MED25 Mediates Shade-Induced Hypocotyl Elongation in Tomato

Avoiding the shade of neighboring plants is essential to optimize light capture and fuel photosynthesis. Shade avoidance is typically sensed through changes in light quality, is mediated by the activity of phytochromes, and modulates other plant stress responses (Courbier and Pierik, 2019). The inactivation of phytochrome B by shade allows Phytochrome Interacting Factor (PIF) transcription factors to bind to (auxin-related) target genes and promote shoot elongation responses. While the molecular mechanisms of shade avoidance and PIF regulation are well understood in the model plant species Arabidopsis (*Arabidopsis thaliana*), whether PIFs play a similar role in crop species remains elusive. In addition, it is unknown how the cell's transcription machinery recruits PIFs to control the expression of target genes.

In this issue of *Plant Physiology*, Sun et al. (2020) demonstrate that tomato (*Solanum lycopersicum*) PIF4 contributes to shade-induced hypocotyl elongation. To functionally assess the role of PIF4 in tomato shade avoidance responses, the authors used the CRISPR/Cas9 gene-editing system to generate tomato *pif4* mutants. They found that *pif4* mutants displayed reduced hypocotyl length under both control and simulated shade conditions when compared with wild-type plants. This reduction in hypocotyl length corresponded to a decline in the expression of (in Arabidopsis) known PIF4 target genes in the *pif4* mutants. Moreover, the authors show that in response to shade, PIF4 levels increased on the promoters of target genes that typically mediate auxin biosynthesis and signaling. Together, these results suggest that tomato PIF4 promotes hypocotyl elongation through direct promoter binding and activation of auxin biosynthesis and auxin-responsive genes (Fig. 1).

Next, the authors searched for potential coactivators of PIF4 in mediating transcriptional activation of its target genes. Previous research identified Mediator Complex Subunit25 (MED25) as an essential regulator of shade avoidance in Arabidopsis (Cerdán and Chory, 2003), but the underlying mechanism remained unknown. Interestingly, the Mediator complex is known to anchor transcription factors with the Pol II machinery to control target gene transcription under a variety of environmental signals (Elfving et al., 2011; Mathur et al., 2011). Therefore, to test if MED25 coactivates PIF4-mediated transcriptional activation in tomato, the authors tested the binding capacity of PIF4 and MED25 and found that they interact both in vitro and in vivo. In addition, they could show that MED25 recruits Pol II to the promoters of PIF4 target genes. Next, Sun et al. (2020) examined whether MED25 is required for shade-induced hypocotyl elongation and transcriptional responses in tomato seedlings. They found that plants impaired in MED25 levels display a reduction in shade-induced hypocotyl elongation. Accordingly, and similar to *pif4* mutants, *MED25* antisense lines were also limited in transcriptional activation of PIF4 target genes. Finally, using a transcriptomics approach, the authors show that PIF4 and MED25 coregulate the expression of a large number of shade-responsive genes. Collectively, the results of Sun et al. (2020) identify MED25 and PIF4 as important transcriptional coregulators of shade avoidance responses in tomato (Fig. 1).

Research over the years has identified MED25 as an important transcriptional coregulator of multiple plant responses that include ethylene signaling (Yang et al., 2014), shade-induced flowering (Cerdán and Chory, 2003), and jasmonic acid (JA)-mediated defense signaling (Chen et al., 2012). The work of Sun et al. (2020) adds shade-induced hypocotyl elongation, through the anchoring of PIF4, to the set of responses controlled by MED25. These reports beg the question of whether

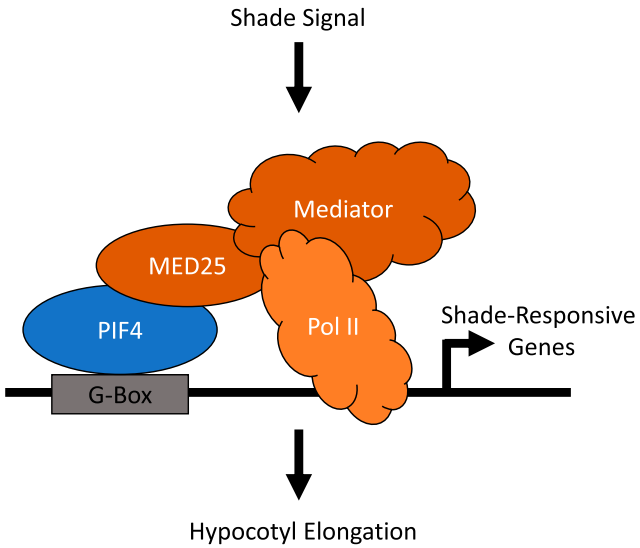

Figure 1. Proposed model for how tomato PIF4 and MED25 regulate shade-responsive gene expression and drive shade-induced hypocotyl elongation. During shade, PIF4 is stabilized and binds to target gene promoters. MED25 physically interacts with PIF4 and recruits RNA polymerase II (Pol II) to induce shade-responsive gene expression and activate hypocotyl elongation. Adapted from figure 5D of Sun et al. (2020).

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MED25 is a universal transcriptional regulator or whether it can function to balance MED25-controlled transcriptional responses in a multistress situation. For instance, recent research in tomato has shown that shade cues reduce the sensitivity to JA-dependent transcriptional responses when attacked by the necrotrophic pathogen *Botrytis cinerea* (Courbier et al., 2020). MED25 is well known to coregulate JA responses through recruitment of the MYC2 transcription factor to its target genes (Chen et al., 2012). Does MED25 contribute to the negative cross talk between shade and JA responses, potentially through direct-binding competition with its respective transcription factors PIF4 and MYC2? In addition, it is likely that MED25-controlled responses achieve higher transcriptional specificity through interaction with other Mediator subunits, such as MED16 (Yang et al., 2014).

While the work of Sun et al. (2020) shows that MED25 and PIF4 control shade-induced hypocotyl elongation in tomato, it remains to be investigated to which extent they also control other shade-mediated responses such as petiole/stem elongation and tomato fruit set (Ji et al., 2019). Such understanding of the regulation of shade responses in crops is crucial to optimally grow our crops in dense vegetations to maximize yield but limit its adverse consequences in the future.

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LITERATURE CITED

Cerdán PD, Chory J (2003) Regulation of flowering time by light quality. Nature **423:** 881–885

Chen R, Jiang H, Li L, Zhai Q, Qi L, Zhou W, Liu X, Li H, Zheng W, Sun J, et al (2012) The Arabidopsis mediator subunit MED25 differentially regulates jasmonate and abscisic acid signaling through interacting with the MYC2 and ABI5 transcription factors. Plant Cell **24:** 2898–2916

Courbier S, Grevink S, Sluijs E, Bonhomme PO, Kajala K, Van Wees SCM, Pierik R (2020) Far-red light promotes *Botrytis cinerea* disease development in tomato leaves via jasmonate-dependent modulation of soluble sugars. Plant Cell Environ, doi:10.1111/pce.13870

Courbier S, Pierik R (2019) Canopy light quality modulates stress responses in plants. iScience **22:** 441–452

Elfving N, Davoine C, Benlloch R, Blomberg J, Brännström K, Müller D, Nilsson A, Ulfstedt M, Ronne H, Wingsle G, et al (2011) The *Arabidopsis thaliana* Med25 mediator subunit integrates environmental cues to control plant development. Proc Natl Acad Sci USA **108:** 8245–8250

Ji Y, Ouzounis T, Courbier S, Kaiser E, Nguyen PT, Schouten HJ, Visser RGF, Pierik R, Marcelis LFM, Heuvelink E (2019) Far-red radiation increases dry mass partitioning to fruits but reduces *Botrytis cinerea* resistance in tomato. Environ Exp Bot **168:** 103889

Mathur S, Vyas S, Kapoor S, Tyagi AK (2011) The Mediator complex in plants: Structure, phylogeny, and expression profiling of representative genes in a dicot (Arabidopsis) and a monocot (rice) during reproduction and abiotic stress. Plant Physiol **157:** 1609–1627

Sun W, Han H, Deng L, Sun C, Xu Y, Lin L, Ren P, Zhao J, Zhai Q, Li C (2020) Mediator subunit MED25 physically interacts with PHYTOCHROME INTERACTING FACTOR 4PIF4 to regulate shade-induced hypocotyl elongation in tomato. Plant Physiol **184:** 1549-1562

Yang Y, Ou B, Zhang J, Si W, Gu H, Qin G, Qu LJ (2014) The Arabidopsis Mediator subunit MED16 regulates iron homeostasis by associating with EIN3/EIL1 through subunit MED25. Plant J **77:** 838–851