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Science and Technology of Fibers in Food Systems

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Preface

This book was conceptualized to thoroughly cover practical and scientific aspects related to the chemistry, analysis, technology, processing, functionality, and health implications of fiber components associated with different food matrices. This volume was thought and designed as a guide to scientists, students, food product developers, nutritionists, medical doctors, and health practitioners interested in the fascinating field of edible food fibers.

Nowadays, different segments of the food industry are constantly developing and launching new products aimed to benefit the health of consumers. Most of these developments include fiber components intended to reduce the caloric density of foods and the levels of cholesterol-containing lipoproteins and improve gastrointestinal function, glycemic index, blood pressure, and levels of antioxidants that protect mammalian systems against oxidative stress. Moreover, different dietary fiber components act as prebiotics that improve the microbiota or microbiome present in the hindgut. The consumption of dietary fiber in most developed and some developing countries is still very low when compared to the recommended daily requirement. This low-fiber intake has been associated with overweight, obesity, metabolic syndrome, chronic or noncommunicable diseases, and cancer, which undoubtedly are the main causes of deaths throughout the globe.

Renowned scientists made their best effort to comprise in each chapter their scientific and technical experiences related to the chemistry, technology, processing, and health implications of diverse fibers associated with different foods. The first section of the book is composed of seven chapters designed to cover the fundamental aspects related to the architecture and structure of cell walls, the chemistry and physical properties of fiber components, the relationship of fiber components with other minor essential nutrients and antioxidants, and the different analytical assays to assess total, insoluble, and soluble fibers and their specific components. Several chapters that detail the fiber composition of cereals, legumes, pseudocereals, fruits, and vegetables are also introduced. Needless to say, these introductory chapters are fundamental to better understand the subsequent sections of the book.

The second section of the book was planned to cover relevant aspects related to the strong relationship between fiber components and health. These chapters deal with causes and prevention of obesity, diabetes, cancer, and hyperlipidemia/hypertension, which are strongly related to cardiovascular diseases, and the important role of fiber in the gut health especially in terms of prebiotic effects and modulation of the microbiota composition. The authors of these chapters made their best effort to explain how different fibers affect key physiological mechanisms and population dynamics of microorganisms present in the large intestine.

The third section of the book consists of chapters that cover how different conventional and emerging processes used in the food industry are used to extract fibers but also how these treatments affect and modify the fiber components to enhance the functional, sensory, and texture properties of fiber-enriched foods. Specific chapters related to various types of thermal and chemical and biocatalytic processes clearly explain how time, temperature, pressure, chemical reactions, and the use of different enzymes affect fiber components and their functionality during the extraction, especially in terms of water absorption, water solubility, oil holding capacity, gel formation capacity, fat emulsification, fermentation capacity, and prebiotic effects. Likewise, the effects of traditional thermal and emerging technologies such as high hydrostatic pressure, ultrasound, and microwave on fiber composition and functionality are comprehensively covered. Finally, the use of dietary fibers in foods and their application during formulation and processing is also discussed. At the end of each chapter, a set of updated references are included with the aim of providing key scientific material useful to expand the knowledge of the readers.

The editors wish to acknowledge the time, effort, and kind contributions of all authors and the editorial project manager, Sofia Valsendur, who dedicated numerous hours in this endeavor during the past 2 years. We especially recognize their tireless efforts through the completion of this volume. Lastly, we certainly hope that this book will positively affect scientists, students, and food developers to upgrade food quality and health of the nearly 7.75 billion people that currently inhabits the planet.

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Contents

Part I Structure and Chemistry of Plant Cell Walls and Dietary Fiber in Foods

Part II Dietary Fiber and Health

Part III Extraction Pretreatments, Treatments and Modification of Dietary Fiber

Part I

Structure and Chemistry of Plant Cell Walls and Dietary Fiber in Foods

Chapter 1
Architecture, Structure and Chemistry of Plant Cell Walls and Their Constituents

Fabiola E. Ayala Soto and Sergio O. Serna Saldívar

1.1 Composition of Plant Cell Walls

The cell wall composition varies according to the plant variety, developmental stage and the environmental conditions. It is composed by mainly polysaccharides that include cellulose, hemicellulose, lignin and pectin, as well as by other minor components such as proteins, and phenolic compounds.

Cellulose is the main constituent in cell walls. The proportion of cellulose varies from 1 to 10% in the primary cell wall of higher plants and red algae, up to 50% in thick secondary structure of higher plants, and 80% or more in some green algae (Krishnamurthy 1999). At tissue level, cellulose commonly comprises about 20–30% of the dry weight of the parenchyma cell wall of fruit and vegetables. Individual cellulose molecules are 1000–4000 residues long in parenchyma cell walls, but in secondary walls they may be up to 12,000 residues long. With respect to legume seeds, the hulls are composed mainly of cellulose which accounts for about 60% of the total fiber components. The cell walls of monocot species such as cereals contain 40 to 50% of cellulose, mainly located in the pericarp cells which constitute about 7% of the total kernel weight (Serna-Saldivar 2010); however, the endosperm cell walls of rice contain high amounts of cellulose (MacDougall and Selvendran 2001).

The hemicelluloses are more abundant in secondary walls than in the primary walls of both dicots (legumes) and monocot (cereals) species. Monocot species have significantly more hemicellulose (more than 50%) than dicots. Xyloglucans (XG) are the predominant hemicellulosic polysaccharides on cell wall parenchyma of fruits, making up 7–10% of the dry weight. In dicotyledons, they represent around 20% of the dry weight (Krishnamurthy 1999). Preliminary evidence (Shiga and

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Lajolo 2006) reported that XG is abundant in beans. However, these polymers and pectic polysaccharides in cereals and grasses are found at relatively low levels (2–5%), while heteroxylans appear to form the most abundant non-cellulosic polysaccharides of most walls (Burton and Fincher 2009; Fincher and Stone 2004; Caffal and Mohnen 2009). The primary cell walls of dicots are made up 5% of polymers that include heteroxylans, arabinoxylans (AX) and glucuronoarabinoxylans (GAX), being GAX the most abundant. In monocot species, these polymers constitute 25% and AX are the most abundant (Caffal and Mohnen 2009). In cereals, such as oat and barley, β-glucans are the most abundant hemicellulose constituting around 70% of the endosperm cell wall whereas in starchy endosperm cell walls in wheat grain comprises about 15% (MacDougall and Selvendran 2001, Burton and Fincher 2014).

Lignin occurs in higher quantities in the secondary walls of particular cells (30–40%), which form parts of woody tissues, such as fibers, xylem vessels, and tracheids. Lower amounts of lignin may be deposited in the primary walls of other cell types, especially in response to stresses. In smaller quantities, lignins are also located in the peridermal/endodermal cell layers, where they play a protective role, forming part of the suberin (Wallace and Fry 1994).

Pectin is found in the middle lamella of cell walls, with a gradual decrease as one passes from primary wall toward the plasma membrane, being a polymer greatly reduced or absent in non-extendable secondary walls (Sundar Raj et al. 2012). Pectic polymers comprise as much as 30% of vegetables, fruits and dicot walls; and from grasses and cereals, represent approximately the 10% by weight (Caffal and Mohnen 2009). Homogalacturonan (HG) can account for greater than 60% of pectins in the fruit cell wall (Caffal and Mohnen 2009). However, the cell wall of legume plants has generally small domains of HG (Shiga and Lajolo 2006). Pectic polysaccharides containing the rhamnogalacturan (RG)-I moiety can be inferred to be present in the highly branched pectin of a range of tissues and comprise about 3–4% of the dry weight of cell walls from fruits, vegetables and dicots (MacDougall and Selvendran 2001).

About 2–5% of the dry weight of cell walls is composed of protein. A small proportion of this comes from contamination by intracellular protein; the remainder comes from the enzymes and structural proteins (extensins) of the cell wall (MacDougall and Selvendran 2001). Several classes of wall structural proteins have been identified and classified according to their predominant amino acid composition such as hydroxproline-rich glycoprotein (HRGP), glycine-rich protein (GRP) and proline-rich protein (PRP). Many of these proteins are highly glycosylated. Typically, these proteins have highly repetitive primary structures and become insolubilized in the cell wall during cell maturation or upon wounding. Structural proteins vary greatly in their abundance, depending on cell type, maturation, and previous stimulation (wounding, pathogen attack). For example, HRGPs are mostly associated with phloem, cambium, and schlerenchyma; GRPs and PRPs are most often localized to the xylem (Cosgrove 1997). Several enzymes may be found associated with cell walls by performing different functions. In synthesis, cellulose synthase proteins that are embedded in the membrane plasma; a superfamily of cellulose synthase-like (Csl) genes rolled in the synthesis of a specific hemicellulose, for example the type A (CslA) involved in glucomannan synthesis. In the integration of newly secreted matrix polysaccharides into existing network are the endotransglycosylases, which cut and ligate glycans together (Cosgrove 2005, Popper 2008). Among structural enzymes are the extensins that are insoluble and highly basic glycoproteins that is built of at least two different polypeptide backbones, both rich in hydroxyproline residues bearing short (mono to tetrasaccharide) side-chains (Fry 1986). Lectins that are widely distributed in seeds, especially in members of the *Leguminosae*, *Solanaceae*, and *Poaceae* families, among others (Krishnamurthy 1999). And other enzymes that are located in the primary cell wall of plants are peroxidases, polyamine oxidase, phosphatases, proteases, nitrate reductase, malate dehydrogenase, prolyl hydroxylase, glycosyl hydrolase and transferases (Krishnamurthy 1999).

It is well established that many plant cell walls contain phenolics and their composition vary according to the type of plant and growth conditions. In fruit and vegetables, phenolics are bound by ester-linkages to polysaccharides, and in cereals and legumes these bioactive compounds may be present in free or conjugated forms (Saulnier and Thibault 1999). Regularly, the primary cell wall contains less phenolics than the secondary walls (Wallace and Fry 1994). Wall-bound phenolic acids are mainly concentrated in the aleurone layer of monocotyledonous species such as commercial cereal grains which belong to the *Gramineae* family (Naczk and Shahidi 2006). The major compounds are derivatives of cinnamic and benzoic acids, predominantly *p*-coumaric and ferulic acids with lesser amounts of vanillic, sinapic and *p*-hydroxybenzoic acid (Wallace and Fry 1994). In all tissues of cereals and grasses, *p*-coumaric acid and ferulic acid are associated with hemicellulosic polymers such as heteroxylans. In maize and barley, phenolic acids can account up to 4% (weight to weight) of monomeric phenolics (Saulnier and Thibault 1999). Additionally, to hydroxycinnamic acids derivatives, the glycosidic forms of flavonoids and tannins have been reported in the seed coat cell walls of sorghum grain, and legumes such as black beans and peas (Awika and Rooney 2004, Chávez-Santoscoy et al. 2014, Stanisavljević et al. 2015). In dicots cell walls, phenolic acids are generally present in lower amounts than flavonoids (flavonols, flavanones, isoflavones, flavan-3-ols, flavones and anthocyanins) (Saulnier and Thibault 1999, Stanisavljević et al. 2015).

In the parenchyma cell wall of fruits phenolics account for about 5% of the dry weight, and the bulk of the phenolics appear to be closely associated with the hemicellulosic polysaccharides (MacDougall and Selvendran 2001). The glycosylated forms of pigmented phenolics (anthocyanins, tannins) and other compounds such as carotenes have been extensively studied in the cell wall of fruits and vegetables (Cartea et al. 2011). Free phenolic acids are present in higher amounts in fruits, being the most common gallic, vanillic, ellagic and syringic acids (Haminiuk et al. 2012).

1.2 Structure and Architecture of Cell Walls

The general constitution of plant cell walls is constituted by the primary wall, middle lamella and the secondary wall (Fig. 1.1).

The primary wall structure contains relative lesser and higher amounts of cellulose and pectin compared to secondary walls. For this reason, the wall strength and pore size in the wall are greatly affected by the flexibility of the pectic network (Fig. 1.2), in which, the structure depends of the inter- and intra-crosslinking of HG domains that are formed according to the degree of methyl esterification and their affinity for calcium ions (Caffal and Mohnen 2009).

In this primary structure, the intra-crosslinking consists of dimers of RG-II domains formed via borate di-ester linkages. In addition, RG-II crosslinks to other cell wall components such as xylans, xyloglucans, heteromannans, heteroxylans and lignin through rhamnose residues branched by arabinan, galactan, and/or AG side chains (Caffal and Mohnen 2009).

Regarding proteins associated to cell walls, the hydroxyproline groups of extensins are recognized as the attachment points for arabinosides of DP 1–4 whereas serine to galactosyl residues. The formation of phenolic bridges between two tyrosine residues have been also identified as other potential mechanism of glycoprotein crosslinking. In the cell walls of parenchyma tissue of dicots are present complexes comprised of pectic polysaccharides and proteins. In addition to cellulose, hemicellulose and lignin, proteins are linked to the aromatic group of phenolic acids and polyphenols present in cell walls (MacDougall and Selvendran 2001, Saulnier et al. 2007, Ayala-Soto et al. 2015). Despite their relatively low proportion, phenolics play a relevant role in crosslinking of cell wall structures by forming complexes not only with proteins but also with polysaccharides such as pectin and hemicellulose structures. In cereals and grasses, ferulic acid plays a pivotal role in the cross-linking process through dimerization reaction because it controls wall organization and structural integrity (Hatfield et al. 1999, Saulnier et al. 2007).

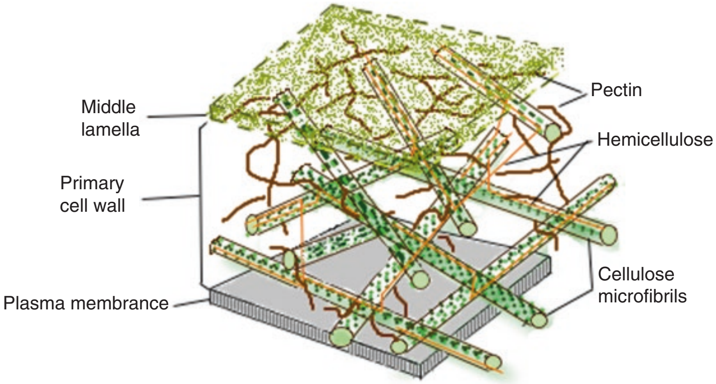


Fig. 1.1 Cell wall structure of plant cells (Adapted from McCann and Roberts 1991)

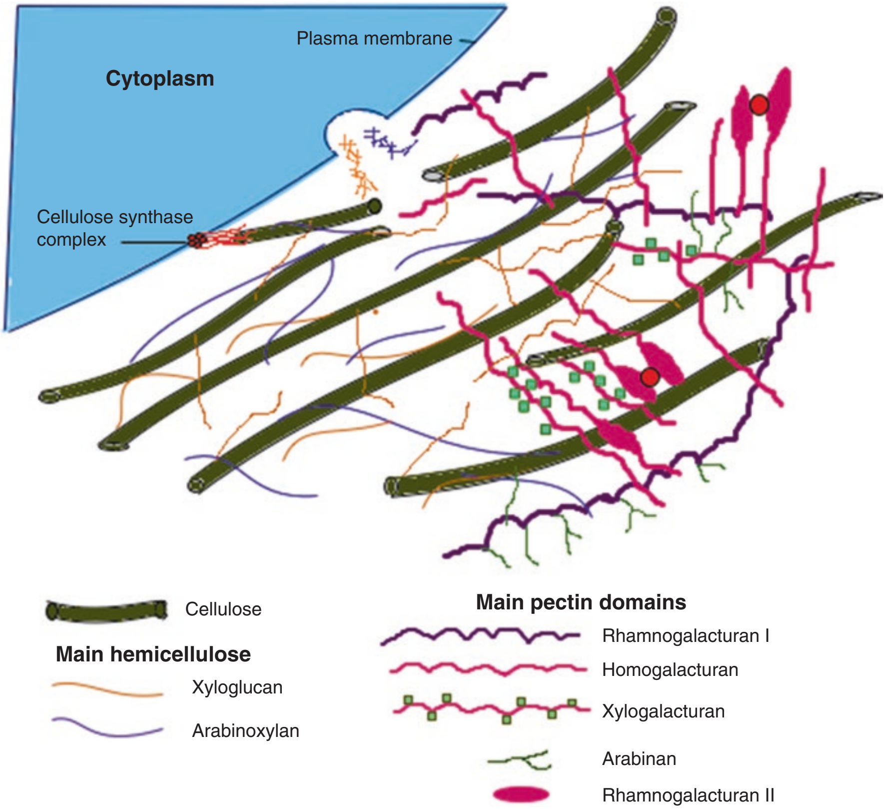


Fig. 1.2 General diagram of the structural features of pectic polysaccharides of the primary cell wall (Adapted from Cosgrove 2005)

In cereals such as oat and rye, β-glucans are other polysaccharides often associated to the primary cell wall structure through β-glycosidic linkages. It is noteworthy to mention that these polysaccharides are not widely distributed outside the primary cell structure (Burton and Fincher 2014; Fincher and Stone 2004).

Position wise, the middle lamella is an intercellular cement that lies between the walls of two daughter cells. This intermediate structure is mainly formed of pectic polysaccharides in their calcium salts (Burton and Fincher 2014). These pectic substances act as adhesive between cells and in the regulation of intercellular bonding (Billy et al. 2008).

The inner secondary wall structure is mostly composed of cellulose, acidic xylans, lignin, and small amounts of glucomannans. This can lead to a massive increase in wall thickness from 0.5 to 5–10 μm (MacDougall and Selvendran 2001).

The equatorial arrangement of the hydroxyl groups in the cellulose molecule and the alternate inversion of the individual residues caused by the β-linkage allows the cellulose molecules to form strong inter- and intra-molecular hydrogen bonds, which render them insoluble. in parenchyma cell walls of fruits, the individual cellulose molecules are 1000–4000 residues long whereas in secondary walls they may be up to 12,000 residues long. Cellulose is laid down in the wall as microfibrils, formed from the association of a large number of individual molecules (MacDougall and Selvendran 2001).

1.3 Types of Plant Cell Tissues

Once cell wall is completed, different plant structural systems and tissues (depicted in Fig. 1.3) are formed according to plant variety and mature. The vascular plant is composed by dermal, ground, and vascular tissue systems. This last system is constituted of the phloem and xylem. The ground system surrounds the vascular tissues, and comprises the parenchyma, collenchyma and sclerenchyma. The dermal system is constituted by the epidermis (Bowes and Mauseth 2008).

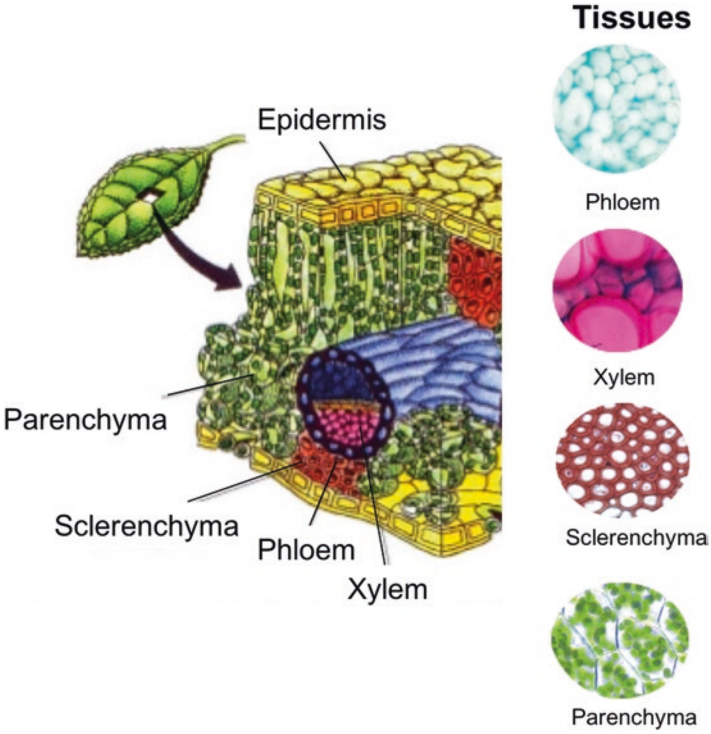


Fig. 1.3 Locations of tissues in the stem of a sunflower (*Helianthus*) (Adapted from Starr et al. 2013)

The parenchyma tissue is comprised of large cells, large vacuoles and thin cell walls which are formed of a primary cell wall separated by the middle lamella region from the adjacent wall (MacDougall and Selvendran 2001, Evert 2006). The tissues with only primary walls play an important role in wound healing, regeneration, the formation of adventitious roots and shoots, and the union of grafts. The parenchyma cells play an important role in the movement of water and the transportation of nutrients to all the plant through the phloem and xylem tissues (Evert 2006, Bowes and Mauseth 2008). Furthermore, the single cells of parenchyma may be considered the phylogenetic precursor of all other tissues, because they have the ability of becoming embryonic cells and then, given proper conditions for growth and development, to develop into an entire plant.

The collenchyma is a tissue formed by the differentiation of primary cells in the growing organs of many plants with walls thickening during and after elongation, including those that are only slightly modified by secondary growth (Leroux 2012). The collenchyma is of great value in the mechanical support of the young shoot but is rare in roots (Bowes and Mauseth 2008). The tissue is composed of extended cells with thick flexible and translucent cell walls and with protoplasts. In older organs, the collenchyma may become more rigid due to changes in cell wall composition or may undergo sclerification through lignification of newly deposited cell wall material (Leroux 2012).

The collenchyma and parenchyma cell walls both have the ability to stretch and/or grow during differentiation, but in the case of the collenchyma the walls thicken throughout elongation and often post-elongation (Jarvis 2007). Similarly, to parenchyma, the collenchyma cells have living protoplasts, essential for controlling the hydration state of the cell wall, but also to enable transdifferentiation and cell wall thickening and modification (Leroux 2012).

The sclerenchyma is a tissue composed of secondary cell walls, often lignified, which its principal function is to provide mechanical support. These cells are supposed to enable plant organs to withstand various strains, such as stretching and bending resulted from the plant weight, and pressure without sustaining damage to the thin walled softer cells. The sclerenchyma cells are divided into two categories, fiber-rich and scleroids cells. Fibrous cells are described as long whereas scleroids as relative short (Evert 2006).

The epidermal tissues form the outer protective layer of the plant provide resistance to desiccation, injury from insects, and attack by phytopathogens. The cuticular membrane that forms the protective layer on the aerial parts of plants (e.g., for leafy vegetables and fruits) is composed of one or more cuticular layers, which are laid down as incrustations of the cell wall or as adcrustations and outside the cuticular membrane are found waxes. Phenolic compounds are also found in the cuticular membrane. It is known that both *m*- and *p*–coumaric acids are released from plant cuticles during de-esterification, and small amounts of ferulic acid are also released from some tissues (MacDougall and Selvendran 2001).

1.4 Morphology of Plants

The groups of cells and tissues which conform the different structural parts of plants vary according to the organ and variety. To provide a better understanding, Table 1.1 depicts some examples of plant organs and their angiosperm (flowering plants) classification: monocotyledons and dicotyledons (Dahlgren et al. 1985). Figure 1.4 depicts the morphology of different types of fruit plants.

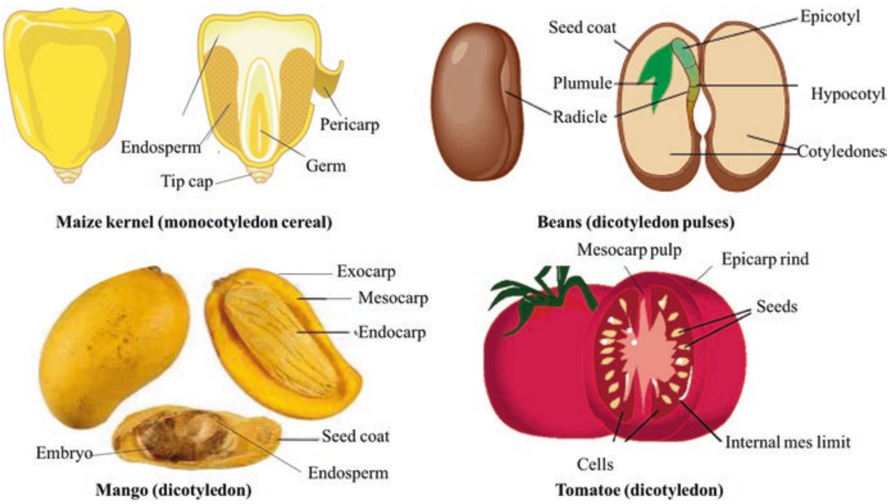
Respecting to monocots, cereal grains are morphologically a fruit botanically named caryopsis containing a single seed. The fruit tissue is constituted by the outer pericarp (beeswing bran) and inner pericarp (cross cells and tube cells), while the aleurone and endosperm are the structures inside that belong to the seed (MacDougall and Selvendran 2001, Serna-Saldivar 2010).

The endosperm is a storage or reserve tissue. The dicots may possess two different types of cell walls depending on whether they are free (i.e., no endospermic, e.g., pea, bean, soybean) or have an endosperm (i.e., endospermic, e.g., guar, locust bean). The cell wall polysaccharides of the cotyledons are similar to those of parenchymatous tissues (fruits and vegetables) and are mainly comprised of pectic substances (usually rich in arabinose and/or galactose), cellulose, and hemicelluloses (e.g., Xyloglucans). On the other hand, the endosperm cell walls of monocot cereals are quite different. They develop initially as a multinucleated cell, and unlike to other dicots plants, fruits and vegetables, their endosperm does not contain pectic polysaccharides, contain little cellulose, and their hemicellulose fraction is

Table 1.1 Examples of mono and dicotyledons and their organ plant classification

Plant organ	Dicotyledons	Monocotyledons
Roots	Carrots Turnip Sweet potato	Palmyra
Tuber, corm, rhizome	Potato	Taro Yam
Stems	Bean shoots	Asparagus Bamboo shoot
Leaves	Cabbage Spinach	Onion Leek
Flowers	Cauliflower Calabrese	
Fruits	Tomato Bean Apple Mango	Pineapple Plantain Banana
Seeds	Peas Pulses	Sweet corn Barley Oats Rice Wheat

Adapted from MacDougall and Selvendran (2001)



Maize kernel (monocotyledon cereal)

Beans (dicotyledon pulses)

Mango (dicotyledon)

Tomatoe (dicotyledon)

Fig. 1.4 Morphology of different fruits belonging to monocotyledon or dicotyledonous plants

composed of a mixture of highly branched neutral arabinoxylans rather than the xyloglucans associated to the parenchyma tissue. In addition, they contain small amounts of mixed linkage β-glucans (MacDougall and Selvendran 2001).

Respecting to cereals, the aleurone layer is composed of cell walls much thicker than the endosperm; therefore, this particular anatomic part contributes a significant amount of the total DF content of the cereal bran. The two main polymers of the aleurone layer cell walls are slightly branched arabinoxylans and mixed linkage β-glucans. In addition, this layer also contains small amounts of cellulose and glucomannans (MacDougall and Selvendran 2001).

The cell walls of the outer covering, testa or "hull" of legume seeds are composed mainly of cellulose, pectic polysaccharides, acidic xylans, and xyloglucans. Importantly, the testa contains small amounts of lignin. The main difference from parenchymatous fruit and vegetable tissues, in the context of DF, is that the seed tissues are dehydrated (MacDougall and Selvendran 2001).

The pericarp is the part that covers the cereal grains to protect them against external agents, to avoid moisture loss, and to conduct and distribute water and other nutrients during germination. The pericarp is the main source of dietary fiber and does not contain starch except in thick pericarp (mesocarp) sorghums (Serna-Saldivar 2010).

The main cellular layers of pericarp are the epicarp, mesocarp, and endocarp, and their thickness varies according to the type of cereal. The endocarp is subdivided into intermediate, cross, and tube cells. The outermost layer, named epicarp, is composed of cells enclosed with thin cell walls rich in hemicelluloses, cellulose, phenolics and lignin and low in proteins. The hemicelluloses are present as highly branched acidic arabinoxylans, slightly branched acidic arabinoxylans, together with acidic arabinoxylan-xyloglucan complexes (in soft tissues and during maturation) (MacDougall and Selvendran 2001, Serna-Saldivar 2010).

1.5 Cell Wall Formation and Biology

The complexity and variability of cell types in each fruit or vegetable begins with the differentiation of the basic cell type. The cell plate formed by nuclear division of meristematic cells, acts as a scaffold on which the new walls are built. Pectic polysaccharides, especially their calcium salts, are deposited on this plate to form a thin middle lamella layer that lies between walls of the two daughter cells. The nascent cell walls are separated by the deposition of cellulosic, non-cellulosic polysaccharides (hemicelluloses, pectic polysaccharides, glycoproteins, proteoglycans) and phenolics at both sides, and then by the formation of primary wall. Despite the relatively low proportion of phenolics in the plant cell wall, they can still play a role in crosslinking contributing to the mechanical strength of cell walls as well as to the regulatory role in plant growth and morphogenesis and in the cell response to stress and pathogens (Naczk and Shahidi 2006). As evidence of this, the phenolics isolated generally appear as polysaccharide-protein-phenolic complexes (MacDougall and Selvendran 2001).

Due to the crosslinking among their components, the primary cell wall structure is thought to contribute to wall integrity, cell adhesion, and signal transduction (Caffal and Mohnen 2009). The structural proteins extensins are involved in cell wall organization, development, wound healing, and plant defense mechanisms (García-Lara et al. 2004). With respect to cellulose-xyloglucan network, the role consists in supplying energy stores in plant seeds and acts as signaling molecule (Caffal and Mohnen 2009). Moreover, it is known that the binding of cellulose to xylose weakens the cellulose networks but increases the expansibility of such networks to improve the mechanical properties suited to the expansion and stresses characteristic of conditions during primary wall synthesis (Brown et al. 1999). At this stage, the wall remains relatively thin to allow its expansion and vacuolation that give rise to a bulky undifferentiated parenchyma. Especially in fruits, the parenchyma cell walls are the largest contributor to DF (MacDougall and Selvendran 2001).

As cell expansion ceases, wall deposition continues in many cells to form a much thicker and stronger secondary wall; in which, the thickening appears to begin with the deposition of xylans and lignin in the preexisted primary wall. In grasses and monocot species, at this stage, the proportion of the wall composed of pectic polysaccharides drops from 30% to less than 3%, suggesting no additional deposition of these polymers (Caffal and Mohnen 2009). Then a further strengthening continues by the deposition of lignin, and through lamination of parallel sheets of cellulose microfibrils that are oriented in different directions (Burton and Fincher 2014; Fincher and Stone 2004).

After their formation, the new cell types are differentiated to form vascular tissues (xylem and phloem), epidermal and storage tissues (endosperm), and a variety of other specialized cell types (sclerenchyma, stone cells, endodermis). In almost all of these examples new polymers are laid down, and in some cases the cell wall may be considerably thickened. These alterations can lead to a large change in the properties of the cell wall (MacDougall and Selvendran 2001).

The phenomenon of lignification is essentially associated with development of the vascular system in the plant body (Barceló 1997). During development, lignification often begins in the middle lamellae and/or primary cell walls and later on spreads into the secondary wall layers; in other tissues, however, only the secondary walls lignify (Wallace and Fry 1986). The monolignols units (the lignin monomers) are synthesized in the cytoplasm, then are transported to the cell wall where they undergo oxidation and polymerization (Li and Chapple 2010). The lignification process in plant cell walls provides mechanical support for the plants to stand upright and enables xylems to withstand the negative pressure generated during water transport, imparting water impermeability (Li and Chapple 2010). The association of aromatic compounds, including lignin and phenolic acids, with plant cell walls may limit the digestibility of wall polysaccharides and increase resistance to microbial attack inhibiting heat attachment process or by limiting access to microbial enzymes (Theodorou et al. 1987).

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Chapter 2
Chemical Composition and Biosynthesis of Dietary Fiber Components

Sergio O. Serna Saldívar and Fabiola E. Ayala Soto

2.1 Properties and Biosynthesis of Cellulose

Cellulose is the most abundant biopolymer on the planet because is the major structural component of green plants in which it is found associated to primary and secondary cell walls where it constitutes between 15–30%. It is also found in cell walls of cyanobacteria, fungi and green algae (Nobles et al. 2001, Bielecki et al. 2002).

In plant cell walls, cellulose is embedded in a matrix of other dietary fiber components such as hemicelluloses, pectins and lignins. The architecture and structural organization of plant cell walls is thoroughly described in Chap. 1.

2.1.1 Chemical and Physical Properties

Chemically, cellulose is a linear polysaccharide consisting of glucans joined by β-D (1–4) bonds (Fig. 2.1) with a degree of polymerization (DP) between 2000–6000 units when associated to primary cell walls or up to 15,000 units when associated to secondary cell walls (Brett 2000, Klemm et al. 2005, Coffey et al. 2006, Somerville 2006, Stick and Williams 2009). However, virtually nothing is known about how the DP is regulated in plants. The linear cellulose chain is inflexible due to the hydrogen bonding occurring between hydroxyl groups on adjacent glucosyl units. Together with van der Waals forces, hydrogen bonding aggregates glucan chains together side-by-side and promotes parallel stacking of microfibrils into crystalline cellulose (Brett 2000, Somerville 2006). This also contributes to its water insolubility (Lineback 1999, Coffey et al. 2006). The long and inelastic microfibrils wrap around

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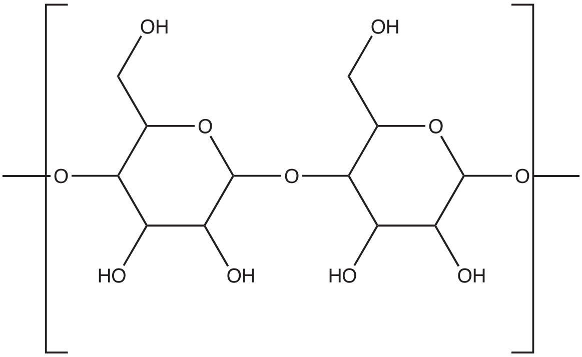

Fig. 2.1 The structure of cellulose

the cell and impart rigidify and strength (Peña et al. 2001, Stick and Williams 2009). In higher plants, 3-nm elementary microfibrils can aggregate into larger size cellulose microfibrils which range from 5–10 nm in width in primary cell walls to 30–50 nm in secondary cell walls (Davies and Harris 2003, Zhang et al. 2014).

The crystalline cellulose is found in nature in four different polymorphic forms commonly known as I, II, III and IV. Cellulose I can be irreversibly converted into a recrystallized cellulose II, a form that is more stable than type I (Brown 1999, Brett 2000). Cellulose I is present in two different holomorphic forms known as I-α and I-β (Peña et al. 2001). Both are composed of parallel glucan polymers, each glucose molecule is rotated 180° in relation to its neighboring counterpart, forming a flat ribbon in which cellobiose is the repeating unit (Maurer and Fengel 1992, Koyama et al. 1997, Somerville 2006). Cellulose produced by bacteria and algae is enriched in I_α while cellulose of higher plants consists mainly of I_β. The conversion of cellulose I to cellulose II is irreversible, suggesting that cellulose I is metastable whereas cellulose II stable. With various chemical treatments, it is possible to produce the structures III and IV. The amorphous region of cellulose can be broken up by strong acids into nanocrystalline cellulose which due to its unique and desirable properties is considered a novel material with many potential applications (Peng et al. 2011).

Physically, the cellulose is strong and chemically water insoluble. These aggregates are resistant to acid hydrolysis compared to other polysaccharides. Treatment with 70% sulfuric acid hydrolyzes cellulose into D-glucose units whereas the partial hydrolysis yields high amounts of cellobiose. This reaction is key to quantify cellulose in the detergent fiber analysis (see Chap. 4). Besides of being water insoluble, pure cellulose is tasteless and odorless with a melting point at 467 °C (Krumm et al. 2016). Many properties of cellulose depend on its degree of polymerization or chain length. For instance, the cellulose found in wood pulp has typical chain lengths between 300 and 1700 units whereas counterparts associated to cotton and other plant fibers as well as bacterial cellulose have chain lengths ranging from 800 to 10,000 units. Plant-derived cellulose is usually found in a mixture with hemicellulose, lignin, pectin and other materials, while bacterial cellulose is quite pure, has a much higher water content and higher tensile strength due to higher chain length or molecular weight (Klemm et al. 2005).

Cellulose is resistant to degradation and only certain microorganisms synthesize the enzyme complex capable of breaking down these high molecular weight molecules. The enzyme complexes known as cellulosomes are found in cellulolytic fungi and bacteria. These complexes contain endo- and exocellulases, and β-glucosidases, as well as carbohydrate-binding proteins that are commonly fused to a glycoside hydrolase. Vertebrates are unable to degrade cellulose although the digestive tracts of ruminants and other herbivores contain symbiotic cellulolytic bacteria (*Ruminococcus albus, R. flavefaciens, Bacteriodes succinogenes, B. fibrisolvens, Eubacterium cellulosolvens, Clostridium cellioboparum*) that convert cellulose into short chain fatty acids that are used as energy source (Stewart et al. 1997). Likewise, other mammals such as equines (Julliand et al. 1999) and rabbits (Boulahrouf et al. 1991) effectively convert cellulose into short chain fatty acids in their functional cecum that is populated by millions of symbiotic cellulolytic bacteria such as *Ruminococcus flavefaciens* and *Eubacterium cellulosolvens.*

Cellulases are used along with other fibrolytic enzymes for the production of second-generation bioethanol either directly or after acid pretreatment. The aim is to convert most cellulose into cellobiose and glucose, so the fermenting yeast or bacteria can convert it into ethanol (Wang et al. 2012).

2.1.2 Biosynthesis

The biosynthesis of cellulose and its complicated regulatory mechanisms were recently reviewed by Li et al. (2014). Cellulose is made at the plasma membrane by an enzyme complex (Fig. 2.2) and is deposited directly into the cell wall in a directional manner (Somerville 2006). All cellulose-synthesizing organisms and higher plants have cellulose synthase proteins, which catalyze the polymerization of glucan chains (Brett 2000, Saxena et al. 2001, Saxena and Brown 2005). Cellulose synthase (CeSA) enzyme is protein complex arranged in hexameric arrays (called rosettes) that are synthetized by 3 different CeSy genes involved in the formation of primary and secondary cell wall. For example, CeSA 1, CeSA 3 y CeSA 6 are required for biosynthesis of primary cell wall, whereas CeSA 4, CeSA 7 and CeSA 8 are required to form secondary wall (Cosgrove 2005). The protein composition of the rosette in higher plants is not well comprehended, but every rosette contains multiple cellulose synthases to accommodate the synthesis of numerous glucan chains with different DP (Taylor et al. 2000, Doblin et al. 2002, Taylor 2003, Desprez et al. 2007, Persson et al. 2007).

The synthesis of cellulose requires chain initiation and elongation reactions. Formation of crystalline cellulose requires a simultaneous synthesis of multiple glucan chains through the plasma membrane rosettes. The rosettes have two distinct functions: intracellular polymerization of glucan chains and extracellular assembly of the chains into crystalline microfibrils (Arioli et al. 1998). Each contains three

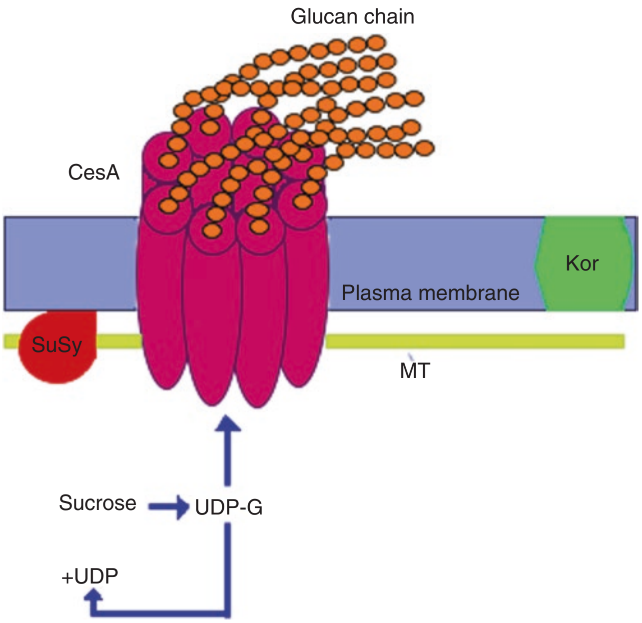

Fig. 2.2 Schematic diagram of cellulose synthesis (Adapted from Maleki et al. 2016). *CeSA*: Cellulose Synthase proteins, MT microtubules play role to regulate *CeSA* tracking; Korrigan cellulase (Kor) has been involved in monitoring of cellulose synthesis. Uridine diphosphate-glucose (UDP-G) substrate to form rosette and glucan chain formation, the UDP formed can be recycled back to SuSy sucrose synthase)

different synthases which yields the individual cellulose polymers and in addition spins resulting microfibrils into cell walls. The *cellulose* synthase *CeSA* glucosyltransferase initiates cellulose polymerization using a steroid primer, sitosterol-beta-glucoside and UDP-glucose. This enzyme system utilizes UDP-D-glucose precursors to elongate the growing cellulose chain. As they are formed, the chains undergo hydrogen bonding to form the partially crystalline microfibrils. (Brown 1999, 2004, Delmer 1999, Saxena and Brown 2001, Kimura and Kondo 2002, Coffey et al. 2006). Each cellulose fiber is proposed to consist of 36 parallel β-glucan chains according to this biosynthetic pathway (Doblin et al. 2002, Stick and Williams 2009, Li et al. 2014).

The regulatory proteins, the underlying mechanisms for cellulose synthesis and the known differences in cellulose structure, especially in terms of cellulose synthesizing complexes, likely evolved independently (Roberts and Roberts 2007, Lei et al. 2012). According to Brabham and Debolt (2012), the synthesis of cellulose in higher plants is a strongly controlled process. For example, the amount of cellulose, the ratio of cellulose to other cell wall polymers, the degree of polymerization, the crystalline cellulose core size, and the orientation of cellulose microfibrils are under tight control (Li and Gu 2012, Li et al. 2014). Glucose, mainly derived from sucrose, is the main substrate for the formation of the disaccharide cellobiose which is considered the basic building block for the synthesis of cellulose (Coffey et al. 2006).

2.2 Hemicelluloses

2.2.1 *Chemical and Physical Properties*

Hemicelluloses are a set of set of non-crystalline hetero linear or branched polysaccharides found in plant cell walls that have β-(1 → 4)-linked backbones with an equatorial configuration. At least 250 of these polymers are known. Hemicelluloses are mainly classified into xyloglucans, xylans, mannans, glucomannans and β-(1–3,1–4)-glucans (Scheller and Ulvskov 2010). The largest group consists of pentosans such as xylans and arabinoxylans. Hemicelulloses are present in the cell walls of all terrestrial plants, except for β-(1–3,1–4)-glucans, which are mainly restricted to *Poales* where the monocotyledonous cereal plants belong. The most relevant biological role of hemicelluloses is their contribution to strengthening the cell wall by interaction with cellulose microfibrils and in some cases with lignin (see Chap. 1, Zablackis et al. 1995). Hemicelluloses are of much lower molecular weight than cellulose. Component monosaccharide units may include xylose, arabinose, galactose, mannose, glucose, glucuronic acid and galacturonic acid. Xylose is the most important monomer followed by galacturonic and mannuronic acids. Hemicelluloses are normally classified by the predominant carbohydrate monomer present into xylans (arabinoxylans and glucoxylans), β-D glucans and xyloglucans. Xylans are constituted by side chains containing D-galactose, L-galactose, and D-xylose sugars. In arabinoxylans there does not appear to be any consistent relationship between solubility and the amount of substitution with arabinose units. Water-soluble arabinoxylans, known as pentosans, are present in minor amounts in cereal grains, but they are of functional importance because of their water-binding capacity and ability to increase viscosity. In rye (*Secale cereale*), the major portion of the arabinoxylans is water insoluble. The water-soluble arabinoxylans from rye exist as a range of polymer structures that differ in molecular weight, arabinose:xylose ratio, ferulic acid, ratio of di- to monosubstituted xylose, and ratio of disubstituted xyloses that are isolated, paired, or present in longer sequences in the xylan chain (1–3). The (1–3)(1–4)-β-D-glucans are major components of the cell-walls of oats (*Avena sativa*) and barley (*Hordeum vulgare*) and scarcely found in the rest of commercial cereal grains. The glucans are known to form viscous solutions and have been shown to be highly prebiotic and effective in reducing serum cholesterol concentrations. The β-glucans of oats are linear polymers containing about 70% 4-O-linked β-D-glucopyranosyl units and about 30% 3-O-linked β-D-glucopyranosyl units. The (1–3) linkages appear to occur singly while the (1–4)-linkages occur in groups of two or three. Thus, the polysaccharide contains β-(1–3)-linked cellotriosyl and cellotetraosyl units. In contrast to cellulose, the hemicellulose chains are easily chemically or enzymatically hydrolyzed by various sorts of cell wall degrading enzymes and importantly have higher fermentability and prebiotic effects in the hind gut or colon (Lineback 1999).

2.2.1.1 Arabinoxylans

Arabinoxylans (AX) are the main constituents of heteroxylans (>70%) and are comprised of a linear β-(1,4)-D-xylopyranose backbone and L-arabinofuranose residues as side chains on O-2 and/or O-3 (Fig. 2.3). Additionally, ferulic acid can be esterified to the arabinose side-chains (O-5 positions) creating cross bonds between the structure and other cell wall components such as lignin and proteins to yield insoluble complexes (Chanliaud et al. 1995, Doner et al. 2001, Carvajal-Millán et al. 2007). As most hemicelluloses, the AX exhibit different physicochemical characteristics such as solubility, viscosity, gelling and hydration properties which are closely related to their chemical structure, molecular size, molecular interaction and spatial arrangement. These features are affected by the source of extraction, extraction conditions and enzymatic hydrolysis. The conformation and interaction properties can be modulated by fine structural changes of the macromolecules (Saulnier et al. 2007).

Water solubility is not only related to structural features of the polymer chain but also to covalent linkage to other cell-wall polymers. Water solubility of AX improves with the increase of arabinose substitutions (Saulnier et al. 2007, Saeed et al. 2011). With respect to water holding capacity, high cross-linked AX do not solve in an aqueous environment but instead swell and imbibe large amount of water (Izydorczyk and Biliaderis 1992). Water extractable-AX form highly viscous solutions in water,

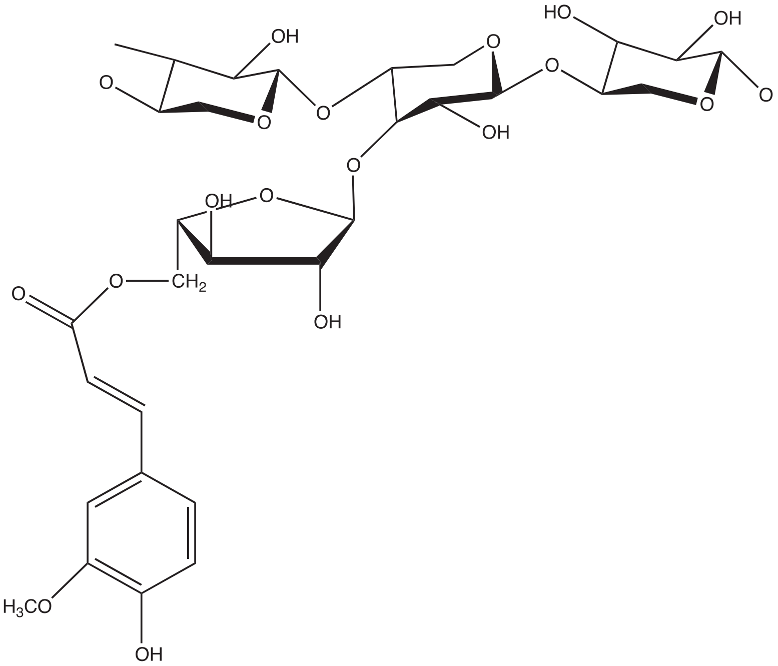

Fig. 2.3 Structure of arabinoxylans, linear β-(1,4)-D-xylopyranose backbone and L-arabinofuranose residues as side chains on O-2 and/or O-3

while water unextractable-AX show a strong water-binding capacity (Izydorczyc and Biliaderis 1995). Water unextractable AX have a strong tendency to absorb water and swell, being able to hold 6.7–9.9 times their weight in water; while the water extractable AX have a capacity to retain 3.5–6.3 times their weight in water. The values were obtained from wheat (*Triticum aestivum*) AX in dough (Courtin and Delcour 2002).

The viscosity of AX solutions has been related with the molecular size and concentration of the polymer. Generally, higher molecular sizes form high viscous solutions (Izydorczyk and Biliaderis 1992). In addition, trace amounts of protein associated with the AX extract would result in even higher viscosities (Courtin and Delcour 2002). Kale et al. (2010) reported that AX solutions exhibit a Newtonian behavior (viscosity increase linearly with shear rate). Carvajal-Millán et al. (2007) showed an extract with a molecular size of 190 KDa and 208 mL/g of intrinsic viscosity; while other sources, as AX from nejayote (the steep high alkaline water residue from the lime-cooking of corn to make tortillas), with lower molecular size (60 KDa), showed lower intrinsic viscosity 183 mL/g (Niño-Medina et al. 2010). These values are quite high when compared with those of other non-starch polysaccharides such as Arabic gum with 12–25 mL/g (Courtin and Delcour 2002).

AX are abundant in cereal endosperm cell walls, where rye and wheat contain the highest contents followed by barley, maize (*Zea mays*), rice (*Oryza sativa*), and oats. These prebiotic compounds have the potential to lower the glycemic index of cereals (Broekaert et al. 2011) and prevent diabetes type II (Van Den Abbeele et al. 2011).

2.2.1.2 Xyloglucans

These polysaccharides are the most abundant hemicelluloses in primary walls of spermatophytes except for grasses. According to Hayashi (1989) xyloglucans constitute as much as 20– 25% of the walls of dicotyledons. Xyloglucans have linear backbones of (1–4)-linked β-D glucopyranoses similar to cellulose but they contain numerous xylopyranosyl units attached along the main backbone (Fig. 2.4). In many plant xyloglucans, the repeating unit is a hepta-saccharide, consisting of a cellotetraose with three subtending xylose residues (Nishinari et al. 2009). Some residues may contain additional galactosyl and fucosyl units. Some plants might contain arabinose instead of fucogalactosyl groups attached to the xylose residues. Xyloglucans from the cotyledons of the dicot tamarind (*Tamarindus indica*) are one of the best characterized (Shirakawa et al. 1998, Nishinari et al. 2009).

Xyloglucans often contain glucose, xylose, and galactose residues in a molar ratio of about 4:3:1 and sometimes also small amounts of arabinose. They have a backbone of 4-linked β-D-glucopyranosyl residues with side chains of α-L-xylopyranosyl residues linked to the sixth position of some of the glucose residues and β-D-galactose residues attached to the second position of some of the xylose residues. The α-1-fucose residues are attached to the second position of some of the galactose residues. Heterogeneity of isolated xyloglucan fractions is linked acidic

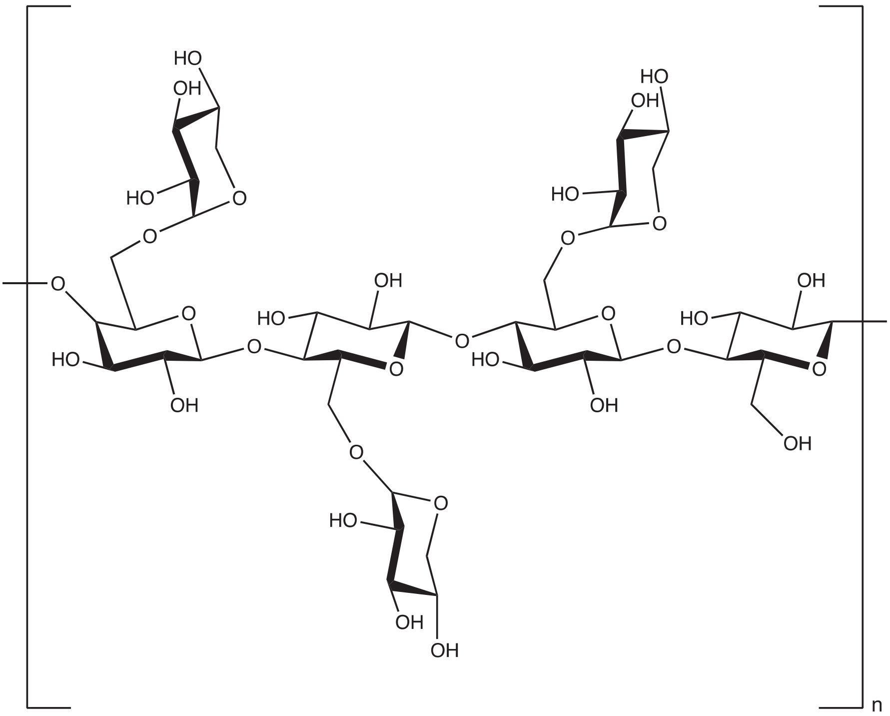

Fig. 2.4 Xyloglucan structure. Linear backbones of (1–4)-linked β-D glucopyranoses

polymers, galacturonans, and rhamnogalacturonan. Less branched xyloglucans are less soluble and this may correlate with their functional aspects. The principal difference in xyloglucan structures is the presence of charged or uncharged side chains. Xyloglucans associated to vascular plants are neutral whereas those found in mosses and liverworts are charged (Albersheim 1975, Andersson et al. 2006).

2.2.1.3 Mannans

Mannans are mainly constituted by mannose units linked by β (1–4) bonds (Fig. 2.5). They are found in higher plants, seaweeds and yeasts where they serve as storage polysaccharides. Linear or branched mannans can contain other sugars such as galactose and glucose. They are broadly divided into galactomannans and glucomannans. The first are mainly found in legume seeds whereas the second in plant and fungal cell walls associated with celluloses. The β-(1–4) linked linear glucomannans are present in minor amounts in cell walls of angiosperms but they are major components of the secondary cell wall of gymnosperms. Glucomannans are the main hemicellulose component of softwood. Structural studies revealed that the galactosyl side chain hydrogen interacts to the mannan backbone intramolecularly