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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.

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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

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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, 1996; Hennig et al., 2002; Heschel et al., 2007, 2008; 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., 1995, 1998; 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

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., 2007, 2008; 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., 2007, 2008; Parks and Spalding, 1999; Reed et al., 1993, 1994; 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., 2007, 2008)
Cryptochrome (cry) 1 (cry1)	Blue (B)/ ultraviolet A (UV-A)	De-etiolation	(Ahmad et al., 1995, 1998; 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)

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