chory et al., 1994). Conversely, BRs were shown to inhibit chloroplast development (Li and Chory, 1999; Nagata et al., 2000; Nakano et al., 2001). ABA impacts expression of nuclear photosynthesis-related genes (Kusnetsov et al., 1998; Staneloni et al., 2008) and chloroplast genes (Yamburenko et al., 2013) in developing seedlings.

7. Conclusions

Light and hormone signaling control distinct aspects of early plant development, especially the critical phase of seed-to-seedling transition. This transitory, but highly important, phase of the life cycle includes a transition from heterotrophic to autotrophic growth characterized by key changes in organ development and chloroplast development. Light and hormones perceived by receptors to initiate signal transduction affect the timing and pattern of

seedling emergence, establishment, and development, and tune these to the external environment. While primary metabolites serve to support the embryo transforming into an independent seedling, the young seedling is left vulnerable to the ecology (predators, abiotic stimuli, etc.) of the environment in which it finds itself. The store of secondary metabolites, thus, serves to mitigate potential damage. Blue and UV in particular rapidly induce the production of phenylpropanoids, which serve in chemical defense and can be deployed in physical defensive structures. Such optimization or fine-tuning of the plants' developmental plasticity and defense mechanisms promotes survival and reproduction over short time scales, and adaptation and influences on plant diversity and population dynamics over longer time scales. In these contexts, understanding this important survival change is vital in the current concerns about accelerated global change.

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Table 1. Role of plant photoreceptors in seed-to seedling transition

Photoreceptor/circadian component	Primary wavelengths detected	Role(s)	Select reference(s)
phytochrome (phy) A (phyA)	red (R)/far-red (FR)	FR-dependent seed germination; de-etiolation	(Botto et al., 1996; Dehesh et al., 1993; Franklin et al., 2003; Heschel et al., 2008; Heschel et al., 2007; Johnson et al., 1994; Nagatani et al., 1993; Parks and Quail, 1993; Parks and Spalding, 1999; Reed et al., 1994; Shinomura et al., 1994)
phyB	R/FR	R/FR-reversible germination; de-etiolation	(Botto et al., 1995; Franklin et al., 2003; Hennig et al., 2001; Heschel et al., 2008; Heschel et al., 2007; Parks and Spalding,

			1999; Reed et al., 1994; Reed et al., 1993; Shinomura et al., 1994)
phyC	R/FR	inhibit germination; de-etiolation	(Arana et al., 2014; Franklin et al., 2003; Monte et al., 2003)
phyD	R/FR	germination; de- etiolation	(Arana et al., 2014; Franklin et al., 2003; Hennig et al., 2001; Heschel et al., 2008)
phyE	R/FR	R/FR-reversible germination; de- etiolation	(Arana et al., 2014; Franklin et al., 2003; Hennig et al., 2002; Heschel et al., 2008; Heschel et al., 2007)
cryptochrome (cry) 1 (cry1)	/blue (B)/ultraviolet A (UV-A)	de-etiolation	(Ahmad et al., 1998; Ahmad et al., 1995; Folta and Spalding, 2001)
cry2	B/UV-A	de-etiolation	(Ahmad et al., 1998; Folta and Spalding, 2001)

phototropin (phot) 1 (phot1)	B/UV-A	phototropism; inhibition of hypocotyl elongation	(Folta and Spalding, 2001; Sakai et al., 2001)
phot2	B/UV-A	phototropism	(Sakai et al., 2001)
UVR8	UV-B	photomorphogenesis; UV-B stress mitigation; phototropism	(Favory et al., 2009; Huang et al., 2014; Rizzini et al., 2011; Vandenbussche et al., 2014)

Table 2. Role of plant hormones in seed-to seedling transition

Hormone	Role(s)	Reference(s)
Abscisic acid (ABA)	Inhibit germination, promote seed dormancy (antagonizes GA and BR)	Reviewed by (Cutler et al., 2010; Miransari and Smith, 2014; Sakata et al., 2014)
Gibberellin or gibberellic acid (GA)	Promote germination (through ABA antagonism); promote stem elongation and leaf expansion	Reviewed by (Gupta and Chakrabarty, 2013; Miransari and Smith, 2014; Peter and Stephen, 2012)
Auxin	Promote cellular elongation and root initiation; promotes phototropism	Reviewed by (Hohm et al., 2013; Miransari and Smith, 2014; Schaller et al., 2015; Zhao, 2010)
Ethylene	Promote germination (partially through ABA antagonism); promote growth and differentiation of shoots and roots	Reviewed by (Corbineau et al., 2014; Miransari and Smith, 2014)
Brassinosteroid (BR)	Promote germination (through ABA antagonism); promote seedling elongation; inhibit chloroplast development	Reviewed by (Clouse, 2011; Miransari and Smith, 2014; Zhu et al., 2013)
Cytokinin	Promote embryonic cell division and root elongation; promote chloroplast	Reviewed by (Binns, 1994; Kieber and Schaller, 2014;

	development	Miransari and Smith, 2014; Perilli et al., 2010; Schaller et al., 2015)
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