

IN BRIEF

Frenemies: Antagonistic bHLH/bZIP Transcription Factors Integrate Light and Reactive Oxygen Species Signaling in *Arabidopsis*

Although plants are autotrophs, they don't start out that way. During early plant growth, reserves stored by the mother plant are mobilized to provide the seedling with energy and carbon until the switch to autotrophic growth occurs (Chen and Thelen, 2010). This crucial developmental switch involves light signal transduction and the production of reactive oxygen species (ROS), including singlet oxygen. ROS act as signaling molecules that regulate multiple processes in plants, including growth and development, stress responses, and programmed cell death. However, high levels of ROS, which are produced under high-light conditions, can cause photo-oxidative damage and inhibit photosynthesis (reviewed in Li et al., 2009). Etiolated seedlings are especially sensitive to high-light levels. ROS signaling is integrated with many signaling networks in plants, but the mechanisms that mediate these interactions are poorly understood. **Chen et al. (2013)** describe how transcription factor modules mediate crosstalk between light perception and ROS production in *Arabidopsis* to help plants optimize their growth in response to light.

The basic-helix-loop-helix (bHLH) and bZIP transcription factors PHYTOCHROME-INTERACTING FACTORS (PIFs) and ELONGATED HYPOCOTYL5 (HY5)/HY5 HOMOLOG (HYH) mediate two distinct signaling branches of the photomorphogenic response in *Arabidopsis*. PIFs, including PIF1 and PIF3, accumulate in the dark to promote etiolation, whereas light induces the rapid degradation of PIFs. PIF proteins prevent singlet oxygen production during seedling greening. Overexpression of *PIF3* results in elongated hypocotyls in plants grown under red light, and *pif* mutants display severe cell death during the dark-to-light transition. By contrast, HY5 and HYH are degraded in the dark and stabilized in the light. These bZIP

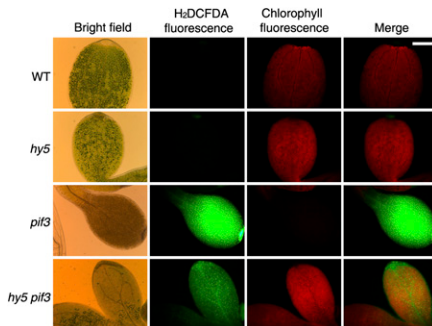


FIGURE LEGEND: Antagonistic roles of PIF3 and HY5 in regulating ROS production. H₂DCFDA fluorescence shows cellular ROS levels of 4-d-old dark-grown seedlings after 24 h of light exposure. Bar=200 μ m. (Reprinted from Chen et al. [2013], Figure 1B and 7C.)

transcription factors negatively regulate the seedling greening process. Despite their antagonistic functions, PIF1/PIF3 and HY5/HYH share similar structures. Using electrophoretic mobility shift assay and co-immunoprecipitation analysis, the authors show that all of these factors directly bind to the promoters of five ROS-responsive genes through their G-box motifs; PIF1/PIF3 act as negative regulators of these genes, while HY5/HYH act as positive regulators. Bimolecular fluorescence complementation and fluorescence resonance energy transfer assays demonstrate that the transcription factors co-exist and interact in the same nucleus at the same time in the dark or after the light transition. In fact, the structural similarity of these transcription factors allows them to form heterodimers, as determined by yeast two-hybrid, pull-down, co-immunoprecipitation, and firefly luciferase complementation imaging assays.

The authors propose that PIF1/PIF3-HY5/HYH heterodimers serve as rheostats to fine-tune the flow of the ROS signaling pathway. In the dark, PIF1/PIF3 are abun-

dant, and their homodimers repress ROS-responsive gene expression in the nucleus. In the light, HY5/HYH are more abundant and form heterodimers with PIF1/PIF3. Since these transcription factors have opposite effects on downstream gene expression, the heterodimers likely function as inactive forms, maintaining ROS-related transcripts at basal levels. Under high-light conditions, PIF1/PIF3 are almost completely degraded, leading to the formation of HY5/HYH homodimers, which increase ROS-responsive gene expression and activate their network. Consistent with this hypothesis, the protein stability of HY5/HYH and PIF1/PIF3 and the expression of downstream ROS-responsive genes are coordinately regulated by the exposure length and intensity of light. Indeed, these transcriptional modules may be crucial for the regulation of the ROS pathway to help plants optimize their growth in response to changing light conditions.

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