

## WRKY transcription factors: links between phytohormones and plant processes

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WRKY transcription factors, which form integral parts of signaling webs that modulate many plant processes, are one of the largest families of transcriptional regulators in plants. More and more findings demonstrate that WRKY transcription factors function as repressors as well as activators, and play roles in both the repression and derepression of important plant processes. Furthermore, a single WRKY transcription factor might be involved in regulating several disparate processes. Recent investigation displayed that WRKY proteins function via interactions with a diverse protein partners, especially the important proteins related to the phytohormone signaling pathways, including JAZs, DELLAs, and IAAs. These illustrate that there might be a complex regulation networks between WRKY transcription factors and the phytohormone signaling pathways.

The first evidence about the function of WRKY proteins suggests that WRKY proteins play roles in regulating plant responses to pathogens. In particular, WRKY factors are positive or negative regulators, of the two partly interconnected branches of plant innate immunity, microbe- or pathogen-associated molecular pattern-triggered immunity (MTI or PTI) and effector-triggered immunity (ETI). Salicylic acid (SA), ethylene (ET), and jasmonic acid (JA) are the main signaling molecules involved in defense responses. The SA signaling pathway is mainly linked to resistance to biotrophic pathogens. The JA and ET signaling pathways mediate resistance mainly to necrotrophic pathogens. Thus,

there are complicated defense networks between phytohormones and WRKY transcription factors that are induced in response to different types of invading pathogens. Several groups have reported on the importance of AtWRKY70, which appears to affect the balance between signaling branches promoting SA-dependent and suppressing JA-dependent responses [1]. Mutations in both of *AtWRKY50* and *AtWRKY51* restored JA-inducible *PDF1.2* expression and basal resistance to *B. cinerea* in the *ssi2* plants, suggesting that AtWRKY50 and AtWRKY51 serve as positive regulators of SA-mediated signaling but negative regulators of JA-mediated signaling [2].

Besides the function of WRKY transcription factors in the plant immune response, several WRKY transcription factors function in the defense response against TMV-cg. For example, AtWRKY8 is involved in the defense response against TMV-cg through the direct regulation of *ABI4*, *ACS6*, and *ERF104* and mediates the crosstalk between ABA and ethylene signaling during the interaction between TMV-cg and *Arabidopsis* [3].

Crosstalk between salicylic acid (SA) and jasmonic acid (JA) signaling is well-studied in pathogen defense, but still at an initial stage during leaf senescence. AtWRKY53 and ESR mediate a negative crosstalk between pathogen resistance and senescence influenced by the JA/SA equilibrium [4]. Recently, our work suggests that AtWRKY57 functions as a regulatory node between auxin and JA signaling in the JA-induced senescence process [5]. Although WRKY transcription factor has been revealed to integrate

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various hormone and environment signals in plants, this study provides a mechanistic understanding of how the crosstalk between the JA and auxin signaling pathways in JA-induced leaf senescence is fine-tuned by AtWRKY57.

Abscisic acid (ABA) mediates plant responses to abiotic stresses, and hence is called a 'stress hormone'. Recent studies reveal that WRKY proteins function in the regulation of ABA signaling. For example, AtWRKY2 serves as a negative feedback regulator of ABA-mediated arrest of seed germination and post-germination growth [6]. *AtWRKY63* is induced by ABA treatment and its mutants are more sensitive to ABA in both seedling establishment and seedling growth and less tolerance to drought [7]. Activated expression of *AtWRKY57* confers the adaption of *Arabidopsis* to drought tolerance by promoting ABA levels and the expression of stress-responsive genes [8]. ABA receptor (ABAR) was identified as a chloroplast-localized protein and the cytosolic C terminus of ABAR interacts with a group of WRKY transcription factors (AD1A/WRKY40, AD1B/WRKY18, and AD1C/WRKY60) that function as negative regulators of ABA signaling in seed germination and post-germination growth [9,10].

Gibberellin (GA) is a key factor helping plants to flower under SD conditions. Our latest study confirms that DELLA proteins interact with two WRKY transcription factors which antagonistically play roles in controlling flowering time under SD conditions in *Arabidopsis*. Further analysis provides a mechanistic understanding of how a precise equilibrium of two WRKYs controlling flowering time under SD conditions (unpublished data). In addition, *AtWRKY27*, a direct target of RGA, was negatively regulated in an immediate/early manner by GA, supporting a potential role of this transcription factor in GA signaling [11].

Above all, these results indicate that WRKY transcription factors function as key components in SA, JA, ET, auxin, ABA and GA signaling pathways. These also give us a hint that WRKY transcription factors might be involved in other phytohormone signaling, such as brassinosteroids (BR), cytokinin (CK), and strigolactone (SL). Although genetic and molecular biology analyses have provided valuable insights into their regulatory roles in diverse plant stress and

hormone responses, it is far from the study how WRKY proteins link different phytohormone signaling pathways. Further investigation is required to grasp the complexity of the signaling networks between WRKY transcription factors and phytohormones.

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