Diversity of Plant Cell Wall

Subjects: Plant Sciences

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The plant cell wall is a complex and dynamic structure composed of many different molecules, which play multiple roles in all aspects of plant life. Today, a new frontier of biotechnology has opened up, which has provided new insights into the structural and functional diversity of cell walls, and is thus serving to re-emphasize the significance of cell wall divergence in the evolutionary history of plant species. The recent availability of plant genome datasets can be used to increase the knowledge regarding the diversity of cell walls among different plant species. Since the growth and development of all types of plant cells are functions of cell wall dynamics, further understanding of the functional diversity of cell walls in relation to diverse biological events will have a significant effect on the broad field of plant sciences.

Keywords: plant cell wall ; dynamic structure, polysaccharide ; cell wall enzyme ; gene family ; genome ; evolution

1. Introduction

A key distinguishing feature of plants is that individual cells are surrounded by a cell wall, which confers mechanical strength that contributes to the maintenance of cell shape and provides sufficient flexibility to facilitate cell expansion [1]. Consequently, the cell wall plays crucial roles in multiple aspects of plant development, growth, and differentiation. The basic framework of the primary cell wall is mainly composed of cellulose microfibrils and hemicellulosic polysaccharides, such as xyloglucan, and embedded in a complex matrix of pectins [2][3][4]. It has previously been proposed that xyloglucan interacts with two or more cellulose microfibrils to form a tether between cellulose microfibrils [5][6][7]. However, recent experimental investigations, along with the development of new technologies, have led to the proposal of a new model, in which the xyloglucan is closely intertwined with cellulose microfibrils at limited sites and mechanically contributes to the network structure [8][9][10]. The entire cell wall is a more complex structure, comprising a diverse range of polysaccharides, highly glycosylated proteins, and phenolic compounds, and its composition is differentially controlled according to cell type and in relation to different stages of growth and development [11][12]. Additionally, some types of cells, such as xylem cells, develop secondary cell walls, which are characterized by an abundance cellulose and xylan, and further reinforced with lignin [13][14][15][16][17].

Recent advances in technology have provided snapshots of plant cell walls from multiple viewpoints. Atomic force microscopy (AFM) has made it possible to directly image the wall architecture at high resolutions, particularly the cellulose microfibrils, and to visualize the alteration in microfibril connectivity involved in wall loosening [18][19][20]. Important insights have also been gained regarding the precise polysaccharide conformation and interactions that underlie cell wall assembly, based on solid-state nuclear magnetic resonance (NMR) studies [21][22]. Additionally, the application of monoclonal antibodies (mAbs) raised against wall polysaccharides has been developed as a powerful tool for examining the precise localization of the polysaccharides and wall microstructures via a wide range of experimental techniques, including immunohistochemical analysis and carbohydrate microarray binding profiles [23][24][25]. Several mAbs can also be used to characterize the different status of wall polysaccharides. For example, LM19 and LM20 are well known to have differing specificities in relation to the methyl-esterification of homogalacturonan (HG), which has roles relating to cell growth and development [26]. Furthermore, the combination of other new technologies has given more powerful tools for analyzing the wall microstructures. The combination of xyloglucan-directed mAbs and high-resolution imaging by field emission scanning electron microscopy has provided insights into xyloglucan conformation and its interactions with cellulose, which are essential features contributing to the basic framework of the plant cell wall [27].

Real-time imaging of cell wall polysaccharides based on chemical staining is also one of the most powerful techniques for monitoring the dynamics of wall microstructures. For example, staining with Pontamine Fast Scarlet 4B, a dye that fluoresces in the presence of cellulose, facilitates the imaging of cellulose dynamics, and has revealed that cellulose bundles rotate in a transverse to longitudinal direction during cell expansion [28][29]. Additionally, we recently developed an imaging technique that can be used to quantitatively evaluate the network of cellulose microfibrils [30][31]. By combining this quantitative imaging technique with a high-yield cell-wall regeneration procedure, we successfully quantified the total length, mean intensity, skewness of intensity distribution, and coefficient of variation of regenerating cellulose microfibrils

in protoplasts derived from *Arabidopsis* leaf mesophyll cells [31]. Furthermore, by adopting a quantitative imaging approach using a xyloglucan-deficient *xxt1/xxt2* mutant of *Arabidopsis thaliana,* we showed that the absence of xyloglucans has almost no influence on either the structure of the cellulose microfibril network or protoplast stability in regenerating protoplasts, thereby indicating that xyloglucan does not directly contribute to the initial assembly of the cellulose network or the mechanical strength of the cell wall of protoplasts [32]. Given that xyloglucan plays an important role in wall loosening, these observations also indicate that the roles of xyloglucan in the initial assembly of cell walls are distinct from those in the cell wall of expanding cells.

2. Cell Wall Diversity and Plant Evolution

In addition to facilitating high-resolution imaging of the cell wall structure, advanced technologies have also revealed that there exists a wide range of structurally and functionally distinct cell walls among different plant species, as well as between discrete developmental stages and cell types within a single plant species.

Unicellular green algae in the division Chlorophyta have a relatively fragile cell wall, or lack a structured cell wall. However, some unicellular green algal species, such as *C. reinhardtii*, have a glycoprotein-layer structure similar in composition to those of land plant species [33]. Additionally, quite a few members of cell wall gene families have been found in unicellular green algae genome sequences [34][35]. For example, the *C. subellipsoidea* C-169 genome reveals cellulose synthase-like domains, although not orthologous to the cellulose synthases and hemicellulose synthases of land plant species [36]. Furthermore, Charophyte green algae have a highly similar cell wall structure to that of land plants, and share many cell wall components with land plants. This is also supported by the presence of genes involved in biosynthesis of the major polysaccharides found in land plants [37]. On the other hand, recent studies have also provided insight into marked differences in cell wall structure and composition between green algae and land plants. For example, although the macromolecular pectic network plays multiple roles in the dynamic structure and ionic environment of the plant cell wall, some pectic network domains, such as arabinans and rhamnogalacturonan I (RG-I), have been found to be less abundant in green algae [38][39][40]. Additionally, the cross-linking of rhamnogalacturonan II (RG-II) via a borate diester, which is essential for the structural organization of the cell wall in angiosperms, has not been found in either bryophytes or charophytes [41]. In contrast, homogalacturonan (HG), which forms complexes with Ca^{2+}, has been characterized as a major component of both land plants and Zygnematophyceaen green algae, the closest relatives of land plants [42]. This diversity in cell wall characteristics may be closely related to certain prerequisites for terrestrial survival, or an adaption to terrestrial habitats that has developed during the evolution of land plants.

Cell wall diversity is also conspicuous with respect to land plant linkages. In many species of terrestrial plants, the primary cell wall is composed mainly of a cellulose–xyloglucan framework embedded in a macromolecular pectic network. However, in commelinid monocotyledons, which include cereals such as rice (*Oryza sativa*), the primary cell walls contain only small amounts of xyloglucan, and instead contain glucuronoarabinoxylan and β1,3:β1,4 mixed glucans as the predominant glycans that interact with the cellulose microfibrils [43][44][45]. This type of cell wall also contains less pectin and higher amounts of hydroxycinnamates, such as ferulate and *p*-coumarate, which form extensive interconnecting networks [46][47]. For example, the residues of ferulic acid are esterified to the arabinosyl side chains of arabinoxylans, and oxidative coupling of the ferulate side chains leads to the formation of cross-links between the arabinoxylans, thereby generating arabinoxylan networks [48][49]. Although the precise roles of polysaccharides and their cross-linkages remain to be elucidated, commelinid monocotyledons may have developed unique cell wall network structures to adapt to the environmental conditions in their respective habitats [50].

The diversity of the cell wall structure and composition provides compelling evidence as to the significant role that this cellular component has played in the evolutionary history of plant species [51][52]. However, our current knowledge of the contribution of the cell wall to plant evolution is still relatively limited. The challenge now is to gain a more comprehensive understanding of the functional diversity of the cell wall in relation to diverse biological events in different species.

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