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The role of pectin in plant morphogenesis

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ABSTRACT

The presence of a polysaccharidic cell wall distinguishes plant cells from animal cells and is responsible for fundamental mechanistic differences in organ development between the two kingdoms. Due to the presence of this wall, plant cells are unable to crawl and contract. On the other hand, plant cell size can increase by several orders of magnitude and cell shape can change from a simple polyhedron or cube to extremely intricate. This expansive cellular growth is regulated by the interaction between the cell wall and the intracellular turgor pressure. One of the principal cell wall components involved in temporal and spatial regulation of the growth process is pectin. Through biochemical changes to pectin composition and biochemical configuration, the properties of this material can be altered to trigger specific developmental processes. Here, the roles of pectin in three systems displaying rapid growth – the elongation zone of the root, the tip region of the pollen tube, and organ primordia formation at the shoot apical meristem – are reviewed.

1. Introduction

Plant development requires cell division, growth, and differentiation. Various combinations of these three processes determine not only the size and shape of the individual cell, but also of the whole plant. Plant cells differ mechanically from most animal cells by the presence of a cell wall, or extracellular matrix, composed largely of polysaccharides that envelop the protoplast with a more or less stiff shell. The presence of this wall prevents plant cells from motion such as crawling and contraction, characteristics that are common to many animal cells. The wall connects neighboring cells and hence essentially locks in place the individual cells composing a mature tissue. However, contrary to what the name may suggest, the cell wall is a complex and dynamic matrix that is constantly assembled, disassembled and deformed. This is particularly true for the primary cell wall that surrounds plant cells that are growing and differentiating. Prior to reaching maturity, plant cells typically undergo a significant increase in size and a change in shape. These changes are crucial for plant development. The cellular volume of a plant cell can increase by several orders of magnitude from typically 10^2 μm^3 (volume of a meristematic cell) to up to 10^7 μm^3 (*e.g.* xylem vessel). Shape changes can entail the modification of a simple cube or polyhedron shaped cell into the intricate form of a star or a complex multifacetted structure. This increase in cellular volume and geometrical complexity are accompanied by an increase in cellular surface, which in plant cells requires the addition of building material in the form of cell wall polymers and membrane. As new cell wall material is incorporated, the existing material is deformed and stretched mechanically. The turgor pressure supplies the driving force for this deformation. However, the dynamic growth process and resulting final cell size and cellular shape are controlled by the mechanical properties of the cell wall (Geitmann, 2010; Geitmann and Ortega, 2009). These mechanical properties are in turn regulated by the biochemical composition of the wall material and it is particularly intriguing to analyze the common principles that allow cellular growth processes to occur despite considerable differences in molecular composition between the cell walls of different plant families (Ovodov, 2009; Popper, 2008).

In general, the cell wall in higher plants is composed primarily of three families of polysaccharides – cellulose, hemi-cellulose and pectin but it is also comprised of proteins, ions and water. The properties and functions of these molecules and their interactions are complex and determine the development of cells and organs as well as the mechanical behavior of plant tissues (Cosgrove, 2005).

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In terms of the mechanical properties of the cell wall, much of the focus has been on the structural network consisting of cellulose microfibrils and xyloglucan links, which is known to confer tensile resistance and mechanical anisotropy to the wall (Baskin, 2005; Geitmann and Ortega, 2009; Wasteneys and Fujita, 2006). This structural network is embedded into a matrix, a principal component of which are pectins, which form up to 35% of the primary walls in dicotyledons and nongrass monocotyledons (Mohnen, 2008). Pectins are among the most complex wall components. Depending on their molecular composition and chemical configuration pectin matrices can change their own mechanical behavior, but their interaction also influences the mechanical behavior of the cellulose–xyloglucan network (Chanliaud and Gidley, 1999). The question of how pectin influences plant development has therefore been at the focus of recent research activities that have successfully combined cell biological approaches with micro-mechanical testing and mathematical modeling.

Pectin molecules are synthesized in the Golgi and inserted into the extracellular matrix by vesicle-mediated exocytosis. They are rich in galacturonic acid (GalA) that have the ability to form a gel-like configuration. They are classified in three families: (a) Homogalacturonan (HG), is made up of linear chains of galacturonic acid residues. (b) Rhamnogalacturonan-I (RG-I), consisting of alternating residues of galacturonic acid and rhamnose, has additional branched side chains containing other pectin domains. (c) Rhamnogalacturonan-II (RGII), has a complex pectin domain that contains 11 different sugar residues and forms dimers through borate esters (Fig. 1) (Caffall and Mohnen, 2009; Jarvis, 1984). The carboxyl groups of the HG chains vary in their degree of methyl esterification which influences their ability to form a gel upon addition of gelling agents such as Ca^{2+} (Proseus and Boyer, 2007). HG with low degree of methyl esterification can be crosslinked by these ions, resulting in a matrix with increased rigidity. The enzyme pectin methyl esterase (PME), therefore, plays an important role in controlling the rheology of the pectin matrix (Wolf and Greiner, in press; Wolf et al., 2009). The mechanical properties of a pectin matrix can also be modulated by altering the molecular structure of the polymers directly, such as by the action of polygalacturonases or pectate lyases (Harholt et al., 2010; Willats et al., 2001). The presence of Ca^{2+} is not easy to visualize in the cell wall, but a rough idea of the degree of pectin methyl-esterification is readily obtained using antibodies specific for the different configurations of pectin polymers (Clausen et al., 2003; Pattathil et al., 2010). Although mechanical properties cannot be deduced with this technique, labeling pectin has helped to identify the roles of the different configurations of the polymer for developmental processes. Complementary information has been produced by analyzing the effects of mutation-induced changes in the activity of enzymes involved in pectin biosynthesis and molecular modification. However, the large number of isoforms for pectin modifying enzymes (*e.g.* 66 ORFs for PMEs in *Arabidopsis*) poses a significant challenge for these approaches because of possible redundancy and because of the resilience of the regulatory system that ensures functionality of cell wall structure even under stress or in the absence of one or several of its components. For detailed information we refer to excellent reviews on the topic (Harholt et al., 2010; Willats et al., 2001; Wolf and Greiner, in press; Wolf et al., 2009). These studies have illustrated the multitude of roles pectin has for plant development ranging from that of a cement connecting the walls of neighboring plant cells in a region known as the middle lamella, to the regulation of morphogenetic processes that require the modulation of the mechanical properties of the wall of the individual cell. In the present review the importance of pectin for plant development will be illustrated using three well investigated developmental processes involving the growth of an individual cell or and entire tissue: (i) linear, diffuse cellular expansion as it typically occurs during root growth, (ii) polar expansion characterizing the pollen tube, and (iii) organogenesis in the shoot apical meristem. Each system offers a unique perspective on the differing roles of pectin in different types of plant cells and we focus in particular on those experimental approaches that have exploited biomechanical or cytomechanical techniques to assess the role of pectin in a quantitative manner and *in situ*.

2. Root Elongation – Pectin Influences Diffuse Cell Expansion

The cylindrical cells composing root and shoot tissues are formed from approximately cube-shaped meristematic cells by an expansion of the lateral walls. In the root, this expansion takes place once a cell leaves the region defined by the apical meristem and becomes part of the maturing root (Fig. 2A). The highest rate of expansion occurs in the elongation zone of the root, immediately adjacent to the apical meristem. This elongation zone is followed by the maturation zone were cells start to differentiate and root hairs are emitted at the root surface (Dolan et al., 1993). Several players have been identified to regulate the onset and termination of cell elongation in the root, as well as the anisotropic manner in which these cells elongate. Among these are the orientation of cellulose microfibrils and alterations to the tensile loadbearing cellulose microfibril–hemicellulose network by factors such as expansins, yieldins and xyloglucan endotransglycosylases (Cosgrove, 2000; Darley et al., 2001; Geitmann and Ortega, 2009). However, the pectin matrix may play an important role as well. The dividing meristematic cells and the cells of the elongation zone of the *Arabidopsis* root the cell walls display abundant methyl-esterified pectin, whereas the central cells of the quiescent center of the root have pectins with low degree of esterification (Dolan et al., 1997). This illustrates that non-growing cell walls are typically associated with the de-esterified, and hence the gelled form of pectin, whereas cellular growth is enabled by a high degree of pectin methyl-esterification. Consistent with this, ectopic overexpression of VANGUARD1, an *Arabidopsis* PME, causes *Arabidopsis* plants to be dwarfed and the abundance of de-esterified pectins in the cell walls to be increased thus suggesting a reduction in wall extensibility to be the cause for the phenotype (Wolf and Greiner, in press). Interestingly, the *Arabidopsis* root region specifically representing the onset of cell elongation, but not the adjacent regions, displays a particular $(1 \rightarrow 4)$-β-D-galactan epitope (McCartney et al., 2003). The authors hypothesize that this transient appearance may be involved in modulating the cell wall properties that are required for the transition to the rapid phase of cell elongation.

Whereas pectins located throughout the thickness of the primary cell wall clearly seem to be involved in regulating cell wall extensibility, it is not clear whether pectins located in the middle lamella influence cell expansion. This region between two neighboring cell walls is extremely rich in pectin and is known to cement cells together (Fig. 2A). The *qua2-1* gene in *Arabidopsis thaliana* encodes a putative methyl transferase specifically located in this region of the cell wall and involved in cell adhesion. A mutation in this gene causes a reduction in the total amount of HG present in the wall and results in reduced cell adhesion (Mouille et al., 2007). Since the protein is solely located in the middle lamella and not in the bulk of the wall, it would seem unlikely that it could be involved in regulating cellular expansion. Consistent with this notion, micromechanical compression testing of isolated single cells from the *qua2-1* mutant does not show significantly altered mechanical cell wall properties (Palin, 2011). However, the mutant does display a significant reduction in root and shoot elongation (Palin, 2011). This suggests that reduced intercellular adhesion resulting from altered pectin deposition into the middle lamella