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Cell wall biomechanics: a tractable challenge in manipulating plant cell walls ‘fit for purpose’!

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The complexity and recalcitrance of plant cell walls has contributed to the success of plants colonising land. Conversely, these attributes have also impeded progress in understanding the roles of walls in controlling and directing developmental processes during plant growth and also in unlocking their potential for biotechnological innovation. Recent technological advances have enabled the probing of how primary wall structures and molecular interactions of polysaccharides define their biomechanical (and hence functional) properties. The outputs have led to a new paradigm that places greater emphasis on understanding how the wall, as a biomechanical construct and cell surface sensor, modulates both plant growth and material properties. Armed with this knowledge, we are gaining the capacity to design walls ‘fit for (biotechnological) purpose’!

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Overview of products made from plant cell walls and their uses

Humans have long had an intricate relationship with plant cell walls (in short, walls), using fibres for clothing, wood for shelter, paper for writing, fuel for heating and transport and as sources of both medicines and foods. Since walls comprise the bulk of the vegetative biomass of plants, interest has focused on walls as a renewable energy resource, particularly secondary cell walls or

lignocellulosic biomass, for second-generation biofuels. The biomaterial properties of walls are also increasingly being exploited, for example, in the use of nano-cellulose for tissue engineering and as building and manufacturing biocomposites [1]. The relationship with walls in our diet is also evident from our teeth and digestive tracts being adapted to a high fibre diet. Diets rich in fibre (mainly walls and resistant starch) containing wholegrains, fruits and vegetables, are known to improve health outcomes and the prevention of certain chronic diseases (reviewed in [2]; see **Box 1**). Understanding the complex structure–function relationships between wall components and improved health benefits, particularly as part of plant-based foods, enables optimisation of foods and food processing for functional outcomes. Likewise, enhancing spinnable fibres for textiles, wood for construction and biomass for biofuels will contribute to a more sustainable and efficient use of plant-based wall products.

Engineering walls ‘fit for purpose’ has many challenges yet with increasing knowledge of wall biosynthesis, regulation, structure, physicochemical and biomechanical properties, processes of secretion and deposition, and compensatory effects to wall changes, the opportunities are endless [3]. The plasticity of biochemical pathways involved in wall polymer synthesis is exemplified by lignin monomer production/polymerisation. A highly recalcitrant polyphenolic polymer, lignin impedes extraction of cellulosic biomass and digestibility of forage crops by ruminants. Attempts to reduce lignin, largely through targeting key biosynthetic genes, has often resulted in negative impacts on either plant growth or biomass quality, or resulted in no change in total lignin content due to the adaptability of the biosynthetic pathways [4,5]. Alternative approaches to generate ‘designer lignins’, for example, with increased proportions of labile ester bonds, have proven successful for both improved degradability and for value-added lignin by-products [6].

Similarly, progress has been made towards elucidating the biosynthetic pathways of polysaccharide synthesis, however, the subsequent steps involving their intricate molecular interactions once deposited within the wall and how this impacts biomechanical properties are rudimentary. We highlight recent progress from the perspective of walls within the context of food and dietary fibre and will therefore largely focus on primary walls.

Box 1 Making the link between cell walls and human health — a new take on dietary fibre.

Wholegrains, fruits, vegetables, legumes and other plant-based whole foods are now generally accepted worldwide as the basis for a healthy human diet, as recommended by all major national and international health agencies. This is largely based on a database of epidemiological observations relating diet and health accumulated over decades. In contrast to other polymeric dietary constituents such as proteins and starch, there are no enzyme activities in either the human mouth, stomach or small intestine capable of depolymerising plant cell walls. Therefore, it is only mechanical actions that can alter the physical structure of plant-based foods during digestion. The wall components that survive to the end of the small intestine transit into the large intestine where microbial fermentation of residual dietary components occurs. In a healthy diet, this will include a large fraction of plant walls and these 'dietary fibres' are recognised as being the preferred energy source for a health-promoting microbiota.

In addition to positively influencing microbial fermentation in the large intestine, four factors can be identified as being important to the functional roles of walls in controlling the digestion of plant-based foods:

1. **Encapsulation.** For nutrients such as lipids and carotenoids, an intact wall represents an impassable barrier. As the biochemical conditions encountered in the mouth, stomach or small intestine are not capable of hydrolysing walls, hydrophobic nutrients in intact cells are transported to the large intestine. Well-studied examples include triglycerides in almond nuts and carotenoids in carrots (reviewed in [10]). The digestion of lipids and absorption of cholesterol can also be hindered by soluble wall components, such as mixed-linkage glucans (MLGs) [72**]. Mechanistic studies in pigs have suggested that the blood lipid-managing and cholesterol-managing properties of soluble wall polysaccharides is related to a masking of triglycerides and cholesterol resulting in a decrease in lipolytic activity and cholesterol absorption.
2. **Binding.** Walls are capable of effectively sequestering and binding both nutrients such as polyphenolics [2] and digestive enzymes such as amylases and proteases [73–76]. This binding has been shown to be effectively irreversible under gastric and small intestinal conditions for polyphenols, suggesting a mechanism for transport to the large intestine [2]. Amylase binding has been shown to be similar for cellulose and starch, leading to essentially a 1:1 repression of starch-hydrolysing activity by cellulose (or wheat bran) with implications for glycemic control and diabetes risk factors [75]. A combination of encapsulation and binding has been shown to result in essentially complete resistance to *in vitro* digestion of starch and protein from intact cells isolated from legume cotyledons [77]. The relatively thick walls of legume cotyledons, compared to for example cereal endosperms, could be a key factor in the positive nutritional value of legumes in the diet.
3. **Transport.** For those nutrients which are either not bound or encapsulated within tissues, walls in multicellular tissue pieces can act as a diffusion barrier that both limits either the ingress of digesting enzymes and the egress of nutrients or the products of enzyme hydrolysis. The solubilisation of polysaccharides from walls during either food processing or digestion can also affect the transport of enzymes and nutrients [78]. This is because the local viscosity generated by high molecular weight soluble polysaccharides such as pectins, arabinoxylans (AXs) and MLGs can slow down the movement of solutes as well as potentially acting as an accessible substrate for binding of nutrients or enzymes. Understanding the factors that control the extent of polysaccharide solubilisation from walls will provide tractable targets for either plant selection or tailored food processing to modify digestion properties.

4. **Rheology.** As walls and their components are not depolymerised enzymatically during digestion, they can impact the physical structure of digesta and how this is perceived, although this will depend on the mixing conditions encountered [78]. For example, wheat AX added to a pig diet caused a more rapid transit through the small intestine, resulting in more protein escaping digestion and becoming a substrate for fermentation in the large intestine [79]. However, there may be a modulating effect of digestive secretions, as very large differences in the rheology of pig diets enriched with pectin *in vitro* were not reflected *in vivo*, probably due to viscosity enhancement of non-pectin diets by gastric mucin [80].

The mechanisms involved in the fermentation of wall polysaccharides within the large intestine are starting to be untangled, with the finding of either individual bacteria or small groups which are capable of 'selfishly' converting complex structures such as xyloglucans (XyGs) and pectins into component monosaccharides for energy generation [81,82]. As this knowledge base expands, we should start to see how the microbial community (microbiome) is shaped and how this impacts on the health of the host. However, these are early days and there is much to be learned about the principles involved in wall fermentation from real foods, how this influences the microbiome, and how this in turn affects human health. In order to realise opportunities to modify food product formulation for improved health benefits, the architecture, physical properties and physiological effects of walls need to be investigated in parallel.

Cell wall structure in relation to mechanical properties

The wall is the key structural element in plants controlling strength, rigidity and flexibility and, in turn, the texture (crispness, mealiness and toughness) of edible plant parts. It is composed of a network of rigid cellulose microfibrils (MFs) embedded in a hydrated gel-like matrix phase containing non-cellulosic polysaccharides (commonly referred to as hemicelluloses). These include the heteroxylans, heteroglucans and heteromannans, pectins (that include homogalacturonans (HGs), rhamnogalacturonans I and II (RG I & II)), (glyco)proteins, and in some differentiated cell types, lignin. There are two main types of walls: primary walls, that are flexible to enable growth but are of sufficient mechanical strength to withstand the turgor pressure of the protoplast; and secondary walls, that are thick, inflexible and deposited on the inner side of the primary wall in specialised tissues.

Although the structural scaffold of both primary and secondary walls are cellulose MFs, the components of the matrix phase vary widely across the plant kingdom [7]. For example, the commelinid monocots (includes the major cereals) are characterised by a matrix phase comprised primarily of (glucurono)arabinoxylans ((G)AXs) and (1,3;1,4)- β -glucans (mixed-linkage β -glucans; MLGs) with low levels of pectic polysaccharides (pectins), xyloglucans (XyGs) and monomeric hydroxycinnamic acids such as ferulic acid [7,8]. By contrast, in dicotyledonous plants, gymnosperms and

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