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## Complexity and health functionality of plant cell wall fibers from fruits and vegetables

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### ABSTRACT

The prevalence of lifestyle-related diseases is increasing in developing countries with the causes for death starting to follow the same pattern in the developed world. Lifestyle factors including inadequate dietary intake of fruits and vegetables and over consumption of nutrient-poor processed foods, are considered to be major causal risk factors associated with increased susceptibility to developing certain diseases (Alldrick, 1998; Kiani, 2007). Recent epidemiological evidence confirms a strong association between dietary fiber and reduced all-cause mortality risk, as well as a risk reduction for a number of non-communicable diseases (Chuang et al., 2012). The relationship between dietary fiber and mortality has been described as “convincing observations that call for mechanistic investigations” (Landberg, 2012). In particular, the health protective roles played by dietary fibers of different origin are not well understood. Whilst Hippocrates was the earliest known physician to study the health benefits of fiber derived from grains (Burkitt, 1987), the functionality of fruit and vegetable fiber, especially in association with other compounds such as polyphenols and carotenoids, is an area of more recent interest. Hence the objective of this review is to assess the complexity and health-related functional role of plant cell wall (PCW) fibers from fruits and vegetables with a particular emphasis on interactions between cell walls and phytonutrients.

### KEYWORDS

Cellulose; pectin; polyphenols; bioaccessibility; cardiovascular; metabolites

### Introduction

From the ancient writings of Homer which details the medicinal use of fruits and vegetables by early physicians (Seymour, 1907), to the promotion of the plant based “Mediterranean” diet by Italian Giacomo Castelvetro to the English population in the Middle Ages (ca. 1600s) (Haber, 1997), fruits and vegetables have historically been promoted as an important part of the human diet. However, in an attempt to address and prevent nutrient deficiencies, animal-based foods were heavily promoted from the 1900s–1970s (Nestle, 1999). Nevertheless, the increasing prevalence rate of chronic disease led scientists to research the dietary differences between Western diets (associated with an increasing rate of chronic disease), and developing countries (and the low prevalence of chronic disease) in the 1960s. As with wholegrains, this was the start of the plethora of epidemiological and intervention studies generally showing positive associations between fruit and vegetable intake and improved health outcomes and/or prevention of certain chronic diseases (Bazzano, 2006; Slavin, 2012). From the 1950s to 1970s, modern medicine focused particularly on the lack of constipation and large bowel conditions (e.g. haemorrhoids, diverticulitis, piles, varicose veins, hernia, gallstones and cancer) amongst populations with high fruit, vegetable and wholegrain dietary intake in comparison to the more meat-based, low fiber Western diets (Jew et al., 2009). From these observational studies it was concluded that high fiber intake is positively associated with a number of health

benefits for the large bowel (Hipsley, 1953; Brownlee, 2011; Miller-Jones, 2013).

The term “dietary fiber” (DF) was first used in Hipsley’s observational study into toxemia rates among pregnant women consuming diets of varying fiber content (Hipsley, 1953). The recommended DF intake for Australian adults is 30 g and 25 g per day for males and females, respectively (NHMRC, 2005). DF was traditionally defined in the 1970s by the AOAC International and AACC International as “...the plant polysaccharides (including cellulose, hemicelluloses, gums, oligosaccharides and pectin) and lignin which are resistant to hydrolysis by digestive enzymes...” (Prosky et al., 1985). However in order to provide a comprehensive definition of DF that also accounts for structural variability and associated health benefits, CODEX Alimentarius recently defined fiber to be “carbohydrate polymers with  $\geq 10$  (or 3, depending on the jurisdiction) monomeric units that are resistant to enzymatic hydrolysis during human small intestinal (SI) digestion on condition that they are either:

- Naturally occurring edible carbohydrate polymers ingested during food consumption;
- Naturally occurring carbohydrate polymers extracted from foods that demonstrate scientifically proven physiological health benefits; and/or
- Synthetic carbohydrate polymers that demonstrate scientifically proven physiological health benefits” (McCleary, 2011; Miller-Jones, 2013).

Whilst vitamins, minerals, antioxidants and polyphenols are promoted as health imparting components, it is important to note that fruits and vegetables are also good sources of DF in the form of the plant cell wall (PCW). Enveloping the plant cell, the PCW is important in maintaining structural integrity while managing the diffusion of nutrients entering in and waste material exiting the plant cell (Doblin et al., 2010). Cell wall structure is typically modified during the maturation process through both the proportions and detailed chemistry of key PCW components (i.e. cellulose, hemicellulose, lignin and pectin) changes (Cosgrove, 2005; Harris and Smith, 2006; Doblin et al., 2010).

It has been noted that the prevalence of certain cancer in countries with a more plant-based diet is considerably lower than the rate in Western countries, where processed foods and meat are the main dietary constituents (von Ruesten et al., 2013; Beliveau and Gingras, 2007). Large-scale cohort and cross-sectional studies have found a considerable decrease in the risk of cardiac and colorectal incidences and related fatalities among participants on a high fruit and vegetable diet (George et al., 2009; Sofi et al., 2010; Martinez-Gonzalez et al., 2011; Andriantsitohaina et al., 2012; Feart et al., 2013; von Ruesten et al., 2013). Several studies have also shown that a daily consumption of a diet high in a range of fruit and vegetables may result in a considerable decrease in the relative risk of developing ischemic stroke (Park, 2010; Griep et al., 2011; Andriantsitohaina et al., 2012; Sherzai et al., 2012). Although cognitive function did not improve with fruit intake, vegetable intake was significantly associated with reduced cognitive decline (Kang et al., 2005; Nooyens et al., 2011; Feart et al., 2013). The health benefits of fiber in maintaining gut motility and health are well established. Due to insoluble fiber's resistance to digestion, foods high in DF are often prescribed as the first line of treatment for constipation due to its laxative effect (Beck, 2008; Kumar, 2012). In addition to this, DF can also affect the health of gut microbial populations during PCW fermentation in the large bowel which may consequently influence nutrient absorption. During DF fermentation, short-chain fatty acids (SCFAs), metabolized for energy, are produced (Macfarlane and Macfarlane, 2012).

The structure and composition of the PCW not only affects the release and absorption of phytonutrients but also the health of gut microbes. Whilst the DF component of fruits and vegetables is usually treated separately from phytochemical components, recent research suggests that these two major health-benefiting aspects of a diet rich in fruits and vegetables act in concert. This review summarizes current knowledge on the effects of fruit and vegetable PCWs as DF and emphasizes the ways in which PCWs interact with phytochemical components in fruits and vegetables, suggesting health-benefiting mechanisms that may underlie epidemiological findings as well as opportunities for food product formulation, whilst also highlighting the gaps in the current knowledge particularly relating to gut microbiome health.

### Plant cell wall structure

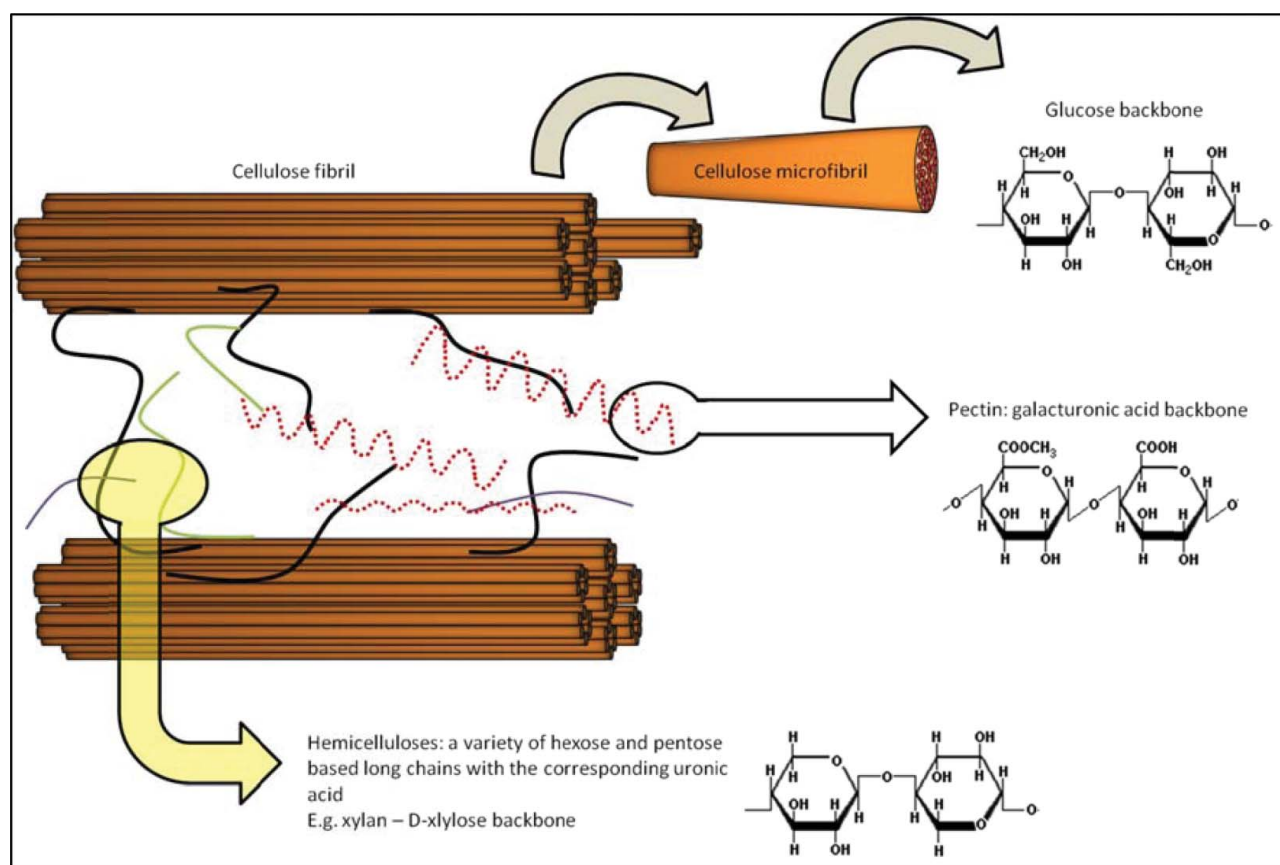
Unlike animal cells, the outer cell membrane of plant cells is completely surrounded by a cell wall which provides structural support to the plant cell (Cosgrove, 2005; Harris and Smith,

2006; Burton et al., 2010; Doblin et al., 2010). The plant cell, like all cells, is a complex system that digests and metabolizes nutrients for energy, stores nutrients and eliminates waste out of the cell in order for continued functioning of the larger organism. Cytoplasm surrounds all components of the cell and creates a turgor pressure which acts against the plasma membrane that forms the boundary of the cell adjacent to the cell wall. The nutrients and energy required by the cell to continue functioning and developing are compartmentalized within the cell (e.g. within the nucleus, vacuole, golgi bodies and ribosomes). Consequently the PCW's role in maintaining the structural integrity of the cell is crucial to the growth, development and survival of the plant as well as directly affecting the textural qualities of edible plant materials (Prasanna et al., 2007). When cell walls are disrupted, for example during eating or food manufacturing, cell components such as polyphenols must pass through the PCW which may result in binding interactions between the PCW and polyphenol compounds (Doblin et al., 2010; Le Bourvellec and Renard, 2012; Padayachee et al., 2012a). It is important to gain an understanding of PCW structure first in order to identify such relationships.

PCWs are classified into two groups; primary and secondary cell walls. Primary cell walls are ubiquitously found in plant tissues, especially the parenchyma cells of food plants. These non-lignified cell walls are initially set in place around the cell allowing room for expansion during the growth stage of the plant (Cosgrove, 2005; Taylor, 2006). However once cell growth has ended, thicker secondary cell walls may then be deposited onto the interior side of the primary wall, providing strength and structural support to the cell (Cosgrove, 2005; Harris and Smith, 2006; Taylor, 2006). Lignified secondary cell walls are generally not present in large amounts in fruits or vegetables as they directly affect the textural qualities and palatability of these foods. For example, the stringiness of asparagus stems can be attributed to the high content of lignified secondary cells as can the distinct grittiness of pears (Harris and Smith, 2006). Indeed, many edible plant tissues are dominated by the primary cell walls characteristic of fleshy plant tissue (Cosgrove, 2005; Harris and Smith, 2006). Cellulose, hemicellulose, lignin and pectin are the key components of the PCW and whilst their proportions differ between individual cell types and plant species, the basic structure and function are generally the same (Cosgrove, 2005; Harris and Smith, 2006).

### Cellulose—Structural supporting rods

Cellulose is the main load-bearing constituent of the PCW and is located within a matrix of hemicelluloses and pectin, and at times lignin (Figure 1) (Cosgrove, 2005; Harris and Smith, 2006; Joshi and Mansfield, 2007). Being one of the most abundant natural biopolymers available, cellulose ( $\beta$ -1,4-glucan) is a polysaccharide made up of hundreds/thousands of glucose monomers (Harris and Smith, 2006; Taylor, 2006). Individual cellulose molecules (10–50) are non-covalently bonded together by lateral alignment to form semi-crystalline cellulose fibers, which are both tough and insoluble, and hence able to resist substantial force and provide support to the plant cells (Taylor, 2006). Cellulose molecules and fibers are held to each other by extensive hydrogen-bonding through—OH groups to



**Figure 1.** The plant cell wall's cellulose-hemicellulose-pectin crosslink network (Adapted from Cosgrove (2005)).

exclude water from between cellulose molecules by forming a secure, firm microfibril (Figure 1) (Taylor, 2006). These microfibrils are extruded out of the cell by a complex biosynthetic assembly that spans the plasma membrane and involves both structural proteins and synthesis enzymes (Joshi and Mansfield, 2007; Morgan et al., 2013). Hemicelluloses may coat and cross-link cellulose microfibrils resulting in a stable cellulosic network that is fairly resistant to enzymatic digestion (Cosgrove, 2005; Doblin et al., 2010). Consequently due to the insolubility and strength reinforcing properties of cellulose, the PCW is able to resist the action of turgor pressure within the cell preventing osmosis and cell rupture (Huxley and Walter, 2007; Doblin et al., 2010).

### Hemicelluloses

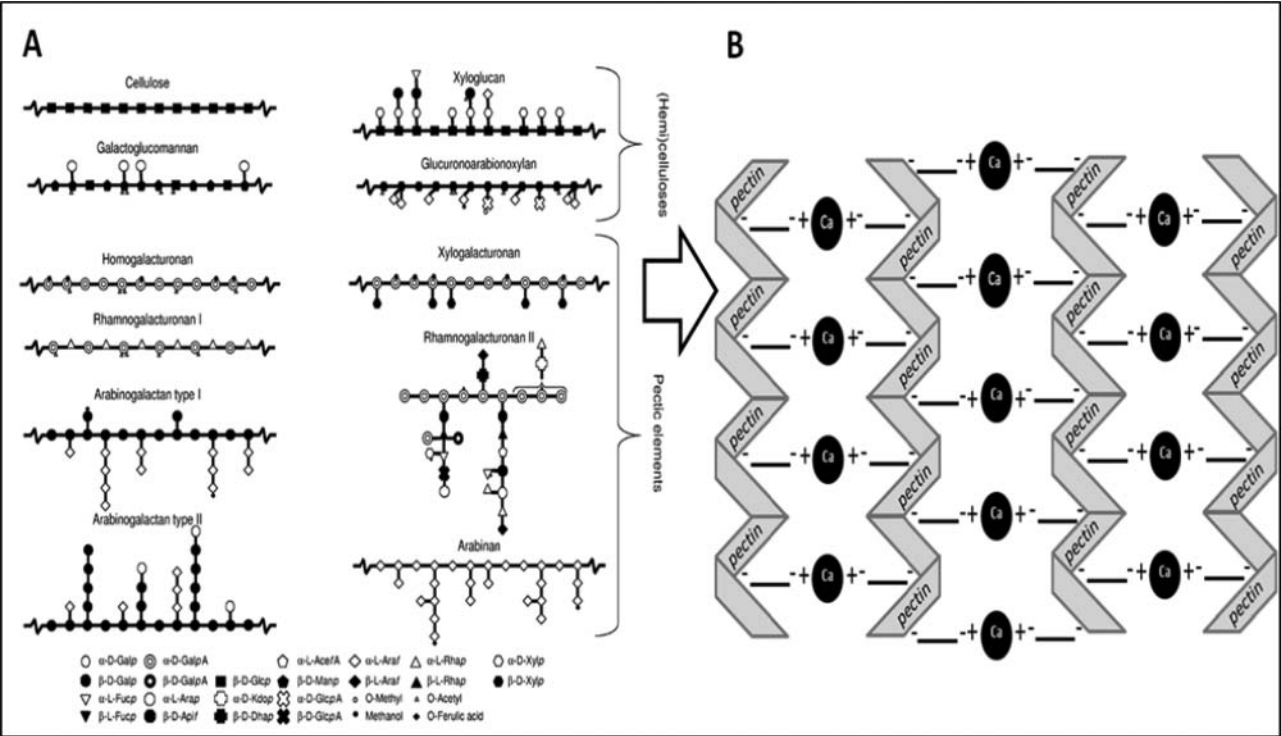
Hemicelluloses are a key non-cellulosic component of both primary and secondary cell walls. Unlike cellulose which is composed entirely of glucose molecules, hemicelluloses may be composed of glucose, xylose, mannose, rhamnose, galactose and/or arabinose (Carpita, 1984; Ebringerova et al., 2005). Xylose and glucose are often the most abundant monomers in hemicelluloses (Figure 1). Therefore hemicelluloses are categorised into four groups: xylans, xyloglucans, mannans and mixed linkage  $\beta$ -glucans (Ebringerova et al., 2005). As hemicelluloses are branched, amorphous polymers, they do not possess the strength properties of the crystalline-structured cellulose polysaccharide. Rather hemicellulose

performs the role of bridging cellulose and pectin together thereby aiding the formation of a cross-linked network structure (Figure 1) (Carpita, 1984; Cosgrove, 2005; Wang and Dixon, 2012).

### Lignin

In conjunction with cellulose and hemicellulose, lignin is also involved in maintaining cell structural integrity by also imparting resistive rigid strength. Lignin is involved in controlling water permeability into the cell by aiding in the transportation of water and solutes into and out of the cell (Boerjan, 2003; Ralph, 2010; Vanholme et al., 2010). Lignin is a heterogeneous set of polymers derived from hydroxycinnamic acids, namely *p*-coumaryl, coniferyl and sinapyl acids. These precursors produce *p*-hydroxyphenyl (H), guaiacyl (G) and syringyl (S) phenylpropanoid units which are integrated into the lignin polymer (Boerjan, 2003; Ralph, 2010; Vanholme et al., 2010). Lignification (i.e. lignin deposition) of the PCW generally takes place during the secondary cell wall thickening phase and is an effective de-watering mechanism that imparts rigidity but reduces plasticity of PCWs. Lignin is deposited in layers, sandwiched between sheets of matrix polysaccharides (usually cellulose and hemicelluloses). However the composition of lignin and concentration in the PCW varies between plants and is affected by environmental and developmental factors (Boerjan, 2003; Ralph, 2010; Vanholme et al., 2010).





**Figure 2.** Pectin structural complexity: (A) Pectin structures; (B) Pectin-Ca<sup>2+</sup> egg-box model of Ca<sup>2+</sup> binding with pectin strands forming a gel structure. (Adapted from Hilz (2007) and Morris et al. (1982)).

**Pectin—Roles in tensile strength and flexibility**

Pectin is a very important component of the PCW, especially the primary cell wall, as it can directly affect cell shape and size (Schols and Voragen, 2002). Being derived from the Greek word “pectos” meaning “gelled,” pectin imparts tensile strength and increases the flexibility of the rigid cellulose based PCW (Figure 2) (Prasanna et al., 2007). Pectin compounds are particularly enriched in the middle lamella between cells and its gelling properties may be important in linking cells together. Consequently during ripening or microbial digestion of plant material, pectolytic enzymatic degradation leads to cell separation as the pectin compounds are degraded resulting in disintegration of the middle lamella (Prasanna et al., 2007).

Unlike cellulose that is exclusively composed of chains of glucose molecules, pectin has a complex structure composed of up to 17 monosaccharides with more than 20 different linkages (Figure 2) (Voragen et al., 2009). There are three categories of pectin based on the method of extraction: water soluble pectins, chelator (calcium) soluble pectins and protopectins that are extracted via alkali or hot dilute acid solutions (Schols and Voragen, 2002; Prasanna et al., 2007). Pectins have a block structure with two distinct domains of polysaccharides, namely linear homogalacturonan (composed of D-galacturonic acid) and branched “hairy” rhamnogalacturonan I or II (composed of D-galacturonic acid, and L-rhamnose), but may also contain xylogalacturonan, apiogalacturonan, arabinan and/or arabinogalactan I or II (containing the neutral sugars D-xylose, D-galactose and L-arabinose) (Figure 2) (Schols and Voragen, 2002; Harris and Smith, 2006; Voragen et al., 2009). The relative

proportion and distribution of these polysaccharide families in conjunction with the number of free carboxyl groups in the homogalacturonan component determines the properties of pectin found within PCW material. Consequently these differences affect the functionality of the pectin impacting the textural qualities of fruits and vegetables. In general the pectin content of vegetables and fruit is approximately 35%, but may be higher in certain fruits (Prasanna et al., 2007; Voragen et al., 2009). The degree of methyl esterification (DE) of carboxyl groups is commonly used to differentiate pectins and represents the percentage of galacturonic acid (GalA) residues that are in the uncharged methyl ester form (Prasanna et al., 2007). The DE of pectin varies between plant species, plant tissues and throughout the development of the plant and it directly influences the firmness and adhesion of cells for example through calcium cross-linking of low DE regions within pectins. For example, during maturation a mango will develop from a hard fruit to a soft, pulpy ripe fruit as the pectin in the middle lamella degrades over time (Prasanna et al., 2007).

Pectin is also used extensively as a stabilizing ingredient in processed foods (e.g. jam, marmalade, jelly, confectionery and certain dairy products) due to its gelling and adhesive properties (Voragen et al., 2009). Commercial pectin is generally extracted from citrus peel or apple pomace, the by-product material of juice processing (CP Kelco, 2011). The acidic conditions typically used to extract pectins commercially remove most of the side chain arabinans and galactans. The DE is deliberately manipulated either during or after extraction. As with plant tissues, DE affects the functionality and textural qualities of processed foods (Voragen et al., 2009).

### Microstructure of the plant cell wall matrix

Primary PCWs characteristic of edible fruits and vegetables contain approximately similar amounts of cellulose and pectin at 20–40% each of PCW dry matter. Water is generally the major component of PCWs as the total dry weight content of fleshy fruit and vegetable tissue is typically 8–14% (w/w) (Prasanna et al., 2007). Research into PCW architecture and development suggest that direct interaction between pectin and cellulose polymers do not occur. Rather, the two polymers are thought to form an inter-penetrating network, that is each polymer forms a network that is entangled with, but not directly attached to, the other network (Figure 1) (McCann and Roberts, 1991). The “egg-box model,” as proposed by Morris et al. (1982), describes the pectin gel network (Figure 2). Basically in the presence of calcium, ionic binding between calcium (divalent) and GalA (monovalent) residues from two separate chains is formed resulting in a stable gel (Morris et al., 1982; Voragen et al., 2009). Low DE pectins particularly favor this type of pectin network formation, whereas very highly esterified pectin (DE > 85) does not gel as there are insufficient charged carboxyl groups available for calcium cross-linking. A second gel mechanism of the high DE (55–75) pectins is through hydrophobic interactions in solutions with soluble solids content greater than 60% due to sugar and water binding together causing association between pectin strands to occur. Clearly not only do PCW have an important functional complex role in plant tissues and processed foods, they are also important in human nutrition as they are a major source of DF (Zhong and Ye, 2007).

### Physical and physiological properties of cell wall fiber

#### Soluble and insoluble dietary fiber

DF can be subdivided into either insoluble or soluble fiber based on chemical, physical and functional properties (McCleary et al., 2012). Insoluble fibers are those fiber (non-starch) polysaccharides that are essentially insoluble in water and gastric-intestinal fluids. As humans do not have enzymes to break down PCW fibers, they travel through the upper gastrointestinal digestive tract (GIT) reaching the colon largely intact. Insoluble fiber is typically present as relatively dense particles which resist penetration by colonic microbiota and therefore show a strong resistance to fermentation by gut bacteria enabling DF to play a major role in bowel scouring, promotion of healthy colonic epithelia, and bulky stool development. Insoluble fiber often contains a high proportion of insoluble cellulose and lignin polymers. Soluble fibers can be swollen or dissolved in water to form viscous solutions or gels. They also resist gastro-intestinal enzymatic digestion and bypass the small intestine to reach the colon. Compared to insoluble fibers, soluble fibers are more readily fermented by the microflora of the large intestine (Brownlee, 2011; Mikkelsen et al., 2011). Pectin is a major soluble fiber component in the PCW, particularly in fruits and vegetables. Whilst insoluble fibers have only limited physiological effects in the upper GIT, soluble fibers can impact on passage rate, rheology, and interactions with digestive enzymes and bile salts in the stomach and small intestine. Thus, both insoluble and soluble fibers play important roles in

digestive health. It is, however, important to realize that “soluble” and “insoluble” are crude measures of a spectrum of physical properties, and that many fruits and vegetables contain components and microstructures that contribute to effects associated with both soluble and insoluble fiber. Although there are some generalities that link molecular composition to fiber solubility (e.g. lignin and insoluble fiber; pectin and soluble fiber), cellulose and hemicellulose components contribute to both soluble and insoluble fiber properties. Thus the physiological effects of PCW fibers are predominantly dependent on its physical properties and do not directly relate in any simple form to their chemical composition (Eastwood and Morris, 1992).

### Physical properties of PCW

Many extracted PCW fibers are hydrophilic and have a natural affinity for water, which makes them ideal candidates as viscosifiers and thickeners of many manufactured foods (Harris and Smith, 2006). From a rheological view point, intact hydrated PCWs can be seen as colloidal dispersions of irregular deformable particles. The viscosity of PCW fibers is due to physical interaction between fiber particles which are strongly associated with PCW fiber microstructure (i.e. fiber particle shape and size distribution). Other factors that influence the rheological properties of fiber dispersions include fiber concentration, particle deformability, particle–particle interactions and hydrodynamic forces arising from the relative motion of particles to the surrounding fluid (Stokes and Frith, 2008; Fischer and Windhab, 2011). Many studies have investigated the rheological behavior of PCW fibers from a variety of fruit and vegetable sources, for example, carrot, broccoli, tomato, apple, kiwifruit, peach, blueberries, etc. (Yoo and Rao, 1994; Valencia et al., 2003; Kunzek, 2006; Bayod et al., 2007; Redgwell et al., 2008; Day et al., 2010a; Day et al., 2010b; Augusto et al., 2011; Kechinski et al., 2011). These studies have shown dominant elastic properties that are dependent on the concentration, stiffness and elastic properties of the solid phase, which is largely controlled by the interactions between the solid particles and deformability of PCW fiber particles.

In general, the flow behavior and viscosity of PCW fibers can be modeled by the Herschel–Bulkley model for non-Newtonian fluids with the viscosity in a power law model as a function of fiber concentration (Krokida et al., 2001; Lopez-Sanchez and Farr, 2012). Recent studies show that the particle size and morphological structure plays an important role in PCW fiber viscosity (Day et al., 2010a; Day et al., 2010). PCW fiber dispersions derived from carrot and broccoli stem tissues exhibit an elastic but weak gel-like rheological behavior within a wide range of particle concentrations (0.5% to 8%). The particles can form colloidal networks at relatively low fiber concentration (~1–2 wt%). Once the fiber concentration reaches an interactive critical threshold (e.g. in the range of 2–4 wt%), interaction between particles leads to a sharp increase in the rheological properties of the dispersion via a power law relationship to the effective volume fraction of the fiber. However, once the interactive critical threshold level has been reached, any further increase in the concentrated packing volume results in increased packing of the particles thus affecting the shape of

fiber particles due to a “jamming” effect similar to concentrated emulsions and elastic particle dispersions (Day et al., 2010).

In vivo, physical properties of the PCW fiber network may be influenced by additional factors, such as pH, ionic environment and the presence of bile acids in the human gastrointestinal system, as well as the presence of other dietary components. However there is direct evidence that consumption of DF affects the viscosity of human gastric and small intestinal digesta (Dikeman and Fahey, 2006; Dikeman et al., 2006).

### **Modulation of viscosity and transport of nutrients in GI Tract**

The physical properties of hydrated and swollen PCW fiber networks can exert strong influences on the viscosity and water-holding capacity of digesta, and can also induce formation of gels in the stomach (Blackwood et al., 2000; Hoad et al., 2004). While substantial research has been conducted on whole grains and individual soluble fibers such as alginate, inulin,  $\beta$ -glucan, psyllium, gums and pectins (Dikeman and Fahey, 2006; Wood, 2007; Chawla and Patil, 2010; Brownlee, 2011; Fiszman and Varela, 2013), few studies have evaluated the physiological effects of natural PCW fiber matrices. Intervention studies have suggested that both fiber content and structure (originating from the ways fruits and vegetables are prepared) can play a role in the feeling of fullness (satiety) with the potential for reduction in subsequent food intakes, plasma-glucose and serum-insulin (Haber et al., 1977; Moorhead et al., 2006; Flood-Obbagy and Rolls, 2009).

Soluble fibers can increase the viscosity of food digesta in the stomach resulting in delayed gastric emptying and the passage of food from the stomach to the duodenum, and thus altering the (rate of) transport of nutrients to the small intestine (Benini et al., 1995; Marciani et al., 2001; Hoad et al., 2004). Such effects have been demonstrated for pectins in human studies (Schwartz et al., 1988; Iftikhar et al., 1994; Sanaka et al., 2007; Strom et al., 2010). Gums prepared from fruits have also been shown to slow stomach emptying (Dall'Agnol and von Poser, 2000). The ability of fibers to absorb large quantities of water in the stomach also increases stomach distension contributing to an increase in satiety (Darwiche et al., 2003; de Graaf et al., 2004).

Within the small intestine, apart from potentially slowing down the transit of the contents, the increased viscosity caused by fibers can also result in a decrease in both digestion processes and in the rate of nutrient release and absorption (Eastwood and Morris, 1992; Brownlee, 2011). The principal mechanisms involved are: (1) the viscous fiber network or intact plant cells act as a barrier slowing or restricting the transport of digestive enzymes to their substrates and digested products from enzymes to the site of absorption (Schneeman and Gallaher, 1985; Eastwood and Morris, 1992; Gidley, 2013); and (2) physical entrapment of nutrients within the structured fiber assemblies which can reduce the bioaccessibility of compounds, such as vitamins, minerals and other micronutrients (discussed in the following sections). The rate of release of nutrients from fibrous particles is inversely proportional to particle size and also affected by the physical structure of the particle (e.g. its deformability and surface properties) (Guillon and Champ, 2000; Brownlee, 2011). One of the examples of the effect of fiber

inclusion on nutrient release and absorption is the alteration of glucose absorption and hence the glycaemic and insulin secretion responses to a meal (Haber et al., 1977; Jenkins et al., 1980; Iftikhar et al., 1994), partly due to the inhibition of  $\alpha$ -amylase activity on starch whilst slowing the diffusion of glucose through the fibrous matrix is also involved to a certain extent (Gourgue et al., 1992). The inclusion of fiber can also have a major effect on the rate of enzymatic digestion of other macronutrients such as proteins and lipids in the small intestine, for example decreasing pancreatic lipase and protease activities (Pasquier et al., 1996; El Kossori et al., 2000).

However, measurements of digesta viscosity within the human gastrointestinal environment is difficult, and the viscosity of food is not necessarily associated with the viscosity of gastrointestinal contents due to the presence of other dietary and endogenous components, as well as the absorption of water throughout the tract resulting in highly variable local concentrations (Dikeman and Fahey, 2006). The ability of fiber to increase the viscosity or gel strength of ingested food is also affected by the pH variation as well as bile salt concentration upon transit through the GIT. It is the viscosity developed by the food/meal within the digestive tract rather than the viscosity of the meal before ingestion that appears to have the greatest effect in slowing down gastric emptying, etc. (Rainbird and Low, 1986; Hoad et al., 2004; Strom et al., 2010). Gastric gelation using alginate, or a combination of alginate and pectin to slow gastric emptying, can be used to achieve prolonged satiety for weight management (Strom et al., 2010). To date, MRI has been the most successful technique to follow digestion of meals in vivo and has been used to study the effect of meal viscosity on gastric dilution and emptying in relation to satiety (Marciani et al., 2001; Hoad et al., 2004). Although in vitro models provide some understanding of physical characteristics of fibers under physiological chemical conditions and provide relative viscosity values of fibers from different sources (Dikeman et al., 2006), development of more sophisticated and realistic in vitro models, particularly accounting for the diffusion and transport of nutrients, will be beneficial to develop mechanistic understanding of fiber matrix microstructure related to physiological functions.

### **Lipid metabolism and cholesterol lowering properties**

Isolated soluble fiber polysaccharides such as  $\beta$ -glucan and pectins have been shown to lower elevated blood cholesterol levels consequently reducing the risk of cardiovascular disease (Bourdon et al., 1999; Jenkins et al., 2002; Brouns et al., 2012). The currently proposed mechanism involves the binding of bile salts to the viscous fiber in the small intestine which leads to an excess faecal excretion of bile salts and limits its re-absorption. The loss of bile salts forces the body to use blood cholesterol for the synthesis of bile salts to replace those lost due to limited re-absorption (Gunnness and Gidley, 2010). Ingestion of DF can also alter plasma lipid concentrations by reducing emulsification of lipids, lowering the rate of lipolysis and decreasing the rate of diffusion of fatty acids (Gruendel et al., 2007).

Several studies have shown that the ex vivo viscosity of intestinal contents containing modified cellulose is inversely correlated with the lower cholesterol absorption efficiency,



lower plasma cholesterol concentration, and lower liver cholesterol ester content (Carr et al., 1996; Juhel et al., 2011). Modified cellulose has also been shown to affect lipid metabolism by lowering total and low-density lipoprotein (LDL) cholesterol in hypercholesterolemic adults (Maki et al., 2000; Maki et al., 2009). Modified cellulose acts like soluble fiber, as it increases the viscosity of the digesta in the GIT, which is suggested to be a major indicator of the cholesterol-lowering potential of fiber (Knarr et al., 2012). This is also consistent with the demonstration that cholesterol lowering by  $\beta$ -glucan is enhanced at higher molecular weights for the same dosage level (Wolever et al., 2010). The structure of three-dimensional cell walls from various fruit and vegetable sources correlate well with bile acid binding, whereas the proportion of soluble to insoluble dietary fiber was much less (Dongowski, 2007). Therefore it is reasonable to suggest that intact PCW fibers, particularly those that generate significant digestive tract viscosity, may also exhibit cholesterol lowering properties.

### **Dietary fiber laxation effect**

Constipation is a common health condition in developed countries affecting nearly one-third of the population (Beck, 2008) and accordingly is considered to be a “disease of affluence” (Kumar, 2012). It is characterized by incomplete defecation as a result of either infrequent bowel movement, long transit time, difficulty in passing stools, hard/dry stools or a combination of these (Beck, 2008; Kumar, 2012). Constipation has been found to be directly related to low dietary fiber intake, with fluid intake and physical activity as secondary contributing factors. Thus consumption of insoluble, non-starch polysaccharides is often prescribed as the first treatment option for constipation (Beck, 2008). The mechanism of constipation mitigation via DF was proposed by Topping and Illman (1986) as a “roughage” model with non-starch polysaccharides resistant to enzymatic degradation in the small intestine resulting in increased faecal bulk which leads to decreased colonic transit, increased colonic bacteria proliferation and water re-absorption resulting in soft, bulky stools and the promotion of laxation (Beck, 2008; Kumar, 2012). Whole grains and legumes are common sources of non-starch polysaccharides however fruits and vegetables are also notable sources of non-starch polysaccharide plant fiber (Table 1).

### **Small molecule micronutrients associated with fruit and vegetables**

The health benefits associated with fruit and vegetables is due in part to these foods being a rich source of a range of micronutrients, such as vitamins, minerals, and a range of phytonutrients including polyphenols and carotenoids.

#### **Vitamins**

The term “vitamin” is based on two root words, *vita* meaning life and *amine* meaning contains nitrogen (Funk, 1912). Vitamins have been recognised as an essential part of a healthy diet since the early 1900s and even though these organic compounds are only required in <1 g/day quantities, absence in the

diet will result in deficiency disease states. Vitamins differ from macronutrients as they are not broken down to produce energy, but aid enzymes in the production of energy from carbohydrates, proteins and fats; are involved in DNA production; and display anti-oxidant behavior in addition to other functions at the cellular level (Lukaski, 2004; Bourre, 2006). Vitamins are divided into two categories: water soluble and fat soluble vitamins. Water soluble vitamins include the B-group (thiamin ( $B_1$ ), riboflavin ( $B_2$ ), niacin ( $B_3$ ), biotin, pantothenic acid, vitamin  $B_6$ , folate and cobalamin ( $B_{12}$ )) and vitamin C (ascorbic acid), and these vitamins are absorbed directly into the blood stream with water and thus are able to circulate to all parts of the body. However as excess water soluble vitamins are excreted via urine, regular intake is required to prevent deficiency. There are four fat soluble vitamins (A (retinol), D (calciferol), E ( $\alpha$ -tocopherol) and K) which are absorbed via the lymphatic system and may require transportation via protein carriers. Fat soluble vitamins are able to be stored in body fat and therefore do not require continual intake (Lukaski, 2004; Bourre, 2006). Whilst vitamins are sourced from all of the food groups, fruits and vegetables are notable sources of certain vitamins, particularly vitamins C and E, as well as some of the B-group. Inadequate dietary intake of vitamins can result in deficiency health conditions such as beriberi ( $B_1$ ), pellagra ( $B_3$ ), megaloblastic anaemia (folate,  $B_{12}$ ), microcytic anaemia ( $B_6$ ), spina bifida and foetal neural tube defects (folate), scurvy (vitamin C), xerophthalmia (A), rickets and osteomalacia (D) and haemorrhage (K) in addition to impaired immunity, nerve and red blood cell damage as well as other health problems (Lukaski, 2004; Bourre, 2006).

#### **Minerals**

Along with vitamins, minerals are also essential nutrients as insufficient dietary intake and/or impaired absorption will result in deficiency disease states as well. Minerals are categorized into two groups—major and trace. Major minerals are present in the body in large amounts and are also required individually in amounts >5 g per day, in contrast to trace minerals which are required in very small amounts (ca. tens of mg or less) (Bourre, 2006). The major minerals are calcium, phosphorus, potassium, sulphur, sodium, chloride, magnesium. There are over a dozen trace minerals required by the human body; however the more commonly known trace minerals include iron, zinc, copper, selenium and iodine. Unlike vitamins, minerals are inorganic compounds and therefore not prone to degradation. Minerals are also unable to be converted into other compounds in the human body and may be absorbed easily into the blood stream like water soluble vitamins or via the more complex lymphatic system. Nevertheless, minerals may interact with binding compounds (e.g. phytates in spinach bind to iron) that decrease or prevent the absorption of minerals in the body (Bourre, 2006). Minerals are essential in maintaining the body's electrolyte balance; however they are involved in many different processes including bone growth and muscle and nerve functionality. Like vitamins, dairy, meat, whole-grains and fruits and vegetables are a source of different minerals (Murphy et al., 2012).



**Table 1.** Dietary fiber content of common fruits and vegetables (adapted from Slavin (2012) and Kumar (2012).

	Vegetables (per 100 g)				Fruit (per 100 g)		
	Total dietary fiber (g)	Soluble dietary fiber (g)	Insoluble dietary fiber (g)		Total dietary fiber (g)	Soluble dietary fiber (g)	Insoluble dietary fiber (g)
Beetroot	7.8	5.4	2.4	Apple	2.4	0.7	1.7
Cabbage	2.5	0.6	1.9	Grapes	0.9	0.4	0.5
Cucumber	0.6	0.1	0.5	Lemon	2.2	1.3	0.9
Celery	1.6	0.1	1.5	Mango	1.8	0.7	1.1
Lettuce	12.3	0.2	10.5	Peach	2.9	1.3	1.6
Onion	0.9	0.4	0.5	Pineapple	1.5	0.04	1.4
Tomato	1.2	0.1	1.1	Strawberry	2	0.5	1.5

**Polyphenols**

**Biological function**

Bioactive compounds are produced by plants as a response to the environment and are important in conducting a variety of functions in the plant including coloration, attracting pollinating insects whilst also providing some protection from ultra-violet light and hence plant-derived foods such as fruits and vegetables are the main source of polyphenols in the human diet (Naczka and Shahidi, 2006; Nichenametla et al., 2006; Denny and Buttriss, 2007). Furthermore as plant bioactive compounds are generally quite unpalatable, tasting bitter, acrid or astringent, they are able to protect the fruit and vegetable against premature consumption by herbivore predators (Drewnowski and Gomez-Carneros, 2000; Le Bourvellec and Renard, 2012). At high amounts, bioactive compounds can be potentially toxic but display bactericidal and biological activities that are beneficial to the plant. However bioactive compounds are generally found in small amounts in plant products, at non-toxic levels which are beneficial to human health (Scalbert et al., 2005).

The strong epidemiological data supporting preventative health benefits and disease reduction with high dietary consumption of fruits and vegetables has been highly influential in facilitating research into the characterization of the bioactive compounds found naturally occurring in fruit and vegetables. Thus in addition to the “essential” vitamins and minerals, it has become increasingly evident that fruits and vegetables are also the main source of polyphenols and other phytonutrients that provide health benefits through diet (Landete, 2012; Murphy et al., 2012). Whilst vitamins and minerals are essential in preventing deficiency diseases and maintaining specific biochemical processes in the body, phytonutrients are considered to be “conditionally essential” for maintaining health and wellbeing due to their complementary actions (Yoshihara et al., 2010). A lack of polyphenols in the diet will not directly result in a deficiency disease. However these compounds facilitate preventative nutrition, as they have important biological roles in achieving and maintaining optimal cellular health leading to an improvement in longevity. These activities are diverse and include, but are not limited to, antioxidant behavior, promoting phytoestrogen activity, inducing enzymatic activity, activating gene transcription and promoting apoptosis (Clydesdale, 2004; Kiani, 2007; Fukuda et al., 2011; Landete, 2012; Le Bourvellec and Renard, 2012).

**Molecular structure**

As with vitamins and minerals, bioactive compounds are mainly found in the vacuole of the plant cell, however some

polyphenols may be found attached to polymers in the PCW such as lignin and xylan polymers (Le Bourvellec et al., 2009; Le Bourvellec and Renard, 2012). In relation to plants, “polyphenol” is the term used to describe water soluble secondary metabolites which possess an aromatic ring that has more than one hydroxyl groups present, are produced via the shikimate/phenylpropanoid or acetate/malonate pathways or both, and perform physiological roles in the plant (Crozier et al., 2009); consequently there are thousands of individual polyphenols with varying chemical structure and functions (Duthie et al., 2003; Denny and Buttriss, 2007). Phenolic acids, with a single C6 ring formation, are the simplest polyphenol compounds, however structures can be quite complex as demonstrated by the highly polymerized tannins (Bravo, 1998; Duthie et al., 2003). Consequently polyphenols are categorized into groups according to their chemical structure and very rarely will a fruit or vegetable contain only one type of polyphenol compound even though there are some polyphenol families that are predominant only in certain families of fruits or vegetables (Denny and Buttriss, 2007). However polyphenols and carotenoids are the most widely distributed compounds available from fruit and vegetables whereas plant sterols, glucosinolates and organosulfur compounds are less widely distributed (Rechner et al., 2001; Denny and Buttriss, 2007; Cheynier, 2005).

**Flavonoids**

Flavonoids are a complex group containing at least 4000 compounds and can be further categorized into 14 groups based on their chemical structures (Bravo, 1998; Lapidot et al., 1999). A well-studied neutral flavonoid is quercetin, but curcumin (common in turmeric), capsaicin (from chilli peppers) and vanillin (found in the vanilla bean) are other common neutral flavonoids. Unlike all other flavonoids and polyphenols, the anthocyanin sub-family are the only major polyphenols that have a positive charge under acidic conditions. Anthocyanins, a main sub-class of dietary flavonoids, are a large group of over 500 water-soluble compounds (McGhie and Walton, 2007; Arscott and Tanumihardjo, 2010), and are responsible for the intense red, purple or blue colors of vegetables and fruits, including purple/black carrot (Gajewski et al., 2007; Arscott and Tanumihardjo, 2010), purple sweet potato (Harada et al., 2004), red cabbage (McDougall et al., 2007), berries (Basu et al., 2010), and red grapes (including red grape products like red wine and juice) (Frank et al., 2003). Cyanidin and its glycoside are the most common anthocyanins found in plant products. The chemical backbone structure of anthocyanins is a glycosylated,

polyhydroxy or polymethoxy derivative of 2-phenylbenzopyrylium with two benzoyl rings separated by a heterocyclic ring (McGhie and Walton, 2007). Structural variation of the chemical backbone results in over 500 different anthocyanin molecules, the six main anthocyanidin families found in fruits and vegetables are cyanidin, pelargonidin, delphinidin, peonidin, malvidin and petunidin (Welch et al., 2008; de Pascual-Teresa et al., 2010).

### Phenolic acids

Common phenolic acids (PAs) in plants are chlorogenic acid, caffeic acid and ferulic acid, and are sourced from a variety of plant-based food, such as coffee, red wine, apples, pears, berries, tomatoes, purple/black carrots and plums in the human diet (Clifford, 2000; Olthof et al., 2001; Crozier et al., 2009). Based on their skeletal structure, PAs are subdivided into either benzoic acid (C1–C6) or hydroxycinnamic acid groups (C3–C6) (Cheynier, 2005). Hydroxycinnamic acids are ubiquitous in plants (Rechner et al., 2001). The most common hydroxycinnamic acid is caffeic acid (3,4-dihydroxycinnamic acid) followed by ferulic acid (3-methoxy, 4-hydroxycinnamic acid) (Clifford, 2000; Crozier et al., 2009). Chlorogenic acids (3-O-, 4-O- and 5-O-caffeoylquinic acids), also widespread, are formed by caffeic acid ester binding to quinic acid (Clifford, 2000; Crozier et al., 2009).

There is strong but circumstantial evidence on the potential health benefits associated with PA intake. PAs, including caffeic, ferulic and chlorogenic acids, have been found to demonstrate free-radical scavenging activity (Rice-Evans et al., 1996; Lu and Foo, 2000; Landete, 2012). These PAs have also been found to display antimutagenic activity (Yamada and Tomita, 1996; Malta et al., 2012). In agreement with in vitro studies where chlorogenic acids were found to suppress LDL cholesterol oxidation (Thilakarathna et al., 2013), the reduction in plasma LDLs in adults has also been attributed to PA rich apple juice leading to a speculation that PAs may be involved in protection against cardiovascular disease (Hyson et al., 2000). Whilst one study has found high consumption of chlorogenic acid rich coffees resulted in an increase in plasma total homocysteine concentrations, a risk factor for cardiovascular disease (Olthof et al., 2001), there is substantial evidence supportive of the health benefits associated with dietary intake of PAs.

### Carotenoids

Being the only lipophilic bioactive group, carotenoids are pigments biosynthesized and localized in the chloroplasts and chromoplasts of plants, including fruits and vegetables, fungi and bacteria (Sandmann, 2001; Schieber and Carle, 2005). Structurally the end group of carotenoids is generally  $\beta$ -ionone although it may be replaced by oxo, hydroxy or epoxy end groups depending on the carotenoid and are characterized by a series of conjugated double bonds (Sandmann, 2001). These structural features control the bio-activity and color of the compound. In nature, carotenoids are generally found as the thermodynamically stable *trans*-isomers and to a lesser extent *cis*-isomers. However during processing, carotenoids have been found to change to *cis*-isomers, altering their bioavailability and antioxidant capacity, for example, as provitamin A (Schieber and Carle, 2005). Carotenoids that have a  $\beta$ -ionone

end group are the precursors for vitamin A in the body. Due to the lipophilic nature of carotenoids, the presence of fat improves release and uptake of these compounds (Rickman et al., 2007). Furthermore carotenoids synthesized and stored in the chloroplasts are harder to extract due to their interactions with proteins as membrane stabilizers and photoprotective pigments in photosynthetic assemblies (Havaux, 2003). Carotenoids are synthesised in either crystalline structure (e.g. in carrots) or as oil droplets (e.g. in mangoes) with the latter expected to have improved extractability (Schieber and Carle, 2005).

Orange carrots, orange sweet potato, nectarines and mangoes are the most well-known dietary sources of  $\beta$ -carotene (Cinar, 2004; Baldermann et al., 2005). Lutein can be sourced from green leafy vegetables whilst zeaxanthin is found in “yellow” foods such yellow squash, sweet corn and yellow carrots (Gajewski et al., 2007). Watermelon, tomatoes, pink grapefruit and red papaya are some of the greatest dietary sources of lycopene (Schieber and Carle, 2005; Karakaya and Yilmaz, 2007). In line with the antioxidant behavior displayed by many bioactive compounds, carotenoids are able to suppress free radical damage (Christaki et al., 2012).

### Epidemiological, in vitro and In vivo evidence for the beneficial effects of fruits and vegetables

There is a substantial body of epidemiological evidence suggesting a beneficial effect of a high fruit and vegetable intake leading to positive health outcomes (Adams and Standridge, 2006; Landete, 2012). Polyphenolic compounds from fruits and vegetables have been found to elicit strong antioxidant and anti-inflammatory behaviors in the body leading to an improvement in plasma lipids and vascular function which may possibly result in a decreased risk of cardiovascular disease (Ruel and Coulliard, 2007). From epidemiological studies, consumption of anthocyanin rich fruits and/or beverages (such as red wine and red grape juice) have been associated with an inverse risk of developing coronary heart disease and cardiovascular disease (Mink et al., 2007; Sesso et al., 2007; Leifert and Abeywardena, 2008). This may be due to an improvement in vasodilation capacity or flow-mediated dilation following consumption of anthocyanin-containing red wine (Kay et al., 2006; Leifert and Abeywardena, 2008). Extensive research into the chemoprotective benefits of plant-based foods has found that such foods contain polyphenols displaying “anti-cancer” behaviors (Beliveau and Gingras, 2007). Although the bulk of epidemiological studies conducted have shown some decreased risk of cancer associated with a high fruit and vegetable intake (Soerjomataram et al., 2010; Reiss et al., 2012; Ding et al., 2013), a beneficial correlation has not been found in some (Hertog et al., 1995).

Animal and in vitro studies have been used to further establish a positive link between polyphenols derived from fruit and vegetables and cancer development. A positive relationship between polyphenol intake on the control and prevention of tumor growths has been shown (Ding et al., 2013; Beliveau and Gingras, 2007) whilst the development and proliferation of particular cancer cell lines could be inhibited in the presence of plant-derived carotenoids (Molnar et al., 2012; Uppala et al., 2013). High doses of flavonoids have demonstrated chemoprevention retarding

cancer cell growth, inflammation, tumour progression by either targeting cell signal pathways (Hou et al., 2003; Hou et al., 2004; Ding et al., 2013) or directly interacting with mammalian enzymes and growth receptors in the inhibition of carcinogen metabolic pathways (Kay and Holub, 2006; Mazza and Kay, 2008) in addition to demonstrating a broad range of biological properties including antioxidant, anti-inflammatory, antimicrobial, and anticarcinogenic activities in *in vitro* and animal studies (Lu and Foo, 2000; Madhujith and Shahidi, 2003; Mazza and Kay, 2008; Basu et al., 2010; Ding et al., 2013). Furthermore anthocyanins and PAs have been found to decrease the progression of oxidative stress, cellular inflammation (Youdim et al., 2000; Serraino et al., 2003; Liu et al., 2008), LDL oxidation and reduce LDL plasma concentration (Hyson et al., 2000; Peng et al., 2011), all risk factors for cardiovascular disease development.

Neurological behavior has been reported to improve with the dietary intake of fresh blueberries and strawberries, high in anthocyanins, resulting in a decrease in age-related cognitive and behavioral deficiencies (Joseph et al., 1999) whereas blueberry extract was associated with a decrease in the development of Alzheimer's disease (Joseph et al., 2003) and common PAs have been found to display antimutagenic activity (Malta et al., 2012; Ding et al., 2013).

Despite these diverse *in vitro*, *in vivo*, and epidemiological lines of evidence, it is not clear what the consequence of delivering vitamins, minerals, polyphenols, carotenoids and other bioactive plant-derived compounds in whole plant foods is compared with individual functional ingredients taken as a supplement or added to fortified foods. The main difference between these two delivery mechanisms is the presence of PCWs in whole plant-based foods, with the consequent potential for controlling the rate and site of release of bioactive components.

### PCW structures affects bioaccessibility

Food composition data alone provides limited information with regard to nutritional effects as the physical state and structure of foods directly affect the bioaccessibility and bioavailability of nutrients (Aguilera, 2005; Parada and Aguilera, 2007; Visioli et al., 2011; Le Bourvellec and Renard, 2012). In order for plant-based polyphenols to exert beneficial effects in the body, they must first be released from the plant matrix and available for absorption (termed bioaccessibility) (Hedron et al., 2002; Palafox-Carlos et al., 2011; Le Bourvellec and Renard, 2012) before absorption and metabolism from the gastrointestinal tract into the blood stream where they can exert biological functions can occur (termed bioavailability) (McGhie and Walton, 2007; Palafox-Carlos et al., 2011; Visioli et al., 2011).

Direct interactions with polysaccharides of the PCW may occur during mastication and/or processing and these interactions may affect the bioaccessibility of polyphenols (Perez-Jimenez et al., 2009; Palafox-Carlos et al., 2011; Saura-Calixto, 2011; Visioli et al., 2011; Le Bourvellec and Renard, 2012). Structural properties of raw fruits and vegetables are altered with the application of processes such as blanching, boiling, cooking, pureeing, homogenization, juicing and canning. Although these processes are applied in order to create food products with increased shelf life by eliminating enzymes and

microorganisms that can cause spoilage, textural changes due to cell wall denaturation inevitably occur (Ormerod et al., 2004). Textural changes are brought about by the softening and rupture of the fibrous cell wall in fruits and vegetables allowing plant cells to split apart from each other resulting in a variety of structures such as pastes and purees as well as intact tissue pieces which may have beneficial or detrimental effects on different aspects of the nutritional profile of these foods. Nevertheless the effect of polyphenols and fiber on health in a combined form is not well established (Palafox-Carlos et al., 2011). Consequently in order to assess the bioavailability of polyphenol and micronutrients from fruits and vegetables, the role of the PCW and food matrix structure in controlling the rate of polyphenol release from the cell during the digestive process must be established first.

Factors affecting the bioaccessibility of polyphenols from food materials are not well understood even though bioaccessibility affects the bioavailability of polyphenols derived from fruits and vegetables and hence directly impacts on the possible health effects these compounds may have *in vivo* (Perez-Jimenez et al., 2009; Palafox-Carlos et al., 2011). Likewise the effect of polyphenols and fiber on health in a combined form is not well established (Palafox-Carlos et al., 2011). Consequently in order to assess the bioavailability of polyphenol and micronutrients from fruits and vegetables, the role of the PCW and food matrix structure in controlling the rate of polyphenol release from the cell during the digestive process must be established first.

The food matrix is an important factor that affects the bioaccessibility of carotenoids (Gartner et al., 1997; Dutta et al., 2005). Within the matrix, intracellular location is one aspect that is involved in polyphenol release. For example,  $\beta$ -carotene is located in the chloroplasts of leaves and the chromoplasts of fruits and vegetables. The bioavailability for  $\beta$ -carotene was found to be higher for carrots and broccoli (up to 34% and 24%, respectively) than green leafy vegetables (6%) which indicates greater disruption of chromoplasts during GI digestion and therefore improved bioavailability (Dutta et al., 2005). A study comparing lycopene bioavailability from fresh tomatoes and tomato paste found that while both fresh tomatoes and tomato paste had the same lycopene isomer pattern, 2.5 times more lycopene was detected in human chylomicrons after ingestion than fresh tomato (Gartner et al., 1997). Likewise consumption of homogenized cooked tomatoes produced significantly greater lycopene,  $\beta$ -carotene and antioxidant activity in human triglyceride-rich lipoproteins and blood plasma than mildly or non-homogenized tomatoes (van Het Hof et al., 2000). Similar results were also found in a recent study assessing bioavailability of carotene from cooked, raw and juiced carrots (Tydeman et al., 2010). Tydeman et al. (2010) found the extensive rupture of the PCW during juicing resulted in greater bioavailability of carotenoids, yet heat treatment did not improve bioavailability from intact cells. Therefore in order to improve bioavailability, degradation of the PCW due to shearing and cell rupture is essential with heat treatment potentially enhancing release from ruptured cells. Consequently this provides fewer constraints for polyphenols and they are able to be liberated easily from broken plant cells thus enhancing the bioaccessibility of carotenoids from the plant cell resulting in



improved bioavailability (Gartner et al., 1997; van Het Hof et al., 2000; Dewanto et al., 2002; Tydeman et al., 2010). Although oxidative and hydrolytic enzymes are also released during disruption of the plant matrix, they can be deactivated with the application of heat (Dewanto et al., 2002).

Studies into the bioavailability of water soluble polyphenols from various food matrices are extensive, yet the effect of the food matrix on the bioaccessibility of water soluble polyphenols has also been investigated to a lesser extent (Yang et al., 2011). From Yang et al. (2011) review on the food matrix's affect on anthocyanin bioavailability it is apparent that due to the variability in anthocyanin bioavailability from various foods (e.g. whole berries, berry juice, wine, puree, jam, powders) not only is anthocyanin structure a factor affecting bioavailability, but the food matrix and interactions with the PCW has a significant role in the release of anthocyanins. In vitro assessment of the bioaccessibility of grape polyphenols found that polyphenols released in the liquid phase were bioaccessible, polyphenols that were trapped or interacted with the PCW were not readily bioaccessible but able to be partially extracted during in vitro gastric and SI digestion due to the mechanical action and acidic environment of the stomach which enabled weakly bound polyphenols to be released (Tagliazucchi et al., 2009). Conversely homogenization, cell rupture and thus exposure to oxygen can result in polyphenol degradation (Le Bourvellec and Renard, 2012) as Ochoa et al. (1999) found by assessing the effect of raspberry processing on anthocyanins.

### **Binding affects nutrient absorption (bioaccessibility)**

From studies into the polyphenol release from whole carrot puree, apple and grape pomace, by-products of apple juice and wine manufacture, as well as polyphenol release during tea steeping, it is clearly evident that polyphenol interactions with the PCW occurs during fruit and vegetable processing. Apple pomace has been found to contain a high content of polyphenols (Lu and Foo, 1997; Lu and Foo, 2000; Vendruscolo et al., 2008; Ibrahim et al., 2011). Sulfite-containing water or alcohols have been used to extract anthocyanins from wine by-products (Metivier et al., 1980; Bocevskaja and Stevcevska, 1997; Ayed et al., 1999). Furthermore it has been found that enzymatic degradation of the PCW has also led to recovery of polyphenols from grape pomace (Meyer et al., 1998; Kammerer et al., 2005). The plant matrix in tea leaves is believed to affect extraction of soluble compounds from tea by providing "physical restraints within the leaf matrix" (Price and Spitzer, 1993). Likewise Zimmerman and Gleichenhagen (2011) also found the leaf structure to be a possible factor affecting polyphenol release as green tea steeped in a low pH solution (pH < 5) at the highest temperature (100°C) for the longest period of time (7 min) had the greatest polyphenol release. A low pH is believed to improve polyphenol extraction by improving the stability of polyphenols whilst simultaneously encouraging structural degradation of the leaf. The high temperature may also contribute to leaf degradation (Zimmerman and Gleichenhagen, 2011).

Polyphenol content of fruits and vegetables are based on the fraction that can be extracted using an aqueous organic solvent yet according to Arranz et al. (2009), this information is limited and underestimates the true polyphenol content, as the non-

extractable polyphenols remaining bound are not taken into consideration. Using acid hydrolysis, Arranz et al. (2009) was further able to extract polyphenols from PCW matter proving the underestimation of polyphenol content in fruits commonly reported, and reinforcing the fact that polyphenols are able to interact with PCW components (Saura-Calixto, 1998; Renard et al., 2001; Arranz et al., 2009; Saura-Calixto, 2011). Saura-Calixto (1998) found that antioxidant-rich dietary fiber, obtained from red grape skins, demonstrated a high antioxidant capacity in preventing lipid oxidation when compared to DL- $\alpha$ -tocopherol (vitamin E). However the author did conclude that the effect in vivo would be dependent on the bioavailability of the polyphenols. It has been shown recently in an ileostomy study that greater delivery of polyphenols to the ileostomy bag (and therefore the colon of healthy individuals) occurred after ingestion of apple smoothie in comparison with cloudy apple juice or apple cider (Hagl et al., 2011). Admittedly the apple smoothie comprising 60% cloudy apple and 40% apple puree had a higher polyphenol content than plain cloudy apple juice or apple cider, but the smoothie also contained more PCW matter which was able to bind available polyphenols. Whilst this reduced the bioavailability of polyphenols in the S.I., increased polyphenolic passage to the colon was predicted.

### **Molecular Interactions**

During plant cell breakage, the cell wall, polyphenols, micronutrients and enzymes are able to come into contact with each other for the first time. Renard and co-workers (2001, 2012) have studied polyphenol-PCW interactions in apples, particularly focusing on procyanidin. By extracting and purifying procyanidin from apple material and then reintroducing it to the original PCW material through a binding experiment, they were able to establish the binding mechanisms between procyanidin and the PCW. From this early study, it was concluded that specific PCW polysaccharides may not contribute to binding interactions, but rather hydrogen bonding and even some hydrophobic bonding may have been the driving factors. A subsequent study on the non-covalent bonding between procyanidin and apple cell walls supported this (Le Bourvellec et al., 2004; Le Bourvellec and Renard, 2012; Le Bourvellec et al., 2012).

In addition to the expected binding by polyphenols stacking on cellulose surfaces, binding interactions with other cell wall components have also been examined. Le Bourvellec et al. (2004, 2005, 2009, 2012) studied procyanidin-polysaccharide binding in apple pomace and showed that individual polysaccharide constituents of the PCW had different rates and extents of binding with procyanidin, favoring pectin over cellulose. This may be due to charge interactions and/or the presence of hydrophobic cavities in the pectin gel (Le Bourvellec et al., 2005; Le Bourvellec and Renard, 2012). Likewise Watrelot et al. (2013) also found whilst interactions between procyanidins of varying degrees of polymerization and pectin occurred, hydrophobic interactions between high DE pectins and highly polymerized procyanidins were stronger. Similar results have also been found with anthocyanins and pectin as well (Padayachee et al., 2012b). At a typical fruit or vegetable pH of ~4–4.3, anthocyanins carry a slight positive charge (Lapidot et al., 1999; Welch et al., 2008) whereas phenolic acids and pectin are



slightly negatively charged (Giacomelli et al., 2002; Ogawa et al., 2004; Almajano et al., 2007; Erdemgil et al., 2007). Interestingly increasing pectin content resulted in increasing binding between anthocyanins and PCW analogues while PAs had varying rates of binding in the presence of negatively charged pectin (Padayachee et al., 2012a).\*\*\*

### Concentration and rate effects

Interactions between polyphenols and the PCW occur with many contributing factors such as PCW concentration, PCW constituents, ionic interactions as well as polyphenol concentrations. Using Langmuir isotherms, Le Bourvellec et al. (2007, 2012, 2012) were able to demonstrate with increased concentration of available procyanidin, greater binding to PCW material occurred up to a predicted capacity of the order of 0.5 g/g. Conversely, maintaining a constant concentration of procyanidin but increasing the amount of cell wall material also resulted in a decrease in free procyanidins in solution (Le Bourvellec et al., 2007; Le Bourvellec and Renard, 2012). Padayachee et al. (2012b) also found that available polyphenolic concentration was a factor that affecting the extent of binding to pure cellulose or cellulose/pectin composites. Doubling the concentration of available anthocyanins in solution led to at least twice as much anthocyanins binding with PCW components suggesting that anthocyanin–PCW interactions are not limited to available binding sites. Although the binding capacity appears to be high, the kinetics of interaction is not uniform, but rather rapid initial binding occurs with slower additional deposition occurring over time on the hours to days timescale. It is possible that initial rapid interactions are directly between polyphenols and PCW components, with subsequent slower increases in binding being due to stacking of polyphenols onto other polyphenols over time (Padayachee et al., 2013).

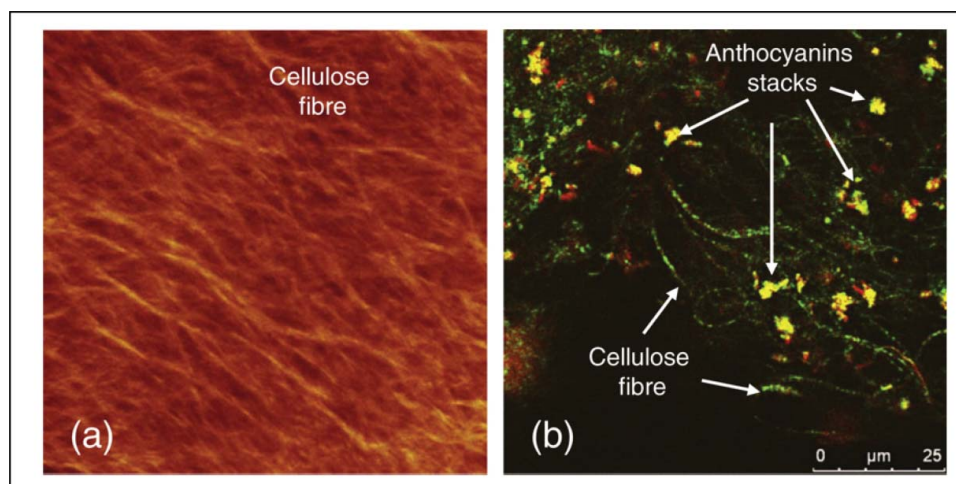
### Polyphenol stacking

The dense but porous structure of PCWs such as apple pomace may allow only limited access of procyanidin molecules to bind. If access of polyphenols to PCWs limits the rate of binding, the pore size of the matrix and molecular weight of procyanidin should both contribute to this size

exclusion effect, which may be an integral part of determining polyphenol–PCW binding and a precursor to the involvement of polyphenolic “stacking” in polyphenol–PCW interactions (Le Bourvellec et al., 2004). In this model, initially small molecules penetrate into the matrix. This is followed by larger procyanidin molecules aggregating on top rather than a universal spread (monolayer) of polyphenol binding across the cell wall material (Renard et al., 2001; Le Bourvellec et al., 2004). A similar phenomena was found with anthocyanins derived from black carrot juice forming clumps on bacterial cellulose strands and intact cell black carrot cell walls in a recent study by Padayachee et al. (2012). Furthermore, confocal analysis of the composites was able to capture anthocyanin stacks on the individual bacterial cellulose strands (Figure 3). This is consistent with initial direct anthocyanin binding with cellulose with slower subsequent stacking of additional anthocyanins over time.

### Polyphenol interactions with other PCW components

Polyphenols have also been found to be able to affect the properties of the protein constituents of the plant cell wall resulting in decreased protein digestion as well as affecting the bioavailability of polyphenols (Baxter et al., 1997; de Freitas and Mateus, 2002; Wu et al., 2011; Le Bourvellec and Renard, 2012). Recently, Wu et al. (2011) characterized the interaction between polyphenols derived from tea and  $\beta$ -glucan derived from oats and proposed the presence of strong H-bonds. It was found that these tea polyphenol– $\beta$ -glucan complexes displayed oxygen scavenging activity indicative of antioxidant behavior. During the wine making process Bindon et al. (2010) found that procyanidins which had become bound to PCW material were difficult to extract due to hydrolysis-resistant interaction with lignin, a plant structural polymer. Furthermore tannin structure, PCW structure (i.e. polysaccharide and lignin composition), binding interactions with the PCW affected the development of strong hydrophobic H-bonds between the polysaccharide and the PCW during wine making (Bindon et al., 2010; Le Bourvellec and Renard, 2012).



**Figure 3.** Confocal microscopy of bacterial cellulose unexposed and exposed to x400 diluted purple carrot juice concentrate: (a) unexposed cellulose; (b) anthocyanin bound to cellulose strands after 24 h incubation; (Adapted from Padayachee et al. (2012)).

### Staining mechanism

From a non-nutritional perspective, yet very similar to the PCW and polyphenolic interactions, berries, a major source of purple-blue anthocyanins, have been used for centuries as a natural dye to color fabric including cotton, which is primarily composed of pure cellulose. Whilst dying, staining and stain removal have been extensively researched, conclusive evidence of the binding mechanism is still lacking, although it is believed that H-bonding, dipolar forces and non-specific hydrophobic interactions are responsible for the staining interactions between non-ionic and positively charged colored ions (e.g. cyanidin) which is enhanced under acidic conditions (Kissa et al., 1991; Holme, 2002) as shown with e.g. coffee staining. Colorless PAs decrease pH and form complexes with colored species thereby aiding in the staining mechanism (Kissa, 1995) whilst also interacting with cellulose via non-ionic Van der Waals or dispersion forces (Kissa, 1995). Furthermore the hydroxyl groups of staining colorants are hypothesized to form H-bonds with cellulose fibers (Saura-Calixto, 2011).

A recent study assessing the extent of release of polyphenols bound to the PCW of black carrots after simulated gastric and SI digestion examines this phenomena. According to Padayachee et al. (2013), the similar binding and extractability behavior of anthocyanins and PAs indicate that binding mechanisms for these polyphenol groups are inter-related. Investigations into binding interactions with PCW components using bacterial cellulose and pectin composites as well as whole carrots found that binding between anthocyanins and PAs with PCW components is initially rapid with deposition due to hydrophobic and H-bond interactions mainly with cellulose (Welch et al., 2008; Padayachee et al., 2013) whereas binding with the negatively charged pectin seems to be more easily disrupted. Accordingly it has been proposed that anthocyanins and PAs stain PCW fibers via a 3-stage deposition mechanism. During initial contact between PCW components and polyphenolic substances (e.g. anthocyanins and PAs), rapid, kinetically controlled randomized adsorption occurs (Figure 4A). Subsequent additional deposition is envisaged to occur on top of the initially bound polyphenols (Figure 4B), and in a third stage, rearrangements occur favoring formation of localized anthocyanin/PA complexes (Figure 4C). Confocal analysis of PCW material provides evidence for such localized deposition (Figure 3; 5) (Padayachee et al., 2013).

### Microbial fermentation of PCW components and their health effects

The human gut contains a large and diverse microbial community, with trillions of microbes present (Lozupone et al., 2012). The lower digestive tract receives food that has been modified during upper gastrointestinal digestion as well as food components resistant to digestion, such as the PCW. As a result, microbial communities of the large bowel are able to interact with and ferment PCW components (digested and undigested) thereby contributing to nutritional absorption, the functionality of plant fiber and human health.

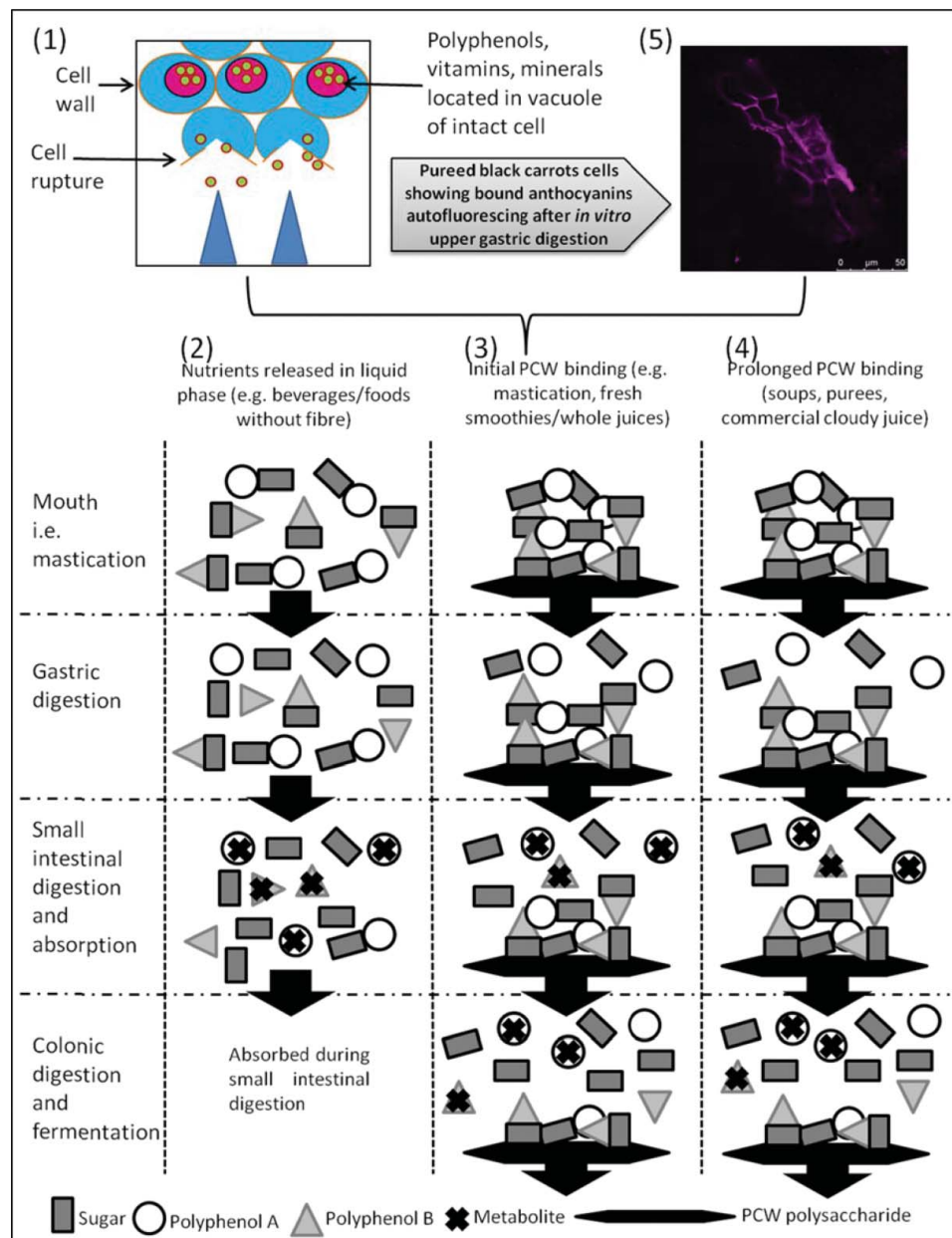
### Microbial diversity in the human gut

The use of high-throughput pyrosequencing has expanded our knowledge of the microbial populations present in the human gut, and how dietary intake and/or the presence of disease affect this composition. Whilst the diversity of gut bacteria differs over time (Lozupone et al., 2012), it does consist of a few core “phylotypes” which contain bacteria belonging to just a few phyla (Arumugam et al., 2011). *Bacteroidetes* and *Firmicutes* are major constituents of the microbiota of most adults, while *Actinobacteria*, *Proteobacteria* and *Verrucomicrobia* form minor proportions of the total bacterial colonies (Eckburg et al., 2005). There are also populations of yeasts, archaea and viruses (Gill et al., 2006). Early studies of human gut microbial diversity indicate that there are distinct patterns and variability amongst different age groups. However more extensive sampling outside of Western societies, encompassing family relationships and geographic distances have shown that there are a few enterotypes common to all humans (Yatsunenko et al., 2012).

Compositional structure of the human gut microbiome may be diverse and changeable, but the functional diversity of the genes and biochemical pathways present provides a broader picture of the gut ecosystem functionality (Clemente et al., 2012; Lozupone et al., 2012). In some cases the metabolic activity of a particular bacterial species can be identified and positioned in the ecological breakdown of human diet components for example, glycan foraging by *Bacteroides thetaiotaomicron* (Sonnenburg et al., 2005). Albeit recent studies have mined genes to predict functionality of the microbiome as a whole (Yatsunenko et al., 2012). Microbiomes of infants can be enriched by genes attributable to breakdown of glycans in breast milk and intestinal mucosa, nitrogen breakdown and vitamin synthesis (Yatsunenko et al., 2012). The microbiota of Malawians and Amerindians are more likely to contain alpha-amylase which is involved in breakdown of starch due to their corn-rich diet (Yatsunenko et al., 2012). Nevertheless evidence of genes involved in the breakdown of PCW components and their synthesizing microbes in the human microbiota is scarce.

### Fiber fermentation and metabolites

Diets rich in fiber, resistant starch and complex carbohydrates produce SCFAs as fermentation products generated by the intestinal microbiota, although they can be produced to a lesser degree by dietary protein, mucus, sloughed cells and gastrointestinal secretions (Cook and Sellin, 1998). SCFAs (containing 1–6 carbon atoms) are produced as metabolites particularly from the activities of the clostridial clusters IV and XIV of the *Firmicutes* and include primarily acetate and propionate, with lesser amounts of butyrate, and even lower amounts of isobutyrate, 2-methylpropionate, valerate, isovalerate and hexanoate (Scheppach, 1994; Wong et al., 2006; Samuel et al., 2008; Chassard et al., 2012; Nicholson et al., 2012). SCFAs are absorbed and metabolized, and are therefore able to contribute to the energy yield of the foodstuff ingested (Macfarlane and Macfarlane, 2012). Up to 95% of the SCFAs produced are absorbed in the large intestine (Cummings et al., 1987). Cellular uptake is via two mechanisms: the first being passive diffusion of the protonated



**Figure 4.** Upon consumption or processing of fruit and vegetable material plant cells are ruptured, allowing for release of polyphenols (1, 2) or interaction with the PCW. Rapid initial binding (3) or prolonged PCW binding (4) results in minimal release from the PCW during gastric and S.I. digestion (5). Whilst some metabolite production occurs in the SI, strong PCW-binding enables polyphenols to be trafficked through the upper GIT to the colon where partial release and modification to produce absorbable metabolites by gut bacteria may occur. (Adapted from Padayachee et al. (2013)).

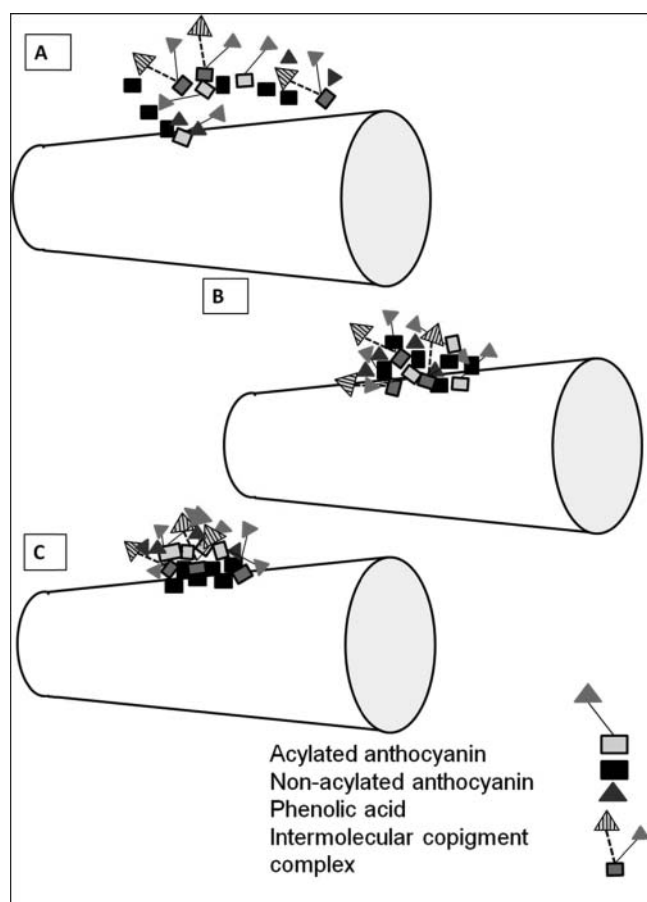
SCFAs and the second via anion exchange (Cook and Sellin, 1998). After uptake, the metabolic fate of the respective SCFA may diverge.

Butyrate is a particularly important fermentation product for its effect in the immediate gut environment, followed by propionate and acetate. Epithelial cells in the colon are able to efficiently convert butyrate to CO<sub>2</sub> and derive up to 70% of their cellular energy by the oxidation of SCFAs (Roediger, 1980). Butyrate also directly influences the metabolic pathways of the gut by affecting cellular growth and metabolism (Macfarlane and Macfarlane, 2012; Nicholson et al., 2012). For example, butyrate influences cellular metabolism to increase lipogenesis from acetyl CoA (Guilloteau et al., 2010) and ketone body synthesis (Roediger, 1980). The presence of SCFAs, particularly butyrate,

is sensed by the G protein-coupled receptors FFAR3 (GPR41) and FFAR2 (GPR43) (Brown et al., 2003). This may then modulate the efficiency of caloric extraction by the human gut by stimulating leptin production in adipocytes (Samuel et al., 2008). Moreover Nicholson (2012) argues that due to the complex interactions of butyrate on the functionality and migration of neutrophils in addition to the ability of butyrate to inhibit cytokine inflammation and chemokine release from immune cells, butyrate itself or groups of bacteria implicated in higher butyrate production could be used as therapeutic aids (Hamer et al., 2008; Guilloteau et al., 2010; Macfarlane and Macfarlane, 2012).

In contrast to butyrate which is mostly metabolized in the colon, propionate and acetate are carried in the bloodstream to the liver to have further effects (Wong et al., 2006; Hosseini





**Figure 5.** Proposed staining mechanism of anthocyanins and PAs on and in cellulose fibers: (A) random external adsorption onto cellulose fiber surface; (B) random agglomeration of polyphenols; and (C) stabilised anthocyanin-PA cluster on the cellulose fiber surface (Padayachee et al., 2013).

et al., 2011; Kau et al., 2011) and then into systematic circulation (Bloemen et al., 2009; Layden et al., 2012). Acetate in particular has been found to interact with the FFAR2 receptor thereby impacting on inflammation and immune responses (Maslowski et al., 2009) whilst also playing an important role in the prevention of infection with *Escherichia coli* (0157:H7) (Fukuda et al., 2011), carcinogenesis, colonic function and adipogenesis (Macfarlane and Macfarlane, 2012).

Propionate also has important functional properties in the body. Like acetate, it interacts with the immune system through interactions with FFAR2 and FFAR3 receptors and regulates carcinogenesis (Macfarlane and Macfarlane, 2012). Diets that stimulate propionate production can alter cholesterol metabolism through inhibition of cholesterol synthesis and reduction of food intake in animals via interaction with leptin regulation (Macfarlane and Macfarlane, 2012). The satiety inducing effects of propionate (and also butyrate) occur via FFAR-dependent and independent mechanisms (Lin et al., 2012).

In general, the presence and concentration of SCFAs is correlated with better health outcomes via the mechanisms indicated above. Enrichment of the diet with particular components, including plant polysaccharides and dietary fiber in the form of the PCW, can influence microbial diversity, concentration of SCFAs and thus health outcomes. These studies are outlined in the following section.

### Dynamic response to change in diet and fiber structure

Fruit and vegetable fiber is composed of plant structural and storage polysaccharides as well as plant secondary polyphenolic compounds. Consequently both the polysaccharide and polyphenols components could potentially interact with the gut microbiota separately or in a joined form (Tuohy et al., 2012). Although there is evidence that dietary change does not affect the make-up of human gut microbial populations (Clemente et al., 2012), the majority of evidence shows that dietary intake does affect gut microbiota composition (Turnbaugh et al., 2009; Wu et al., 2011). Dietary polysaccharides that reach the human large intestine have been found to impact on gut microbial ecology and health (Jacobs et al., 2009; Li et al., 2009). Studies have also shown that changing to plant polysaccharide-rich and high-fiber diet stimulated changes in the microbial composition and dominance within 24 hours (Turnbaugh et al., 2009; Wu et al., 2011). Over the long-term, fiber-rich diet triggered a shift in microbial composition so that the community was dominated by *Prevotella* spp. in contrast to a high-fat, high-protein diet where *Bacteriodes* dominated. Wu et al. (2011)

In an influential study by De Filippo et al. (2010) compared the microbial communities of children in a rural African village to those of children living in Florence, Italy. Not only were the African children's microbiota enriched in *Bacteriodes* when compared to the microbiota of Italian children, but unique species of bacteria were found in the African children's gut bacteria population including *Xylanibacter*, *Prevotella*, *Butyrivibrio*, and *Treponema* species. The faecal concentrations of SCFAs, including butyrate, acetate and propionate, were higher in the African children, and correlated with the presence of these unique species of bacteria. The authors concluded that as the African children consume a plant based diet (rich in whole grains and higher proportions of fruits and vegetables), the higher concentration of dietary fiber, resistant starch, and oligosaccharides resulted in the specific bacterial population to produce the greater amounts of SCFAs (De Filippo et al., 2010). In another study, higher fruit and vegetable intake was found to correlate with a diverse and stable microbial community, enriched in particular enterotypes with high frequency of SCFA biosynthetic genes (Claesson et al., 2012).

It has been demonstrated that the molecular structure of individual polysaccharides, the matrix structure and the particle size of the fiber can significantly affect availability of substrate for bacterial enzymes and the ability of bacteria to colonize and invade fragments of plant tissue and cell walls. (Guillon and Champ, 2000; van Laar et al., 2000; Mikkelsen et al., 2011). Cellulose, which exists as highly crystalline fibrils, is fermented slower than soluble fiber such as pectin, and is a major component of the dietary fiber that survives and contributes faecal bulk in plant-containing diets. Soluble polysaccharides are generally more rapidly fermented than equivalent polysaccharides included in an organised network such as cellulose-based composites (Mikkelsen et al., 2011). The combined effects of increasing amounts of crystalline cellulose and lignin was seen to be the cause in the contrast between fermentation of parenchymatous pith cells and the secondary thickened rind (cortex) cells of broccoli stem in the hind gut (Monro & Mishra 2010). While the parenchyma cells are almost completely consumed by the



bacterial flora, rind cells, containing a high proportion of secondary thickened and lignified xylem tissue, remain apparently intact and recognizable in the faeces. Even within tissues consisting entirely of parenchyma cells, the rate of fermentation can be modulated by structure. The particle size of cell wall structures also leads to different fermentation rate as multi-cell clusters of carrot fiber were found to be more rapidly fermented than cell wall fragments (Day et al., 2012). This may be due to the inter-cellular spaces and the junctions between cells providing more easily accessible colonization sites for colonic bacteria thereby outweighing the greater specific surface area of smaller particles as a driver for more rapid fermentation.

Clearly, there is a strong influence of fiber content and its structure on microbiome population and function and it has important consequences for general health and susceptibility to disease. An important advance in this area would be to understand how plant cell wall components (collectively and individually) are able to influence gut microbe diversity and metabolic output as important health gains could be made. As the majority of plant polyphenols escape upper GIT digestion and absorption and consequently pass through into the colon, PCW-bound polyphenols inadvertently become substrates for the gut bacteria to produce small PAs and SCFA, thus modifying the bio-availability and metabolic activity of these compounds (Visioli et al., 2011). The consequences in terms of fermentation rates / products and microbial population shifts of polyphenols or other plant metabolites being delivered to the colon due to binding with PCWs have not yet been studied, but such studies may shed light on the mechanisms underlying nutritional benefits of consuming phytonutrients as part of whole foods rather than as an isolated supplement or food additive.

### **Food industry opportunities**

Processed fruits and vegetables produce approximately 50% by-product waste in the form of peels, cores, pomace, unripe and/or damaged fruits and vegetables (Virk and Sogi, 2004). For example out of the annual global watermelon production of 95 million tons (FAO, 2011), up to approximately 53% of the total melon is discarded (Aguayo et al., 2004; Tarazona-Diaz et al., 2010); approximately 8% waste was produced from the 98 million kg of apples processed in New York State in 2000; New Zealand apple product manufacturing produces 20000 tons of by-product waste (Wolfe and Liu, 2003a); up to 60% of processed mangoes end up as waste by-products. In recent years, effective management of the high amounts of by-product waste output from fruit and vegetable processing and wine manufacture has become an area of major environmental and economic importance world-wide (Peschel et al., 2006). However due to the nutritional content of fruit and vegetable by-products, advancement in waste streams as value-added ingredients is also of importance and is a growing research area.

By-product waste is a very high source of both PCWs and polyphenols. Pomace (i.e. skins, pulp, seeds, fruit stem) has been found to contain more antioxidant content than the flesh/ juice according to Wolfe and Liu (2003a; 2003b). Watermelon waste is mainly composed of rind, a rich source of citrulline (Rimando and Perkins-Weazie, 2005), an amino-acid displaying strong antioxidant and vasodilation behaviors (Ikeda et al.,

2000; Fang et al., 2002). As O'Shea et al. (2012) review, apple pomace and peels have been found to be rich sources of magnesium, calcium, quercetin (a flavonoid), procyanidin (a flavanol) and phenolic acids; grape pomace is a notable source of anthocyanins (flavonoid), flavonols and gallic acid (phenolic acid); mango peel and kernel have been found to be high sources of carotene and flavonoids;

Polyphenol rich apple pomace has found to be an effective apple juice stabiliser and is consequently recommended to be used as a value-adding ingredient in functional food manufacture (Lu and Foo, 1997; Lu and Foo, 2000; Vendruscolo et al., 2008; Ibrahim et al., 2011) whilst apple peel removed during the manufacture of dried apples was successfully used in the creation of a dried powder ingredient with the potential to be used in various processed foods (Henriquez et al., 2010).

Similarly carrot pomace, produced from juice manufacture, was found to not only be a substantial source of polyphenols and carotenoids, but also able to successfully stabilize carrot juice (Stoll et al., 2003a; Stoll et al., 2003b) and milk protein gel such as yoghurt (McCann et al., 2011). Recently Pedroza et al. (2011) were able to produce rosé wines after incubating red grape waste skins in white wine. With increased maceration time, anthocyanins in the skins were able to leach into the white wine thus producing the rosé wine product. Peach fiber high in polyphenols, vitamin C and carotene, has been used successfully as a functional ingredient developed from peach pomace and by-products, and has been found to be a functional substitute for flour in muffins (Adil et al., 2007). Likewise cauliflower fiber created as a functional ingredient from cauliflower stalks is a source of protein, hydroxycinnamic acids, quercetin, kaempferol and glucosinolates and has been successfully used as a fat substitute in beef sausages (Abdul-Fadl, 2012) and has also been incorporated into extruded ready-to eat snack foods (Stojceska et al., 2008). Other uses of processed fruit and vegetable by-products include antimicrobial protection of the fresh-cut surface of fruit via antioxidant enrichment (Ayala-Zavala et al., 2010). One potential drawback is that any pesticide residues are likely to be concentrated in peel and pomace by-products, and may impact on the use of by-products as a functional ingredient - an area which requires more research. Furthermore while polyphenol-rich fruit and vegetable by-products have been found to display exceptional *in vitro* antioxidant and anticarcinogenic properties (Stockhammer et al., 2009; Wijngaard et al., 2009; Tow et al., 2011), research demonstrating comparable properties of polyphenols *in vivo* is lacking.

### **Conclusion**

Numerous health benefits are associated with dietary intake of polyphenols derived from fruits and vegetables including anti-carcinogenic, antioxidant and anti-mutagenic activities. Similarly dietary fiber (PCW) is known to play an important role in bowel health, weight management and lowering blood cholesterol, glycaemic and insulin responses. Recent research has shown that polyphenols are able to interact with and bind to cellulose, pectin, and other components of the PCW, with the majority of polyphenols in fruit and vegetable systems likely to be bound to PCW material when the PCW is ruptured either during consumption or processing. Binding interactions are

strong resulting in minimal extraction with acidified methanol (a normally effective solvent used typically for the analysis of polyphenols) and during in vitro simulated upper gastrointestinal digestion. The results suggest that plant fiber plays an important role in transporting polyphenols through the upper gastrointestinal tract to the colon where colonic bacteria have the potential to release and metabolise these compounds. Whilst polyphenol metabolites may be absorbed from the colon, delivery of polyphenols to the colon via plant fiber can have an impact on the environment of the colon as well through influencing microflora ecology. Further research should focus on the effect that polyphenols bound to PCW matter have on colonic bacteria. Metabolites produced and the mode of absorption from the colon should also be assessed. The potential role that polyphenols bound to PCW matter have on the prevention or treatment of large bowel health conditions could also be assessed with a view to optimising food processes for functional benefit. Future research may also focus on the role of dietary fiber as a delivery system of medications to the colon for the treatment of certain health conditions, including colorectal cancers. Consequently future work in digestive release and metabolism of PCW-bound polyphenols in vivo, will provide further evidence on the release mechanism of polyphenols and how this may be maximised through diet and food structure design.

Binding of polyphenols to the PCW is not surprising, considering the persistent color of e.g. fruit fibers in purees. Even though evidence is emerging to demonstrate that the food matrix is a key contributor to the release of polyphenols from the plant cell, detailed understanding of the nature of interactions between polyphenols and the PCW, and how this affects polyphenol bioaccessibility and bioavailability during digestion is lacking. Whilst DF has traditionally been viewed as having beneficial effects due to inherent physical properties of solution viscosity and insoluble particles coupled with fermentation by colonic microflora, it is now clear that acting as a carrier for phytonutrients is an additional important function. This is particularly important for fruits and vegetables which often have high contents of bioactive phytonutrients such as polyphenols. The consequence of DF as a carrier of these bioactives in whole foods may be part of the reason why diets rich in whole foods are considered to have greater health benefits than isolated bioactive nutrients administered in purified form. Binding to DF not only alters the site (and therefore the rate) of phytonutrient uptake from the small to large intestine, but may also alter the molecular nature of the absorbed species because phytonutrients may be metabolised by the colonic microbiota prior to uptake. Clearly (fruit and vegetable) DF provides a series of much more complex functions in the human body than affecting bowel motility. By gaining a greater knowledge in this area, this will lead onto the development of procedures that can bind or de-bind polyphenols from food matrices, thereby controlling the release rate during digestion.

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