

Spatial-specific regulation of root development by phytochromes in *Arabidopsis thaliana*

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Distinct tissues and organs of plants exhibit dissimilar responses to light exposure—cotyledon growth is promoted by light, whereas hypocotyl growth is inhibited by light. Light can have different impacts on root development, including impacting root elongation, morphology, lateral root proliferation and root tropisms. In many cases, light inhibits root elongation. There has been much attention given to whether roots themselves are the sites of photoperception for light that impacts light-dependent growth and development of roots. A number of approaches including photoreceptor localization in planta, localized irradiation and exposure of dissected roots to light have been used to explore the site(s) of light perception for the photoregulation of root development. Such approaches have led to the observation that photoreceptors are localized to roots in many plant species, and that roots are capable of light absorption that can alter morphology and/or gene expression. Our recent results show that localized depletion of phytochrome photoreceptors in *Arabidopsis thaliana* disrupts root development and root responsiveness to the plant hormone jasmonic acid. Thus, root-localized light perception appears central to organ-specific, photoregulation of growth and development in roots.

Introduction

Proper onset and fine-tuning of developmental transitions and adaptive processes in plants not only require detection of the presence or absence of light, but also spectral quality, quantity, directionality

and periodicity. To perceive fluctuations in the temporal and spatial patterns of light, photoreceptors function at the interface between plants and the environment. The regulation of plant growth and development by light signals, otherwise known as photomorphogenesis, involves several classes of photoreceptors: blue (B)/Ultraviolet-A (UV-A)-absorbing photoreceptors, including cryptochromes, phototropins and Zeitlupes; red (R)/far-red (FR)-absorbing phytochromes and Ultraviolet-B (UV-B) photoreceptors.^{1,2} One of the most well-studied families of photoreceptors, phytochromes, regulates a range of developmental and adaptive responses, such as seed germination, de-etiolation, gravitropic orientation, stomatal development, shade avoidance, entrainment of the circadian clock and flowering in *Arabidopsis thaliana*.^{1,3,4}

Phytochromes are soluble chromoproteins and consist of an apoprotein and a light-absorbing chromophore.⁵ A nuclear gene family encodes the apoproteins, five of which (*PHYTOCHROME A-PHYTOCHROME E* (*PHYA-PHYE*)) are found in *A. thaliana*.⁶⁻⁸ Multiple genes encode the enzymes responsible for chromophore synthesis, which occurs in the chloroplast.⁹⁻¹² A single chromophore, i.e., phytychromobilin, is used by all higher plant phytochrome family members and is essential for phytochrome photoperception.⁵

Plants exhibit diverse growth and developmental responses in distinct tissues and organs in response to light. For example, growth of cotyledons is promoted by light, whereas the growth of the hypocotyl is inhibited by light exposure.

Keywords: morphogenesis, photomorphogenesis, photoreception, photoregulation, photoreceptor, phytochrome, red light, far-red light, blue light

Abbreviations: B, blue light; cry, cryptochrome; FR, far red light; phy, phytochrome; R, red light; UV, ultraviolet; W, white light

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Photoreceptors regulate such distinct tissue- and organ-specific photoresponses or inter-organ, light-dependent growth and developmental responses. The most widely known of these inter-organ responses include the perception of light by cotyledons that results in the inhibition of hypocotyl elongation and the perception of light by leaves that results in the induction of flowering, or a transition from vegetative to reproductive growth at the shoot apical meristem, under permissive photoperiods.¹³⁻¹⁵ The regulation of physiological responses depends upon complex intracellular, intercellular and inter-organ signaling cascades.^{13,14} Through inter-tissue and inter-organ signaling, opposing physiological responses in different plant tissues or organs can be regulated by the same light stimulus.^{13,14}

Recently, insight into the molecular bases of such tissue- and organ-specific photoreceptor-dependent responses has begun to emerge. For example, tissue-specific expression of genes that encode photoreceptors in photoreceptor-deficient backgrounds has resulted in insight into the sub-organismal pools of phytochromes and cryptochromes that regulate distinct developmental or growth responses.¹⁶⁻¹⁸ Using such an approach, mesophyll-localized phyB was shown to regulate flowering.¹⁸ Likewise, cryptochrome molecules localized to vascular bundles were shown to be the pool of cryptochromes that regulate flowering.¹⁶ Also, an approach to inactivate phytochromes in specific tissues has yielded insight into tissue-specific roles of phytochromes in the regulation of distinct phytochrome responses.¹⁹⁻²² These studies demonstrated that mesophyll-localized pools of phytochromes have tissue-specific roles in anthocyanin synthesis and/or accumulation,^{21,22} and inter-organ roles in the inhibition of hypocotyl elongation.^{20,21} Also, root-localized phytochromes have a role in the photoregulation of root elongation.¹⁹

Apart from the photoreceptors themselves, additional insight into the tissue-specific roles of effectors that function downstream of the photoreceptors has also begun to emerge. For example, a recent study demonstrated distinct-tissue specific roles for SUPPRESSOR OF PHYTOCHROME A 1 (SPA1), a

key repressor of photomorphogenesis.²³ SPA1 in the phloem and mesophyll impacts light-dependent leaf expansion, whereas phloem-specific SPA1 regulates the photoperiodic induction of flowering.²³ Likewise, factors that function in the photoperiodic induction of flowering, which is a photoreceptor-regulated process, have also been shown to function in specific tissues and/or organs. For example, CONSTANS, a key flowering regulator, functions in the phloem to regulate the photoperiod-dependent flowering, whereas FLOWERING LOCUS T (FT), another flowering regulator, functions in the phloem and meristem in the photoperiodic induction of flowering.²⁴ Although tissue-specific, light-dependent responses have been long recognized (for reviews, see refs. 13 and 14), the application of new experimental tools, some of which have been recently reviewed in reference 25, has allowed progress to be made in understanding the molecular bases for such tissue- and organ-specific photoresponses.

Spatial-Specific Regulation of Root Development by Photoreceptors

Although definitive information on the molecular mechanisms of light-dependent inter-tissue and inter-organ signaling is limited, tissue-specific gene expression analyses suggest that there are distinct subsets of light-mediated genes in discrete tissues in several plant species. In Arabidopsis, in cotyledons, hypocotyls and roots, less than 1% of light-regulated genes are common to all three types of tissues.²⁶ Despite the similarity in the mechanism of photoperception and initial signaling in cotyledons and roots in Arabidopsis,^{27,28} distinct subsets of light-regulated genes have been identified from cotyledons vs. roots.^{26,29} In rice, roots appear to have more light-regulated genes than shoots.^{26,29} Tissue-specific, light-regulated gene expression in tissues such as roots suggests that the perception of light by root-localized photoreceptors has biological importance and specific physiological relevance for accurate development or photoresponses of roots. Notably, ecotypic differences in root lengths for Arabidopsis plants grown under white (W)

illumination have been recognized.^{19,30,31} In these experiments, ecotype Col-0 has longer roots than No-0 or C24.^{19,30,31} Our recent analyses show that differences in photobiological responses under distinct light conditions also exist, resulting in the Col-0 ecotype also being longer than No-0 or C24 under B and R, but Col-0 being similar to No-0 or C24 ecotypes under FR (see Fig. 4 in ref. 19).

Light penetration has been observed in the upper layers of soil up to several millimeters in natural environments.³² Phytochromes, cryptochromes, phototropins and perhaps other photoreceptors are localized in roots and render the capability to roots of sensing and responding to light.³³⁻³⁵ In Arabidopsis, B-absorbing phototropins in roots contribute to root development and function in natural environments.³⁶ MYC2, which functions as a negative regulator in B-dependent photomorphogenesis,³⁷ also impacts root elongation under white illumination.^{19,38} Also, phyB has been shown to effect root system morphology in soil-grown plants.³⁹ Apart from *A. thaliana*, light has also been shown to impact root development in some rice varieties. For example, light promotes helical growth of seminal roots and regulates root morphology in some varieties of rice.^{40,41}

Spatial-Specific Regulation of Root Elongation by Phytochromes

In many controlled photobiological experiments, phytochromes have been shown to impact root development. PhyA promotes root elongation in R,⁴² FR,^{19,42,43} and B.¹⁹ Similarly, phyB promotes R-dependent root elongation.¹⁹ Both phyA and phyB also have been shown to contribute to root hair formation in *A. thaliana*.^{44,45} Photoreceptor phyA regulates root hair formation in response to FR illumination, whereas both phyA and phyB contribute to root hair formation under R conditions.^{44,46} Lateral root production also is regulated by phytochromes, with phyA, phyB and phyE stimulating lateral root production, whereas phyD inhibits the formation of lateral roots in Arabidopsis.³⁹ Notably, recent results related root-localized expression of a gene associated with

phytochrome chromophore production, i.e., *Brassica napus* haem oxygenase-1 (*BnHO1*), with the early stages of lateral root formation in *B. napus*.⁴⁷ These intriguing results suggest a potential role for phytochromes in lateral root development in this plant species.⁴⁷ A role for phytochromes in root hair formation also has been recognized in lettuce.⁴⁸ The site of light perception by phytochromes for this response was localized to a specific portion of the root using microbeam irradiation of lettuce seedlings.⁴⁹

Recent evidence also has emerged for phytochrome-dependent regulation of root development in rice.⁵⁰ The noted response is the light-dependent inhibition of seminal roots, i.e., cell elongation of roots, not cell division, is inhibited.⁵⁰ The authors argue that the site for this photosensory response in rice appears to be the roots themselves, as irradiation of shoots alone does not result in inhibition of seminal roots.⁵⁰ Additionally, phytochromes were localized to roots, as assayed immunohistochemically in rice, which suggests that photoreceptors in the roots themselves can regulate this photoresponse of seminal roots.⁵⁰ Both phyA and phyB have been implicated as the phytochromes regulating this light-dependent inhibition of seminal root elongation in rice.⁵⁰

Recent results arising from a line that has the phytochrome chromophore inactivated specifically in roots of *Arabidopsis* demonstrates that phytochromes in roots regulate root elongation under W, B and R illumination.¹⁹ The impact of W light in this instance is due to the combined effect of photoreceptors. The R-dependent root response may be regulated by any of the phys capable of R absorption. However, the B-dependent response is attributed to phyA.¹⁹ phyA is a strong B sensor⁵¹ and contributes to a number of B-dependent responses, including anthocyanin accumulation,^{22,52} hypocotyl elongation,^{20,52-57} and circadian entrainment.⁵³ Although, as stated above, B absorbed by phyA has been associated with the photoregulation of root elongation, our recent results demonstrated that phyA localized in roots themselves contributes locally to this BL-dependent

regulation of root development,¹⁹ whereas prior results suggest that cryptochromes in shoots, rather than root-localized pools, contribute to regulation of root development.⁵⁸ Furthermore, root-localized phytochromes contribute significantly to the local response of the plant hormone jasmonic acid on root inhibition.¹⁹

Conclusions

Photoreceptors localized in roots regulate light-dependent root elongation responses. Although several photoreceptors are localized in the roots, root-localized phytochromes have been shown to impact root development directly, as opposed to cryptochromes, which appear to impact root development long distance, i.e., shoot-localized cryptochromes appear to exert control through inter-organ signaling. A determination of whether distinct signaling components are utilized in roots or in shoots to impact light-dependent root growth and development requires additional investigations. The fact that distinct subsets of light-regulated genes have been identified in different tissues or in shoots to impact light-dependent root growth and development suggests that distinct signaling components may contribute to photoregulation of root development.

Note added in proof: Recent studies using covered seedling parts and grafting studies confirm that roots directly perceive light and that regulation of the actin cytoskeleton in roots contributes to root-localized photoregulation of elongation.⁵⁹

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