Cell

Information Integration and Communication in Plant Growth Regulation

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Plants are equipped with the capacity to respond to a large number of diverse signals, both internal ones and those emanating from the environment, that are critical to their survival and adaption as sessile organisms. These signals need to be integrated through highly structured intracellular networks to ensure coherent cellular responses, and in addition, spatiotemporal actions of hormones and peptides both orchestrate local cell differentiation and coordinate growth and physiology over long distances. Further, signal interactions and signaling outputs vary significantly with developmental context. This review discusses our current understanding of the integrated intracellular and intercellular signaling networks that control plant growth.

Introduction

Cell-to-cell communication is essential for the life of multicellular organisms, in which growth and development requires coordination of cell proliferation and differentiation between cells. Survival also requires an organism to respond properly to a wide range of environmental signals, and such adaptive responses require both intracellular signal transduction and information flow from cells receiving the signal to the rest of the body. In animals, cell-to-cell communication is facilitated by both hormones and the neuronal systems. Plants lack neuronal systems and rely largely on hormones and secreted small peptides for communication. Further, plants are sessile and must adapt to the environment by altering growth, development, and metabolism. Consequently, plants have evolved robust intracellular information processing systems and sophisticated intercellular signaling networks.

At least nine groups of plant hormones have been studied extensively. Auxin, cytokinin, brassinosteroid (BR), gibberellin (GA), and strigolactone (SL) play essential roles in normal growth and development. Abscisic acid (ABA) and ethylene mediate responses to abiotic stresses. Jasmonic acid (JA) is required for defense responses to herbivore wounding and anther development, whereas salicylic acid (SA) activates immune responses to pathogen infection (Larrieu and Vernoux, 2015). In addition, many secreted peptides have been shown to have hormone-like functions as mobile signals (Tavormina et al., 2015). While different hormones play predominant roles in growth promotion or stress responses, each hormone affects a wide range of developmental and physiological processes, and every developmental process is co-regulated by multiple hormones. Plant development is also highly sensitive to many environmental factors, such as light, temperature, pathogens, and herbivores. Extensive studies have elucidated the molecular pathways that transduce these signals and revealed many connections between these pathways. Further, recent studies have revealed a central growth-regulation module that controls cell elongation in shoot organs and different signaling outputs and hormone interactions between shoot and root. These studies shed light on important general questions of how a cell processes complex signals into coherent responses and growth decisions, how a hormone induces cell-type-specific responses, and how hormone signaling and crosstalk are rewired in different developmental context. Here, we provide an overview of the intracellular circuits that integrate multiple signals into cellular decisions, as well as intercellular signal circuits that program development locally and globally. We cover classic phytohormones and peptide signals, and their interactions with environmental signals in regulating shoot and root growth. Proteins and RNA molecules that move between cells through the plasmodesmata also play important roles in communication; these topics have been covered in recent reviews (Otero et al., 2016), and will not be discussed here. Given the broad scope of the topic and high complexity of the system, we will use selected key examples to illustrate principles rather than giving a comprehensive coverage of the literature.

Regulation of Shoot Cell Elongation by Integration of Environmental and Hormonal Signals

Growth in plants is driven by cell division in the stem cell populations maintained at the shoot apical meristem (SAM) and root apical meristem (RAM), followed by cell elongation. The balance between stem cell division and differentiation is crucial for maintaining the continuous growth (Sparks et al., 2013). However, cell elongation contributes to the majority of growth of shoot and root length and is controlled tightly by key environmental signals such as light and temperature, as well as major growth promoting hormones including auxin, BR, and GA (Figure 1).

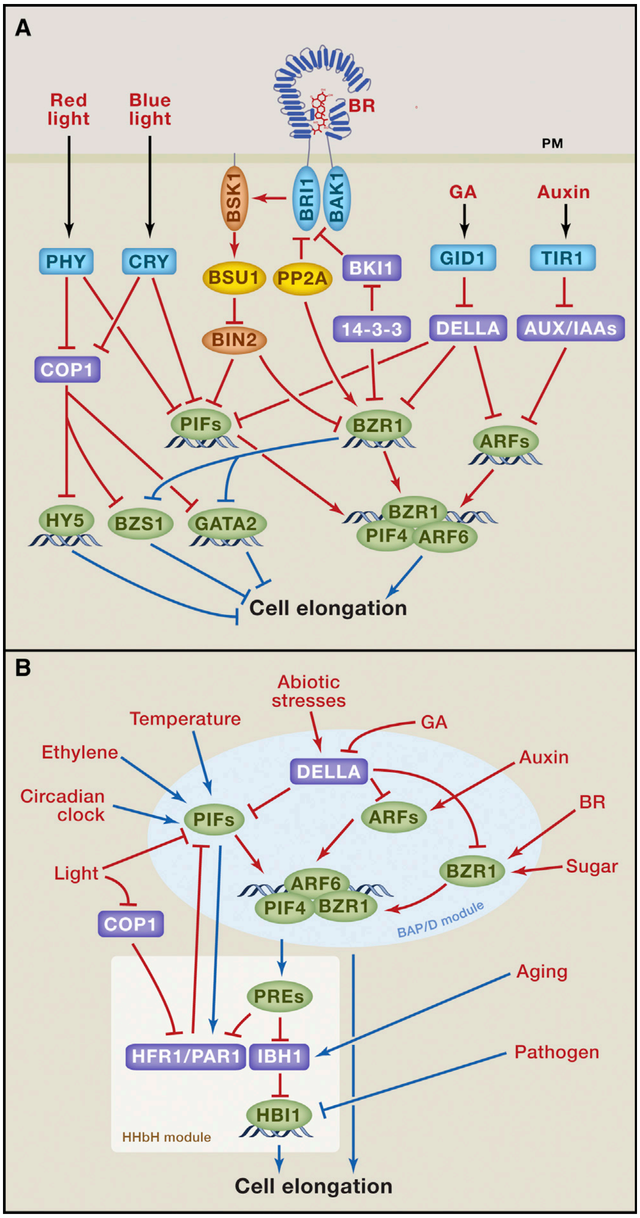

Figure 1. Integration of Light and Hormone Signaling Pathways Regulates Hypocotyl Elongation

(A) Light and hormonal signals (red text) are perceived by cell-surface or intracellular receptors (blue), which regulate transcription factors (green) through signaling/posttranslational mechanisms (red lines), whereas the transcription factors transcriptionally regulate (blue lines) downstream responses and components of other pathways. Orange: kinases; yellow: phosphatases; purple: inhibitors of transcription factors.

(B) Transcriptional integration by the BAP/D-HHbH circuit. Red and blue lines show regulation at the protein and RNA (transcriptional) levels, respectively.

The light-mediated morphological changes in *Arabidopsis* seedling, so called photomorphogenesis, has been a model system for studying the interactions between light and hormones and the regulation of cell elongation. Upon seed germination in the dark (under soil in nature), an *Arabidopsis* seedling undergoes skotomorphogenesis (also called etiolation), which is characterized by maximum hypocotyl elongation, limited root growth, closed cotyledons with an apical hook, and suppression of chloroplast development. Upon exposure to light, seedling development switches to photomorphogenesis (also called de-etiolation), which is characterized by inhibition of hypocotyl elongation, opening/expanding and greening of cotyledons and leaves, and acceleration of root growth. Deficiency in synthesis or signal transduction of BR, auxin, and GA all cause photomorphogenesis in the dark, suggesting intimate relationships between light and these growth hormones in co-regulating cell elongation and seedling photomorphogenesis. While some previous studies proposed hierarchical relationships of light regulating hormone levels, or one hormone regulating another, in order to control cell elongation, recent studies have revealed that these light and hormonal signals also converge at a central module of interacting transcription factors/regulators to co-regulate overlapping sets of genes. Furthermore, additional environmental and endogenous signals impinge on this central module to control shoot cell elongation (Figure 1).

For developmental regulation, plants detect light of different wavelength using several classes of photoreceptors (Galvão and Fankhauser, 2015), among which the red/far-red photoreceptor phytochromes and blue light receptor cryptochromes play major roles in seedling morphogenesis (Chory, 2010; Liu et al., 2011). Phytochromes exist in two photo-switchable forms: the red-absorbing Pr form, which is biologically inactive, and the active far-red-absorbing Pfr form. Light absorption switches phytochromes between Pr and Pfr forms. Such photo-reversibility allows phytochromes to measure not only light intensity but also wavelength, which changes with season and canopy (Chen and Chory, 2011).

Phytochromes and cryptochromes regulate cell elongation primarily through two classes of transcription factors that have opposite functions. The phytochrome interacting factors (PIFs), a class of basic helix-loop-helix (bHLH) factors, are major positive regulators of shoot cell elongation. Photo-activated phytochromes inactivate PIFs by inhibiting their DNA-binding activities and promoting their phosphorylation, ubiquitination, and degradation (de Lucas and Prat, 2014; Ni et al., 2014). Several PIFs are also inactivated by direct interaction with cryptochromes (Ma et al., 2016; Pedmale et al., 2016). Elongated hypocotyl5 (HY5), GATA2/4, and B-box factors including BZS1 are negative regulators of cell elongation, and they are degraded in the dark through the E3 ubiquitin ligase constitutive photomorphogenic1 (COP1), which is inactivated by both phytochromes and cryptochromes (Lau and Deng, 2012; Liu et al., 2011; Wang et al., 2012).

Auxin (primarily indole-3-acetic acid, IAA) regulates gene expression and promotes shoot cell elongation by activating the auxin response factor (ARF) family of transcription factors. ARFs are repressed by the Aux/IAA proteins, which are removed by auxin-induced degradation. Auxin binds to the TIR1/AFB family of F-box proteins, which recruit the Aux/IAA proteins to the $SCF^{TIR1/AFB}$ complex for ubiquitination and proteasome-mediated degradation, leading to de-repression of ARFs (Salehin et al., 2015).

BR acts through the cell surface receptor kinase brassinosteroid-insensitive1 (BRI1). BRI1 represents one of over 220