Food Hydrocolloids 25 (2011) 257–262

Contents lists available at ScienceDirect

Food Hydrocolloids

journal homepage: www.elsevier.com/locate/foodhyd

Plant cell walls: Supramolecular assemblies

Michael C. Jarvis*

Department of Chemistry, University of Glasgow, University Avenue, Glasgow G12 8QQ, Scotland, UK

ARTICLE INFO

Article history:
Received 14 August 2009
Accepted 17 September 2009

Keywords:
Pectic
Cellulose
Xyloglucan
Cross-linking
Porosity
Dietary fibre

ABSTRACT

The primary walls of plant cells comprise a large part of our dietary fibre. Their properties depend on the polysaccharides comprising them but also on the manner in which they are interlinked to form the three-dimensional, functional structure of the intact cell wall. This structure is far from homogeneous, but includes local adaptations to withstand local stresses at the cell corners and the margins of intercellular spaces. There is also variation in cell-wall structure at the tissue, organ and species levels. Interlinking of cell-wall polymers by covalent, ionic and hydrogen bonding varies at all these levels and affects the mechanical properties of the cell walls. Cross-linking of pectins in particular, by a variety of covalent as well as non-covalent mechanisms, determines what kind of disruption of the cell wall is necessary to bring them into solution. Solubilisation of pectins has dietary significance in its own right but also leads to an increase in the pore size of the cell wall and hence reduces the extent to which it impedes the entry of enzymes such as α-amylase and the outflow of intracellular macromolecules during the digestion process. The nutritional value of cell walls as 'dietary fibre' may then depend on the extent to which the cell walls remain physically intact during the digestion process.

1. Introduction

Much of what we call dietary fibre consists of the primary walls of plant cells (Englyst, Liu, & Englyst, 2007; Ha, Jarvis, & Mann, 2000). Cell walls are unusual materials. Their structures, functions and properties show wide and complex biological variation (Knox, 2008; Moller et al., 2007). If we wish to understand cell walls in all their variability a good starting point is their functional biology within the living plant (Somerville et al., 2004).

The primary cell walls of plants have the following functions:

(1) to support the cell membrane and prevent it from bursting under the turgor pressure contained osmotically within the cell (Cosgrove, 2005; Fricke, Jarvis, & Brett, 2000);
(2) to expand, under turgor pressure, at a precisely controlled rate and direction that will ultimately define the cell's contribution to the growth and form of the plant (Boyer, 2009; Cosgrove, 2005);
(3) to cooperate with adjacent cells under similar turgor pressure to build a mechanically competent three-dimensional tissue with every cell wall maintained in tension (Niklas, 2004; Somerville et al., 2004).

Secondary (woody) cell walls are minor components of dietary fibre. They are deposited inside pre-existing primary cell walls, normally in tissues that will require mechanical strength greater than can be provided by the strategy of using turgor pressure to carry macroscopic compressive loads and to maintain the cell walls in constant tension (Niklas, 2004). In contrast to primary cell walls they do not grow, are usually not tensioned by turgor and function equally well under external tension or compression (Bruchert & Gardiner, 2006; Mellerowicz & Sundberg, 2008). Secondary cell walls are usually thicker and have greater polymer mass per unit volume (i.e. lower water content) than primary cell walls. Secondary cell walls of an exceptional type are found in many seeds, where their mechanical role is secondary to an energy storage function and the abundance of one particular cell-wall polysaccharide, the identity of which varies from one species to another, is greatly increased (Buckeridge, dos Santos, & Tine, 2000; Crombie, Chengappa, Hellyer, & Reid, 1998, 2002; Edwards et al., 1999).

This review deals with the primary cell walls of non-graminaceous plants. In view of their mechanical function it is natural to describe primary cell walls as solids, and to attribute to them a wide variety of mechanical parameters such as strength, stiffness, Poisson ratio and fracture energy (Niklas, 2004). But primary cell walls have water contents that are usually well in excess of the mass of solid polymers present. Typical water: polymer ratios vary from 3:1 to 10:1, and still higher ratios may be found in cell walls from ripe

* Tel.: +44 141 330 4653; fax: +44 141 330 4888.
E-mail address: mikej@chem.gla.ac.uk

0268-005X/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.foodhyd.2009.09.010

fruit (Redgwell et al., 1997; Rondeau-Mouro, Defer, Leboeuf, & Lahaye, 2008; Woehlecke & Ehwald, 1995). It may therefore be more accurate for some purposes to describe cell walls as hydrogels. That is, they are permeable to aqueous solutes of low molecular-mass, show ion-exchange and Donnan effects (Dainty & Hope, 1961; Michael & Ehwald, 1996; Rufyikiri, Genon, Dufey, & Delvaux, 2003), and shrink or swell in response to charge repulsion and the dielectric constant of the solvent (Redgwell, Curti, & Gehin-Delval, 2008; Shomer, Novacky, Pike, Yermiyahu, & Kinraide, 2003).

Because low-molecular solutes can move more through the cell-wall space the network of cell walls throughout the plant, and the intercellular spaces and xylem channels interconnected with them, can be considered as a single entity called the apoplast. The above-ground part of the apoplast is waterproofed by the cuticular layer of the epidermis, otherwise the plant would dry out. The outer epidermal cell wall resembles other primary cell walls in its general polysaccharide composition but is thickened, to the point where it comprises a substantial fraction of the cell-wall mass of leaves and some kinds of fruit, and is reinforced in its outer layers with the polyester cutin and waterproofed with waxes (Franke et al., 2005). In underground plant parts the phenolic/aliphatic polyester suberin (Yu et al., 2006) replaces cutin. The influence of cutin and suberin on the digestion of polysaccharides associated with them is a neglected area. While generally these waterproofing polymers separate the hydrated cell-wall network from the atmosphere, an exception of nutritional interest is the seed coats of some species of plants where a specialised cell-wall layer is capable of swelling outward in the presence of free water and surrounds the seed in a protective, mucilaginous coating (Fekri, Khayami, Heidari, & Jamee, 2008; Lindberg et al., 1990; Naran, Chen, & Carpita, 2008). Mucilaginous surface layers are also found on the outside of root caps, where they are continually renewed from within (Iijima, Morita, & Barlow, 2008). In these mucilages cellulose microfibrils are absent or dispersed, unlike conventional primary cell walls where the reinforcement provided by the microfibrils confers the mechanical properties expected of a conventional solid material.

2. Structure of primary cell walls

The constituent polymers of the primary cell wall are normally classified as follows.

2.1. Cellulose

The unbranched, β(1,4′)-linked glucan chains of cellulose aggregate together by hydrogen bonding to form microfibrils each about 3 nm in diameter.

2.2. Hemicelluloses

These polymers have some degree of conformational resemblance to cellulose and are capable of hydrogen bonding to cellulose microfibrils, possibly in a similar manner to the aggregation of the cellulose chains themselves (Jarvis, 2009). The principal hemicelluloses of primary cell walls in most plants (Harris & Smith, 2006; Moller et al., 2007) are xyloglucans and glucomannans, but arabinoxylans and mixed-linkage β-glucans replace these in grasses, cereals (Cui & Wang, 2009) and a small number of other plants such as palms.

2.3. Pectins

The distinguishing feature of the pectic group of polysaccharides is a partially methyl-esterified α(1,4′)-linked galacturonan chain (Mohnen, 2008). Associated with the pectic galacturonan are a number of other polymers or polymer segments, the most abundant being the highly branched rhamnogalacturonan I which has α(1,5′)/(1,3′)-linked arabinan and β(1,4′)-linked galactan side-chains attached to a core chain of alternating galacturonosyl and rhamnosyl residues (Popper, 2008; Willats, Knox, & Mikkelsen, 2006). Less abundant pectic chain types include the complex rhamnogalacturonan II, which has binding sites for borate esters (O'Neill, Ishii, Albersheim, & Darvill, 2004), and galacturonan segments with xylosyl side-units (Nakamura, Furuta, Maeda, Takao, & Nagamatsu, 2002; Willats et al., 2004). From the fact that these heterogeneous building blocks are often extracted together it is commonly assumed that there are glycosidic linkages between them, and branching visible by atomic force microscopy confirms this (Kirby, MacDougall, & Morris, 2008). The nature and position of the linkages has been difficult to elucidate (Vincken et al., 2003) but their presence is supported by experimental evidence for attachment of rhamnogalacturonan II to galacturonan (Ishii & Matsunaga, 2001) and for a common core chain in galacturonan, rhamnogalacturonan I and xyloglucan (Coenen, Bakx, Verhoef, Schols, & Voragen, 2007).

The relative abundance of these building blocks is not constant. Variation occurs at every scale. Within one primary wall of a single cell the cellulose microfibrils are arranged 10–20 nm apart in loosely parallel layers, with at least some of the hemicelluloses more or less closely associated with them and pectins arranged between. There is therefore variation in composition on the nm scale depending on distance from the centre of the nearest microfibril, and periodic variation across successive layers of the cell wall. The mechanical properties of the cell wall in its own plane are largely dependent on the orientation and interconnection of microfibrils within each layer, and these are the properties that permit and direct the growth of the cell (Kerstens & Verbelen, 2003). Between one layer and the next pectins predominate and the middle lamella is composed largely or wholly of pectins with no cellulose microfibrils (Guillemin et al., 2005; Knox, 2008). The pectic component is in general less rigid than the hemicellulose-cellulose network and, carrying charged functional groups on the main chain and having more flexible side-chains, the pectins interact more strongly with water. It follows that when primary cell walls swell or shrink they do so largely in thickness by expansion or contraction of the interlayer pectic gel (Jarvis, 1992).

Because turgor pressure tends to inflate each plant cell into a rounded shape, it generates forces pulling cells away from one another at the corners. These localised stresses are carried by specialised pectic domains with reduced methyl esterification (Jarvis, Briggs, & Knox, 2003; Knox, 2008). Triangular intercellular spaces are frequently present at these locations, reducing the turgor-generated forces and transferring them to the corners of the intercellular spaces where similar low-ester pectic polysaccharides are found (Jarvis et al., 2003; Knox, 2008).

In elongating tissues the origins of the side and end walls of each cell differ, with the side walls being formed by extension and the end walls inserted as the cells divide. These differences are reflected in the pectic composition, particularly the relative abundance of arabinan side-chains in rhamnogalacturonan I (McCartney & knox, 2002; McCartney, Steel-King, Jordan, & Knox, 2003).

Within one plant tissue the cell-wall composition changes with development and, partly in consequence of this, there are substantial differences between tissues (Guillemin et al., 2005; Muller et al., 2003). Distinctive polymer compositions are a particular feature of fruit cell walls, where the disassembly of the cell-wall structure is an integral part of the ripening process (Brummell, 2006; Cantu et al., 2008).

Apart from the taxonomic dichotomy between graminaceous and non-graminacous plants, different species have different