Short Reviewer

Current Thought of Plant Cell Wall: Structure, Biosynthesis, and Future Application

Opini Terkini Tentang Dinding Sel Tanaman: Struktur, Biosintesis, dan Aplikasinya

Dina Yulia dan Bintarti Yusriana

Department of Biology Education, Faculty of Teaching and Education, University of Muhammadiyah Purwokerto, Jalan Raya Dukuh Waluh Purwokerto, 53182, Indonesia. E-mail:dinayulia1101@yahoo.com

Introduction

Plant cell walls are unique, complex, diverse and dynamic structures that change throughout the process of cell division, growth and differentiation. Plant cell walls are not only a single key determinant of overall plant form, but they also play an important role in sustaining human societies. Evidence of how cell walls are crucial for plant structure is that without cell walls, plants would be elastic piles of protoplasm, more like slime moulds than stately trees. Unlike animals, in which specialized skeletal system provides physical support, the strength, flexibility, texture and overall shape of higher plants depend on the cumulative properties of walls. Moreover, plants are composed of approximately 35-40 cell types that are distinguished from each other by the chemistry and organization of their walls. In human societies, cell walls directly affect the quality of most plant-based products, including paper and pulping, textile, food quality and texture, dietary fibre, malting and brewing and bioethanol production (Cosgrove, 2005; Farrokhi *et al*., 2006).

The chemical structure of most wall components has been intensively studied and defined in detail, however, the enzymes responsible for cell wall biosynthesis and also its restructure remain poorly understood. However, currently, there has been real progress towards understanding the cell wall biosynthesis, using various emerging approaches, such as genetic and biochemical approaches (Farrokhi *et al*., 2006).

This review will elaborate on recent advances in our knowledge of the structure cell walls of flowering plants, particularly the structure of primary cell walls. Moreover, this review will also explain the current knowledge towards understanding primary wall biosynthesis and also the future application of cell wall study in biotechnology.

Structure of primary cell walls of flowering plant

Primary walls are formed initially in the cell plate during cell division and rapidly increase in the surface area during cell expansion. The primary walls of neighbouring cells are separated by interface called middle lamella (Carpita and McCann, 2000). The figure of primary walls and middle lamella observed by transmission electron microscopy is shown in Figure 1.

Composition of the primary wall has been studied using a variety of techniques. Classically, cell wall fractionation by precipitation using solvents that vary in their ionic strength, pH and capacity to bind divalent cation, was done by chromatography or by electrophoresis (Morrison, 1996). Then, the polysaccharide composition of each fraction could be determined quantitatively by methylation or nuclear magnetic resonance (Carpita and Gibeaut, 1993). Recently, the use of probes such as antibodies offers the opportunity to analyse wall composition at the single cell level (Knox, 1997; Willats *et al*., 2000). Although antibodies are powerful tools, their availability is confined to a small number of wall epitopes and is not representative of the structural complexity of the wall. An alternative technology, chemical imaging, is becoming available, which combines spatial information with chemical information deduced from relative infrared absorbance (Chen *et al*., 1998; Mc Cann *et al*., 2001; Mouille *et al*., 2003).

In general, composition of primary walls of flowering plants are described in Table 1 and illustrated in Figure 2. Based on their composition, there are two distinct types of architecture of primary walls of flowering plants, the Type I and Type II walls as. Type I walls belong to most of dicots and the non-commelinoid monocots, whereas Type II walls are found in commelinoid monocots (Carpita and McCann, 2000).

The main component present in both types of walls is cellulose microfbrils. This component accounts for 15-30% of the dry mass of primary walls and is embedded in different classes of non-cellulosic components called hemicellulose (Carpita and McCann, 2000; Cosgrove, 2005). Apart from cellulose, Type I walls are predominantly composed of hemicellulose xyloglucan (XG) and pectin and also significant amount of wall proteins. Instead of XG, Type II walls have glucuronoarabinoxylan (GAX) and pectins as the main hemicellulose and also marked level of aromatic substances. A unique constituent o Type II walls is mixed-linkage glucan (MLG) which is only synthesized when the cells ar undergoing elongation (Carpita and McCann 2000).

Enzyme involved and subcellula location of cell wall biosynthesis

As mentioned previously, unlike th structure of primary wall that has been deeply studied, its biosynthesis is poorly defined. Prio to the development of extensive sequenc databases, advance molecular biology an bioinformatics techniques, the finding of gene involved in cell wall biosynthesis were don through biochemical approach. Biochemica technique has been proved difficult, whic might be because the enzymes involved in cel wall biosynthesis are large in size an membrane-bound and frequently loss activity during extraction (Farrokhi *et al*., 2006 Scheible *et al*., 2003).

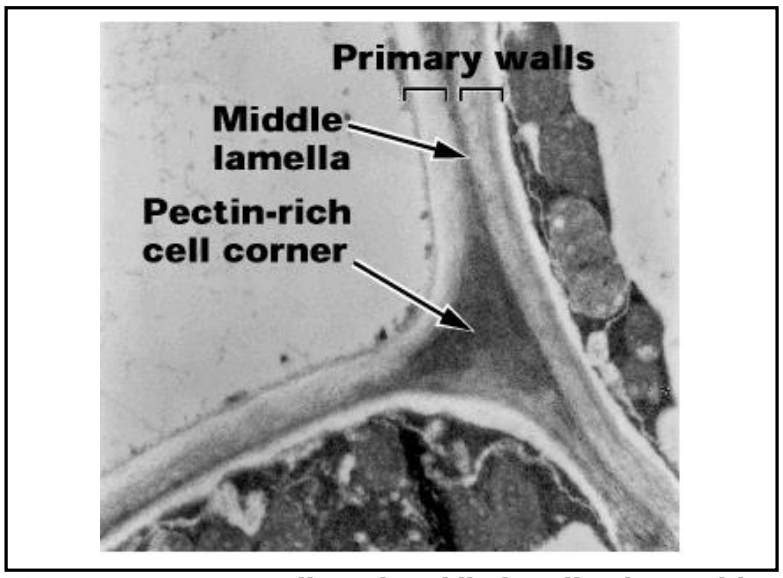

Figure 1. Primary walls and middle lamella observed by transmission electron microscopy.

Table 1. Composition of type I and type II primary plant cell walls

Cell wall component	Type I walls (dicots, gymnosperms and non-commelinoid monocots)	Type II walls (commelinoid monocots)
Fibrillar phase	Cellulose microfibrils	Cellulose microfibrils
Matrix-phase (non-cellulosic polysaccharides)	Xyloglucans (XGs)	Glucuronoarabinoxylans (GAXs)
	Arabinoxylan (low)	Mixed-linkage glucan (MLG)
	Pectins	Pectins (low)
Phenolic acids	Ferulic acid only in Caryophyllales	Ferulic acid (and small amounts of other phenolic acids)
Proteins	HRGPs, PRPs, AGPs, extensins and GRPs	HRGPs (less than type I) AGPs

HRGPs, hydroxyproline-rich glycoproteins; PRPs, proline-rich proteins; AGPs, arabinogalactan proteins; GRPs, glycine-rich proteins (Carpita and McCann, 2000).

Progress, however, has been made recently using various current genetic approaches, the forward and reverse genetic, in addition to classical biochemical approach (Burton *et al*., 2004; Colombani *et al*., 2004; Dhugga *et al*., 2003; Liepman *et al*., 2005). Moreover, the availability of increasing amount of genome sequence, precise genetic and physical maps also contribute to the success of identifying new cell wall related genes (Scheible *et al*., 2003). In this section, progresses in understanding cellulose biosynthesis and synthesis of backbone of non-cellulosic component, heteromannan, will be briefly reviewed.

Plant cellulose synthase (CESA) gene has been proved to be involved in cellulose biosynthesis, either in primary or secondary cell wall. CESA family contains more than one gene, which are expressed in different tissues and cell types (Burton *et al*., 2004; Taylor *et al*., 2003). Cellulose is thought to be synthesized by cellulose synthase complex called rosettes and consists of six CESA proteins and other proteins, such as korrigan (KOR) and sucrose synthase (SuSy, Read & Bacic, 2002). This rosette structure was identified in the plasma membrane (PM, Itoh *et al*., 2004). The six CESA proteins that compose rosette are known to be encoded by three CESA genes (Cosgrove, 2005).

The CESA family belongs to a larger superfamily of genes called cellulose synthase-like (CSL), which include eight other gene families, named CSLA, CSLB and so on, up to CSLH (Richmond and Sommerville, 2000). While CESA proteins are involved in cellulose biosynthesis, these CSL proteins are considered to be good candidates for the synthesis of backbone of hemicellulose that are localized in Golgi apparatus (Cosgrove, 2005).

Understanding the functions of CSL genes has never been easy for several reasons, including low abundance of mRNA transcript of CSL genes that make it hard to correlate the mRNA abundance and the level of particular cell wall components (Farrokhi *et al*., 2006). However, recent studies indicate that CSLA genes encode β-mannan synthases, the enzyme required for the formation of the mannan backbone of certain hemicellulose (Dhugga *et al*., 2003; Liepmann *et al*., 2005).

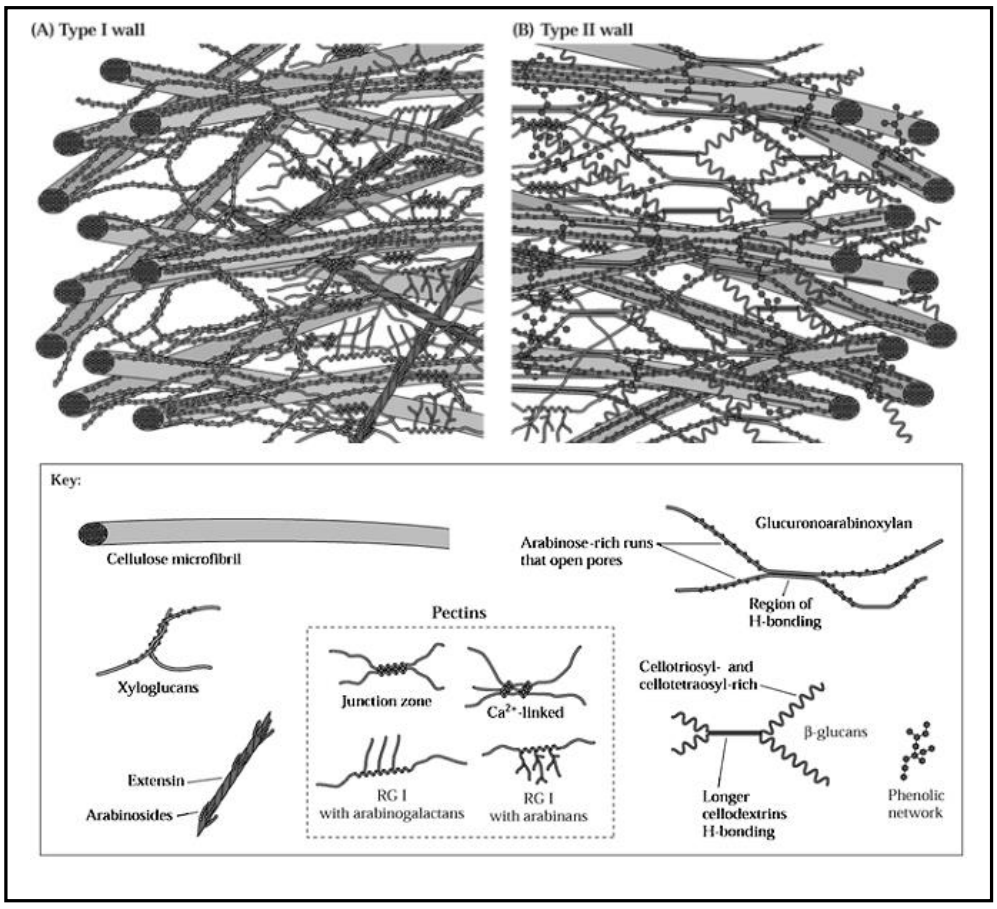

Figure 2. Models of type I and type II cell walls. The cell wall components, as shown in the key, form structurally independent but interacting networks (Carpita and McCann, 2000)

Summarizing existing knowledge of cell wall biosynthesis enables us to draw conclusions about where the cell walls might be made in the cells. The possible location of enzymes involved in cell wall biosynthesis in a highly idealized plant cell is illustrated in Figure 3. XG, GAX and pectin are synthesized Golgi apparatus (GA) and transported to the cell surface in secretory vesicles. After fusing with the PM, the contents of these vesicles can be incorporated into the wall. While MLG are also synthesised in the GA, cellulose is made directly at PM (Cosgrove, 2005).

Future applications of cell wall study in biotechnology

As plant cell walls are principal textural components of fruits, vegetables and cereals, the plant cell walls play important role in a human society. Therefore, understanding cell wall biosynthesis is crucial for determining genes and enzymes involved in thei biosynthesis. This, in turn, enables us t modify the quality and quantity of wal components for the need of people throug genetic manipulation.

Here are some examples of th application of cell wall study in improvin food and fibres quality via biotechnology Firstly, cereal MLG (mixed-linkage glucan) i useful in bread- making, where it could be use as flour supplement to increase wate absorption of dough. In any case, manipulatio of expression of genes involved in MLG synthesis could significantly enhance th bread-making properties and nutritional valu of wheat (Farrokhi *et al*., 2006). Secondly changes in pectin components are regarded a the obvious components of fruit cell walls tha impact wall structure during ripening, whic involve cell softening and separation (Chappl and Carpita, 1998).

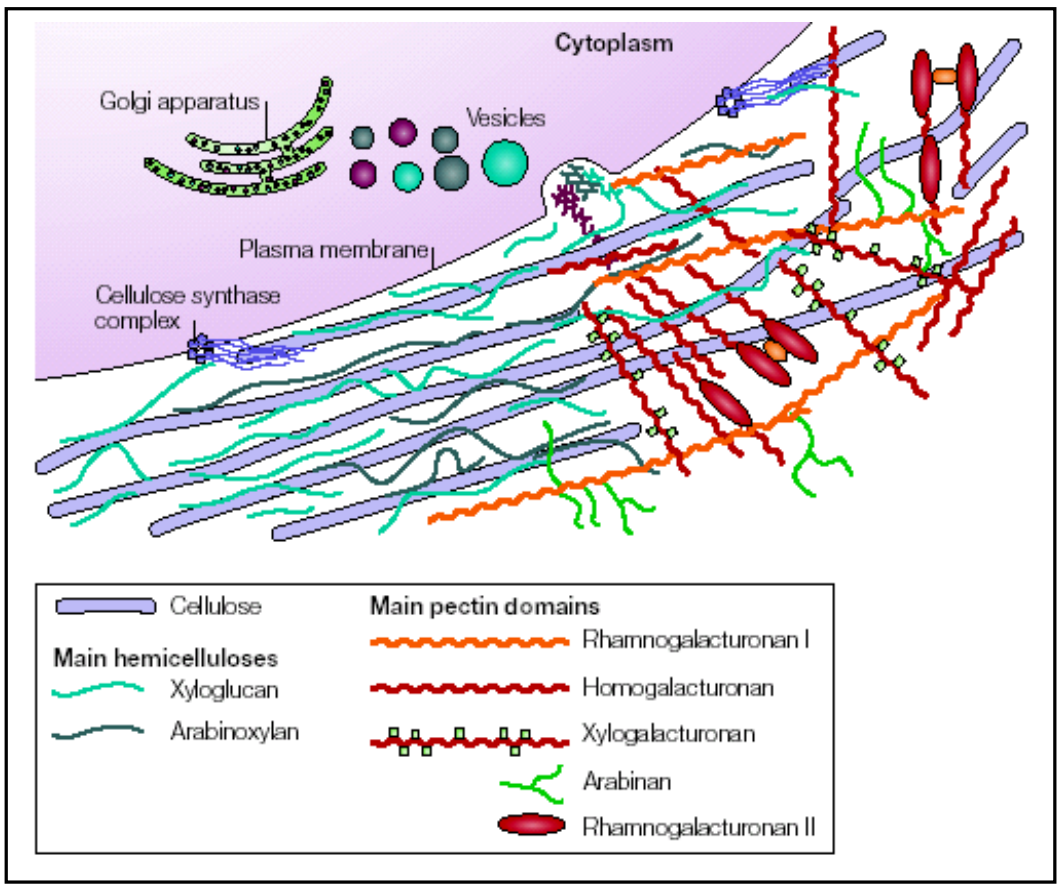

Figure 3. Summary of the structure of flowering plant cell wall and subcellular locations where the cell wall components are possibly synthesized (Cosgrove, 2005)

Finding gene and enzyme responsible for pectin biosynthesis, such as pectin methylesterase (PME) and polygalacturonase (Pgase), might enable us to prolong desirable texture during ripening, which is the key to prolonging the shelf-life of the fruit (Chappel and Carpita, 1998). Moreover, crystalline cellulose is the main components of flax and cotton, the principal fibre crops in the world. Flax has greater crystalline nature of cellulose than cotton, which makes flax fibres stiffer and stronger than cotton (Chappel and Carpita, 1998). Understanding how glucan chains are packed into para-crystalline cellulose is important to enable us to improve properties of plant fibres important for textile industries.

Conclusion

It cannot be denied that plant cell walls are not only crucial for plant form, but also important for mankind. While the cell wall structure and composition have been studied and defined years ago, cell wall biosynthesis is still in progress. However, identification of some genes involved in cellulose and non-cellulosic components using various current techniques is a breakthrough. By understanding the genes and enzymes involved in cell wall biosynthesis, manipulation of quantity and composition of cell wall can possibly be a complished, to improve the quality and quantity of cell wall-based products.

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