Editorial: An Emerging View of Plant Cell Walls as an Apoplastic Intelligent System

Kazuhiko Nishitani¹,* and Taku Demura²

¹Laboratory of Plant Cell Wall Biology, Graduate School of Life Sciences, Tohoku University, 6-3 Aoba, Aramaki, Aoba-ku, Sendai, 890-8578 Japan
²Graduate School of Biological Sciences, Nara Institute of Science and Technology, 8916-5 Takayama-cho, Ikoma, Nara, 630-0192 Japan

*Corresponding author: E-mail, nishitan@m.tohoku.ac.jp; Fax, +81-22-795-6669.

An overview of plant cell walls from a conventional perspective

Cell walls of land plants (embryophytes) are multifunctional cellular structures characterized by a framework of cellulose microfibrils embedded in an amorphous matrix containing various structural and functional components. The wall consists of three layers: the middle lamella, the primary cell wall and the secondary cell wall (Popper 2008, Albersheim et al. 2010).

The middle lamella is derived from the cell plate, which is formed during cytokinesis, and remains deposited between the two layers of the primary cell wall, which are formed after the completion of cell division and continue to be remodeled during cell expansion. These two layers are ubiquitous in all tissues of land plants. They contain abundant hydrophilic matrix polysaccharides including pectins and xyloglucans, and are responsible for regulation of cell–cell adhesion, cell expansion and determination of cell shape (Yokoyama et al. 2014). In contrast, secondary cell walls are deposited internally to primary cell walls in specific cell types, such as vessels and fiber cells of vascular plants, once cell expansion ceases. The secondary wall is characterized by deposition of lignin and/or suberin, which render the wall chemically hydrophobic and impermeable to water, and is mechanically resistant to compression stress. These physical and chemical properties are evidently crucial for all vascular plants to remain upright, to take up and translocate water and nutrients, and to defend themselves from external biotic stress and abiotic attack (Oda and Fukuda 2012, Demura 2014, Malinovsky et al. 2014).

Three and a half centuries of cell wall research

It was the suberized secondary cell walls derived from cork oak (Quercus suber L.) that Robert Hooke first observed under his microscope in 1665, and which he termed ‘cells’ (Hooke 1665). His observation was followed by a more comprehensive microscopic dissection of cell walls in plant tissues and organs by Nehemiah Grew in the 17th century (Grew 1682). These pioneering studies described plant cell walls as static and rigid. Although by the 19th century the cell wall became recognized as dynamic and critical for plant growth and development, it was not until the 1970s that Peter Albersheim and colleagues proposed a molecular–structural model of the primary cell wall (Keegstra et al. 1973). The basis of this model was that certain cross-links between cellulose microfibrils serve as load-bearing linkages of the cell wall, and that their separation and reunion are required for the cell wall to loosen and expand during cell growth and differentiation. By the end of the last century, a set of key enzymes implicated in cell wall construction, modification and disassembly had been isolated and characterized, and their genes identified (reviewed by Cosgrove 2005). Since the beginning of this century, integrated-omics approaches based on genomic, transcriptomic and proteomic databases have facilitated the comprehensive molecular dissection of cell wall construction and function (Albenne et al. 2009, Usadel and Fernie 2013, Demura 2014, Mewalal et al. 2014). More recently, plant cell wall research has entered a new era thanks to the development of advanced imaging technologies, such as high-speed atomic force microscopy (HS-AFM) (Igarashi et al. 2011) and super resolution confocal live imaging microscope (SCLIM) (Fujimoto et al. 2015).

Emerging views of the plant cell wall

To date, the plant cell wall is progressively being considered not simply a structure or even an apparatus, but a system in charge of sensing, processing and responding to internal and external cellular signals (Somerville et al. 2004), thereby functioning as an intelligent frontier capable of processing information from the environment and co-ordinating whole-plant growth by optimizing individual cell growth and differentiation (Engelsdorf and Hamann 2014). Despite its importance and unique features, both the process of cell wall construction and the mechanisms of its intelligent function remain largely unknown, the elucidation of which could pave the way for understanding how individual cells of land plants can co-ordinate each other to control the whole body in the absence of a nervous system.

Three approaches to elucidate plant cell wall function

In this issue, we focus on three aspects pertaining to recent advances in research on the plant cell wall as an information processing system: (i) the molecular mechanisms for its construction; (ii) the molecular bases for its function; and (iii) the...
function of the cell wall as an interface between cells and their environment.

Molecular mechanisms for cell wall construction

Several thousand genes in plants are known to be involved in cell wall construction, and their expression is highly regulated during growth and differentiation of plant cells (Carpita et al. 2001). Only little is known about transcriptional regulation of genes related to construction of primary cell walls, e.g. the brassinosteroid-activated transcription factor BRI1-EMS-SUPPRESSOR 1 (BES1) might regulate the expression of genes encoding cellulose synthase catalytic subunits (CESAs) for primary cell walls. On the other hand, the transcriptional regulation of genes related to secondary cell wall construction has been very well illustrated since the identification of a number of key transcription factors, such as VASCULAR-RELATED NAC-DOMAIN6 (VND6), VND7, NAC SECONDARY WALL THICKENING PROMOTING FACTOR (NST1), SECONDARY WALL-ASSOCIATED NAC DOMAIN PROTEIN (SND1), MYB46 (AT5G12870) and MYB83 (AT3G08500) (Demura and Ye 2010, Zhong et al. 2010, Demura 2014). In this issue, Zhong and Ye (2015) provide an update on the latest research regarding transcriptional regulation, where they comprehensively review genes involved in the biosynthesis of secondary cell wall components including cellulose, hemicellulose and lignin. Such information is valuable for the genetic engineering of secondary cell walls and, in this issue, Sakamoto and Mitsuda (2015) clearly demonstrate that transmuted/artificial secondary cell walls with different characteristics can be synthesized in Arabidopsis nst1 snd1/nst3 double mutants, which lack secondary cell walls in fiber cells, by the expression of chimeric proteins comprising certain key transcription factors. While it has been demonstrated that NAC transcription factors including VND1–VND7, NST1 and SND1 are the main master switches in this transcriptional network (Zhong and Ye 2015), knowledge about the upstream elements regulating the expression of such master switches is lacking. In this issue, Endo et al. (2015) have now found that 14 transcription factors including VND1–VND7, GATA12 and ANA075 are putative positive regulators of one of these master switches, VND7.

The proper construction of plant cell walls is strongly dependent on the membrane trafficking system for a variety of cell wall components (Sanchez-Rodriguez and Persson 2014). In this issue, Fujimoto et al. (2015) reveal that phosphoinositides potentially contribute to the localization and transport of one of the primary cell wall CESAs, CESA3, and Oda et al. (2015) show that novel coiled-coil proteins VETH1 and VETH2, which interact with the conserved oligomeric Golgi complex 2 (COG2) protein, recruit an exocyst subunit EXO70A1 to cortical microtubules to ensure correct deposition of secondary cell walls. During cell wall construction, various complex and branched polysaccharides including pectins and hemicelluloses are synthesized in the Golgi apparatus by Golgi membrane-localized glycosyltransferases. In this issue, Chou et al. (2015) propose that several glycosyltransferases involved in xyloglucan biosynthesis, including CSLC4, MUR3, XLT2, XXT2, XXT5 and FUT1, form functional multiprotein complexes in the Golgi.

Molecular bases for cell wall function

As mentioned earlier, the cell wall model proposed by Albersheim’s group in the 1970s envisaged pectin and xyloglucans as key components responsible for tethering cellulose microfibrils, with xyloglucan coating most of the available cellulose surface (Keegstra et al. 1973). Since then, this model has been challenged and revised repeatedly (Carpita and Gibeau 1993, Nishitani 1997, Cosgrove 2014). In this issue, Park and Cosgrove (2015) put forward a revised structural model for the cellulose-xyloglucan complex, in which they propose that cellulose microfibrils are directly cross-linked via xyloglucan at limited sites that function as load-bearing bridges between cellulose microfibrils, termed ‘biochemical hotspots’.

Pectin, on the other hand, seems to be more complicated and versatile than xyloglucan in terms of both structure and function (Atmodjo et al. 2013). It consists of several complex domains including rhamnogalacturonan-I, rhamnogalacturonan-II and homogalacturonan. Although the biosynthesis steps of these components are slowly being revealed, their overall structures are still controversial and their biological roles remain largely unknown, especially in cereal plants. To address this question, Sumiyoshi et al. (2015) targeted genes encoding UDP-arabinopyranose mutase, which is responsible for synthesis of the arabinan side chain on rhamnogalacturonan-I. In this issue, they demonstrate the critical role of the arabinan side chain for development of reproductive tissues in rice.

The cell wall in rice is unique in that it contains abundant (1:3/1:4)-β-D-glucan (or mixed linkage β-D-glucan; MLG) and silicon. Although the individual roles of MLG and silicon in growth and defense responses are known and their possible association has been suggested (Fry et al. 2008), the molecular bases for their interactions are not well known. To gain insight into the functional relationship between both compounds, Kido et al. (2015) have investigated the function and distribution of silicon in the cell wall of transgenic rice in which the MLG content is reduced. The authors propose that MLG affects the function and distribution profile of silicon in rice tissues without altering the uptake of silicon by the plant.

The cell wall as an intelligent interface between cells and their environment

A trade-off between growth promotion and resistance to environmental stress is a crucial strategy for the survival of all organisms. In land plants, in which the cell wall plays a central role in both growth regulation and defense response, such a trade-off is often also mediated via the additional ‘intelligent function’ of the cell wall. In this issue, Hofte (2015) reviews the literature pertaining to an emerging view of how plant cells can sense disruption of its cell wall and maintain its integrity via an interplay between a positive (yin) and a negative (yang) signaling module. In addition, Hamann (2015) reviews the currently available literature on the cell wall integrity maintenance mechanism of yeast and plants, paying special attention to the role of turgor pressure in the latter.
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