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Review

Complexity of the transcriptional network controlling secondary wall biosynthesis

Ruiqin Zhong, Zheng-Hua Ye*

Department of Plant Biology, University of Georgia, Athens, GA 30602, USA

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ABSTRACT

Secondary walls in the form of wood and fibers are the most abundant biomass produced by vascular plants, and are important raw materials for many industrial uses. Understanding how secondary walls are constructed is of significance in basic plant biology and also has far-reaching implications in genetic engineering of plant biomass better suited for various end uses, such as biofuel production. Secondary walls are composed of three major biopolymers, i.e., cellulose, hemicelluloses and lignin, the biosynthesis of which requires the coordinated transcriptional regulation of all their biosynthesis genes. Genomic and molecular studies have identified a number of transcription factors, whose expression is associated with secondary wall biosynthesis. We comprehensively review how these secondary wall-associated transcription factors function together to turn on the secondary wall biosynthetic program, which leads to secondary wall deposition in vascular plants. The transcriptional network regulating secondary wall biosynthesis employs a multi-leveled feed-forward loop regulatory structure, in which the top-level secondary wall NAC (NAM, ATAF1/2 and CUC2) master switches activate the second-level MYB master switches and they together induce the expression of downstream transcription factors and secondary wall biosynthesis genes. Secondary wall NAC master switches and secondary wall MYB master switches bind to and activate the SNBE (secondary wall NAC binding element) and SMRE (secondary wall MYB-responsive element) sites, respectively, in their target gene promoters. Further investigation of what and how developmental signals trigger the transcriptional network to regulate secondary wall biosynthesis and how different secondary wall-associated transcription factors function cooperatively in activating secondary wall biosynthetic pathways will lead to a better understanding of the molecular mechanisms underlying the transcriptional control of secondary wall biosynthesis.

Contents

* Corresponding author. Tel.: +1 706 542 1832; fax: +1 706 542 1805.
E-mail address: zhye@plantbio.uga.edu (Z.-H. Ye).

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1. Introduction

Secondary walls are deposited between the plasma membrane and the primary walls in specialized cells after the cessation of cell expansion. The most abundant cell types with secondary wall deposition are tracheary elements (tracheids in gymnosperms and vessels in angiosperms) and fibers in xylem/wood. Secondary walls provide mechanical strength and hydrophobicity for tracheids and vessels, facilitating their function as conduits of water transport. At the same time, the mechanical strength and rigidity conferred by secondary wall-reinforced tracheary elements and fibers provide structural support to plant organs, which enables vascular plants to reach great heights and compete for light. In addition to tracheary elements and fibers in xylem, secondary walls are also found in other cell types, such as sclereids in some fruits, seed coats and leaves, endothecium in anthers, valve margin fibers in seed pods, trichomes, and extraxylary fibers [1]. The ability for plants to deposit secondary walls was evolved when the first vascular plants evolved during the Silurian period around 430 million years ago. Thus, it is conceivable that plants might have co-opted the same regulatory mechanisms that activate the secondary wall biosynthetic program in various cell types. Dissecting the molecular mechanisms controlling secondary wall deposition would facilitate ascertaining the molecular signals and signaling pathways that initiate the program of secondary wall deposition, how the biosynthesis genes for secondary wall components are coordinately activated, and whether vascular plants evolved common regulatory mechanisms controlling secondary wall deposition in different cell types. Considering that secondary walls in the form of wood and fibers are the most abundant plant biomass widely used in our daily life, uncovering the molecular mechanisms controlling secondary wall deposition will also have important implications in tree biotechnology.

Secondary walls are mainly composed of cellulose, hemicelluloses and lignin, the proportions of which may vary in different cell types and plant species. All the biosynthesis genes for cellulose, hemicelluloses and lignin need to be turned on as well as the genes responsible for the supply of nucleotide sugars, phenylpropanoid pathway precursors, methyl and acetyl donors and many other secondary wall biosynthetic pathway precursors need to be upregulated to make secondary walls. The secondary walls in tracheary elements are constructed in annular, helical, reticulated and pitted patterns. Thus, it is likely that specific genes responsible for the patterning of secondary walls are also induced. Genomic, coexpression and molecular analyses have provided ample evidence demonstrating the coordinated activation of genes involved in secondary wall biosynthesis during xylem and fiber differentiation [2,3]. In the past decade, comprehensive molecular and genetic studies have led to the breakthrough discovery that this coordinated activation of the secondary wall biosynthetic program is controlled by the secondary wall NAC (NAM, ATAF1/2 and CUC2)- and MYB-mediated transcriptional network (Fig. 1). This article will focus on recent findings on transcriptional regulation of secondary wall biosynthesis and attempt to postulate how different players in the transcriptional network function concertedly in the activation of secondary wall biosynthesis genes.

2. Secondary wall NAC master switches

2.1. Discovery of secondary wall NACs

Secondary wall NACs are master transcriptional switches controlling secondary wall deposition (Fig. 1; Table 1). They were first discovered during the study of xylem and fiber differentiation in the model plant *Arabidopsis thaliana*. Transcriptome profiling of Arabidopsis in vitro-induced xylem cells revealed the upregulation of 7 closely-related NAC domain genes, namely VASCULAR-RELATED NAC DOMAINs (VNDs), whose expression is specifically associated with vessel elements [3]. Overexpression of VND6 and VND7 in Arabidopsis induces ectopic deposition of vessel-like walls, and their dominant repression results in inhibition of metaxylem and protoxylem formation, respectively. This led to the conclusion that VNDs are transcriptional switches controlling protoxylem and metaxylem vessel formation. Similarly, VND1 to VND5 are specifically expressed in vessels and their overexpression results in ectopic deposition of secondary walls in normally parenchyma cells [4]. A role of NACs in regulating secondary wall thickening in anther endothecium was discovered by dominant repression of two Arabidopsis NAC genes, namely NAC SECONDARY WALL THICKENING PROMOTING FACTOR1 (NST1) and NST2, which results in an anther dehiscence defect [5]. NST1 and NST2 function redundantly in activating secondary wall biosynthesis in anther endothecium, and their overexpression induces the expression of secondary wall biosynthesis genes and concomitantly causes ectopic deposition of secondary walls in parenchymatous cells of various organs.

The most abundant secondary wall-forming cell types in Arabidopsis are fibers located in the xylem (xylary fibers) and outside the xylem (extraxylary fibers). Extraxylary fibers are present in various organs, such as the interfascicular regions (interfascicular fibers) of stems (Fig. 2A) [6] and the valve margin and the endocarp layer of siliques [7]. Studies of NAC genes that are preferentially expressed in developing stems led to the discovery of the role of SECONDARY WALL-ASSOCIATED NAC DOMAIN PROTEIN1 (SND1; also called NST3) in controlling secondary wall deposition in fibers [6,8,9]. The *SND1* gene is specifically expressed in xylary fibers and interfascicular fibers but not in vessels in stems, and dominant repression of SND1 results in a specific loss of secondary wall thickening in fibers but not in vessels. Simultaneous RNA interference inhibition or loss-of-function mutations of *SND1* and *NST1* lead to a loss of secondary wall thickening in xylary fibers and interfascicular fibers of stems (Fig. 2B) and a pendent stem phenotype, demonstrating that SND1 functions redundantly with NST1 in activating the secondary wall biosynthetic program in fibers [8,9]. Simultaneous mutations of *NST1* and *SND1* also cause a loss of secondary wall thickening in endocarp and valve margin fibers of siliques, resulting in resistance to pod shattering [7]. In contrast, the resistance to pod shattering seen in domesticated soybeans was proposed to be due to an increased expression of a secondary wall NAC ortholog, *SHAT1-5*, which results in a significant secondary wall thickening of fiber cap cells in the pod [10]. Overexpression of SND1 activates the biosynthesis genes for cellulose, xylan and lignin, similar to NST1, NST2, and VND1 to VND7. This leads to ectopic deposition of secondary walls in leaf parenchyma cells (Fig. 2E) and concomitantly curly leaves and reduced plant growth [6]. These findings provide