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# The Role of Pectin Phase Separation in Plant Cell Wall Assembly and Growth

**Alexis Wightman***

*Department of Urology, University of Cambridge, Bateman Street, UK*

**Abstract**

A growing body of literature suggests that phase separation within polymer mixtures drives many biological processes. The formation of membrane-less organelles by liquid-liquid phase separation is thought to play a variety of roles in cell metabolism, gene regulation, and signalling. One of the characteristics of these systems is that they are poised at phase transition boundaries, which makes them perfectly suited to elicit robust cellular responses to often very small changes in the cell's "environment". Recent findings suggest that phase separation not only plays a role in wall patterning, hydration, and stress relaxation during growth, but may also be a driving force for cell wall expansion in the semisolid environment of plant cell walls.

**Keywords:** Epigenetics • Hypomethylation • Diagnosis • Prostate cancer

## Introduction

When the interaction energy favouring like neighbours and disfavoring unlike neighbours exceeds the mixing entropy of polymers, liquid-liquid phase separation occurs. See for a great introduction to the physics of phase separation in biology. Many regulatory processes in the cell are thought to influence phase separation, such as posttranslational modifications that change the strength of interactions between cellular components. Increasing polymer affinity transforms liquid droplets in the cytosol into a gel, where the crosslink lifetime distinguishes between liquid and solid behaviour. Interestingly, gels can exhibit spectacular reversible volume transitions caused by phase separation of the gel into high and low density domains in response to small environmental changes.The semi-solid environment of plant cell walls also experiences phase separation, which contributes to their remarkable nanoscale organisation and materiality.

After reaching an equilibrium, this layer phase separates via an as-yet unknown mechanism, resulting in more dense aggregates that form highly reproducible patterns. These surface patterns are stabilised by impregnation with sporopollinin, a highly resistant polymer composed of long chain fatty acids and phenolics secreted by adjacent tapetum cells. The primexin phase separation is kinetically arrested in some species, presumably due to premature sporopollinin release, resulting in variable deposition patterns. These arrested patterns appear to evolve faster than equilibrium patterns. Another example is the cell wall maturation of the singlecelled freshwater desmid alga Penium margaritaceum. Desmids are Charophycean green algae that have a similar cell wall composition to land plants, including an important role for pectins in cell wall architecture [1].

## Literature Review

How cell wall metabolism can control cell expansion and plant growth is a major mystery in plant biology. According to the acid growth theory, the growth hormone auxin promotes turgor-driven cell expansion by promoting cell wall acidification, which increases cell wall extensibility. Numerous studies on isolated cell walls have found acid-induced "creep," or long-term plastic deformation of the cell wall. Expansins have been identified as the proteinaceous agents responsible for acid-induced creep. These proteins appear to specifically remove the aforementioned cellulose-xyloglucan-cellulose crosslinks via a non-enzymatic mechanism that is still unknown. In the context of living expanding cells, this activity, which is characterised on isolated and heat-inactivated walls, appears to be only a part of the picture. The removal of cellulose-XG crosslinks was catalysed by sin.

Pectin fibrils with diameters ranging from 20 to 30 nm have been reported to extend into the lumen from the corners of poplar xylem fibre cells. The authors proposed that these hydrophilic fibres play a role in water storage in the xylem. As with previous research, these structures can be species, cell type, and even subcellular location specific. The presence of pectin fibrils begs the question of how the HG chains came to be uni-axial. Is this due to interaction with equally oriented cellulose, a self-assembling nematic crystalline phase, or oriented deposition? The latter, seemingly contradictory possibility should not be dismissed given the precedent of tubular exocytosis in neurons and the recent discovery of extracellular vesicular-tubular structures.

## Discussion

Cellulose is the most condensed phase in the cell wall, consisting of semi-crystalline microfibrils made up of multiple ß-1,4 linked glucan chains. Microfibrils are formed by hexameric complexes in the plasma membrane, with each globule containing three distinct catalytic subunits. The proximity of these subunits within the complex ensures the aggregation of 18 parallel glucan chains into elementary microfibrils with typical diameters of 3 nm. Depending on the nature of the matrix polymers present during deposition, these elementary microfibrils can form higher order aggregates. Indeed, some matrix polymers or polymer domains, such as certain xyloglucan, xylan, and pectin species, readily condense onto cellulose and act either as a double-sided tape crosslinking microfibrils or as a sterically and electrostatically repulsive barrier.

The remarkable ability of pollen grains and seeds to dehydrate and rehydrate is one of the characteristics of seed plants' success in colonising terrestrial habitats. Volume transitions in pectin gels can occur during rehydration processes. Below the exine layer of dicot pollen grains is an intine layer rich in pectin. This pectin's de-methylesterification prior to germination is required for normal pollen hydration and germination. Indeed, a mutation in one of the 13 PME genes expressed in Arabidopsis pollen resulted in significantly delayed pollen swelling and germination. According to a recent study on chemically deesterified sunflower pollen, swelling is driven by pectin charges and limited by $Ca^{2+}$ crosslinks. Indeed, neutralising the charges at low pH prevented swelling and chelator removal of $Ca^{2+}$ with a chelator at neutral pH [2].

The fungus attacks the bark of hazelnut trees, causing cankers and branch

***Address for Correspondence:** Alexis Wightman, Department of Urology, University of Cambridge, Bateman Street, UK, E-mail: alexiswightman@gmail.com*



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girdling. This reduces nutrient and water uptake, resulting in stunted growth, dieback, and eventual tree also known as grey mould, is a fungal disease that affects the hazelnut's flowers, buds, leaves, and nuts. The fungus causes a grayish-brown mould to grow on the affected areas, resulting in a lower yield and quality of nuts. Powdery mildew is a fungal disease caused by various Erysiphe species. The disease attacks hazelnut leaves, flowers, and young nuts, causing white powdery patches to appear on the affected parts. The disease can reduce crop yield and quality.

The presence of a specialised outer cell wall, which yields to the pressure of the swelling gel at predefined fragile spots at cell edges, where the cell wall is thinner, facilitates mucilage release from the Arabidopsis seed coat. According to a recent elegant study, the formation of these fragile spots requires the local action of the peroxidase PRX36. Cell wall thinning at this site can be explained by cell wall densification caused by PRX36-catalyzed oxidative crosslinking of cell wall polymers, though other scenarios involving hydroxyl-mediated polymer cleavage cannot be ruled out. Interestingly, the authors demonstrated that RFP-tagged cell edges require the PME inhibitor to be targeted. Immunofluorescence experiments revealed that this inhibitor, most likely in conjunction with an unidentified PME [3-5].

## Conclusion

We discussed a number of examples in this review that demonstrate how phase separation in polymer mixtures is widely used in the control of biological processes not only in the cytosol, nucleoplasm, and at membrane interfaces, but also in the extracellular matrix of plant cells. Recent findings implicate phase separation in the spatial organisation of exine in pollen grains, the surface features of Penium cells, the regulated hydration of pollen grains and seed mucilage, and the possible recruitment of a cell wall modifying enzyme in specific wall domains of seed coat cells. We also talked about how pH-induced changes in pectin assemblies and enzyme-regulated volume transitions in crystalline pectin fibres may contribute to cell wall expansion and how this may fit into the picture. We are entering an exciting new era in plant cell wall research that combines glycochemistry, soft matter physics, and cell biology to provide new insights into the control of cell wall architecture, plant growth, and, most likely, abiotic stress resistance and immunity. Understanding the emergent properties of co-evolved polymer assemblies should also inspire the development of new functional nanomaterials. Finally, it will be interesting to see if the concepts discussed in this review apply to other biochemically distinct cell walls, such as those of algae, bacteria, oomycetes, or fungi.

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## Conflict of Interest

There are no conflicts of interest by author.

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