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Roles of Phytochrome-interacting Factors in Light Signaling

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As sessile organisms, plants have acquired a high degree of developmental plasticity to optimize their growth and reproduction in response to their ambient environment, such as light, temperature, humidity and salinity. Light is one of the key environmental signals that influence plant growth and development. It controls multiple developmental processes in the plant life cycle, including seed germination, seedling de-etiolation, leaf expansion, stem elongation, phototropism, stomata and chloroplast movement, shade avoidance, circadian rhythms and flowering time. In *Arabidopsis*, there are five distinct phytochromes, namely phyA to phyE. Phytochromes regulate plant gene expression by absorbing red and far-red light and play an important role throughout the life cycle of plants [1]. A small subset of basic/helix-loop-helix (bHLH) transcription factors called Phytochrome-Interacting Factors (PIFs) act to repress seed germination, promote seedling skotomorphogenesis and promote shade-avoidance [2]. Light activated phytochrome molecules directly reverse these activities by inducing rapid degradation of the PIF proteins. Light-induced degradation of these PIFs does not lead to the total disappearance of the protein, but rather results in a new, lower steady-state level of the protein in sustained light, such as that experienced during the day of a normal day-night cycle. Moreover, degradation ceases upon Pfr removal and the return of plants to darkness, resulting in rapid reaccumulation of PIF proteins to high levels over the dark period. Recent advances in dissecting PIFs signaling pathways, include the gibberellin pathway, the circadian clock and high temperature. These studies indicated that PIFs have broader roles than previously appreciated, functioning as a cellular signaling hub that integrates multiple signals to orchestrate regulation of the transcriptional network that drives multiple facets of downstream morphogenesis.

Seven *Arabidopsis* bHLHs (HFR1, PIL1, PIF3, PIF4, PIL5/PIF1, PIL6 and SPT) have been shown to regulate various light responses [3]. PIF3, PIF4, PIL5/PIF1 and PIL6/PIF5 interact directly with phytochromes. PIF3, the foundation member of the PIF subset, was initially identified in a yeast two-hybrid screen for phyB-interacting proteins, and subsequently shown to bind conformer specifically, in photoreversible fashion, to the Pfr forms of both phyA and phyB. PIF3 regulates hypocotyl elongation, as well as anthocyanin and chlorophyll biosynthesis by directly binding to the promoters of its target genes. Genetic analysis showed that monogenic *pif3, pif4, pif5* and *pif7* null mutants exhibit light-hypersensitive seedling phenotypes, that is, short hypocotyls and large cotyledons, at the completion of de-etiolation after several days of exposure to light.

Light mediated plants development is the switches from skotomorphogenesis to photomorphogenesis. Seedling development undergoes critical changes during the transition from life in the dark just after germination, toward life in a light environment when seedlings emerge through the soil surface. In the preparation for this switch, dark grown seedlings accumulate the chlorophyll precursor protochlorophyllide to permit rapid assembly of functional photosynthesis machinery upon initial light irradiation [4]. In consequence, cotyledons of etiolated *pif* mutant seedlings are severely bleached when transferred to light [5]. Light-triggered degradation of PIFs results in a rapid production of carotenoids in coordination with chlorophyll biosynthesis. In addition, PIF3 acts similarly and additively to PIF1 to repress chloroplast development and chlorophyll synthesis in the dark to rapidly assemble functional photosynthetic machinery [5, 6].

Phenotypic and genetic evidence indicate that PIF3 mainly acts as a negative regulator in light responses, repressing light-mediated cotyledon expansion and chlorophyll biosynthesis in the dark [5,7, 8]. Recent studies have revealed that PIF3 represses the majority of chlorophyll biosynthetic and photosynthetic genes in etiolated seedlings. In *vitro* binding assays showed that PIF3 binds specifically to cis-acting regulatory elements, such as G-boxes and E-boxes in promoters of a variety of light-responsive genes [9]. Our recent study reveals that the RPD3/HDA1 type histone deacetylase HDA15 directly interacts with PIF3 *in vivo* and *in vitro*, suggesting that PIF3 and HDA15 are in the same protein complex [10]. Genome-wide transcriptome analysis revealed that HDA15 acts mainly as a transcriptional repressor and negatively regulates chlorophyll biosynthesis and photosynthesis gene expression in etiolated seedlings. Both HDA15 and PIF3 repress gene expression involved in chlorophyll biosynthesis and photosynthesis by decreasing the histone acetylation levels and RNA Polymerase II-associated transcription. The binding of HDA15 to the target genes depends on the presence of PIF3. In addition, PIF3 and HDA15 are dissociated from the target genes upon exposure to light. Taken together, these results indicate that PIF3 repress chlorophyll biosynthetic and photosynthetic genes in etiolated seedlings *via* recruiting the histone deacetylase HDA15. Further research is required to determine whether other PIFs are also associated with histone deacetylases to regulate gene expression in light responses.

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