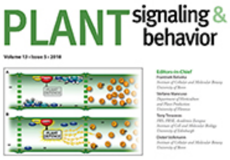

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SHORT COMMUNICATION

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Abscisic acid-mediated phytochrome B signaling promotes primary root growth in *Arabidopsis*

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ABSTRACT
Plant photomorphogenic responses have been studied mostly using the shoots, the core part of plant architecture that perceives light for photosynthesis and influences the overall processes of growth and development. While the roots are also known to respond to aboveground light through multiple routes of light signal transduction, root photomorphogenesis has been less highlighted until recently. A long-standing, critical question was how the underground roots are capable of sensing aerial light and how the root-sensed light signals trigger root photomorphogenesis. When the roots are directly exposed to light, reactive oxygen species (ROS) are rapidly produced to promote primary root elongation, which helps the roots to escape from the abnormal growth conditions. However, severe or long-term exposure of the roots to light causes ROS burst, which impose oxidative damages, leading to a reduction of root growth. We have recently found that phytochrome B (phyB) promotes abscisic acid (ABA) biosynthesis in the shoots and the shoot-derived ABA signals mediate ROS detoxification in the roots, lessening the detrimental effects of light on root growth. On the basis of these observations we propose that the phyB-mediated ABA signaling contributes to the shoot-root synchronization that is essential for optimal growth and performance in plants.

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ROS; ABA; root photomorphogenesis; phyB

Text

In nature, the root system is mostly embedded in soil and thus assumed to be blocked from light exposure. On the other hand, the shoots are exposed to aerial light and known to possess various light-sensing molecules, which mediate photosynthesis and photomorphogenesis. However, recent accumulating evidence strongly support that the roots are also capable of sensing and responding to aboveground light to trigger root morphogenic dynamics and developmental changes, which mediate primary root growth, lateral root formation, nutrient uptake, and greening process.[1–3] In particular, the light-induced promotion of root growth is emerging as a major topic in the field of sensory root biology.[4] The light-mediated promotion of root growth is known to function as an escape tropism of the light-stressed roots through the ROS-mediated signaling pathways, further supporting the physiological relevance of root photomorphogenesis.

There are multiple routes of light signal transduction to the roots. When plants are exposed to drought or strong wind, the roots are often exposed to light that penetrates through the soil particle or cracks of the soil layer.[5,6] Under this condition, the roots are directly exposed to ambient light. It is well-known that photoreceptor genes are expressed in the roots, and the root photoreceptors would be able to sense the soil-penetrating light. It has been recently demonstrated that light is transmitted through the plant body to the underground roots, and the stem-piped light activates phyB in the root to trigger primary root growth and root gravitropism.[7,8] The vascular tissues would serve as a potential path of light transmission. The shoot-sensed light also trigger biosynthesis of light signaling molecules, which are subsequently transported to the roots via the vascular system. For example, the shoot-to-root transport of auxin affects lateral root formation
via phyA and phyB signaling.[9] In *Lotus japonicas*, jasmonic acid (JA) – mediated phyB signaling is proven to regulate root nodulation.[1]

Our recent findings indicate that shoot phyB promotes ABA synthesis in the shoot, and the shoot-derived ABA itself or signals induces root elongation by detoxifying ROS.[10] Consistent with this notion, ROS accumulate in the roots of *phyb* mutant that exhibits reduced primary root growth upon exposure to long-term light illumination. This entails that shoot ABA itself or as-yet unknown ABA signaling molecule links the shoot phyB-sensed light perception and ROS homeostasis in the underground roots. The proposed role of ABA in phyB light signaling is further supported by treatments of seedlings with fluridone, a potential inhibitor of ABA biosyntehsis.[11] It was found that while fluridone reduced the primary root growth of wild-type Col-0 seedlings, that of *phyb-9* mutant was insensitive to fluridone (Figure1A). It has been suggested that low levels of ABA in *phyb-9* mutant reduced the primary root growth of the mutant. [7,8] Furthermore, grafting experiment using Col-0 plants and *aba1-6* mutant, which is defective in ABA production[12], revealed that chimeric

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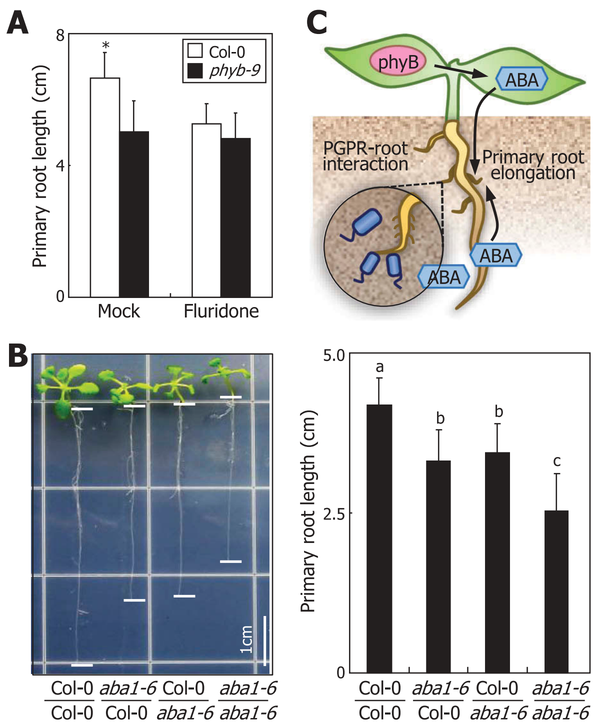

Figure 1. Effects of ABA on root photomorphogenesis.

(A) Effects of fluridone on primary root growth. Seedlings germinated and grown on horizontal MS-agar plates for 3 days were transferred to vertical MS-agar plates containing 100 μM fluridone, an inhibitor of ABA biosynthesis, for additional 10 days in the light. Fifteen measurements of primary root lengths were statistically analyzed using Student *t*-test (*$P < 0.01$). Bars indicate standard deviation of the mean (SD).**(B)** Primary root growth of grafted seedlings between Col-0 plants and *aba1-6* mutant. Grafted seedlings were grown for 2 weeks on MS-agar plates in the light before measurements of primary root lengths. Different letters represent a significant difference ($P < 0.01$) determined by one-way analysis of variance (ANOVA) with *post hoc* Tukey test. Bars indicate SD.**(C)** Schematic model illustrating ABA function in root photomorphogenesis and interactions of the roots with plant growth-promoting rhizobacteria (PGPR).

plants having *aba1-6* scion or *aba1-6* stock exhibited an intermediate phenotype of wild type and *aba1-6* seedlings (Figure 1B), suggesting that ABA produced in both the shoots and the roots is essential for the phyB-mediated primary root elongation.

We have previously demonstrated that phyB mediates ABA biosynthesis in the shoots and ABA triggers the expression of PEROXIDASE1 gene by stabilization ABA INSENSITIVE5 transcription factor.[10] Considering the importance of the synchronization and communication between the shoot and root parts, more works are required for further understanding root photomorphogenesis.

It is notable that root photomorphogenesis and associated growth hormones, such as ethylene and ABA, are critical for the cultivation of crop plants. Plant growth-promoting rhizobacteria (PGPR) are soil bacteria that improve plant productivity and immunity, forming symbiotic relationships with many plants. It is known that the root-bacteria relationship is modulated by endogenous ABA content of the host plant; PGPR inhibits plant growth in ABA-deficient plants, while it stimulates growth of wild-type plants.[13] It is interesting to propose that root photomorphogenesis might be linked with the rhizobacterial system. Stem-piped light would regulate not only the primary root growth but also the symbiotic relationship with surrounding rhizobacteria in the soil (Figure 1C). Further understanding of morphological and architectural dynamics in root photomorphogenesis and symbiosis with rhizobacteria would contribute to development of crop plants with improved productivity and environmental adaptation.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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