

## Review

# Dietary fiber in plant cell walls—the healthy carbohydrates

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## Abstract

Dietary fiber (DF) is one of the major classes of nutrients for humans. It is widely distributed in the edible parts of natural plants, with the cell wall being the main DF-containing structure. DF content varies significantly in different plant species and organs, and the processing procedure can have a dramatic effect on the DF composition of plant-based foods. Given the considerable nutritional value of DF, a deeper understanding of DF in food plants, including its composition and biosynthesis, is fundamental to the establishment of a daily intake reference of DF and is also critical to molecular breeding programs for modifying DF content. In the past decades, plant cell wall biology has seen dramatic progress, and such knowledge is of great potential to be translated into DF-related food science research and may provide future research directions for improving the health benefits of food crops. In this review, to spark interdisciplinary discussions between food science researchers and plant cell wall biologists, we focus on a specific category of DF—cell wall carbohydrates. We first summarize the content and composition of carbohydrate DF in various plant-based foods, and then discuss the structure and biosynthesis mechanism of each carbohydrate DF category, in particular the respective biosynthetic enzymes. Health impacts of DF are highlighted, and finally, future directions of DF research are also briefly outlined.

**Keywords:** Dietary fiber; carbohydrate; plant cell walls; polysaccharide; glycosyltransferases; healthy food.

## Introduction

Dietary fiber (DF) is generally considered an essential class of nutrients. Compared with other traditional nutrient classes, namely, water, proteins, sugars, fats, vitamins, and minerals, the concept of DF was established rather late, only after the Second World War. In 1953, Hipsley used the term DF for the first time to refer to certain high-molecular-weight substances from food, including cellulose, hemicellulose, and lignin (Hipsley, 1953). In 1972, Trowell defined DF as ‘the skeletal remains of plant cells that are resistant to digestion by enzymes of man’ (Trowell, 1972a; Trowell, 1972b). This widely spread concept was also adopted by the Association of Official Analytical Chemists, which released a similar physiological definition of DF (together with its chemical composition) in 1994 (Lee and Prosky, 1995). In 2001, the American Association of Cereal Chemists (AACC) provided a comprehensive definition of DF: ‘the edible parts of plants or analogous carbohydrates that are resistant to digestion and absorption that include polysaccharides, oligosaccharides, lignin, and associated plant substances’ (AACC, 2001). This is the current, internationally recognized, and relatively authoritative definition of DF.

Similar to the definition of DF, the classification methods of DF are also diversified. In general, DF is grouped into

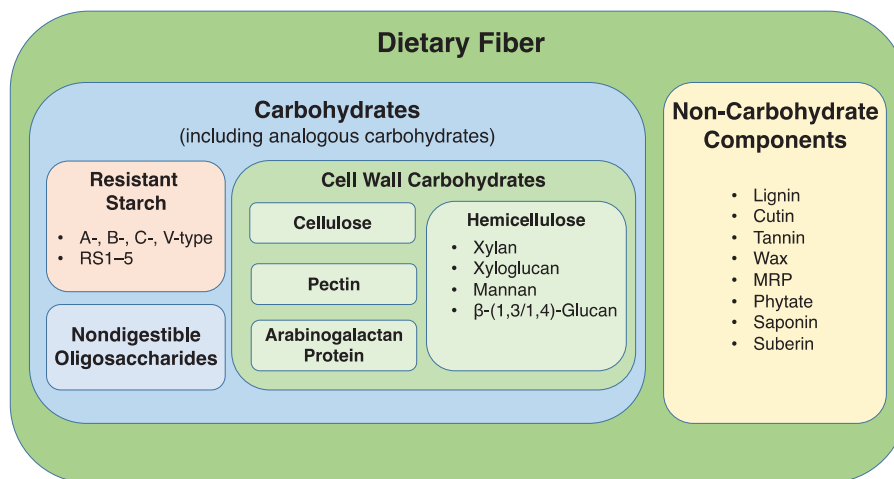
carbohydrates and non-carbohydrate components (Slabaugh *et al.*, 2014; AACC, 2001; Figure 1). Additionally, DF can be classified according to its food origin and solubility. Plants are the major source of our DF intake, while animals, fungi, and microorganisms also contain DF. Recently, artificially synthesized DF has also been developed. In plants, DF largely exists as part of their cell walls, a polysaccharide-rich structure outside of the plant plasma membrane, mainly consisting of cellulose, hemicellulose, lignin, pectin, and glycoproteins. Some of these cell wall-derived DFs are insoluble dietary fiber (IDF), such as cellulose and lignin. Despite their high nutritional value, they are less beneficial in food-processing operations than soluble dietary fiber (SDF), as the latter provides viscosity and has the ability to form gels and/or act as emulsifiers (Mudgil and Barak, 2013).

Among these DF categories, plant polysaccharides represent the main source of DF intake for humans, and plant cell wall-derived DF is therefore the most studied and exploited DF category. In this review, we focus on carbohydrate DF derived from the plant cell wall, aiming to integrate the latest knowledge of cell wall biology with DF research and thus prompt new research opportunities. In the following sections, we first provide a breakdown of DF from various common daily diets, summarizing the distinct

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**Figure 1.** Classification of common dietary fiber (AACC, 2001; Mudgil and Barak, 2013). MRP, Maillard reaction product; RS, resistant starch.

DF content in different plant-based foods. Subsequently, we compare the chemical/molecular structure of cell wall DF, and the composition and biosynthesis are also discussed. Furthermore, the health benefits of cell wall DF are also briefly explored.







## DF in Plant-Based Foods

The main sources of plant DF obtained from the diet are cereals, fruits, vegetables, legumes, nuts, and edible seeds. While DF is found in all these plant-based foods, its concentration and composition vary considerably depending on product characteristics and the processing method (e.g. fresh, blanched, frozen, dried, cooked, canned, juiced, and sauced; Welti-Chanes *et al.*, 2020).

## Cereals

As the most important energy supply in human food, cereals are certainly the top supplier of our fiber intake (Table 1). DF in cereals include non-starch polysaccharides, oligosaccharides (fructo-oligosaccharides (FOs)), resistant starch, and lignin (Bach Knudsen *et al.*, 2017). DF is found in all four structures of cereal grains, namely, germ, endosperm, bran, and glume. The cell wall of the outer kernel of cereals (bran) is thick, hydrophobic, and is mainly composed of IDF (i.e. cellulose, insoluble arabinoxylan, and lignin). For example, in wheat and rye bran, around 50% and 30% of the dry matter (DM) are IDF, respectively (Bach Knudsen *et al.*, 2017). By contrast, the cell wall of endosperm is narrow and hydrophilic, mainly consisting of arabinoxylan and/or  $\beta$ -glucan and a small fraction

**Table 1.** Content of dietary fiber (DF) in cereal grains

Cereals	DF content (g/100 g DM)	Reference
 Wheat ( <i>Triticum</i> )	9.2–17.0	De Santis <i>et al.</i> , 2018; Dodevska <i>et al.</i> , 2013
 Rice ( <i>Oryza sativa</i> )	2.5–9.9	Amalraj and Pius, 2015; Bach Knudsen <i>et al.</i> , 2017
 Maize ( <i>Zea mays</i> )	3.7–19.6	Prasanthi <i>et al.</i> , 2017; Vitaglione <i>et al.</i> , 2008
 Oat ( <i>Avena sativa</i> )	9.8–37.7	Bach Knudsen <i>et al.</i> , 2017; Vitaglione <i>et al.</i> , 2008
 Barley ( <i>Hordeum vulgare</i> )	10.1–27.9	Djurle <i>et al.</i> , 2016; Messia <i>et al.</i> , 2017; Tang and Tsao, 2017
 Rye ( <i>Secale cereal</i> )	9.6–20.9	Bucella <i>et al.</i> , 2016; Hansen <i>et al.</i> , 2003

DM, dry matter.

of fructans (Nilsson *et al.*, 1986). The DF content in the grain not only varies among grain structures, but it could also be largely influenced by the processing method. For example, maize is known to be rich in DF that consists mainly of heteroxylan and cellulose (Hamaker *et al.*, 2019); however, fresh sweet maize kernels contain only a small amount of DF (2.4% of the fresh weight), of which up to 80% is cellulose (Welti-Chanes *et al.*, 2020), while in maize bran prepared by dry milling, cellulose and heteroxylan are the dominant components, accounting for 22% and 70% of DM, respectively (Ai and Jane, 2016).

### Fruits

Fruits represent another important source of DF intake. Among a very wide range of fruits, some popular ones have been well studied in terms of their DF and are therefore discussed here as examples. Citrus fruits are a well-known source of DF rich in pectin. In the peels of different major citrus species, namely, orange (*Citrus sinensis*), grapefruit (*Citrus grandis*), lemon (*Citrus limon*), gonggan (*Citrus reticulata* × *Citrus sinensis*), and ponkan (*Citrus reticulata*), the proportion of DF content ranges from 60.92 to 65.36 g/100 g DM (Wang *et al.*, 2015). Pectin is the predominant polysaccharide in citrus pulp, accounting for 42% of the fresh weight, followed by cellulose (16%) and hemicellulose (10%) (Lundberg *et al.*, 2014). In addition to citrus fruits, some other tropical fruits such as mango (*Mangifera indica*), pineapple (*Ananas comosus*), passion fruit (*Passiflora edulis*), banana (*Musa paradisiaca*), and coconut (*Cocos nucifera*) have also been subjected to intensive research for their attractive flavor, color, and texture, as well as their DF contents (Bicas *et al.*, 2011). Pineapple pulp has a higher DF content (69.6%) than passion fruits (56.9%) and mango (31.6%); however, the content ratio of SDF to IDF in pineapple (around 1:34) is lower than that of passion fruits (around 3:16) and mango (around 1:4) (Selani *et al.*, 2016). In mango peel, an important by-product in the food industry, the DF percentage of DM ranges from 40.6% to 72.5%, typically higher in ripe mango peels in comparison with non-ripe ones (Ajila and Prasada Rao, 2013).

### Vegetables and legumes

The DF concentration varies among different vegetable species and varieties, and it also largely depends on the evaluated plant part/tissue and ripening stage. Many cruciferous vegetables are consumed in large amounts, such as cabbage (*Brassica oleracea* var. *capitata*) and broccoli (*Brassica oleracea* var. *italica*). The DF constituents of boiled white cabbage vary greatly, with a range of approximately 17.7%–31.7% of DM (Wennberg *et al.*, 2003). In broccoli, the overall DF content is relatively low (around 11.3%, DM; Bouzari *et al.*, 2015), but in its stems, large amounts of DFs (around 30%, DM), mostly IDF, have been measured (Schäfer *et al.*, 2017). Some popular root and tuber vegetables, such as carrot (*Daucus carota*), onion (*Allium cepa*), and potato (*Solanum tuberosum*), are also rich in DF. In carrot, there are large amounts of DF (63.5%, DM) in pomace, higher than fresh carrot peels (Chantaro *et al.*, 2008). In onion, DF is present at the highest level (68.3%, DM) in the skin, whereas the inner part has the lowest DF content (11.6%, DM; Jaime *et al.*, 2002). The major DF types contained in potato are cellulose (10%–40%, DM), hemicellulose (10%–15%), pectin (15%–20%), and lignin (4%–25%; Camire *et al.*, 1997; Kaack *et al.*, 2006).

Legumes provide a large proportion of dietary proteins for humans. The most utilized oil-bearing legume species are soybean (*Glycine max*) and peanut (*Arachis hypogea*). An intact soybean contains around 10% IDF and 7% SDF (Anderson *et al.*, 1999). Peanuts are primarily consumed as nuts, but they are also ingredients for producing nutritious bars, pastes, and peanut butter. It has been reported that the mature Okrun seeds generally contain 13.6% DF of DM (Jonnala *et al.*, 2006).

### Nuts and edible seeds

Nuts are the seeds of a hard-shelled dry fruit, and the main edible part is the cotyledon or endosperm. The fact that nuts may contain even higher DF content than grains contributes to nuts' highly appreciated nutrient value (Fitzgerald *et al.*, 2020). Flaxseeds have the highest DF content (>27%, DM) among all nuts and edible seeds, followed by almonds, whose DF content is also remarkably high (12% DM). Some widely consumed nuts, such as cashew nuts, hazelnuts, pecans, pistachio, and walnuts, are also excellent DF sources (Table 2). All the fiber-rich nuts listed in Table 2 are healthy additions to our diets (Ozturkoglu-Budak *et al.*, 2016), with around 30–60 g of nuts being the recommended daily portion size.

### Chemical Structure of Dietary Carbohydrates

Despite the substantial variation in DF composition among different plant-based foods, the chemical structure of each DF category is relatively conserved and has been unraveled. In particular, extensive biochemical characterization of the plant cell wall in different plant species has dramatically improved our understanding of these dietary carbohydrates. In this section, we describe the chemical structure of this cell wall-derived DF in detail and also briefly discuss the structure of some non-digestible oligosaccharides (NDOs), most of which are degradation products of cell wall polysaccharides.

### Cell wall polysaccharides

#### Cellulose

Cellulose is the most abundant biopolymer in our planet (representing more than half of Earth's total carbon) and the main weight-bearing element of plant cell walls (Kumar *et al.*, 2012; Polko and Kieber, 2019). Cellulose is a complex structure consisting of  $\beta$ -(1,4)-glucose (Glc) chains (Figure 2). These chains may crystallize into cellulose microfibrils (CMFs) through inter- and intramolecular hydrogen and Van der Waals bonds, which give the majority of native cellulose a quasi-crystalline structure (Saxena and Brown, 2005; Somerville, 2006; Nishiyama, 2009). Compared with secondary cell walls, CMFs of the primary wall are highly crystalline, and they have an orientation parallel to the direction of elongation (Kataoka and Kondo, 1998). For many years, CMFs were thought to be composed of 36 cellulose chains, based on the structure of the cellulose synthase complex (CSC; see more in the section of 'Synthesis of Dietary Carbohydrates'; Kubicki *et al.*, 2018). These 36-cellulose polymer layers are presumably arranged in a '12 345 654 321' pattern (Matthews *et al.*, 2012). Recently, based on the trimeric nature of cellulose synthase (CESA), a new model of a CSC rosette containing 18 CESA subunits synthesizing 18-cellulose polymer chains was proposed (Hill *et al.*, 2014). Transmission electron microscopy imaging of CSCs of *Physcomitrella patens* coupled with computational

**Table 2.** Contents of dietary fiber (DF) and water in daily intake of raw foods (Rhodes et al., 2020)








































































Fruits	Content (g/100 g)		Vegetables	Content (g/100 g)		Nuts	Content (g/100 g)	
	DF	Water		DF	Water		DF	Water
 Apple, without skin	1.3	86.7	 Asparagus	2.1	93.2	 Almond	12.5	4.4
 Avocado	6.7	73.2	 Bean, black	15.5	11.0	 Cashew nut	3.0	1.7
 Banana	2.6	74.9	 Bean, snap, green	2.7	90.3	 Chestnut, European	5.1	40.5
 Blackberry	5.3	88.2	 Beet	2.8	87.6	 Hazelnuts or filbert	9.7	5.3
 Blueberry	2.4	84.2	 Broccoli	2.6	89.3	 Pecan	9.6	3.5
 Cantaloupe	0.8	82.3	 Cabbage	2.5	92.2	 Pine nut	3.7	2.3
 Cherry, sweet	2.1	47.0	 Carrots	2.8	88.3	 Pistachio nut	10.3	1.9
 Coconut meat	9.0	67.6	 Cassava	1.8	59.7	 Walnut, black	6.8	4.6
 Coconut milk	2.2	80.8	 Cauliflower	2.0	92.1	 Peanut	8.5	6.5
 Guava	5.4	83.9	 Chickpea	12.2	7.7	 Flaxseed seed	27.3	7.0
 Kiwifruit, green	3.0	80.9	 Chive	2.5	90.7	 Pumpkin seed kernel	6.5	2.0
 Kumquat	6.5	89.0	 Collard	4.0	89.6	 Sesame seed kernel	11.6	3.8
 Lemon, without peel	2.8	88.3	 Cucumber, with peel	0.5	95.2	 Sunflower seed kernel	11.1	1.2
 Lime	2.8	81.8	 Eggplant	3.0	92.3			
 Litchi	1.3	83.5	 Garlic	2.1	58.6			
 Mango	1.6	90.2	 Ginger root	2.0	78.9			
 Nectarine	1.5	89.0	 Hot chili	1.5	88.0			
 Orange	2.4	86.8	 Kale	4.1	89.6			
 Papaya	1.7	88.1	 Lentil	10.7	8.3			
 Passion-fruit juice, purple	0.2	85.6	 Mung bean, sprouted	1.8	90.4			
 Passion-fruit, purple	10.4	72.9	 Okra	3.2	89.6			
 Peach	1.5	88.3	 Onion	1.7	89.1			
 Pear	3.1	84.0	 Potato	2.1	79.3			
 Pineapple	1.4	86.0	 Pumpkin	0.5	91.6			
 Plum	1.4	87.2	 Radicchio	0.9	93.1			
 Pomegranate	4.0	77.9	 Radish	1.6	95.3			
 Strawberry	2.0	91.0	 Spinach	2.2	91.4			

Table 2. Continued

	Fruits	Content (g/100 g)		Vegetables	Content (g/100 g)		Nuts	Content (g/100 g)	
		DF	Water		DF	Water		DF	Water
	Tangerine	1.8	85.2		Taro	4.1	70.6		
	Watermelon	0.4	91.5		Tomato	1.2	94.5		

modeling further supports this hypothesis (Nixon *et al.*, 2016). More recently, Kubicki *et al.* (2018) predicted the exact structure of CMFs by the  $\delta^{13}\text{C}$  nuclear magnetic resonance values obtained from performing density functional theory calculations on the energetic and spectral parameters of the CMF habit, and by comparing the calculated  $s\text{C}_4$  and  $s\text{C}_6$  values with the observed  $\delta^{13}\text{C}$  values, the authors concluded that cellulosic polymer layers are more likely to be arranged in a five-layer diamond model of 34 443 per layer.

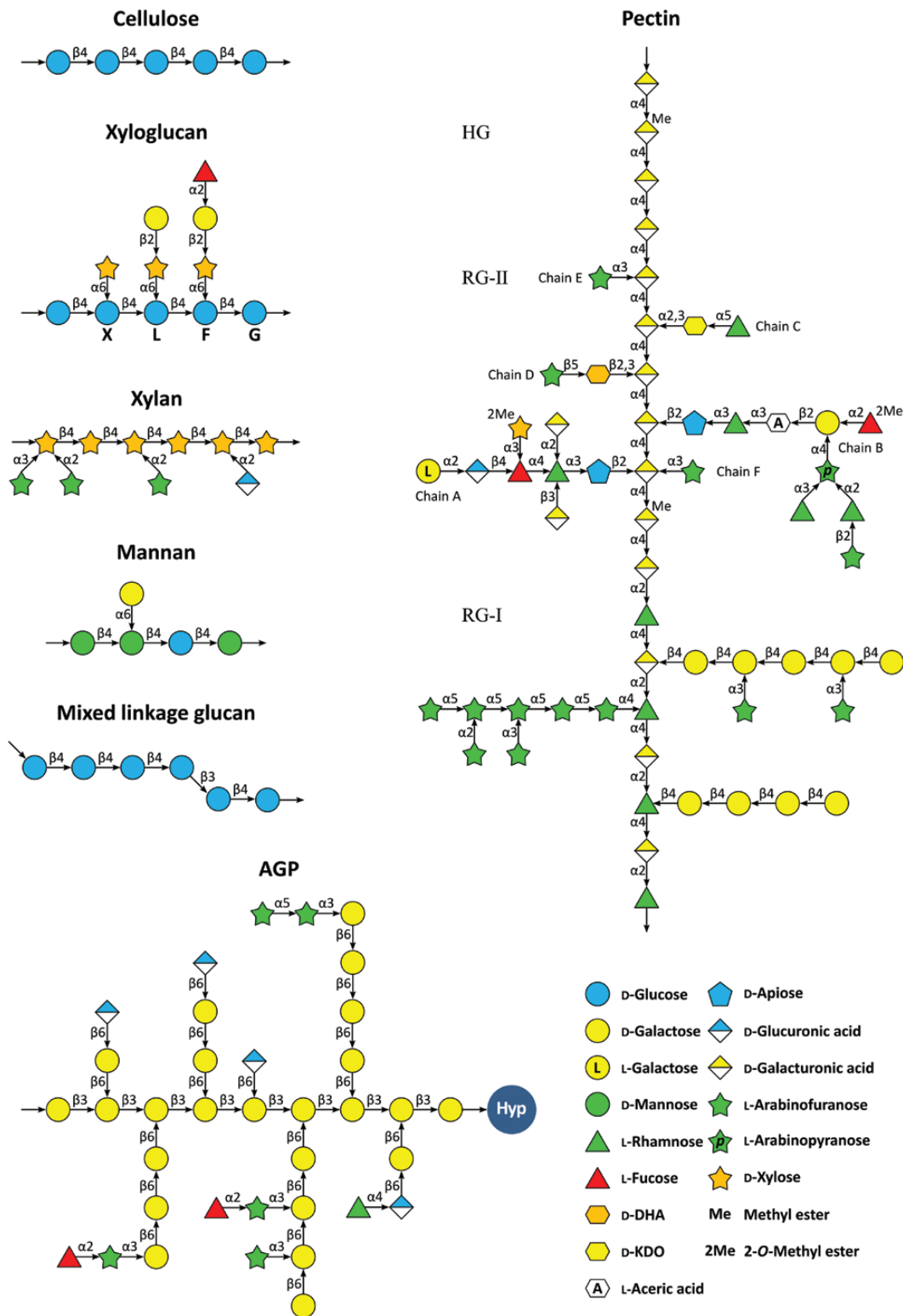
### Hemicelluloses

Hemicelluloses are branched polysaccharides with a backbone featuring linked Glc, xylose (Xyl), or mannose (Man) residues, termed xyloglucan, xylan, or mannan, respectively, with the exception of  $\beta$ -(1,3/1,4)-glucan (mixed linkage glucan, MLG), which has no carbohydrate side chain decorations (Scheller and Ulvskov, 2010). Xyloglucan is the major hemicellulose component in the primary cell wall of eudicots. It has a  $\beta$ -(1,4)-glycan backbone with  $\alpha$ -(1,6)-Xyl side chains that can be further substituted with extra monosaccharides (e.g. galactose (Gal) and fucose (Fuc); Figure 2). A single letter is used to stand for the Glc residues with a certain side chain or without (Fry *et al.*, 1993); for example, G represents a Glc residue without a side chain, and X represents  $\alpha$ -Xyl- $\alpha$ -(1,6)-Glc (Figure 2). Two common types of xyloglucan structures are XXXG and XXGG, mainly present in dicots and grasses, respectively. For instance, commelinid monocots' primary walls contain xyloglucan that is predominantly of the XXGG structure (Scheller and Ulvskov, 2010; Pauly and Keegstra, 2016). The backbone of xylan is composed of Xyl residues linked by  $\beta$ -(1,4) glycosidic bonds, and is modified by glucuronic acid (GlcA), arabinose (Ara), and Xyl (Figure 2). The structure of xylan varies in different plant species and tissues. Glucuronoxyylan is the major non-cellulosic polysaccharide of the secondary wall of eudicots, whereas glucuronoarabinoxylan is the major non-cellulosic polysaccharide in the primary wall of commelinid monocots (Scheller and Ulvskov, 2010). In wheat endosperm, up to 70% of the cell wall is composed of arabinoxyylan (Faik, 2010). In plantago, the seed mucilage is mostly composed of heteroxyylan, a xylan that is heavily branched with pentoses (Xyl and Ara; Yu *et al.*, 2017). Surprisingly, in conifers and several eudicots, the reducing end of the xylan backbone has a conserved oligosaccharide structure:  $\text{-D-Xylp-}\beta$ -(1,3)-L-Rhap- $\alpha$ -(1,2)-D-GalpA- $\alpha$ -(1,4)-D-Xylp (Rha, rhamnose; Peña *et al.*, 2007), but not in grasses (Ratnayake *et al.*, 2014). Heteromannans are a class of ancient polysaccharides abundant in early-evolved terrestrial plants such as mosses (Moller *et al.*, 2007). Galactomannans

have a backbone entirely composed of  $\beta$ -(1,4)-mannosyl residues, whereas glucomannans and galactoglucomannans have a backbone that is composed of Glc and Man and substituted with an  $\alpha$ -1,6-linked galactosyl residue on the mannosyl residues (Figure 2). Compared with early land plants, mannan and glucomannan tend to be much less abundant in spermatophytes, and in gymnosperms, galactomannan has become a major component of their secondary walls (Ebringerová *et al.*, 2005). MLG is largely composed of  $\beta$ -(1,4)-linked Glc (around 70% of the polymer), with individual  $\beta$ -(1,3)-linked Glc (around 30%) interspersed, and this polysaccharide is commonly found in plants in the Poaceae family (Smith and Harris, 1999; Ebringerová *et al.*, 2005; Figure 2).

### Pectins

Pectins are a family of galacturonic acid (GalA)-rich polysaccharides, generally being grouped into three major types: homogalacturonan (HG), rhamnogalacturonan I (RG-I), and rhamnogalacturonan II (RG-II). Two less-common pectin types, apiogalacturonan (AGA) and xylogalacturonan (XGA), are also found in some cell walls. These pectic components are often crosslinked with each other, forming a pectic network, and the network is further enlarged as pectin may be crosslinked with other components of the cell wall (e.g. xylans, xyloglucans, proteins, and lignins), as well as some non-cell wall substances (e.g. calcium ions, borate esters, and phenolic compounds; Caffall and Mohnen, 2009). The backbone of the dominant pectin type HG (around 65%) is a polymer of  $\alpha$ -(1,4)-linked D-GalA, and methylation and acetylation may occur at the C-6 position and O-2 (or O-3), respectively (Ridley *et al.*, 2001; Figure 2). HG can be further substituted. AGA is predominantly found in the cell wall of aquatic plants (Hart and Kindel, 1970), and it is HG substituted with D-apiose in the form of apiose monomers or dimers (also called apibiose, the disaccharide of apiose (Apif-1,3-Apif-1-); O'Neill and York, 2003). XGA is HG decorated with D-Xyl residues at C-3 of the backbone (O'Neill and York, 2003). The most abundant XGA polysaccharide structure in plants features a GalA backbone decorated by Xyl at the O-3 and by two linked Xyl residues at the O-2 (Caffall and Mohnen, 2009). RG-I's backbone structure is  $[\alpha$ -(1,4)-D-GalpA- $\alpha$ -(1,2)-L-Rhap-] $_n$ , and it often contains arabinan, galactan, or arabinogalactan (AG) side chains. Type-I AG is the most abundant in RG-I (Western *et al.*, 2004; Caffall and Mohnen, 2009), and it is composed of  $\beta$ -(1,4)-linked galactan mainly substituted by  $\alpha$ -(1,5)-L-Araf residues at the O-3 position (Huisman *et al.*, 2001). RG-II is a complex substituted HG that accounts for only a small



**Figure 2.** Typical chemical structure of carbohydrate dietary fiber except for non-digestible oligosaccharides and resistant starch. Glycans symbols were drawn using the SNFG (Symbol Nomenclature for Glycans guidelines) standard (Neelamegham et al., 2019). AGP, arabinogalactan protein; HG, homogalacturonan; DHA, docose hexaenoic acid; KDO, 3-deoxy-D-manno-octulosonic acid; Hyp, hydroxyproline; RG-I, rhamnogalacturonan I; RG-II, rhamnogalacturonan II.

amount of cell wall material. It contains multiple side chain types composed of at least 13 different types of monosaccharides linked by more than 20 glycosidic bonds (Anderson and Kieber, 2020).

### Arabinogalactan proteins (AGPs)

AGPs are a group of heavily glycosylated, hydroxyproline-rich proteins (HRGPs) present in virtually all land plants. As approximately 90% of the AGP molecule is the carbohydrate

part (AG glycan structure), AGPs are also termed proteoglycans (Peña *et al.*, 2000) and are available to human gut microbiota (Munoz-Munoz *et al.*, 2021). For most AGPs, one or more hydroxyproline residues are O-glycosylated by Type II AGs, which consist of a  $\beta$ -(1,3)-Gal backbone with  $\beta$ -(1,6)-AG side chains (Figure 2). The side chains can be further modified with the addition of GlcA, Rha, Xyl, and Fuc. AGPs can be categorized broadly into classical and non-classical AGPs (Ma *et al.*, 2018). A classical AGP contains a signal peptide at the N-terminus, a central domain rich in Pro, Ala, Ser, and Thr for glycosylation, and often a C-terminal glycosylphosphatidylinositol lipid (GPI) anchor. Classical AGPs can be further classified into GPI-AGPs, non-GPI-AGPs, lysine (K)-rich AGPs, and AG-peptides (Schultz *et al.*, 2000). Non-classical AGPs have domains such as histidine-rich and cysteine-containing ones, and other hybrid HRGPs (Showalter *et al.*, 2010; Ma *et al.*, 2018). Some of these non-classical AGPs are also called chimeric AGPs, which have a recognized domain in addition to the AGP domain; for example, fasciclin-like arabinogalactan-proteins feature an additional fasciclin domain (Ma *et al.*, 2017).

### NDOs

NDOs are certain dietary oligosaccharides that are not easily digested or hydrolyzed by gut digestive enzymes. Such resistance of NDOs is in part because most NDOs have a  $\beta$ -configuration, making them difficult to be degraded by  $\alpha$ -glycosidic bond-specific gastrointestinal digestive enzymes (Swennen *et al.*, 2006). However,  $\beta$ -galactosidase enzymes are also present, so the low degradation rate might also result from weak enzyme activities and/or substrate selectivity. The degree of polymerization (DP) is an important determinant of the oligosaccharide's properties. NDOs' DP could range from 2 (e.g. lactulose) to 60 (e.g. chicory inulin). In addition, the chain lengths and composition of NDOs are diverse, and they also affect the physicochemical properties of the food (Delzenne, 2003), such as the ability to bind water, the gelling state, and the fat substitution value. Table 3 shows the structure and source of some common NDOs that we consume in our daily lives (Roberfroid and Slavin, 2000; Murphy, 2001; Delzenne, 2003; Nakakuki, 2003; Liu *et al.*, 2020).

### Synthesis of Dietary Carbohydrates

Over the past decades, the synthesis of cell wall carbohydrates has been extensively studied using the model plant *Arabidopsis* and a number of agriculturally important crop plants (Ciudad-Mulero *et al.*, 2019; Verbančič *et al.*, 2018). Notably, a large number of key enzymes and pathways have been identified, and such knowledge has been widely utilized in developing the sustainable energy industry via tailoring plant biomass production (Anderson and Kieber, 2020; Han *et al.*, 2020). By contrast, less attention has been paid to strategies for improving the health benefits of food crops through modifying their DF contents, for which a comprehensive understanding of its synthesis is a prerequisite. To this end, here we outline the synthesis mechanisms of some major cell wall DF and NDOs.

### Biosynthesis of cell wall polysaccharides

#### Cellulose

CMFs are synthesized by plasma membrane-localized CSCs, and the core of the CSC in *Arabidopsis* consists of six CESA

trimers, which form a rosette structure (Polko and Kieber, 2019). The substrate of CESAs is uridine diphosphate-Glc (UDP-Glc; Verbančič *et al.*, 2018), which is converted from phosphorylated hexose sugars (Barnes and Anderson, 2018). The CESA protein comprises a cytoplasmic N-terminal domain involved in the dimerization/oligomerization process of CESA subunits (Kurek *et al.*, 2002), two transmembrane domains flanking a large cytoplasmic loop that contains the substrate binding domain and catalytic domains, six additional transmembrane domains (Sethaphong *et al.*, 2013; Slabaugh *et al.*, 2014), and an intracellular C-terminal domain (Polko and Kieber, 2019). In *Arabidopsis*, CESA1, CESA3, and CESA6 are involved in primary wall cellulose synthesis, while CESA4, CESA7, and CESA8 participate in secondary wall cellulose synthesis (Desprez *et al.*, 2007; Persson *et al.*, 2007). Primary cell wall CSCs are completely replaced by secondary cell wall CSCs during the transition of primary to secondary wall deposition, but they may appear concurrently for a short period of time (Watanabe *et al.*, 2018). Other non-CESA proteins are also involved in cellulose synthesis, mostly playing regulatory roles. The Golgi-located STELLO proteins contain a structural domain homologous to proteins of glycosyltransferase (GT) family 75, and they can interact with CESAs. Elegant cell biology experiments have revealed that they can regulate the assembly of CSCs (Zhang *et al.*, 2016). COBRA, a glycosylphosphatidylinositol-anchored protein, can regulate the orientation of cellulose microfibrils and cellulose crystallinity (Roudier *et al.*, 2005; Liu *et al.*, 2013). Furthermore, in response to environmental changes, cellulose biosynthesis is also modulated through phosphorylation, which occurs mainly at the N-terminal and cytoplasmic loop of CESAs (Nühse *et al.*, 2004; Speicher *et al.*, 2018).

#### Hemicellulose

Members of the cellulose synthase-like (CSL) superfamily are involved in the synthesis of various hemicelluloses, such as xyloglucan, glucomannan, and  $\beta$ -(1,3/1,4)-glucan (Scheller and Ulvskov, 2010). The backbone of xyloglucan is synthesized by CSL proteins of the CSLC family. So far only CSLC4 of the five CSLC proteins in *Arabidopsis* has been evidently identified with activity of synthesizing the xyloglucan backbone (Cocuron *et al.*, 2007). For the side chains, at least three  $\alpha$ -(1,6)-xylosyltransferases (xyloglucan xylosyltransferase1 (XXT1), XXT2, and XXT5) from the GT34 family are involved in adding Xyl residues to xyloglucan in *Arabidopsis* (Faik *et al.*, 2002; Cavalier and Keegstra, 2006; Zabolina *et al.*, 2008). FUT1 of the GT37 family, an  $\alpha$ -(1,2)-fucosyltransferase, is one of the first xyloglucan-glycosyltransferases identified and seems solely responsible for transferring Fuc to the backbone (Perrin *et al.*, 1999). MUR3, a GT belonging to subgroup A of the GT47 family, has been first identified with xyloglucan galactosyltransferase activity, but it only adds Gal to the third Xyl-substituted Glc in the xyloglucan XXXG core unit (Madson *et al.*, 2003; Li XM *et al.*, 2004). Later on, it was found that the other Gal on the second position X is incorporated by xyloglucan L-side chain galactosyltransferase2 (XLT2; Jensen *et al.*, 2012). Characterization of mutants displaying irregular xylem phenotypes revealed that irregular xylem9 (IRX9), IRX14 (GT43 family), and IRX10 (GT47 family), as well as their homologs, are involved in the synthesis of the xylan backbone in *Arabidopsis* (Brown *et al.*, 2007; Lee *et al.*, 2007; Brown *et al.*, 2009). Moreover, in conifers and several dicots, fragile fiber8/IRX7 (GT47 family),

**Table 3.** Dietary non-digestible oligosaccharides (NDOs) structure and origin (Delzenne, 2003; Liu et al., 2020; Murphy, 2001; Nakakuki, 2003; Roberfroid and Slavin, 2000)

NDO	Chemical structure	Food origin and/or preparation method
Fructo-Os (GFn)	$\alpha$ -(2,1)-Glc-[ $\beta$ -(2,1)-Fru] <sub>n</sub>	Extraction from natural sources and/or partial enzymatic hydrolysis
Fructo-Os (FFn)	[ $\beta$ -(2,1)-Fru] <sub>n</sub>	Hydrolysis from chicory root inulin; degraded by a fructan polymer inulin
Galacto-Os	[ $\beta$ -(1,6)-Gal] <sub>n</sub> - $\alpha$ -(1,4)-Glc	Enzymatic synthesis from lactose
Lactulose	Gal- $\beta$ -(1,4)-Fru	Synthesis from lactose
Lacto-sucrose	Gal- $\beta$ -(1,4)-Glc- $\alpha$ -(1,2)- $\beta$ -Fru	Enzymatic synthesis from lactose and/or sucrose
Mannan-Os	[ $\beta$ -(1,4)-Man] <sub>n</sub>	Naturally occurring in coffee beans, konjac; extracted from <i>Amorphophallus konjactubers</i> , and the extracellular wall of the yeast <i>Saccharomyces cerevisiae</i> .
Iso-malto-Os	[ $\alpha$ -(1,6)-Glc] <sub>n</sub>	Partial enzymatic hydrolysis or glycosyl transfer from starch, naturally occurring in fermented foods (fermented sourdough bread and kimchi)
Palatinose (isomaltulose)	Glc- $\alpha$ -(1,6)-Fru	Enzymatic synthesis from sucrose
Polydextrose	[ $\alpha$ -(1,6)-Glc] <sub>n</sub> , mainly	Thermal treatment of starch with citric acid
Raffinose	Gal- $\alpha$ -(1,6)-Glc- $\beta$ -(1,2)-Fru	Found in vegetables (cabbage, broccoli, beans, ginger)
Resistant dextrins	[ $\alpha$ -(1,4/6)-Glc] <sub>n</sub> , mainly	Synthesis from starch
Soybean-Os	[ $\alpha$ -(1,6)-Gal] <sub>n</sub> - $\alpha$ -(1,6)-Glc- $\beta$ -(1,2)-Fru	Extraction from natural source
Stachyose (raffinose)	Gal- $\alpha$ -(1,6)-Gal- $\alpha$ -(1,6)-Glc- $\beta$ -(1,2)-Fru	Naturally present in soyabean
Xylo-Os	[ $\beta$ -(1,4)-Xyl] <sub>n</sub>	Partial enzymatic hydrolysis of polyxylan; found naturally in fruits, vegetables, honey bamboo shoots

-Os, -oligosaccharides; Fru, fructose; Gal, galactose; Glc, glucose; Man, mannose; Xyl, xylose.

galacturonosyltransferase12 (GAUT12)/IRX8 (GT8 family) and galacturonosyltransferase-like1 (GATL1)/PARVUS (GT8 family) are associated with the synthesis of the conserved structure at the reducing end of the xylan backbone (Lee et al., 2007; Peña et al., 2007). It is noteworthy that some GT proteins may form a complex to cooperatively synthesize both the xylan backbone and its side chains. For instance, wheat arabinoxylan is synthesized by a synthase complex containing members of the GT43, GT47, and GT75 families (Zeng et al., 2010; Jiang et al., 2016). Furthermore, the GT61 family genes are also studied in grasses and plantago and are thought to be involved in the xylan pentose sidechain incorporation (Phan et al., 2016; Zhong et al., 2021). Following the identification of a mannan synthase, which is a CSLA protein (GT2 family), in guar (*Cyamopsis tetragonoloba*; Dhugga et al., 2004), several CSLA members have been found to have mannan and glucomannan synthase activity in *Arabidopsis*, such as CSLA2, CSLA7, and CSLA9 (Liepman et al., 2005). Recently, an innovative synthetic approach has revealed that mannan-synthesis related proteins may affect CSLA activity through protein glycosylation (Voiniciuc et al., 2019). In addition to this, fenugreek enzymes from GT34 are involved in the side chain galactosylation of mannan (Edwards et al., 1999). As mixed-linkage glucan has not been found in dicots, its synthesis has been primarily studied in some grass species; these efforts revealed that members of the grass-specific CSLF and CSLH families are involved in  $\beta$ -(1,3/1,4)-glucan biosynthesis (Burton et al., 2006; Doblin et al., 2009).

### Pectin

Due to the difficulties in high-quality enzyme preparation, only a small number of pectin biosynthetic enzymes' activities have been unambiguously or putatively demonstrated, and most of them localize to the Golgi apparatus, where pectic polysaccharides are synthesized (Moore et al.,

1991; Zhang and Staehelin, 1992). For the backbones, a complex consisting of GAUT1, a proven HG: $\alpha$ -1,4-D-galacturonosyltransferase, and GAUT7 is known to catalyze the HG backbone biosynthesis in *Arabidopsis* (Sterling et al., 2006; Atmodjo et al., 2011), and recently, the  $\alpha$ -(1,4)-rhamnosyltransferases responsible for the synthesis of the RG-I backbone have been identified (Takenaka et al., 2018). For the side chains, two GT47 family members arabinan deficient1 (ARAD1) and ARAD2 have been assigned putative arabinosyltransferase activity, forming a complex to participate in the synthesis of RG-I side chains (Harholt et al., 2006, 2012), and only some xylosyltransferases (GT77) involved in RG-II side chain biosynthesis were characterized (Egelund et al., 2006), although many more GTs are apparently required. Pectic polysaccharides may be methylesterified and acetylated (Ishii, 1997; Lennon and Lord, 2000; Willats et al., 2001), yet so far only some putative pectin methyltransferases and acetyltransferases have been identified (Atmodjo et al., 2013).

### AGPs

The biosynthesis of AGPs is complex, because it involves amino acids, carbohydrates, and lipids. For the AGP glycans, at least 10 functionally distinct GTs are required, such as galactosyltransferases (GALTs), including hydroxyproline O-galactosyltransferases (HPTGs), fucosyltransferases (FUTs), and glucuronosyltransferases (GLCATs). The GT31 family appears to be important for the synthesis of AGPs' sugar backbone, as the members of this family are responsible for both its initiation and elongation. In this family, GALT2–6 and HPGT1–3 specifically add the first Gal residue to the hydroxyproline of the peptide chain in *Arabidopsis* (Basu et al., 2013, 2015; Ogawa-Ohnishi and Matsubayashi, 2015). AT1G77810 and KAONASHI4/GALT14 were found to be able to extend the  $\beta$ -(1,3)-Gal backbone by adding multiple Gal residues (Qu et al., 2008; Suzuki et al., 2017). In addition,

one GT31 family protein from cotton was also characterized as AGP  $\beta$ -(1,3)-galactan synthase and it affects the fiber development (Qin *et al.*, 2017). Given the diverse nature of AGP side chains, it is not surprising that multiple families of GTs need to participate. Some relatively well-characterized families are GT47, GT14, GT37, and GT77. Members of the GT47 family may be able to synthesize Ara side chains onto AGPs (Harholt *et al.*, 2012; Lampugnani *et al.*, 2016). GLCAT14A from the GT14 family is able to add GlcA residues to the terminals of the  $\beta$ -(1,3)-Gal sugar backbone and  $\beta$ -(1,6)-Gal side chains (Knoch *et al.*, 2013; Dilokpimol and Geshi, 2014; Xuan *et al.*, 2021). AtFUT4 and AtFUT6, two GT37 family members, are capable of adding Fuc residues to the Ara residues of the side chains (Wu *et al.*, 2010; Tryfona *et al.*, 2014). Moreover, REDUCED ARABINOSE YARIV1 of the GT77 family has a putative function of adding AraF residues (Gille *et al.*, 2013).

### *In vitro* biosynthesis of NDOs

Some naturally occurring NDOs are present in plants, such as FOs (Delzenne, 2003; Liu *et al.*, 2020). Meanwhile, many more non-naturally occurring oligosaccharides can be prepared from plant-based ingredients (Table 3). The preparation can be easy. For example, polydextrose can be prepared by heat-treating Glc in the presence of citric acid (Roberfroid and Slavin, 2000). Nowadays, many NDOs are produced through enzyme processing, which is considered to be more efficient and environmentally friendly than the chemical synthesis approach. Glycosylhydrolases (GHs) and GTs are two commonly used enzyme categories. Most NDOs are produced using GHs, which can use xylan, inulin, and starch as substrates (Swennen *et al.*, 2006). In addition, GTs (or glycosidases with transferase capacity) are employed for the enzymatic synthesis of oligosaccharides using both activated donor carbohydrates bound to nucleoside monophosphates or diphosphates (cytidine monophosphate, UDP, guanosine diphosphate, or thymidine diphosphate) and non-activated donors (Chakdar and Pabbi, 2016). Combined activities of GTs and GHs can synthesize some simple sugars such as lactulose (Kim and Oh, 2012; Wang *et al.*, 2013), FOs (Ganaie *et al.*, 2013; Dominguez *et al.*, 2014), and gentiatriose (Fujimoto *et al.*, 2009). The current commercial methods for NDO production are shown in Table 4. In addition to these listed methods, some automated synthesis systems for oligosaccharides are being intensively investigated (Zhang JB *et al.*, 2018).

## DF and Human Health

DF exerts many important physiological effects on human health (Lunn and Buttriss, 2007). In recent years, there have been two major categories of health-related DF studies: (i) characterization of physiochemical properties that affects DF's physiological effects, and (ii) exploitation of their biological mechanisms.

### Beneficial effects of DF on disease prevention and treatment

Sufficient DF intake has been positively associated with the prevention of several common chronic diseases, such as diabetes, cardiovascular diseases, and inflammation, all of which are leading causes of death and disability worldwide (Meijer *et al.*, 2010; Ottevaere *et al.*, 2011). Epidemiological evidence shows that insufficient DF intake is associated with

increased incidences of obesity and diabetes (Howarth *et al.*, 2001; Trinidad *et al.*, 2006), and fiber treatment may help prevent or alleviate these conditions. For example, it has been shown that barley fiber treatment can reduce postprandial glycemia and insulin response (Behall *et al.*, 2006) and improve the Glc-tolerance of patients with type II diabetes, in addition to reducing systolic blood pressure, fasting plasma glycemia, glycosylated hemoglobin, and free fatty acid levels (Li *et al.*, 2003, 2004). Regarding cardiovascular diseases, many studies also have demonstrated that DF treatment plays a positive role in reducing them. Garcia *et al.* (2007) reported that arabinoxylan consumption can significantly reduce postprandial glycemia, insulin, and triglyceride responses. In the process of lipid metabolism, DF can inhibit or delay the absorption of cholesterol and triglycerides in the lymphatic system, thereby maintaining the normal metabolism of blood lipids and lipoproteins. In addition, John *et al.* (2002) found that *Plantago ovata* husk and a high daily intake of fruits and vegetables are associated with lower blood pressure and can reduce cardiovascular risk. Multiple types of cancer, such as lung, ovarian, and breast, also appear to occur in a lower frequency when patients are supplied with certain plant DF (Narita *et al.*, 2017; Li *et al.*, 2020). Detailed biochemical analyses revealed that metabolites produced in the intestinal tract from certain antioxidant phytochemicals in DF may be able to effectively scavenge free radicals and therefore create an antioxidant environment to prevent cancer (Quirós-Sauceda *et al.*, 2014; Del Pino-García *et al.*, 2016).

Although DF has many health benefits, there are also potential health risks if DF is overconsumed. Some DF may not only cause adverse irritation of the mucous membranes of intestines, but it can also be over-fermented in the colon to produce gas and cause bloating. Additionally, excessive DF intake may inhibit the absorption of certain nutrients in the body, such as calcium, iron, zinc, and fat-soluble vitamins (Shah *et al.*, 2009; Hayes *et al.*, 2014; Ötles and Ozgoz, 2014; Folkerts *et al.*, 2018). Therefore, a better understanding of the effectiveness and exact physiological roles of DF is needed to achieve a more balanced diet.

## Physiochemical properties that influence DF's physiological effects

### Physical properties

Various physical properties of DF can influence its health-related effects. In general, DF increases the viscosity of intestinal contents and the volume of feces (diluting potentially harmful substances); thus, it shortens the time of proteolytic fermentation and the production of harmful substances, and reduces the contact of potentially harmful substances with mucosal cells (Lattimer and Haub, 2010; Macfarlane and Macfarlane, 2012). Therefore, the molecular weight, water/oil-holding capacity and bulk density of DF are all important factors, and many studies confirm their relationships to DF's physiological effects. For instance, low-molecular-weight SDF of potato pulp has potent hydroxyl radical scavenging activity (Cheng *et al.*, 2017). Low-molecular-weight pectin has the potential to inhibit carcinogenic effects (Maxwell *et al.*, 2012). High water-holding capacity DF can modify the structure of formulated foods and reduce their caloric content (Lv *et al.*, 2017). DF with high oil-holding capacity can reduce fat digestion and absorption in the intestinal tract (Cui *et al.*, 2019). Lower bulk density DF has higher porosity and larger surface area, and therefore tends to display greater binding

**Table 4.** Commercial enzymatic synthesis methods for NDOs

NDO	Enzyme	Reference	Material	Product
CDs	Cyclodextrin glycosyltransferase (CGTase)	Li <i>et al.</i> , 2007	Starch or starch derivatives	CDs
FOs	2,1- $\beta$ -Fructan fructanohydrolases	Mutanda <i>et al.</i> , 2014	Inulin	Inulotriose, inulotetraose, inulopentaose
	$\beta$ -Fructohydrolases	Apolinário <i>et al.</i> , 2014	Inulin	High fructose syrup
	Endolevanase from <i>Bacillus licheniformis</i>	Porras-Domínguez <i>et al.</i> , 2014	Levan	$\beta$ -(2,6)-FOs
	Fructosyltransferases (FTase) and $\beta$ -fructofuranosidases (FFase)	Porras-Domínguez <i>et al.</i> , 2014	Sucrose	FOs
	Levan-sucrase from <i>Zymomonas mobilis</i>	Vigants <i>et al.</i> , 2013	Levan and sucrose	6-Ketose of FOs
GOs	$\beta$ -Galactosidases from <i>Kluyveromyces lactis</i> , <i>Streptococcus thermophilus</i>	Rodríguez-Colinas <i>et al.</i> , 2011	Lactose	$\beta$ -(1,6)-GOs
	$\beta$ -Galactosidases from <i>Bacillus circulans</i>	Song <i>et al.</i> , 2011	Lactose	$\beta$ -(1,4)-GOs
	$\beta$ -Galactosidases from <i>Bifidobacterium bifidum</i>	Goulas <i>et al.</i> , 2009	Lactose	$\beta$ -(1,3)-GOs
	$\beta$ -Galactosidases from <i>Kluyveromyces lactis</i> and glucose-isomerases from <i>Streptomyces murinus</i>	Wang <i>et al.</i> , 2013	Lactose without fructose	Lactulose
	Thermostable cellobiose-2-epimerase from <i>Caldicellulosiruptor saccharolyticus</i>	Kim and Oh, 2012	Lactose without fructose	Lactulose
MOs	Dextranase from <i>Leuconostoc mesenteroides</i>	Lee <i>et al.</i> , 2008	Sucrose and maltose	Iso-MOs with DPs (around 4–9)
	$\alpha$ -Glucosidases from <i>Aspergillus niger</i> , <i>Saccharomyces cerevisiae</i> , <i>Xanthophyllomyces dendrorhous</i>	Duan <i>et al.</i> , 1995	Maltose	Iso-MOs with DPs (around 2–4)
XOs	Xylanases and $\alpha$ -arabinofuranosidase	Manisseri and Gudipati, 2010	Wheat bran	XOs
	Xylanase from <i>Trichoderma viridere</i>	Samanta <i>et al.</i> , 2012	<i>Sehima nervosum</i>	Xylobiose, xylotriase, xylose
	Xylanase from <i>Aspergillus foetidus</i>	Chapla <i>et al.</i> , 2010	Alkali-treated corncobs	XOs
	Thermophilic xylanases from <i>Humicola insolens</i>	Du <i>et al.</i> , 2013	Wine industry waste	Xylobiose, xylotriase, xylose

CDs, cyclodextrins; COs, chito-oligosaccharides; DP, degree of polymerization; FOs, fructo-oligosaccharides; GOs, galacto-oligosaccharides; MOs, malto-oligosaccharides; XOs, xylo-oligosaccharides.

capacity (Benítez *et al.*, 2011). It has also been reported that oat  $\beta$ -glucan, due to its high lipid-binding capacity, can reduce obesity and abdominal fat via improving lipid distribution (Chang *et al.*, 2013). Moreover, the cholesterol and bile acid binding capacity of DF is also more marked when the surfaces are large, porous, and loose (Niu *et al.*, 2018; Song *et al.*, 2018). Also due to its enhanced binding capacity, DF with high porosity and charge density has hypocholesterolemic activity and can prevent heavy metal toxicity (López-Vargas *et al.*, 2013).

### Chemical properties

While the detailed mechanisms remain elusive, the chemical structure of DF appears to be crucial for the regulation of intestinal activity and microbiota, thereby affecting DF's physiological effects (Lupton, 2004; Cui *et al.*, 2019). For pectin, the degree of methylation is a major factor affecting the cation binding capacity (Celus *et al.*, 2018), and the percentage of methyl-esterified carboxyl groups in the pectin chain is associated with its gelling properties (Zhang H *et al.*, 2018). Furthermore, it has been reported that low- and high-methoxyl pectins interact differently with intestinal

environment. Low-methoxyl pectin is fermented faster than high-methoxyl pectin and can protect epithelial cells by stimulating the secretion of intestinal mucins (Dongowski *et al.*, 2002; Hino *et al.*, 2013). The proportion of *Faecalibacterium prausnitzii* can be increased by high-methoxyl citrus pectin, while the low-methoxyl pectin can effectively reduce *Prevotella copri* (Cui *et al.*, 2019). For some disaccharides, the linkage type seems to be critical. Disaccharides with 1–2, 1–4, and 1–6 linkages are more effective than those with other linkages in increasing the growth of certain probiotics (Sanz *et al.*, 2005; Liu *et al.*, 2020). Meanwhile, disaccharides with 1–4 linkages seem to be more digestible than those with 1–6 and 1–2 linkages (Hernández-Hernández *et al.*, 2012). For many polysaccharides, the branching degree can also determine their behavior and function in the intestinal environment. Highly branched DFs (e.g. oat bran, pectin, and guar) are susceptible to fermentation with multiple glycosidases produced by colonic bacteria, whereas DFs with a lower degree of branching (e.g. cellulose and wheat bran) are usually poorly fermented (McBurney and Thompson, 1990; Lupton, 2004; Ndeh *et al.*, 2017). Moreover, DP is also considered to be a factor affecting the selective stimulation of DF on the

colonic microbiota (Gibson *et al.*, 1995; Bosscher *et al.*, 2009; Christophersen *et al.*, 2013; Chong, 2014).

### Mechanisms underpinning DF's physiological effects

DF has positive health effects largely because it is fermented by the gut microbiota, a process that provides energy to promote the proliferation of microorganisms and regulates host metabolism to affect the physiology (Queiroz-Monici *et al.*, 2005; Roberfroid, 2005). DF resists digestion in the small intestine, and when DF enters the colon, it is fermented to produce short-chain fatty acids (SCFAs), which are considered to be the end-products of DF fermentation with a multitude of positive roles both within the gut and beyond (Zeng *et al.*, 2014). Predominant SCFAs are acetate (around 60%, molecular ratio), propionate (around 25%), and butyrate (around 15%) (Wong *et al.*, 2006; Tan *et al.*, 2014), and the concentration of SCFAs can reach around 13 mmol/L in the terminal ileum, around 130 mmol/L in the cecum, and around 80 mmol/L in the descending colon in humans (Cummings *et al.*, 1987).

There are two mechanisms by which SCFAs may confer their beneficial effects. One is to serve as energy substrates, and the other is to function as signaling molecules (Koh *et al.*, 2016). There are many biological processes and tissues that require SCFAs as the major energy substrate. For example, acetate is a major substrate for cholesterol synthesis (Cui *et al.*, 2019), and therefore it may be involved in apoptosis in cancer cells (Hague *et al.*, 1995) and prevention of DNA oxidative damage (Abrahamse *et al.*, 1999). Propionate is the main precursor of Glc production in the liver with hypolipidemic effects (Morrison and Preston, 2016). Butyrate provides approximately 60%–70% of the energy requirement of colonic epithelial cells (Robles Alonso and Guarner, 2013). In addition, both acetate and propionate can act as substrates for lipogenesis and gluconeogenesis in the liver and its peripheral organs (Tremaroli and Bäckhed, 2012).

The role of SCFAs as signaling molecules is now well-known, and among the SCFAs, butyrate has been investigated most extensively in this aspect. First, butyrate can act as a histone deacetylase (HDAC) inhibitor, and butyrate-mediated HDAC has been revealed as an anti-tumor agent (Waldecker *et al.*, 2008; Vinolo *et al.*, 2011; Zimmerman *et al.*, 2012). Histone hyperacetylation triggered by butyrate results in decreased expression of miR-106b, which in turn induces cyclin-dependent kinase inhibitory protein p21/Cip1 and cyclin D3 to enable cell cycle arrest (Blottière *et al.*, 2003), and therefore inhibits tumor growth and migration (Song and Chan, 2018). In addition, butyrate can also suppress the migration and invasion rate of cancer cells, and such anti-metastatic function is the net effect of increasing the expression of both pro-metastatic and anti-metastatic genes (Emenaker *et al.*, 2001; Zeng and Briske-Anderson, 2005). Apart from the anti-tumor role, butyrate-mediated HDAC is also a potent anti-inflammatory agent. By inhibiting the production of HDAC (Morrison and Preston, 2016), butyrate also downregulates the expression of genes coding pro-inflammatory mediators and increases anti-inflammatory cytokine release in immune and colonic epithelial cells (Zeng *et al.*, 2014). Second, butyrate is also a ligand for G protein coupled receptors, many of which are vital signaling proteins in our immune system and may be regulated by butyrate (Lazarova *et al.*, 2004; Kimura *et al.*, 2013; Park *et al.*, 2015).

For example, butyrate exerts anti-inflammatory effects in part through activating GPR109A, a receptor for macrophages, dendritic cells, and neutrophils. As a result, the recruitment and pro-inflammatory activity of these three cell types are inhibited, inducing the generation of regulatory T-cells and interleukin-10-producing T-cells (Singh *et al.*, 2014; Liu *et al.*, 2018).

### Conclusions and Future Perspectives

With rapid economic growth and an improving standard of living, the demand for healthy food is also increasing. As one of the indispensable nutritional elements for human beings and an essential ingredient in many nutraceuticals, the importance of DF in the food industry is manifest. Consequently, we propose that development of new foods with optimized DF content or with DF possessing improved medical/pharmacological activities would be an attractive future research direction and that interdisciplinary collaborations are of importance to reach these goals.

As outlined earlier, our knowledge on DF's food origin, composition and biosynthesis, and nutritional and pharmacological properties has been gradually accumulated. However, little effort has been made to integrate these aspects. The basic research on polysaccharide biosynthesis has been primarily conducted on the model plant *Arabidopsis*, and for food crops, DF studies centered around nutritional and pharmacological values. It is noteworthy that the rapidly accumulating genomic resources of food crops now enable us to explore the parallel synthesis mechanisms of DF in these target plants. Such effort would be the first step for developing healthier food based on DF-related knowledge, and it involves the identification of key enzymes and characterization of their precise roles and relationships with the nutritional and pharmacological properties. Certainly, many of the *Arabidopsis* genes introduced earlier would be greatly informative. Thanks to a wider application of genome-editing techniques, in the next step, we may not only attempt to tailor DF composition (e.g. the content ratio of SDF to IDF), but also engineer novel DF with desired properties. Importantly, for food crops tissue-specific approaches can be employed to control the expression of DF biosynthetic genes in target tissues, ensuring nutrients (including DF) and other desired traits are produced in specific plant organs. Such a roadmap is challenging if research on DF is divided, and we anticipate that combined efforts from food technologists and plant physiologists will potentially bring revolutionary developments into the food industry.

### Author Contributions

Yi An, Weitai Lu, Wenze Li, and Wei Zeng drafted the manuscript; Langlang Pan helped collect data and edited the figures; Mengzhu Lu, Zheng Li, Igor Cesarino, and Wei Zeng conceived and edited the manuscript.

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## Conflict of Interest

The authors declare no conflict of interest.

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