

Guide to Plant Transcription Factors

Edited by
Aryadeep Roychoudhury



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School of Sciences, Indira Gandhi National Open University,
New Delhi, India



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Transcription factors in regulating the synthesis of secondary metabolites in plants

Aisha Kamal¹, Garvit Verma¹, Sanaya¹, Nida Sultan², Sazia Siddiqui², and Ayeesha Khatoon²

¹Department of Bioengineering, Integral University, Lucknow, Uttar Pradesh, India, ²Department of Biosciences, Integral University, Lucknow, Uttar Pradesh, India

Plants produce an extensive array of organic compounds that can be broadly categorized into two groups: primary and secondary metabolites (SMs). Primary metabolites are indispensable for growth and development of plants, serving fundamental roles that are consistent across most plant species. SMs, on the other hand, play critical roles in defense mechanisms, environmental interactions, and adaptive responses to biotic and abiotic stresses, despite not being directly involved in primary growth processes (Al-Khayri et al., 2023; Obata, 2019). These compounds are integral to various ecological functions, including imparting flavor and taste to fruits, providing coloration to flowers, and attracting pollinators and seed dispersers. Additionally, they protect plants from herbivores, pathogens, and environmental challenges (Vranová et al., 2012; Yang et al., 2012). SMs also hold significant value for humans, being utilized extensively in the production of natural fragrances and medicinal compounds (Duan et al., 2012; Garba Mikail et al., 2022; Wink, 2015). On the basis of their structure and biosynthesis, these metabolites are generally grouped into three major groups: terpenoids, phenolic compounds, and nitrogen-containing compounds. Terpenoids are composed of C₅ units and are synthesized via two pathways—the cytosolic mevalonate pathway and the plastidial methylerythritol phosphate pathway. Phenolic compounds encompass a variety of structures, including phenylpropanoids, flavonoids, coumarins, and stilbenes, and are primarily derived from the shikimate pathway, sometimes in conjunction with the mevalonate pathway. Nitrogen-containing compounds, such as alkaloids, amines, and nonprotein amino acids, are synthesized through diverse biosynthetic routes, typically originating from amino acids. Thus far, scientists have identified more than 10,000 flavonoids, 12,000 alkaloids, and 36,000 terpenoids, though these numbers represent only a portion of the immense chemical diversity present in nature (Cheng et al., 2007).

The biosynthesis, as well as accumulation of SMs in plants, is highly specific to tissues and developmental stages. For example, gossypol in cotton accumulates in pigment glands of shoots and roots, while artemisinin in *Artemisia annua* is found in glandular trichomes (Olsson et al., 2009). Similarly, terpenoid distribution in *Arabidopsis thaliana* is driven by tissue-specific terpene synthase expression (Tholl et al., 2005; Tholl and Lee, 2011). In tobacco, nicotine is synthesized in the roots and transported to leaf vacuoles via a MATE-type transporter (Hashimoto and Yamada, 2003; Shitan et al., 2009). SMs also respond to environmental stimuli, such as herbivore damage or microbial infection. Phytoalexins, like gossypol in cotton (Li et al., 2014; Xu et al., 2004) and zealexins in maize, are produced during defense responses, triggered by fungal elicitors (Huffaker et al., 2011). This blurs the distinction between primary metabolites and SMs, leading researchers to use the term “specialized metabolites” to highlight their critical roles in stress responses.

The production of SMs is highly regulated at the transcriptional level by specialized regulatory proteins called transcription factors (TFs), also referred to as trans-acting factors. TFs are DNA-binding proteins with sequence specificity, enabling them to recognize specific cis-regulatory elements within the target gene promoters. In this way, they regulate gene expression in response to diverse developmental and environmental cues (Ng et al., 2018). Researchers have identified and extensively studied more than 2000 TFs in *A. thaliana*, which clearly emphasizes the importance of transcriptional control (Wehner, 2011). Certain TFs crosstalk with other proteins to form complexes that modulate gene expression, even without directly binding to DNA. For instance, the production of flavonoids and terpenoid indole alkaloids (TIAs) is regulated by TFs that are influenced by internal cues, such as plant hormones, as well as external