Sci. Bull.
DOI 10.1007/s11434-016-1061-7

www.scibull.com
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Review

Life & Medical Sciences

Transition of primary to secondary cell wall synthesis

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Received: 14 January 2016 / Revised: 15 March 2016 / Accepted: 24 March 2016

Abstract The construction of a secondary cell wall is an important and necessary developmental decision that supports cell function and plant stature. Unlike the primary cell walls, which are initiated during cell division and develop along with the expansion of the cells, secondary cell walls are constructed after the cells have stopped growing. Hence, the transition from primary to secondary wall synthesis marks an important and distinct metabolic investment by the plant. This transition requires a coordinated change of a plethora of cellular processes, including hormonal, transcriptional and post-transcriptional activities, metabolic flux re-distributions and enzymatic activities. In this review, we briefly summarize the hormonal and transcriptional control of the primary to secondary wall transition, and highlight important gaps in our understanding of the metabolic framework that support the transition. Several tools that may aid in future research efforts to better understand the changes in cell wall synthesis during the trans-differentiation are also discussed.

SPECIAL TOPIC: Plant Development and Reproduction.

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Keywords Secondary cell wall · Primary cell wall transition · Hormone · Transcriptional network · Metabolism

1 Introduction

A major developmental difference between animals and plants is that plant cell morphogenesis and pattern formation are accomplished largely through asymmetric cell divisions and cell enlargement [1, 2]. These events are underpinned by extensive synthesis and re-modelling of the plant cell wall, a glycan-enriched extracellular structure. In the course of cell division, a nascent cell wall is deposited usually perpendicular to the dividing axis of a mother cell following mitosis [1, 3]. The completion of this cross wall marks the end of cytokinesis and thus the formation of two daughter cells. Importantly, the position of the cross wall may be regarded as a first "decision point" of cell fate as it results in two daughter cells with different shape [1]. After cytokinesis, the two daughter cells typically expand to obtain their final form and function. Cell expansion requires rapid synthesis, localized deposition, and extensive re-modelling of cell wall material to allow anisotropic cell growth. One impressive example of cell form and function is the dramatic differentiation of the xylem tissue [4]. Xylem vessels consist of interconnected cells that can reach over a meter in length, which is approximately 10,000 times larger than the size of newborn cells [5]. However, the elongation of these cells, and their interconnectedness, are not sufficient to ensure solute transport through the vessels. To sustain this capacity, the maturing vessel cells produce a secondary and much thicker cell wall. Due to the developmental order, these two types of cell walls were historically termed as primary and secondary cell walls (PCWs and SCWs), respectively.

Published online: 09 May 2016

SCWs are specialized cell wall structures that support plant stature and cell functions [6, 7]. While SCWs are deposited around xylem vessels, they may also be found at anther endothecium, and around tracheids and fibres in woody tissues. The SCW structure represents a key advance for plants to adapt to terrestrial environments, and was a necessity for land plants to evolve. The PCWs of most plants consist of three major glycan structures; cellulose, hemicelluloses and pectins. The relative amounts of these three components can vary depending on species, on cell and tissue types, and on the developmental and environmental contexts [8]. For example, a typical dicot primary wall consists of cellulose, xyloglucans, a mixture of homo- and rhamnogalacturonans, and heavily glycosylated protein [8]. While the SCWs also contain large amounts of cellulose, they have a different set of hemicelluloses and reduced amounts of pectins [7]. Hence, the SCWs typically contain xylans and mannans, but also a significant amount of the polyphenolic structure lignin [7]. In contrast to PCWs, which are relatively elastic due to effective cell wall re-modelling, SCWs are characterised by their high rigidity. In both cell wall types, cellulose provides the main mechanical strength and steers plant cell morphology. For example, in the SCW, cellulose prevents vessels from collapsing due to the negative pressure inside of the cells [7]. Nevertheless, both xylan and lignin provide SCW strength as they aid in cross-linking cellulose microfibrils, and to an interconnected SCW framework. In addition, lignin confers water-repellent characteristics to the SCWs due to its inherent hydrophobicity and is thus crucial for the water transporting efficiency of the vessels [9]. Understanding how plants produce SCWs is therefore of significant biological interest.

Apart from the biological significance, SCWs also constitute the bulk of biomass a plant produces. This biomass is of major economic importance as it is used for a variety of industries, such as textile, lumber, feed and fuel [8, 10, 11]. While we understand a great deal of the enzymes involved in SCW synthesis, and how the corresponding genes are transcriptionally regulated, we know surprisingly little concerning the transition of the primary to SCW synthesis. That is, what aspects of the PCW synthesis are shut down when SCW synthesis is turned on, and what are the drivers for these processes? How is the metabolic framework changing during this transition? And, how can we begin to address these questions with the tools we currently have at hand? Here, we highlight aspects that are related to some of these questions, and also attempt to underline tools that may be used for future endeavours in this direction. With a few exceptions, this review mainly focuses on tracheary elements and xylem/interfascicular fibres due to length restrictions.

2 Hormonal control of the initial onset of secondary wall production

Almost every aspect of plant growth and development is under the control of various hormones [12–15]. It is therefore not surprising that also the transition from the primary to the SCW is controlled by their coordinated action [16, 17]. Given the pleiotropic effect of single hormones, and the added combinatorial effects of multiple ones, it is difficult to dissect aspects of SCW formation the hormones regulate. However, it is clear that auxin, cytokinin and brassinosteroids contribute to the onset of SCW in vessels of *Arabidopsis thaliana* [18–20]. Various combinations of these hormones have also been used to induce SCW synthesis in cell suspension cultures, e.g., in *Zinnia elegans* and *Arabidopsis* [21–24], supporting an active role of them in SCW production.

Several vessel-specific transcription factors (TFs) that drive SCW synthesis are under the control of auxin, cytokinin and brassinosteroids. These include the central NAC TFs, VASCULAR-RELATED NAC-DOMAIN (VND)6 and VND7 that are referred to as master TFs as expression of them in cells that do not normally undergo SCW synthesis triggers SCW production [7, 25]. Notably, robust activation of these TFs requires the presence of auxin, cytokinins and brassinosteroids, while each hormone alone has no major impact [25] (Fig. 1). Other VND TFs, namely *VND1–5* and the *NAC SECONDARY WALL THICKENING PROMOTING FACTOR (NST)3/SECONDARY WALL-ASSOCIATED NAC DOMAIN PROTEIN (SND)1*, may be induced by abscisic acid (ABA) [26]. While the ABA induction of SCW inducing TFs is interesting it is currently not clear whether this activation is part of an *in planta* activation process [26] (Fig. 1). Based on recent reports it appears that there may be at least an additional layer between the hormone tier and the master TFs. For example, the expression of *VND6* and *VND7* is regulated via a feedback-loop by *ASYMMETRIC LEAVES-LIKE* (*ASL)19* that in turn are controlled by the auxin induced *AUXIN RESPONSE FACTOR7* (*ARF7*) [27] (Fig. 1).

Both primary and secondary wall cellulose synthesis is regulated by cortical microtubules that guide the cellulose synthase complex (CSC) [10, 28–31]. This guidance is essential to maintain cell wall strength, cell morphology and function [32–35]. The microtubule array undergoes a dramatic re-organization during the transition between the two wall types. In elongating cells, the microtubule array is evenly dispersed across the cell cortex and is typically transversely oriented with regards to the cell's growth axis [36]. However, during SCW synthesis the microtubules form distinct and evenly distributed bands and/or lattices that mark synthesis of cellulose and other cell wall components [30, 37–39] (Fig. 1). Hormones, such as AUX, BR