Virtual issue: cell wall functions in plant growth and environmental responses

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Abstract

Plant cell walls have multiple functions, including determining cell shape and size, cell–cell adhesion, controlling cell differentiation and growth, and promoting abiotic and biotic stress tolerance. This virtual issue introduces the physiological functions of cell walls in growth and environmental responses. The articles detail research on (1) embryogenesis and seed development, (2) vegetative growth, (3) reproductive growth, and (4) environmental responses. These articles, published in the *Journal of Plant Research*, will provide valuable information for future research on the function and dynamics of cell walls at various growth stages, and in response to environmental factors.

Cell wall components make various contributions to plant growth (Somerville et al. 2004). Various cell wall components have been detected in different plant organs, such as roots, leaves, stems, and flowers. Plant cell walls are dynamic structures composed of three main polysaccharide types: cellulose, hemicellulose, and pectin (Gigli-Bisceglia et al. 2019). These polysaccharides interact with structural proteins inserted in the cell wall matrix by various chemical bonds and physical arrangements to form a network (Cafall and Mohnen 2005; Cosgrove 2005; Scheller and Ulvikov 2010). These structures allow plant cells to maintain a defined shape, provide mechanical support, and maintain cell-to-cell communication in various organs. The composition and chemical structure of these polysaccharides change during plant growth in response to environmental and endogenous signals. The cell wall composition varies among species and cell types, and even by intracellular domains within the cell wall of a single cell (Yokoyama and Nishitani 2004). This variation in cell wall composition suggests that the plant cell wall is highly dynamic and regulated in a very specific manner (Carpita et al. 1993). The cell wall plays an important role in plant morphogenesis and environmental

responses (Bethke et al. 2016; Bidhendi and Geitmann 2016; Le Gall et al. 2015).

In this virtual issue, we list 16 recent papers published in the *Journal of Plant Research* that have contributed to our understanding of cell wall functions. These include papers on (1) embryogenesis and seed development, (2) vegetative growth, (3) reproductive growth, and (4) environmental responses.

Embryogenesis and seed development

In the tomato (*Solanum lycopersicum* L.), cell proliferation and rapid cell expansion occur in the ovary and embryo during early fruit development after pollination and early fruit formation. Terao et al. (2013) revealed changes in the distribution of cell wall polysaccharides, especially pectic galactans and arabinans, in ovules and fruit during early fruit development, via immunolocalization analyses using monoclonal antibodies specific for various cell wall epitopes. Du et al. (2020) also observed embryogenesis and dynamic changes in cell wall components of the Chinese chestnut (*Castanea mollissima* Blume) ‘Huaihuang’. Their results also suggested rapid metabolism of pectin and the presence of hemicellulose (galactan, arabinan, and xylan) during embryogenesis. The distributions of cell walls during embryogenesis and reproduction have been observed not only in angiosperms but also in mosses. Henry et al. (2020) localized cell wall components in liverwort (*Marchantia polymorpha* L.) placental cells. Dynamic changes in cell

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wall components have been implicated in embryonic developmental processes. During seed development, a unique cell wall protein, seed and root hair protective protein (SRPP), has been reported. (Tanaka et al. 2014). The *SRPP* gene (At4G02270) is significantly induced in root hairs under phosphate deficiency. Using an SRPP mutant, Uno et al. (2019) focused on the relationship between SRPP and seed viability; loss of SRPP function results in small, shriveled seeds with low germination rates. The absence of SRPPs in the cell wall may trigger the defects in cell wall structure seen in the seed coat. These results suggest that SRPP is important for normal development of seeds.

Vegetative growth

The ability of plants to grow upright and penetrate the soil comes from the mechanical strength of the organism, which is provided by the solidification of semi-rigid cell walls. The cell wall also gives the plant the strength and plasticity it needs to withstand adverse environmental conditions. The primary cell wall is produced during cell division and expansion, and determines the shape and volume of the cell. After cell expansion, some plant cells produce lignified walls, called secondary cell walls, which support plant growth. Fernandes et al. (2016) determined the response of cell walls, specifically the rearrangement of components, to depletion of key individual nutrients using grape shoot internodes as an experimental model. Honta et al. (2018) showed that arabinan and UDP-arabinopyranose mutase (UAM) are involved in pectin side chains and arabinoxyloglucan, especially in vegetative development, using RNA interference-induced tobacco transformants. UAMs are required for the biosynthesis of arabinose side chains in both pectin and arabinoxyloglucan in Solanaceae, and the arabinan-mediated cell wall network is important for normal leaf development in tobacco. The arabinan-mediated cell wall synthesis and network affected normal cell differentiation during the development of various organs (Kotake et al. 2016). Saelim et al. (2018) analyzed *AP2/EREBP* genes in Group IIIId *Arabidopsis thaliana* (L.) Heynh.. These genes are homologs of rice *ERF* genes previously proposed to be associated with secondary cell wall biosynthesis. However, they are involved in the transcriptional regulation of the primary cell wall-type *CESA* gene in *Arabidopsis thaliana*. Xylogenesis, the process of woody tissue formation, is accompanied by qualitative and quantitative cell wall changes. Shinohara et al. (2015) used cell wall-directed monoclonal antibodies from a *Zinnia elegans* Jacq. xylogenic culture system to identify two molecular events during xylogenesis. Stem mechanical strength is an important quantitative trait in agriculture closely related to host resistance in rice, which is reduced when fertilizers with high nitrogen contents are applied.

Secondary cell wall thickness is mainly responsible for stem strength (Aohara et al. 2009). Zhang et al. (2017) focused on nitrogen-induced gene regulation and demonstrated that nitrogen fertilizer affects stem mechanical strength by altering secondary cell wall synthesis in culm tissue. It was also reported that the cell wall thickened under Si-deficient conditions. Rice (*Oryza sativa* L.) is a typical Si-accumulating plant, in which more than 10% of the shoot dry weight may be accumulated Si. Under Si-deficient conditions, rice is sensitive to several stresses. The expression of genes involved in secondary cell wall synthesis was increased to compensate for the reduced stress tolerance, and the contents of cellulose and lignin increased (Yamamoto et al. 2012).

Reproductive growth

Plant reproduction requires active communication between cells and changes in the cell wall, which also play an important role in pollen development. The tapetum plays an important role in anther development by providing material for pollen wall formation and nutrients for pollen formation.

Takebe et al. (2020) reported the properties of a male-sterile glycine-rich protein 2 (OsGRP2) mutant, which was found to have irregular cell division and reduced tapetum function. GRP is a structural protein found in the cell walls of diverse plants. This paper revealed that OsGRP2 plays an important role in tapetum differentiation and function. Reproductive tissues are particularly rich in pectin compared to other tissues and play an important role in various developmental processes. The degree of methylesterification of pectin is an important determinant of its adhesive properties. After pollination, the pollen tube entering the stigma extends through the adhesive cells of the transmitting pistil tissue toward the ovary. In higher plants, the transmitting tissues along the pollen pathway contain large amounts of pectin (Iwai et al. 2006). In addition, the growing pollen tube actively synthesizes a pectin-rich cell wall at its tip. In pectin methyltransferase mutants, the level of pectin methylesterification in the cell wall of the transmitting pistil tissue is reduced, resulting in abnormal cell wall properties and the inability of pollen tubes to advance through the pistil transmitting tissue (Hasegawa et al. 2021). Maintaining the cell wall properties of the pistil transmitting tissue by pectin methylesterification may regulate the mechanical guidance of pollen tubes. The degradation of cell wall polysaccharides by various cell wall hydrolases during fruit softening causes structural changes in hemicellulose and pectin, which affect fruit physical properties and softening. Changes in cell wall degradation and cell wall polysaccharide biosynthesis and cross-linking, which are involved in fruit softening and fruit shape maintenance during ripening, vary among fruit tissues in tomato (Takizawa et al. 2014). The extent of cell wall

modification, and the modifying enzymes activated during fruit softening, vary among fruit types. Expansins are proteins involved in the modification of plant cell walls, including cell expansion. Expansins also play an important role in fruit ripening by loosening the cell wall, making it more accessible to other cell wall-related enzymes. Expansins have been proposed to induce cell wall disassembly by breaking the non-covalent bonds between cellulose and matrix polysaccharides (Cosgrove 2000). Using strawberry fruit, Nardi et al. (2013) showed that expansins bind not only cellulose, but also to a wide range of cell wall polymers. After fruit development following pollination, the abscission zone of the pedicel strengthens its adhesion to keep the fruit attached. Non-pollinated flowers drop off at each abscission zone, but the same tissue expansion is observed in pollinated flowers. As the fruit grows and ripens, it readily sheds at the abscission zone, indicating that shedding is accelerated. Cell wall degradation and synthesis play important roles in these processes (Tsuchiya et al. 2015). Iwai et al. (2013) showed that different mechanisms regulate floral shedding, which is determined by successful pollination, and fruit shedding, which occurs after ripening, i.e., remodeling of cell wall polysaccharides and lignification, respectively.

Environmental responses

Various stresses affect plant growth, including pathogen attack, insect herbivory, high salinity, drought, and excessive temperature. Most plant cells are attached to neighboring cells through a common interface, the cell wall, and maintain their position during development. Since plant development depends on harmonious cell division, expansion, and differentiation, it is essential that individual cells are in harmony with developing neighboring cells in terms of adhesion and separation. Plant-parasitic nematodes parasitize many rhizomatous plants and take up nutrients, resulting in severe growth disorders in the host plant. During infection, root hump nematodes induce the formation of characteristic hyperplastic structures, called root humps or galls, in the roots of host plants. Ishida et al. (2020) showed that plant-parasitic nematodes modulate host developmental mechanisms to reduce secondary cell walls and establish feeding sites.

Various mechanisms are involved in the detoxification of heavy metals in plant cells. Most of the heavy metals taken up by plants accumulate in the roots. Inoue et al. (2012) clarified the properties of lead deposited in the cell walls of radish roots grown in a glass bead bed containing lead pellets; they showed that the root cell wall has high affinity for Pb^{2+} and that the carboxyl groups of pectin play a role in Pb binding. Aluminum toxicity is another major cause of poor crop growth, especially in areas with acidic soils. Pectin in

the cell wall also functions in aluminum toxicity and plays an important role as a barrier to prevent aluminum from entering rice (Nagayama et al. 2019).

I hope that these 16 articles provide valuable information for future research on cell wall function in plant growth and environmental responses.

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