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Review

Biomimetic plant foods: Structural design and functionality

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ABSTRACT

Background: The rising number of people living with chronic conditions, such as diabetes and cardiovascular disease, along with the widespread demand for healthier foods have posed significant challenges to the food industry. Plant-based foods, beyond simple nutrition, can provide health-benefiting functionalities within the complex environment of the human gastrointestinal (GI) tract. Biomimetics is defined as taking inspirations from nature to solve problems. Biomimetic plant foods (BPFs) can offer solutions for the future with the design of nature-inspired food structures for improved health and well-being.

Scope and approach: This review provides an insight into the assembly of plant food structures and their disassembly in the human GI tract. Their role in controlling the digestive fate of nutrients is elucidated. Recent developments and future perspectives on designing BPFs are also presented and discussed.

Key findings and conclusions: Plant foods in nature possess hierarchically self-assembled structures. During processing and GI digestion, these structures are disassembled to enable liberation and assimilation of nutrients and bioactive molecules contained within the food matrix. The assembly and disassembly are linked to a hierarchy of structure in plants within which different levels (molecule, polymer, cell wall, cell, tissue, organ) and their interactions can modulate nutrient bioaccessibility and digestion. Inspired by nature, BPFs can be engineered to deliver in-body functionality. The emerging trend of biomimetics will potentially pave the way for the future of food.

1. Introduction

Spanning millions years of trial and error, natural structures have evolved to well-adapted forms with optimal efficiency via the process of natural selection. The great diversity of structures and functions in nature has always been a source of inspiration for the design and making of various man-made materials. This establishes the foundation for the field of biomimetics (Bhushan, 2009). Biomimetic materials science is not a new field. However, we have recently begun to see a growing interest in research and innovation on this dynamically developing area, thanks to the expanding interface between biological and material sciences (Fratzl, 2007).

In terms of scope, biomimetics is concerned with the imitation of biological models, systems, processes and structures found in nature for the purpose of solving a variety of complex human problems (Bhushan, 2009; Fratzl, 2007). Natural and biomimetic food systems are vastly different in their design strategies to achieve the desired functionality (Table 1). Indeed, nature uses a limited range of molecules and self-assembly principles to build a vast array of larger, more complex plant structures with remarkable functional properties. Unlike nature, humans utilise a large variety of base elements to fabricate structures following an exact design. In addition, the functionality of natural foods, such as fruits and vegetables, is largely imparted by their highly organised, hierarchical structures. In contrast, biomimetic foods rely on the choice of materials and selection of processing technologies to acquire specific functions (Fratzl, 2007).

Recent years have witnessed pioneering work on the biomimetics of foods with the development of cultured meat and plant-based burgers. This serves as a starting point to introduce the novel concept of biomimetic plant foods (BPFs). BPFs is an emerging platform of research that examines fundamental aspects of the structure-functionality relationships in plant foods from nature. This underpinning knowledge

Abbreviations: BC, bacterial cellulose; BPF, biomimetic plant food; ES, encapsulated starch; GI, gastrointestinal; LB, lipid body; NCS, normal corn starch; PB, protein body; PL, phospholipid; RS, resistant starch; SCFA, short-chain fatty acid; SDS, slowly digestible starch; SG, starch granule; SM, starch-entrapped microsphere; TAG, triacylglycerol

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Table 1
Natural versus biomimetic food systems, adapted with permission from Fratzl (2007).

Characteristics	Natural food system	Biomimetic food system
Choice of base elements	Limited types of molecules available: C, O, H, N, S, etc.	Large variety of elements (isolated ingredients): starch, protein isolates, refined oil, soluble fibers, etc.
Mode of assembly	Growth by biologically controlled self-assembly (approximate design)	Fabrication from colloidal dispersions, emulsions, amorphous and crystalline phases, gel networks, etc. (exact design)
Functionality	Hierarchical structuring over multiple length scales, functions imparted by natural structures	Formulation and re-assembling, choice of materials and selection of processing technologies according to functions

will then inform the creative design of innovative, bio-inspired food materials for the delivery of targeted in-body functionality. Such foods are expected to have potential health benefits for the management and prevention of chronic diseases.

This review provides a brief overview of the hierarchical assembly of plant foods and their disassembly during processing and various stages of human digestion. This forms the basis for our understanding of the multi-scale plant structure and its impact on the digestive fate of nutrients with special emphasis on macro-nutrients (carbohydrates, proteins and lipids). This review will be concluded by presenting recent trends and future outlook in designing BPFs.

2. Assembly of plant foods in nature

Plant foods in nature exhibit highly complex and diverse structures. Plants have formed these intricate structures for numerous reasons. Interestingly, most plants have not evolved to serve the primary purpose of being foods and eaten by humans and animals to sustain life. Notable examples include fruits consumed by animals as a way to scatter seeds around (for the spreading of plants and trees), and starches contained in tubers, grain seeds and bulbs to provide reproductive functions for plants (Ubbink, Burbidge, & Mezzenga, 2008). According to Parada and Aguilera (2007), the classification of most plant foods cultivated for human consumption mainly falls into two broad categories, namely fleshy structures and encapsulated embryos (Table 2).

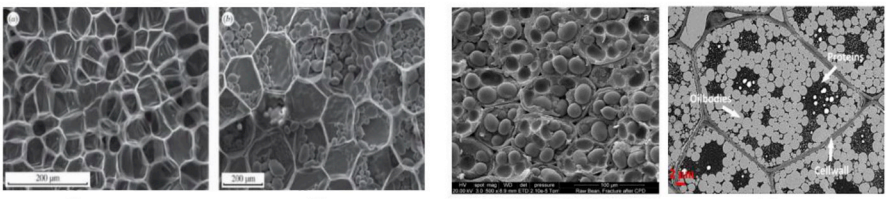
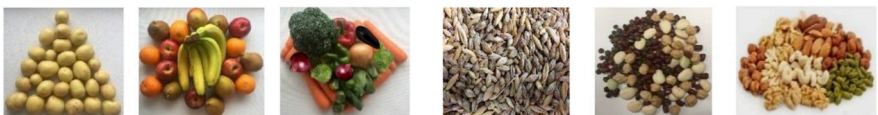
It is generally accepted that edible plants display hierarchical structures; *i.e.* structures of increasingly higher organisation are progressively assembled from the molecular to macro scale until achieving desired functions and properties. Nature utilises a limited number of available molecules as building blocks to synthesize numerous polymers and organelles, and then compartmentalises them into cells and tissues at multiple length scales (Aguilera & Stanley, 1999). This hierarchical self-assembly in plant foods is shown in Fig. 1, with several levels of structure that range from molecular (nm), through microscopic (μm), to macroscopic (mm) scales.

There is still a long way to go towards fully understanding the assembly of such complex structures in natural foods. With the aid of sophisticated microscopy techniques, considerable progress has been made in gaining insights into food structures that can be defined as spatial arrangements of various elements and their interactions at different length scales (Aguilera & Stanley, 1999). Principal structural assemblies present in plant foods are cell walls, starch granules, protein bodies, lipid bodies, cells and tissues. These elements can impart physicochemical and sensory attributes along with nutritional functionality to foods.

2.1. Plant cell walls

Plant cell walls have a complex hierarchical structure that comprises of four levels, namely, cellulose molecules, cellulose microfibrils, macrofibrils from primary cell walls, and plant cell walls (made up of primary and secondary walls) (Gibson, 2012). The primary walls, a major source of dietary fiber, essentially consist of three-dimensional interacting networks of highly ordered, crystalline cellulose microfibrils

Table 2
Classification of plant foods in nature.

Classification	Fleshy structures	Encapsulated embryos
Description[a]	Hierarchical composites of hydrated cells (spherical or polyhedral) that are bound together at cell walls and middle lamella and exhibit turgor pressure	Assembly of dispersed starch, protein and lipid into discrete pockets
Microstructure[b]	 Carrot Potato Navy bean Almond	
Examples of plant foods	 Tubers Fruits Vegetables Cereals Legumes Tree nuts	

[a] The description by Parada and Aguilera (2007). [b] The microstructural images reprinted for carrot and potato from Gibson, Ashby, and Harley (2010) with permission from Cambridge University Press; navy bean from Berg, Singh, Hardacre, and Boland (2012) with permission from Elsevier; and almond from Grundy, Lapsley, and Ellis (2016b).

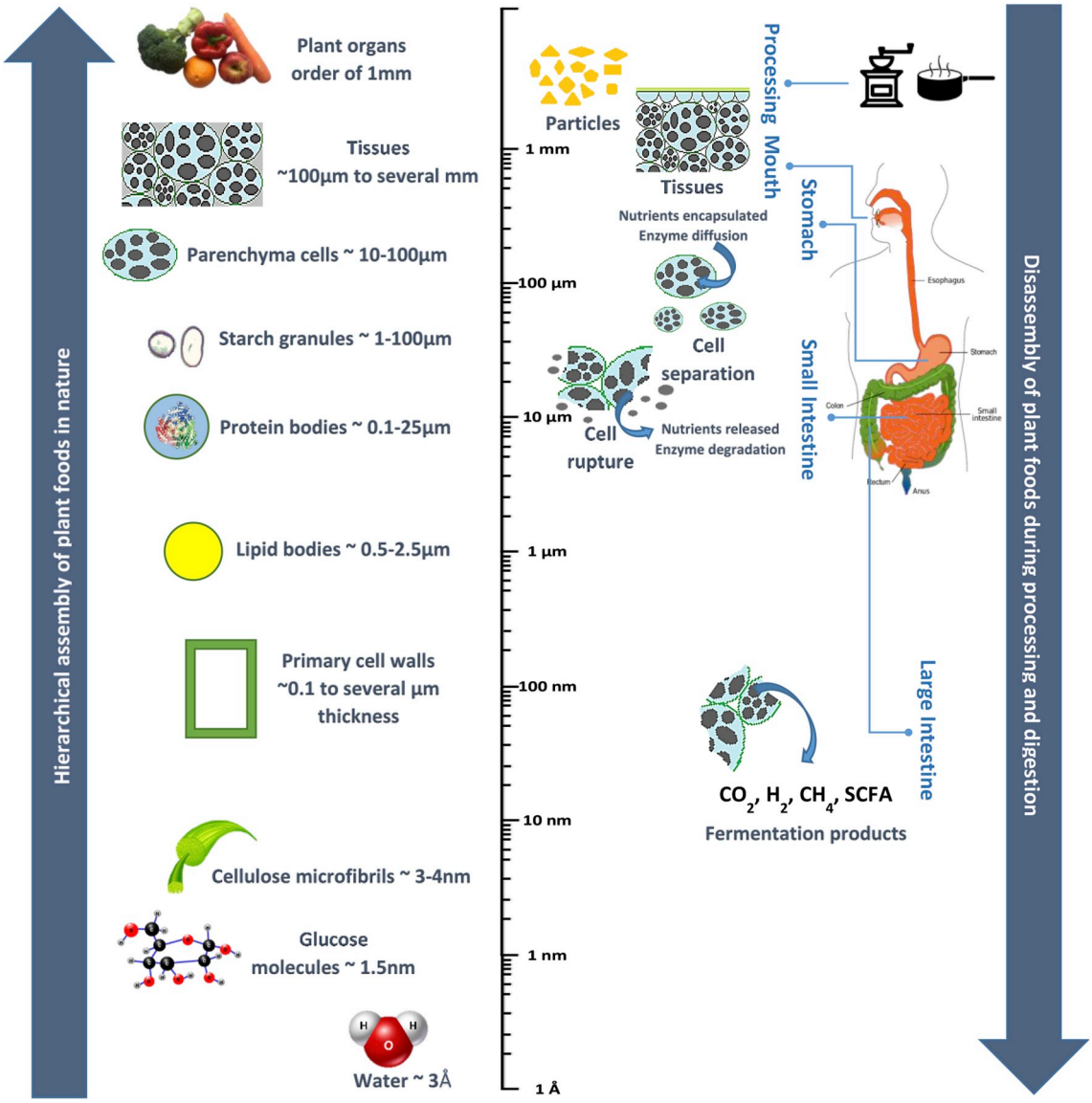


Fig. 1. Hierarchical assembly of plant food structures in nature and their disassembly during processing and digestion in the human GI tract. The disassembly process was adapted with permission from Grundy et al. (2016a). Picture of the human GI tract was reproduced from https://en.wikipedia.org/wiki/Gastrointestinal_tract (Copyright free).

(organised phase) embedded in a continuous, non-cellulosic matrix (amorphous phase). The matrix phase is composed of pectins, hemicelluloses and some minor structural proteins. The cellulose microfibrils are bound together via hemicellulosic tethers to form the load-bearing cellulose-hemicellulose framework, while pectins are thought to function as a plasticiser and control wall porosity (Cosgrove, 1997; Gibson, 2012).

2.2. Starch granules

Starch is a principal energy reserve in edible plants and forms the bulk of carbohydrates in the human diet (Singh, Dartois, & Kaur, 2010). Native starch granules (SGs) are made up of two different types of anhydroglucose polymers – amylose and amylopectin. They exhibit a hierarchical structure, which can generally be classified into four levels, ranging in scale from nm to µm: individual linear branches – consisting of glucosyl links, whole starch molecules – slightly branched amylose and highly branched amylopectin, lamella – double helices of short chains of amylopectin in crystalline regions and possible entanglement between amylose and amylopectin chains in amorphous regions, granules – made up of concentric growth ring shells of radially alternating semi-crystalline and amorphous lamella (Dona, Pages, Gilbert, & Kuchel, 2010).

2.3. Protein bodies

Proteins are accumulated in storage tissues of seeds. They are deposited in specialised subcellular organelles, commonly known as protein bodies (PBs) or aleurone grains. PBs are typically spherical and small with a size range from 0.1 to 25 µm in diameter. They contain an amorphous protein matrix enveloped by an external single membrane (Weber & Neumann, 1980). In sorghum endosperms, three major classes of storage proteins (prolamins), namely α-, β- and γ-kafirins, are not homogenously distributed within the PBs. The α-kafirin appears to occupy the central region, whereas the cross-linked β- and γ-kafirins are localised at the periphery (Mesa-Stonestreet, Jhoe, Alavi, & Bean, 2010). Likewise, a typical maize PB consists of an outer shell of primarily β- and γ-zeins and an interior of mainly α-zein. The interactions between these proteins have been postulated to play a role in the PB assembly (Lending, Kriz, Larkins, & Bracker, 1988).

2.4. Lipid bodies

Storage tissues of seeds, including cotyledons and endosperms, contain lipids within small, discrete subcellular organelles. These are referred to as lipid bodies (LBs) that are usually spherical in shape and have diameters ranging between 0.5 and 2.5 μm. Triacylglycerol (TAG) is a predominant form of storage lipids. The stable packing of suspended LBs in an aqueous environment of cytoplasm in plant cells resembles the structure of an oil-in-water emulsion. Generally, a LB consists of a central core of hydrophobic TAG molecules that are encapsulated and stabilised by a phospholipid (PL) monolayer embedded with integral proteins. These proteins include a major structural one (oleosin) and at least two minor ones (caleosin and steroleosin). The specific interactions among surface proteins, PLs and TAGs confer exceptional structural integrity and stability to LBs against destabilisation (coalescence and aggregation), regardless of whether they are inside cells or in intact, isolated forms (Tzen, 2012).

2.5. Cells and tissues

The most common tissue of edible plant organs is parenchyma. It constitutes the cotyledon of legumes and tree nuts, the endosperm of cereals, the cortex and pith of tubers, the pulp of fruits and the mesophyll of leaf vegetables. Plant tissues are made up of parenchyma cells, which usually have thin and non-lignified walls. Middle lamella, which is rich in pectic substances, glues the primary walls of adjacent cells (Brooker, Widmaier, Graham, & Stiling, 2017). From a food structure – digestion perspective, parenchyma cells are of particular interest to food scientists, since nutrients are assembled in storage compartments (SGs, PBs and LBs) within these cells.

3. Disassembly of plant foods during processing and digestion

While plant foods undergo processing and traverse the GI tract, they experience extensive structural transformations from the highest-order level of a storage organ, through intermediate levels (particle, tissue and cell), to a complete break-up to molecular-level components. This breakdown of food structure facilitates the enzymatic digestion and absorption of nutrients (Fig. 1).

3.1. Disassembly during processing

Processing causes irreversible alterations to structural integrity of plant foods. One of the primary consequences of processing is particle size reduction. This is a break-up of organs into smaller particles of various sizes, which is accompanied by an increase in available surface area for enzymatic action (Al-Rabadi, Gilbert, & Gidley, 2009). Processing can further reduce food particles to structures of tissues and cells. Depending upon the processing conditions that plant foods undergo and their tissue characteristics (*e.g.* cell-cell adhesion strength), cells can either separate along the middle lamella or rupture across cell walls. High pressure processing or mechanical grinding of intact tissues (*e.g.* legume cotyledons and almond kernels) fractures cell walls and liberates nutrients enclosed within cells (Berg et al., 2012; Grundy et al., 2016b). On the other hand, hydrothermal processing of plant foods (*e.g.* legumes and carrots) and subsequent mechanical shear applied within the resulting puree induce separation of intact cells without breaking them open (Berg et al., 2012; Tydeman et al., 2010a). Processing can also modify cell wall architecture (*e.g.* swelling, increased solubility and porosity, etc.) and alter structures and physicochemical properties of subcellular nutrients (*e.g.* starch gelatinisation/retrogradation, protein denaturation/aggregation, lipid emulsification/coalescence, etc.) (Grundy et al., 2016a). Due to all these aforementioned changes generated under various processing operations, a significant change in the overall properties of plant foods (*e.g.* colour, texture, rheology, etc.) occurs, thereby affecting the quality of final products.

3.2. Disassembly during digestion in the human GI tract

Digestion is characterised by a series of mechanical and enzymatic processes whereby ingested plant foods are physically and chemically disintegrated to facilitate the reduction of food particle size (mainly in the mouth and stomach), and the enzymatic hydrolysis and absorption of nutrients (mainly in the small and large intestine) (Guerra et al., 2012).

The digestion process begins with mastication of foods in the mouth to form a mass bolus. This is followed by the transport of bolus via the esophagus into the stomach (Bornhorst & Singh, 2014; Guerra et al., 2012). During mastication, cells of raw nuts and unripe fruits (*e.g.* almonds) tend to rupture and liberate intracellular contents as a consequence of cell wall disruption at the surface of chewed particles (Ellis et al., 2004). In contrast, cells or cell clusters of hydrothermally processed plant foods (*e.g.* cooked legumes) tend to separate rather than rupturing (Grundy et al., 2016a).

During gastric digestion, the swallowed boluses are further softened and physically broken down with the aid of secreted gastric juice and peristalsis contractions of the stomach wall, along with nutrient hydrolysis by actions of digestive enzymes (*i.e.* pepsin and lipase) (Bornhorst & Singh, 2014; Guerra et al., 2012). The disintegration of solid particles in the stomach can be governed primarily by either surface erosion or fragmentation (Kong & Singh, 2009b). Kong and Singh (2009a) provided a closer look at the digestion of raw almond particles in simulated gastric environment. It was revealed that cell separation occurred, possibly due to the weakening of cell-cell adhesion caused by the acidic hydrolysis of the middle lamella. Acid-induced breakage in cell walls was also observed for most internal cells within the almond tissue, facilitating the release and hydrolysis of intracellular lipid and protein bodies.

The partially digested foods expelled from the stomach, termed chyme, pass into the small intestine where their extensive enzymatic breakdown into molecules takes place. Segmentation and peristaltic contractions assist in the transport and mixing of chyme and nutrient absorption into the bloodstream through the epithelial cells (Bornhorst & Singh, 2014; Guerra et al., 2012). During this stage, intact plant cells preserve their structural integrity and enzymes diffuse into the cells in order to hydrolyse the enclosed nutrients. Ruptured cells, though, expose their cellular contents, rendering the entrapped nutrients readily available for enzymatic digestion and intestinal absorption (Berg et al., 2012).

The digestion process terminates in the large intestine, which is inhabited by a community of various species of microorganisms. Their role is to perform fermentation of incompletely digested food particles, including carbohydrates (resistant starch (RS) and cell wall polysaccharides), proteins and peptides. The colonic fermentation generates primary products of short-chain fatty acids (SCFAs), principally acetate, propionate and butyrate, with other by-products. These SCFAs are considered to have positive physiological effects on the colonic epithelial cells, particularly the protective effects of butyrate against colorectal cancer (Macfarlane & Macfarlane, 2012). Intact cells, as previously observed in legumes and carrots, can survive gastro-small intestinal digestion. These cells, carrying encapsulated nutrients (starch and carotenoids), may remain undigested and pass on to the colon where they serve as a substrate for microbial fermentation (Noah et al., 1998; Tydeman et al., 2010b).

4. Complex structure and functionality of plant foods

Fig. 2 depicts the inherent hierarchy of plant food structures in nature in conjunction with two processes: (1) assembly (developmental change) and (2) disassembly (processing/digestion change). Six levels make up the hierarchy within which molecules are essential building blocks for the assembly of higher-order structures such as polymers. Cell walls consist of an intricate network of polymers. Cell walls and

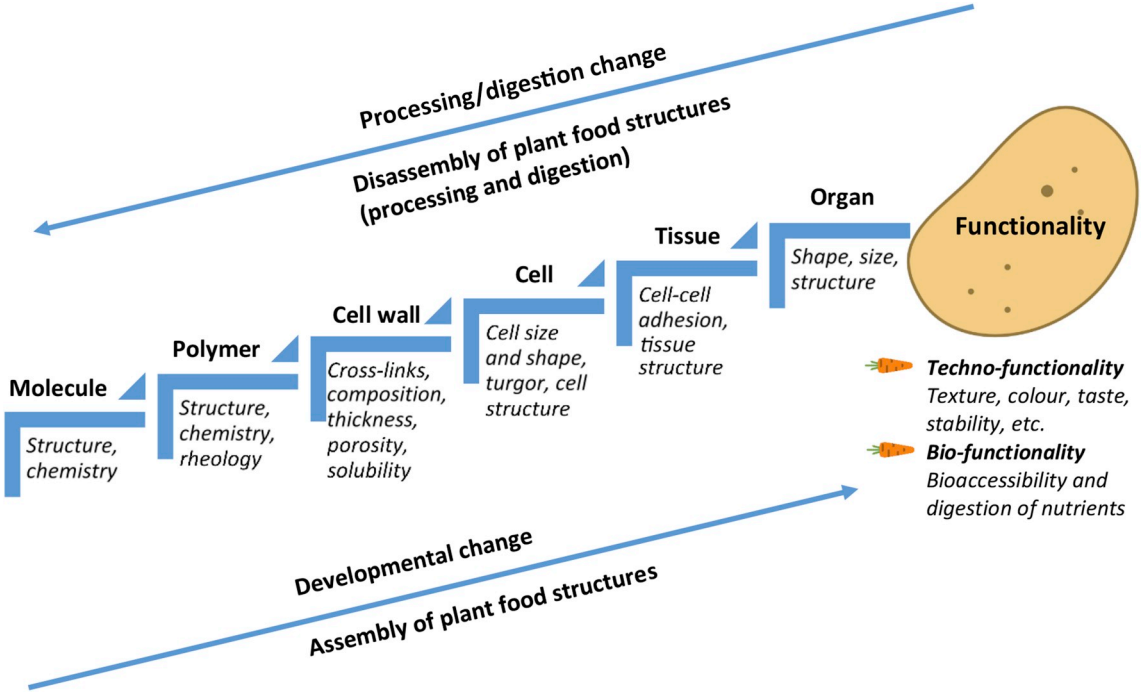


Fig. 2. Schematic representation of hierarchy of structures that contribute to the functionality of plant-based foods, adapted with permission from Parker, Parker, Smith, and Waldron (2001).

cellular components (*e.g.* SG, PB and LB) are assembled in plant cells. Tissues, which are made up of numerous cells, constitute plant organs. The characteristics of, and interactions between, the different structural levels can contribute to the: (i) techno-functionality relating to organoleptic and stability properties (*e.g.* texture, colour, taste, aroma release, shelf-life, etc.) and (ii) bio-functionality relating to nutritional value and health (*i.e.* controlling bioaccessibility and digestion of nutrients contained within the food matrix during GI digestion) of plant foods; we will focus on the latter aspect in this review.

During digestion, foods and their constituents are exposed to certain physiological conditions in the human GI tract, such as mastication, pH, actions of digestive enzymes and peristalsis contractions. Food macro- and micro-nutrients are susceptible to enzymatic hydrolysis and molecular degradation under these conditions. The natural food matrix provides protection for nutrients from degradation in the gut environment. An all-encompassing body of research has provided compelling evidence suggesting that plant food structure affects the GI fate of nutrients (Ellis et al., 2004; Berg et al., 2012; Tydeman et al., 2010a; Parada & Aguilera, 2007). For instance, the entrapment of nutrients within plant matrices is detrimental to their digestion and absorption in the body. This is because the protection by the plant matrix and/or interactions with other matrix constituents tends to lower their bioaccessibility (release from the food matrix) (Parada & Aguilera, 2007; Tydeman et al., 2010b). However, such a structure proves to be favourable in some cases, *e.g.*, digestion of starch-containing legume cells gives rise to gradual release of glucose in the small intestine and delivery of RS to the colon (Dhital, Bhattarai, Gorham, & Gidley, 2016; Noah et al., 1998).

The hierarchy in plant foods contains specific structural features at different levels of organisation and length scales that can play a role in controlling nutrient bioaccessibility and digestion (Fig. 3). For example, Berg et al. (2012) reported that the cotyledon cell structure of navy beans, consisting of SGs enveloped within intact cell walls, was the limiting factor for *in vitro* starch digestion. However, when the cell wall barriers were removed due to processing (starch extraction and milling), intrinsic properties of starch (as for isolated starch) and interactions of starch with proteins and lipids (as for milled flour) could be the key determinants for starch digestion.

5. Structural basis for bioaccessibility and digestion of nutrients in plant foods

5.1. Molecular and polymer level

The molecular and polymer structures of nutrients from plant foods (*e.g.* starch, proteins and lipids) greatly influence their digestion properties. Starch is composed of a mixture of two polymers: amylose and amylopectin, whose structural characteristics and properties can affect starch digestibility. It has been extensively reported that factors, such as amylopectin chain length distribution with lower proportions of short branch chains and higher proportions of intermediate and long branch chains, high amylose content, formation of amylose-lipid complexes and amylose/amylopectin retrogradation, can decrease starch digestibility (Singh et al., 2010).

Digestibility of plant proteins is influenced by their structural conformations, amino acid sequences and cross-linking (Duodu et al., 2002; Duodu, Taylor, Belton, & Hamaker, 2003). For example, Clemente et al. (2000) has pointed out that the formation upon heating of inter- and intra-molecular disulfide bonds that are resistant to proteolytic attack is deemed to be a major factor in reducing protein digestibility of chickpea albumins.

Triacylglycerols are the main plant-based source of dietary lipids. Their molecular structure and chemical composition can have a considerable impact on lipid digestion. Previous studies have shown that the molecular weight, stereospecific distribution and unsaturation of fatty acid chains on the glycerol backbone of TAGs could play a critical role in manipulation of lipolysis. In fact, the presence of long-chain saturated fatty acids in TAG structures in tropical plant oils, particularly at sn-1 and sn-3 esterified positions, has been found to exert detrimental effects on lipid digestion and absorption (Gallier & Singh, 2012b; McClements, Decker, & Park, 2008). Additionally, results from a human clinical trial indicated that the higher degree of fatty acid unsaturation appeared to promote more effective lipolysis along with slower gastric emptying and longer satiety (Maljaars, Romeyn, Haddeman, Peters, & Masclee, 2009).

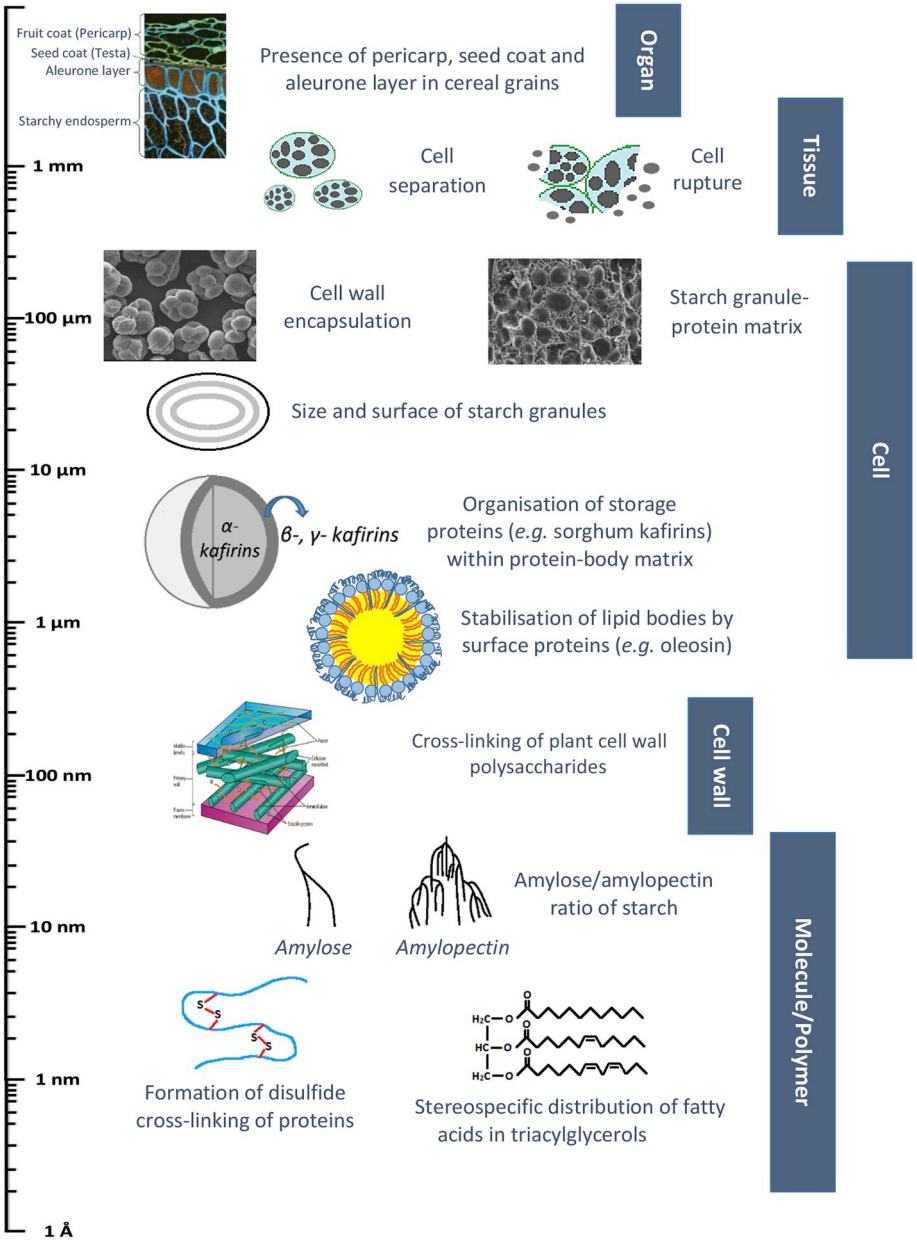


Fig. 3. Examples of structural features affecting nutrient bioaccessibility and digestion at different hierarchical levels of plant food structures. Permission given for the image reproduction of cell wall from Sticklen (2008); cell wall encapsulation from Do, Singh, Oey, and Singh (in preparation); starch granule-protein matrix from Black (2001) and wheat microstructure from Kamal-Eldin et al. (2009).

5.2. Cell wall level

Primary cell walls constitute the bulk of dietary fiber intake from plant foods. Their dietary consequences are strongly linked to the mechanisms whereby they directly affect the physiology of human digestion and the gut function (Capuano, 2017; Grundy et al., 2016a; Padayachee, Day, Howell, & Gidley, 2017). The primary walls are viewed as supramolecular assemblies consisting of a mixture of polysaccharides with broad variations in structural and functional characteristics. Their physical, physicochemical and digestion properties depend on the constituent polysaccharides, but perhaps more importantly, on the way in which these polymers are interlinked by ionic, covalent or hydrogen bonding to construct the three-dimensional cell wall architecture (Jarvis, 2011). Knowledge on their properties is crucial to the understanding of their behaviour during digestion. These properties are also believed to determine nutritional effects of the primary walls, including the effects on the rate and location of nutrient release in the stomach and small intestine, and on the amount of indigestible substances (*e.g.* RS) that can be subjected to microbial fermentation in the colon.

5.2.1. Solubility

Cellulose has a strong and insoluble structure that is more resistant to any form of degradation than other cell wall polysaccharides. Non-cellulosic polysaccharides (hemicelluloses and pectins) in native states can be soluble in appropriate aqueous solvents. Nevertheless, their solubilisation within the cell wall matrix is limited due to their strong molecular interactions with other wall components (Comino, Collins, Lahnstein, Beahan, & Gidley, 2014; Cosgrove, 1997). Despite being known for its insoluble nature, the intact cell wall inevitably undergoes structural and chemical modifications that affect its solubility during cooking and GI digestion. Indeed, solubilisation of pectins in the cell

wall/middle region upon thermal treatments enhances the cell wall permeability with increasing pore size. This facilitates the entry of enzymes into cells for hydrolysis of intracellular nutrients during digestion (Capuano, 2017). Crosslinking between matrix polymers in the cell wall may impart wall strength that resists solubilisation. Frost et al. (2016) have recently identified the presence in abundance of RG-I galactan firmly attached to cellulose in the cell walls of three distinct potato cultivars that have low levels of pectin loss during cooking and *in vitro* starch digestibility. The fact that the rigid cell walls of these potatoes could withstand pectin solubilisation and suppress access of amylases for starch hydrolysis may be uniquely linked to the strong interactions between cellulose and RG-I galactan.

5.2.2. Thickness

Variations in cell wall thickness among different edible plant tissues have possible implications for starch digestibility. Indeed, thicker and more rigid cell wall structures are more likely to impose greater restrictions on the gelatinisation degree of starch trapped within intact parenchyma cells and remain less degraded throughout digestion; this may therefore reduce starch susceptibility to amylolysis (Alminger, Eklund-Jonsson, Kidman, & Langton, 2012; Edwards et al., 2015).

5.2.3. Viscosity

Cell walls of cereals (*e.g.* oats and barley), owing to their soluble fiber of mixed linkage β-glucans, have been known to swell and exert viscosity effects on the food bolus in the stomach. The desirable effects arising from the increase in bolus viscosity include delayed gastric emptying, extended satiety, and reduced rate of starch hydrolysis with lowered postprandial glycemic response in humans (Tosh, 2013).

5.2.4. Porosity

Living plant cells communicate with their extracellular environment through a complex cell-wall-polysaccharide matrix, which is inherently porous and selectively permeable to certain molecules (Burton, Gidley, & Fincher, 2010). In order to facilitate the hydrolysis of nutrient molecules inside plant cells during digestion, enzymes must be able to penetrate into cells by crossing cell wall barriers. Alternatively, intracellular molecules must diffuse to the outside environment containing digestive fluids. Berg et al. (2012) reported on the *in vitro* starch digestion of cooked navy beans. It was suggested that amylolysis could take place partly inside the intact cotyledon cells as the result of enzymatic diffusion through the permeable cell walls.

The transport of molecules in and out of cells is controlled by pores located on intact cell walls. Hence, the pores impose restrictions on molecules that cells can allow to pass through. From a nutritional standpoint, the pore size governs diffusion of enzyme molecules and ultimately affects nutrient bioaccessibility (Jarvis, 2011). Grundy et al. (2016c) estimated the pore size of almond cell walls between 3.4 and 5.0 nm. Despite the relatively smaller radius of gyration of pancreatic lipases (50 kDa, $R_g \sim 1.9$ nm), it was found that the enzymes seemed to permeate only into damaged almond cells, but not into intact ones. It was then suggested that the digestion of intracellular lipids could be facilitated by a slow mechanism whereby, with great difficulty, lipases diffused through the cell wall matrix into the intact cells for hydrolysing the lipids and hydrolysis products leaked out of the cells to be made available for absorption. Evidently, in this case, cell wall porosity is a predominant factor responsible for limiting the bioaccessibility and digestibility of almond lipids.

5.2.5. Binding interactions

In a starch-cellulose system, α-amylases tend to have affinity for cellulose by non-specific binding on its surface, which in turn has an inhibitory effect on the enzyme activity from hydrolysing the starch (Dhital, Gidley, & Warren, 2015). This phenomenon has direct implications for the diminished digestibility of enclosed starch in plant food tissues because α-amylases can effectively bind to cellulosic components in the cell walls (Bhattarai, Dhital, Wu, Chen, & Gidley, 2017; Dhital et al., 2016). Food micronutrients such as polyphenols can also bind to polysaccharide constituents in the cell walls from fruits and vegetables. These binding interactions prevent liberation of nutrients from the food matrix and lower their bioaccessibility (Padayachee et al., 2017).

5.2.6. Digestibility

The endogenous enzymes secreted in the human upper gut cannot hydrolyse plant cell wall polysaccharides. As a result, the cell walls remain unaffected by digestive enzymes and reach the colon where it is fermented by the intestinal microbiota. A number of studies have recently revealed that their chemical composition and structure remain largely unaltered during processing and simulated *in vitro* upper GI digestion (Carnachan, Bootten, Mishra, Monro, & Sims, 2012; Mandalari et al., 2014). Since the cell walls are chemically inert and impervious to enzymatic attack, their intact structures can provide substantial protection to nutrients located inside plant cells throughout digestion.

5.3. Cellular level

5.3.1. Starch granules

Native SGs vary in their morphology, composition, structure and digestibility according to different botanical sources of plant foods. In general, starches in cereals are more digestible than those in tubers and legumes (Liu, Donner, Yin, Huang, & Fan, 2006). This can be attributed to a combination of several microstructural factors found in cereal starches at the granular level, including their smaller granule sizes and corresponding larger surface area, their crystal form (A-type) that is more prone to amylolysis than those of tubers (B-type) and legumes (C-type), and the presence of numerous pores and channels on granule surfaces (Singh et al., 2010). Since plant foods are usually processed prior to consumption, the effects of processing are of crucial importance in determining the ultimate starch digestibility of a particular food. Food processing at both industrial and household scales (*e.g.* cooking, extrusion, roasting and refrigeration) causes permanent changes in starch structure (gelatinisation and retrogradation) that can lead to either a notable increase or decrease in starch digestibility (Singh et al., 2010).

5.3.2. Protein bodies

The digestion of PBs is not well understood, however, few prior studies have offered some suggestions on the possible relationship between PB structure and protein digestibility. Teuber (2002) pointed out that certain proteins may not be made easily accessible to enzymes and readily bioavailable for uptake in the human upper gut due to the nature of their assembly into PB organelles. The ability of PBs to maintain their structural stability in the GI tract may be associated with delayed digestion and low digestibility of some plant proteins. Studies on sorghum have revealed the critical importance of PB structure in affecting the resistance of α-, β- and γ-kafirins to digestion. Oria, Hamaker, and Shull (1995) showed a protein degradation pattern of native PBs in uncooked sorghum flour during in vitro pepsin digestion. The PB digestion was initiated at the periphery, where β- and γ- kafirins are situated, then moved gradually towards the α-kafirin localised in the interior. It was suggested that its internal location was able to shield the α-kafirin away from exposure to enzymatic attack. The α-kafirin had a tendency to be degraded after "peeling off" of the more enzyme-susceptible β- and γ- kafirins at the outer surfaces of the PBs. As a result, the α-kafirin was found to be more slowly and less digested than the other two kafirins. Upon cooking, the formation of enzyme-resistant, disulfide-bonded polymeric network of the β- and γ-kafirins further impaired access of pepsin to the inner α-kafirin, therefore reducing the digestibility of all three kafirins (Oria et al., 1995).

5.3.3. Lipid bodies

The "oil-in-water-emulsion-like" structure of plant LBs stabilised by coating layers of PLs and integral proteins is a natural vehicle for the delivery of pre-emulsified lipids in digestible forms, similar to the nature of milk fat globules and processed lipid foods (Golding & Wooster, 2010). The behaviour of isolated plant LBs during GI digestion has been examined in the literature, highlighting a key role of intact oleosin for their stability against lipolysis and coalescence. A loss of emulsifying properties of oleosin at oil-water interfaces under GI conditions (low gastric pH and pepsin action) is conducive to destabilisation and aggregation/flocculation of LBs (Gallier & Singh, 2012a; Maurer et al., 2013). Evidence has shown that the PL/protein coat may be involved in delayed TAG hydrolysis by reducing lipase specific activities. Kinetics studies have demonstrated that the specific activity measured on almond LBs is much lower compared to that measured on almond lipid emulsions stabilised by gum arabic (Beisson et al., 2001). This is consistent with the finding of White, Fisk, Makkhun, and Gray (2009), who observed a slower rate of lipase-catalysed hydrolysis and lower bioaccessibility of α-tocopherol and fatty acids for sunflower LBs relative to that for artificial lipid emulsions stabilised by Tween 20 or whey protein isolate. Hence, it was postulated that native LBs could act as a natural emulsion in food systems with slow digestion properties. This can provide beneficial physiological consequences, such as reduced energy intake and increased satiety. Further, it is clear that LBs serve as an exemplar of naturally designed structures with unique functionality for the regulation of lipid digestion.

5.3.4. Cell wall encapsulation

Most plants at the cellular level are examples of microencapsulation in nature, with each living cell representing a microcapsule (Shahidi & Han, 1993). Cell walls act as a "shell" that not only fulfils their functional biology within the living plant, such as conferring structural support for the cell membrane against its bursting under the influence of turgor pressure (Jarvis, 2011), but also provides protection and stability to "core" materials of subcellular nutrients. One of the most important functions of food encapsulation is the controlled release rate of active "core" ingredients (Shahidi & Han, 1993). This is analogous to the role of cell wall encapsulation in modulating the rate and extent of nutrients released from the plant food matrix during digestion (Berg et al., 2012; Ellis et al., 2004; Melito & Tovar, 1995; Tydeman et al., 2010a).

Cotyledon cells of legumes (except oilseeds) provide effective encapsulation for starch. The cotyledons are made up of numerous parenchyma cells. Within each cell, a thick, mechanically robust cell wall encloses tightly-packed SGs that are embedded in a protein matrix of cytoplasm (Berg et al., 2012; Brummer, Kaviani, & Tosh, 2015). During traditional cooking of cotyledon tissues (*e.g.* boiling and steaming), cell walls form physical barriers that impose restrictions on water availability, heat transfer and space, which is required for the swelling and gelatinisation of SGs inside cells (Edwards et al., 2015). Such thermal cooking techniques promote dissolution of pectic polymers that are involved in cell-cell adhesion, followed by the separation of intact cells (instead of rupturing). These cells are also highly resistant to subsequent enzymatic digestion. Since these cells cannot be disrupted by either cooking or digestion and the partially-gelatinised starch is of too high molecular mass to escape via the cell wall pores, the starch remains trapped within the cells and its exposure to amylases is reduced to a large degree. The combined effects of the restricted starch gelatinisation and the enzyme barrier properties of the cell walls decrease the *in vitro* rate and extent of starch hydrolysis (Berg et al., 2012; Brummer et al., 2015). Recent evidence has indicated that, among several key factors including the intrinsic properties of starch (*e.g.* amylose content and retrograded amylose), interactions between starch and fiber/proteins, and the presence of amylase-inhibitors (Thorne, Thompson, & Jenkins, 1983), the rigidity and intactness of cotyledon cell structure (Berg et al., 2012) is the predominant contributing factor to the slow digestion property of carbohydrates in legumes and its lowering effect on the postprandial elevation in blood glucose levels.

Legume cotyledon tissues can be reduced to a suspension of single cells following heat or chemical maceration. The gelatinisation and digestion behaviour of starch within these cells has been investigated. A single intact cell has sufficient capacity to limit *in vitro* starch digestibility by providing an efficient cell wall barrier restricting intracellular starch gelatinisation and enzyme accessibility (Dhital et al., 2016; Do et al., in preparation; Fujimura & Kugimiya, 1994). Other possible mechanisms have been postulated to explain the reduced amylolytic susceptibility of starches inside isolated cells, including non-specific binding of amylases to cell wall components (Bhattarai et al., 2017), the protein matrix in cytoplasm acting as an additional barrier against starch-amylase interactions, and enzyme diffusion restricted by permeable cell walls (Rovalino-Córdova, Fogliano, & Capuano, 2018).

An *in vivo* study on starch digestion in healthy humans confirmed a significant proportion of starch in a physically inaccessible form (trapped within intact cells), recovered in samples of ileal digesta (*i.e.* the effluent collected at the end of the small intestine) after 3 h following ingestion of cooked white beans. The formation of RS was largely attributed to partially degraded starch molecules that escaped small intestinal digestion due to the effect of cell wall encapsulation (Noah et al., 1998). Drastic food processing, such as milling and high pressure, can disrupt cell wall integrity and liberate starch. This renders the starch more susceptible to amylolytic attack and leads to a marked increase in the starch hydrolysis rate (Berg et al., 2012). Therefore, minimal processing for preservation of intact cell structures is a crucial strategy for maintenance of the low glycemic features of legumes and delivery of RS to the large intestine.

Apart from starch, cell walls also provide encapsulation for other subcellular nutrients, including proteins, lipids and micronutrients. The physical impediment of cell walls is one of the key structural features that play a pivotal role in limiting protein digestibility in legumes (Melito & Tovar, 1995). Previous studies have identified cell wall encapsulation as a major determinant in modulating bioaccessibility and digestibility of lipids in almond seeds (Ellis et al., 2004; Grundy et al., 2016c; Grundy, Wilde, Butterworth, Gray, & Ellis, 2015; Mandalari et al., 2014). The cell wall barrier hinders the release of lipids out of almond cells and impairs the entry of lipases into the intracellular environment. A significant proportion of cells preserve their intact structures and the encapsulated lipids remain undigested at the end of *in vitro* upper gastric and duodenal digestion (Grundy et al., 2015, 2016c). A fraction of cells even survives *in vivo* bacterial fermentation in the large intestine and could be observed intact in human faecal samples (Ellis et al., 2004). Therefore, it seems paradoxical that the regular consumption of nuts (high in lipid contents) has actually been linked to lowered energy intake and decreased risks of cardiovascular diseases (Berry et al., 2008). Food processing techniques and oral mastication induce varying degrees of cellular rupture in almond tissues, which in turn enhances lipid bioaccessibility (Grundy et al., 2016b). There is also a large volume of research exploring the role of cell wall encapsulation in reducing bioaccessibility of micronutrients, such as carotene in carrots (Tydeman et al., 2010a, 2010b), iron in common beans (Glahn, Tako, Cichy, & Wiesinger, 2016), and the effects of processing in breaking down the cell walls and making the micronutrients more bioaccessible for gut uptake (Bengtsson, Brackmann, Enejder, Alminger, & Svanberg, 2010).

5.3.5. Starch-protein matrices

The parenchyma cell in cereal endosperms (*e.g.* maize, sorghum, barley and wheat) contains densely-packed SGs and numerous PBs that are both embedded in a protein matrix. The PBs are firmly cemented to the surrounding SGs or sometimes indented onto starch surfaces (Black, 2001; Mesa-Stonestreet et al., 2010). In raw grains, the compactness of protein matrices and the tight association between SGs and PBs have been known to attenuate starch digestion. The mechanisms for this

attenuating effect may involve a hindering effect of the protein barrier against enzymatic accessibility and a weak binding of protein components to α-amylases during *in vitro* digestion. The nature of these starch-protein interactions has significant relevance to human and animal nutrition (Choct, Bird, Littlefield, Balogun, & Rowe, 2001; Yu et al., 2017).

Kafirin proteins are responsible for the nutritional functionality of food sorghum in cooking. Since kafirins are buried within the PB structure, they must be released to enhance their functional capacity. This can be achieved through physical disruption of PBs by the application of shear forces in food processing (Hamaker & Bugusu, 2003). Kafirins (particularly β- and γ-) are rich in sulfur-containing amino acids (cysteine and methionine). They are prone to network formation of intra- and inter-molecular disulfide bonds (Mesa-Stonestreet et al., 2010). Upon cooking sorghum flour, kafirins form extended web-like and rigid sheet-like structures. This is because cooking promotes their hydrophobic nature and the propensity of kafirin monomers for forming large disulfide-bonded oligomers and polymers, along with an evident increase in cross-linked glutelins present in non-kafirin protein matrices. These physicochemical changes inhibit swelling and water absorption capacity of the disulfide-mediated protein network surrounding starch. This compact protein matrix, in turn, restricts starch granular expansion/gelatinisation during cooking and limits accessibility of starch to amylases during in vitro digestion. This situation effectively reduces availability of entrapped starch for amylolysis by restricting granule expansion and gelatinisation during cooking and impairing enzyme accessibility during *in vitro* digestion (Ezeogu, Duodu, Emmambux, & Taylor, 2008; Ezeogu, Duodu, & Taylor, 2005). In order to enhance the starch digestibility of sorghum, the protein barrier must be broken down to enable amylolytic enzymes to gain entry to starch reserves in endosperms. Processing techniques (*e.g.* germination and high-pressure cooking) or the use of reducing agents (*e.g.* 2-mercaptoethanol) can disrupt the starch-protein matrices to varying extents. These drastic treatments improve starch digestion by inducing open protein structures or limiting the degree of disulfide-bonded polymerisation of the prolamins, thus increasing susceptibility of the exposed starch to amylase action (Choct et al., 2001; Ezeogu et al., 2005).

The structure of cereal proteins varies within and between grain species, and so do their physicochemical properties and their effects on starch digestion. Kafirin and zein are both classified as alcohol-soluble prolamins (Mesa-Stonestreet et al., 2010). Despite the high homology in amino acid sequences between these two prolamins, kafirin contains more cross-linked protein fractions and is generally more hydrophobic than zein. This explains the more extensive formation of disulfide cross-linkages and possibly more complex structures of high-molecular-weight protein aggregates upon cooking (boiling in water) in sorghum flour compared with that observed in maize flour. Consequently, the protein network and starch in sorghum flour are less accessible to digestive enzymes and less digestible than their maize counterparts (Duodu et al., 2003; Ezeogu et al., 2005, 2008). Besides, Yu et al. (2017) characterised barley proteins and found that variations in the protein content and composition (notably hordein fractions) existed across cultivars. These variations could probably result in different levels of inhibitory activity against starch-hydrolysing enzymes. This finding will potentially give rise to a selection of barley varieties with a range of starch digestibility characteristics that will deliver nutritional and health benefits for humans (slowly digestible foods) and animals (easily and rapidly digestible feeds).

5.4. Tissue level

At the tissue level, the effects of particle size on the kinetics of starch digestion have been investigated by studying different size fractions of milled plant tissues. Al-Rabadi et al. (2009) and Roman, Gomez, Li, Hamaker, and Martinez (2017) observed an inverse correlation between the particle size of cereal flours and rate coefficients for amylolysis. One possible explanation for this finding is that coarse flours appeared to possess a lower amount of peripheral damaged starch and a smaller surface area for enzyme binding compared with fine flours. Flour particles could also preserve their structural integrity (*e.g.* cell walls and protein matrix), restricting water ingress for starch granular swelling/gelatinisation and limiting diffusion-controlled starch hydrolysis by amylases; this effect being greater for coarse flours.

There is also a growing body of evidence suggesting that at the tissue level, cell adhesion and cell separation/rupture may play a role in governing the rate and location of nutrient release during the process of digestion (Tydeman et al., 2010a; Berg et al., 2012). Developing plants use adhesion between adjacent cells, a central characteristic of multicellular organisms, as a strategy to acquire mechanical strength. The pectin-rich middle lamella is thought to play a crucial role in maintaining cell-cell adhesion and protecting tissue integrity (Jarvis, Briggs, & Knox, 2003). Tissue failure affects organoleptic quality attributes (texture and aroma release) of plant-based foods. It often occurs in the form of cell separation or cell rupture or a combination of both. The type of failure is determined by the relative strengths of the cell walls and cell adhesion forces (Waldron, Parker, & Smith, 2003). Thermal cooking of starch-based plant foods (*e.g.* potatoes) results in cell separation and a mealy texture. This can be attributed to a loss of turgor pressure and a dual effect of cell wall/middle lamella disassociation and starch swelling pressure (Jarvis, Mackenzie, & Duncan, 1992). During fruit ripening, cell separation is facilitated by pectin degradation in the primary wall/middle lamella by active pectin-degrading enzymes (Jarvis et al., 2003). Once there has been a substantial level of cell separation, it becomes rather difficult to fracture individual cells by any mechanical means (Jarvis, 2011). On the other hand, mechanical or oral processing of unripe fruits causes breakage across the cell walls. This is immediately followed by a release of cell contents and a resulting juicy texture (Waldron et al., 2003). Intact cells preserve their structural integrity and protect entrapped nutrients against enzymatic degradation. Hence, they remain resistant to digestion for a longer way down the GI tract as opposed to ruptured cells, but their ability to retain any of the cellular contents may rely on the degree to which the cell wall porosity is altered (Jarvis, 2011). These findings reinforce the paramount importance of the underlying principles of cell separation/rupture in regulating nutrient release at the tissue level. Furthermore, it is essential to select suitable processing methods/conditions so as to achieve efficient separation and minimal fracture of plant cells or vice versa for targeted nutrient bioaccessibility (Tydeman et al., 2010a; Grundy et al., 2016b).

5.5. Organ level

The structure of edible plants, such as cereal grains, possesses several physical characteristics at the organ level that can influence nutrient digestion. The organs of cereal grains possess physical barriers that can influence nutrient digestibility. The outer layers and their associated components (pericarp and polyphenols, gem and lipids) present in sorghum may be involved in lowering *in vitro* protein digestibility of both uncooked and cooked whole grain flours when compared to endosperm flours devoid of these structures (Duodu et al., 2002). Additionally, a study by Tamura, Singh, Kaur, and Ogawa (2016) on starch digestibility of cooked rice pointed out that the aleurone layers in rice endosperm could inhibit penetration of digestive fluids containing starch-hydrolysing enzymes into the core of cooked, intact grains. As a result, the *in vitro* starch hydrolysis rate of homogenised rice was found to be eight times higher than that of intact rice. Moreover, Bornhorst, Chang, Rutherfurd, Moughan, and Singh (2013) conducted an *in vivo* study to examine the gastric digestion of cooked rice meals using growing pigs as a model for adult humans. They found an accumulation of the bran layers from brown rice in the pig gastric antrum after meal consumption, which could explain a lower gastric emptying rate for

protein in brown rice compared to white rice (bran layers had been removed by processing).

6. Recent trends in designing biomimetic plant foods (BPFs)

In recent decades, there has been a shift from the traditional view of examining nutritional benefits of a food simply based on its composition, to the recognition of the critical importance of its structure in influencing nutrient digestion and nutritionally-related health (Wahlqvist, 2016). The topic of designing foods to control the GI fate of nutrients for improved health and wellness is a rapidly expanding area of research. Within the context of the current understanding of food digestion for health, BPFs emerge as a novel approach for the future of food structure design.

Despite scientific progress, public opinion has been divided over the notion of biomimetic foods. Dietary guidelines frequently recommend natural foods being an essential basis of a healthy diet as well as avoidance of ultra-processed foods (Wahlqvist, 2016). For example, minimal processing of legumes is advantageous to retain their intact cotyledon cells and the associated benefits of low glycemic features (Berg et al., 2012). Clearly, consuming unrefined or minimally-processed plant foods provides us with the full benefits. And if so, why should we create biomimetic ones? This is a reasoning often given by health-conscious consumers favouring wholesome foods of natural origin over processed or fabricated products. To address this point, the concept of biomimetics should be fully realised. In fact, the ultimate vision is not to make a replica of natural foods, but rather to be inspired by structure-functionality linkages encoded in them, to enable the design of nature-like food systems with similar or enhanced functionality. The advantage of biomimetic foods is their versatility of being tailored to specific shape, size, structure or composition, and being utilised in different food matrices according to the type of application.

In this review, we have highlighted plant foods as a naturally-occurring delivery system for nutrients and bioactive compounds. More importantly, we have shown that all hierarchical levels of food structures are involved in manipulating the bioaccessibility and digestion of these constituents. Therefore, we propose that structural design principles derived from plants can potentially serve as inspiration for the invention of high-value healthy BPFs. As illustrated in Fig. 4, plant cell and lipid body are examples of natural templates for creating BPFs with targeted functionalities in the GI tract such as delayed digestion of starch/lipid and reduced postprandial glycemia/lipemia.

We envisage a new category of BPF products that can be tailored to allow their uses in specific health-promoting applications to help prevent or combat chronic diseases. Examples include lowered caloric content and prolonged satiety for obesity management; slow and sustained release of glucose in the small intestine and delivery of resistant starch to the large intestine for decreased risks of diabetes and improved colonic health; preservation of functionality and targeted delivery of bioactive food components for cancer prevention; and so on. Recent studies have shed light on many possibilities of engineering BPFs that can be fabricated from isolated food-grade ingredients using processing technologies.

6.1. Artificial plant cell walls

Artificial plant cell walls can be reassembled from their basic building blocks of cellulose, xyloglucan, and pectin. In a biotic (living) system, the *in vivo* assembly of cell walls occurs during the deposition of bacterial cellulose (BC) synthesized extracellularly by the bacterium *Gluconacetobacter xylinus* into a culture medium containing xyloglucan and pectin (Fig. 5A) (Cybulska et al., 2010; Gu & Catchmark, 2012). An alternative mode of *in vitro* assembly can be adopted in an abiotic (non-living) system. A mixture of isolated polymers, containing extracted cellulose fibers, is incubated with constant mixing to mimic the reconstruction of cellulose/xyloglucan network in the primary cell wall (Hayashi, Marsden, & Delmer, 1987; Whitney, Brigham, Darke, Reid, & Gidley, 1995). Artificial cell walls produced by BC exhibit some

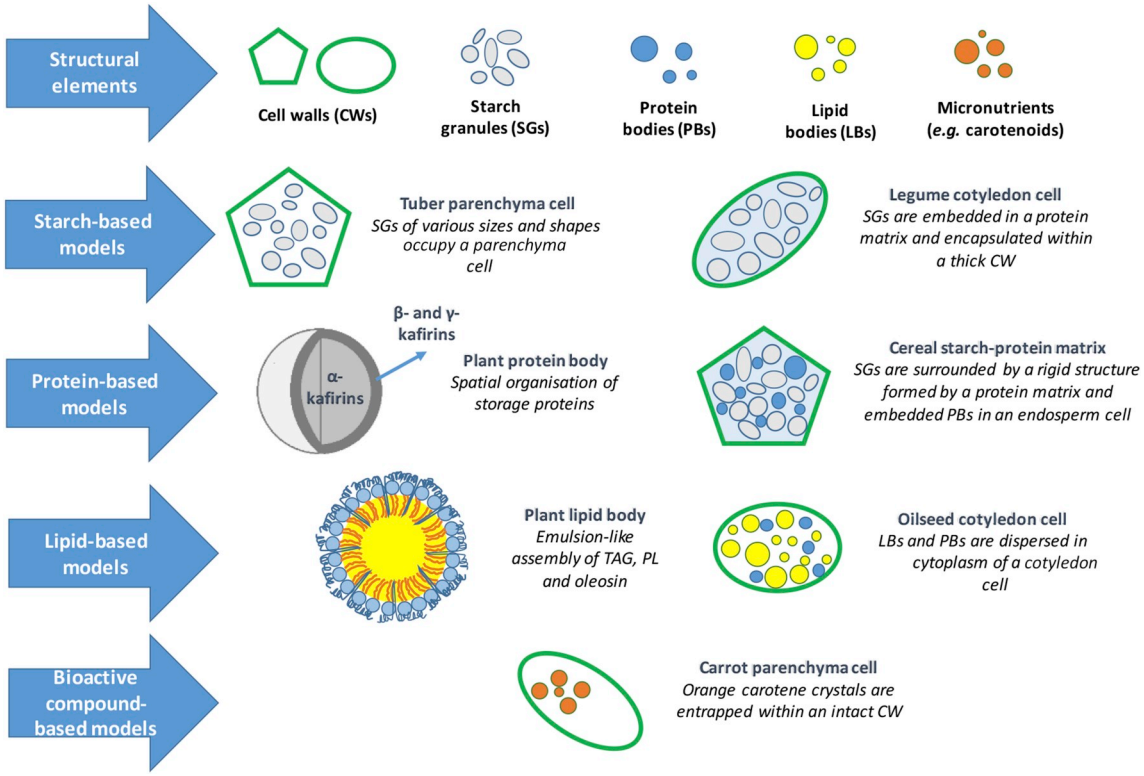


Fig. 4. Structural design of plant foods in nature serves as a template for biomimetics. The illustrations do not necessarily represent exact replication of the natural structures.

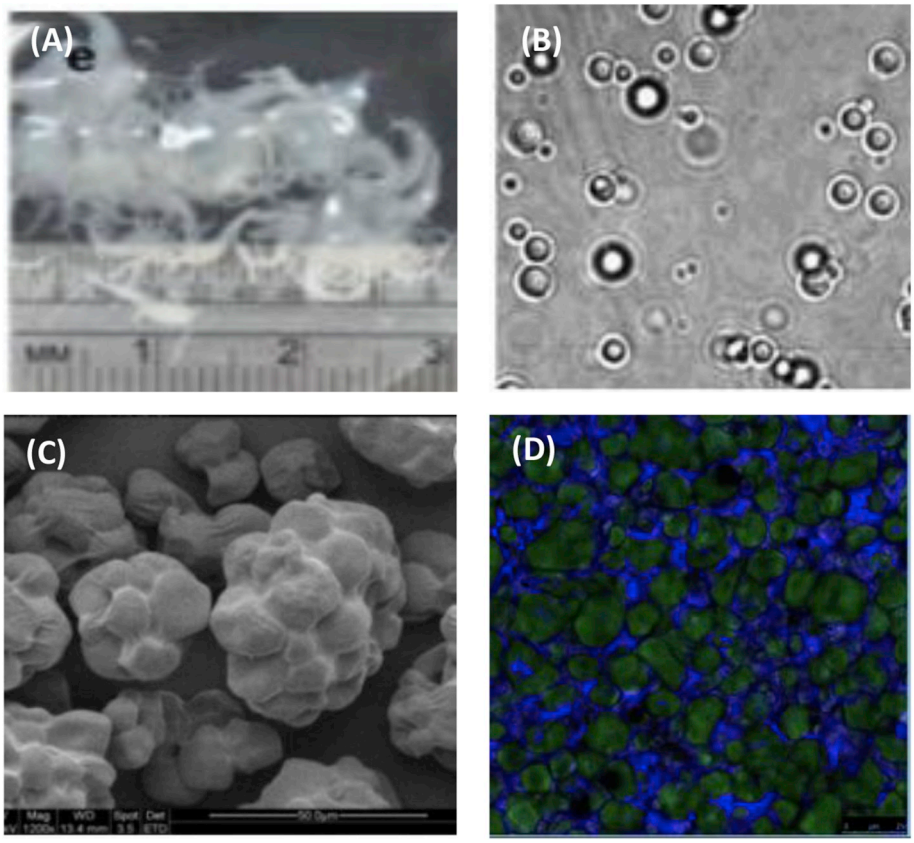


Fig. 5. Examples of BPFs. (A) Assembly of primary cell walls from a blend of BC, xyloglucan and pectin after 7 days of incubation, reprinted from Gu and Catchmark (2012) with permission from Elsevier, (B) Stable LBs reconstituted from TAG, PL and oleosin, reprinted with permission from Chen, M. C., Chyan, C. L., Lee, T. T., Huang, S. H., & Tzen, J. T. (2004). Constitution of stable artificial oil bodies with triacylglycerol, phospholipid and caleosin. *Journal of Agricultural and Food Chemistry*, *52*(12), 3982–3987. Copyright (2004) American Chemical Society, (C) Encapsulation of SGs within the zein protein matrix, reprinted from Xu and Zhang (2014) with permission from Elsevier, (D) Entrapment of SGs (green) within the alginate-β-glucan gel network (blue), reprinted from Luo and Zhang (2018) with permission from Elsevier. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

similarities to native ones in terms of their chemical composition and microstructure (Cybulska et al., 2010). Whitney and colleagues have demonstrated that the level of xyloglucan incorporation into the cellulose network in an actively growing BC system is comparable with that in native cell walls, but is considerably higher (approximately an order of magnitude) than that in a corresponding polymer mixture.. Xyloglucan is capable of penetrating BC fibrils and altering their structures and properties, whereas only xyloglucan binding/cross-linking was found at the surface of cellulose particles under *in vitro* conditions (Whitney et al., 1995). In light of these observed molecular interactions, it becomes evident that the biosynthesis of BC in the presence of xyloglucan and pectin bio-mimics the assembly of primary cell walls in nature. In practice, BC-based cell wall composites have been used as a model system for the understanding of plant cell walls regarding their permeability, porosity and mechanical characteristics, as well as their fermentation as dietary fiber. The insoluble and enzyme-resistant nature of plant cell walls is also a source of inspiration for structuring novel encapsulating materials using cell wall polysaccharides to be used in food delivery systems for nutrients and probiotics in food systems. Encapsulation of probiotic bacteria (*Bacillus coagulans*) in a composite matrix consisting of bacterial nanocellulose and pectin could protect them against thermal drying and gastrointestinal conditions. This could be attributed to intermolecular interactions between functional groups of bacterial nanocellulose and pectin, which have a synergistic effect on crystallinity of the composite. The mixing of these two constituents also results in a compact surface morphology that could limit diffusion of acids and digestive enzymes into the composite matrix (Khorasani & Shojaosadati, 2016).

6.2. Artificial lipid bodies

In order to mimic the unique structure of lipid storage organelles within oilseeds, artificial LBs (Fig. 5B) could be formulated and reconstituted from three principal isolated components (TAGs, PLs, and integral proteins) under the same weight proportions as they are found in nature. Artificial LBs could be stabilised by oleosin or caleosin, but not by steroleosin. Their average sizes could be controlled by varying the ratio of TAGs to lipid-body proteins (Peng, Lin, Lin, & Tzen, 2003). In comparison with native LBs, oleosin-stabilised ones are comparable in size (0.5–2 μm), whereas caleosin-stabilised ones are 10 times smaller (50–200 nm) (Chen, Chyan, Lee, Huang, & Tzen, 2004). Interestingly, similar to the stability of native LBs both inside and outside the environment of plant cells, artificial LBs display excellent stability against heat, oxidation and flocculation/coalescence during storage (Wijesundera & Shen, 2014). Wijesundera et al. (2013) prepared artificial LBs from tuna fish oil, PL, and oleosin extracted from canola meal. They were found to readily disperse in water to produce physically stable oil-in-water emulsions which showed no evidence of coalescence during storage at 4 and 40 °C. No creaming was also observed when these artificial LB emulsions were subjected to standard conditions of commercial pasteurisation (low temperature long time or high temperature short time). In addition, accelerated oxidation tests demonstrated that these artificial emulsions were significantly more resistant to lipid oxidation when compared with oil-in-water emulsions prepared from tuna fish oil and stabilised with various emulsifiers (Tween 40, sodium caseinate and commercial canola protein isolate). The *in vitro* lipid-body self-assembly has led to a variety of food applications. Examples include development of novel flavouring and emulsifying agents, structuring food emulsions to control lipid oxidation and digestion, encapsulation of probiotics in dairy products, and carrier for delivery of lipid-soluble bioactive compounds (Tzen, 2012).

6.3. Biomimicking of plant cells

Plant cell wall encapsulation of nutrients modulates their release and assimilation in the digestive tract (refer to 5.3.4). This principle can provide creative ideas for the design of biomimetic food systems for nutrient delivery applications. Venkatachalam, Kushnick, Zhang, and

Hamaker (2009) first reported on the development of a novel carbohydrate ingredient for controlled delivery of glucose to the body. Starch-entrapped microspheres (SMs) could be fabricated by entrapment of SGs in calcium-induced gel networks of pectin or alginate. These SMs bear some resemblance to starch-encapsulated plant cells. It is important to note that the biopolymer matrix in SMs has a much less complex structure than the intricate cell wall polymer network. Nevertheless, it could act as a physical barrier controlling starch digestion in a similar manner to the cell wall. Indeed, *in vitro* starch digestion assays combined with scanning electron microscopy techniques demonstrated that gelatinised starch, which is tightly packed within biopolymer matrices in cooked SMs, was enzyme-digested in a layer-by-layer fashion. This means that digestion progressed from the outer towards the centre of the SM over time. The dense biopolymer matrix appeared to hinder the free access of amylolytic enzymes to the encapsulated starch, therefore providing a slow and extended release of glucose during *in vitro* digestion. Aside from exhibiting slow digestion properties, SMs could also be tailored for specific *in vitro* glucose release profiles and desired contents of slowly digestible starch (SDS). A range of glycemic properties could be achieved by manipulating a number of factors such as biopolymer type and concentration, starch type and microsphere size (Venkatachalam et al., 2009). *In vivo* studies in humans have shown that the incorporation of slowly digestible SMs into meals results in delayed gastric emptying (Cisse et al., 2017) and decreased postprandial glycemic and insulinemic responses (Venkatachalam et al., 2009). Furthermore, a recent clinical trial conducted on human subjects has suggested that the consumption of SM supplementation as a novel source of dietary fiber with slow fermentation properties could improve bowel habits in those with constipation (Rasmussen et al., 2017).

6.4. Biomimicking of starch-protein matrices

Protein matrices of natural origin modulate starch digestion (refer to 5.3.5), which may inspire food scientists to devise biomimetic approaches to developing foods with low and slow glycemic features. Xu and Zhang (2014) reported on the microencapsulation of corn starch by zein protein via spray drying for the imitation of natural starch-protein matrices in corn grains. Their alcohol-soluble and film-forming properties make zeins an ideal shell material for the encapsulation of corn starch. Following a low-temperature spray drying process, spherical particles of encapsulated starch (ES) were formed and made up of tightly packed SGs embedded in the zein protein matrix (Fig. 5C). *In vitro* digestion of raw ES of various compositions showed that a zein to starch ratio of 1 to 6 yielded materials with the lowest level of rapidly digestible starch and the highest levels of SDS and RS. This ratio is likely the optimal level for maximum encapsulation of SGs with minimal hydrophobic-interaction-induced aggregation of zein molecules. After high-temperature pre-treatments, the ES exhibited *in vitro* digestion profiles that were different from those of the control of normal corn starch (NCS). When the starch samples were treated at 50 °C (below the NCS gelatinisation temperature), the ES had much lower digestibility than the NCS. After pre-treatment temperatures were raised to 80, 90 and 100 °C (above the NCS gelatinisation temperature), the ES showed higher levels of SDS and RS compared to the NCS. Based on these results, it was then speculated that the zein matrix could play a key role in the slow digestion of ES. Indeed, the zein matrix formed a hydrophobic physical barrier limiting the free access of amylases to the encapsulated SGs. During high-temperature pre-treatments, the zein barrier could be highly effective in resisting water adsorption and restricting granular swelling, hence limiting starch exposure to enzymatic attack. The incorporation of plasticizers, including glycerol and oleic acid, during microencapsulation was found to substantially further improve the resistance of starch to thermal treatments and amylolysis. One possible explanation for this is that, apart from forming amylose-lipid complexes, these two plasticizers could act synergistically to improve tensile strength of the zein film. This presumably could decrease heat-induced swelling of the embedded SGs and prevent mechanical breakdown of the zein matrix during digestion. The study also proposed a promising application of this particular nature-inspired structure that can be directly incorporated into beverages with acceptable sensory quality for postprandial glycemic control (Xu & Zhang, 2014).

6.5. Biomimicking of whole grain tissues

Luo and Zhang (2018) reported on a very recent attempt to biomimic the microstructure of endosperm tissues within whole cereal grains of oat and barley. In order to construct whole-grain-like matrices, SGs were embedded in a calcium cross-linked gel network formed by alginate and β-glucan, acting as pectin and hemicellulose constituents of plant cell walls respectively. The artificial grain tissue contains cell-like compartments that are morphologically similar to starch-containing endosperm cells as found in cereal grains (Fig. 5D). *In vitro* starch digestion data of cooked artificial grains showed that their SDS content was comparable to that of native corn starch, but was significantly higher than that of cooked, gelatinised corn starch. This difference may have been due to the co-formed gel matrix of alginate-β-glucan could act as a physical barrier impeding amylase accessibility to the encapsulated starch, in a similar manner to that seen with cell walls in whole grains. For comparison with artificial grains, a physical mixture was prepared by combining the same amounts of isolated ingredients (corn starch, alginate and β-glucan). Interestingly, the SDS of the physical mixture was markedly lower than that of its counterpart. This finding is indicative of the important role of physical intactness of the whole-grain structural form in limiting starch digestion. This whole-grain-like structure can serve as a model to study interactions between starch and other co-existing components within the natural grain matrix. Regarding food application, this type of structure can potentially be used as a functional ingredient for the development of foods for glycemic control (Luo & Zhang, 2018).

7. Conclusions and future perspectives

The increase in prevalence, incidence and mortality associated with modern chronic diseases has placed substantial health and economic burden on global societies. This alarming situation has accentuated the growing demand for foods that can help curb the risks or ameliorate the effects of these debilitating conditions. The design and manufacturing of such foods is a challenging task and has attracted considerable interest from the food industry and academics in recent years. Throughout history, solutions to many practical problems facing humanity have come from emulating nature via lessons learned through observations. As we have finally come to understand the complexity behind the process-structure-function relations of plant foods, we can begin to explore the opportunities to develop BPFs for optimal nutrition and health.

The novelty of BPFs presents technical difficulties that need to be overcome. Firstly, it is extremely challenging to mimic the self-assembly process and hierarchical structuring that are inherent in foods of nature. Scientific evidence has suggested that intact, minimally-processed natural foods seem to have more compact, cohesive matrices and stronger interactions between nutrients. This means they are disassembled and release nutrients in the digestive tract at a slower rate with greater satiety as opposed to artificially reconstructed foods (Fardet, 2015). Furthermore, drastic processing conditions may inadvertently cause undesirable changes in structures and properties of food elements during isolation or reassembly. Finally, the application of BPFs can be problematic in new product development for commercialisation. Despite these technical challenges, the prospects are very exciting. Ongoing and future research initiatives should be directed towards exploring the possibility of designing BPFs for better health

outcomes. An interdisciplinary approach should be taken and this is reflected in conducting research at the dynamic interface of a wide range of disciplines in food science and technology, including structure-digestion, chemistry, engineering, physiology, microbiology and human nutrition.

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