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DEPT-BOTANY
PREPARED BY DR. RUMA HAJRA

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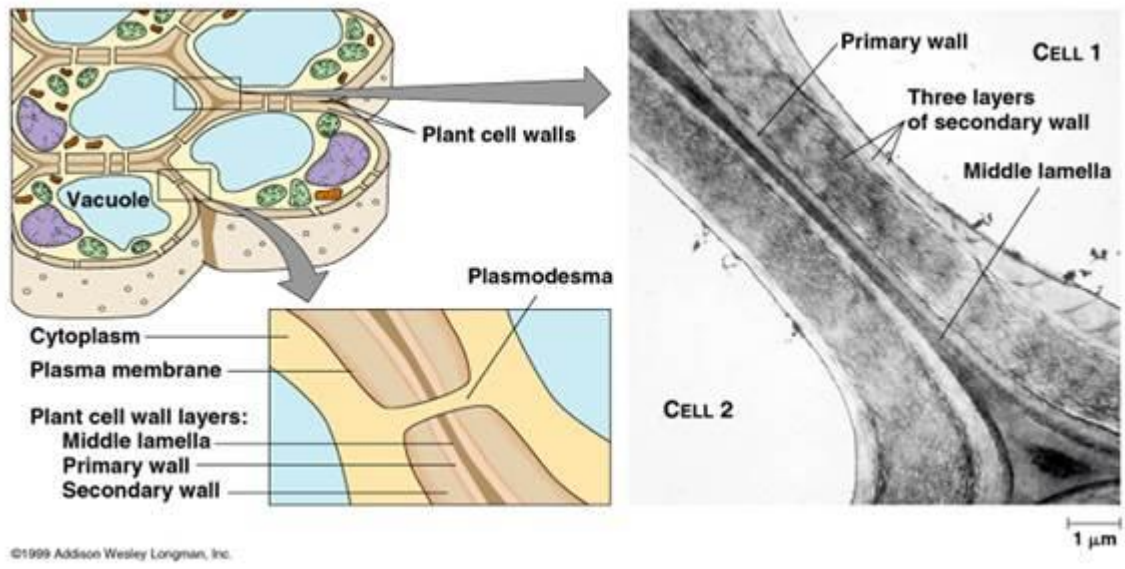
CELL WALL



One of the most important distinguishing features of plant cells is the presence of a cell wall. The relative rigidity of the cell wall renders plants sedentary, unlike animals, whose lack of this type of structure allows their cells more flexibility, which is necessary for locomotion. The plant cell wall serves a variety of functions. Along with protecting the intracellular contents, the structure bestows rigidity to the plant, provides a porous medium for the circulation and distribution of water, minerals, and other nutrients, and houses specialized molecules that regulate growth and protect the plant from disease.

Cell walls are significantly thicker than plasma membranes and were visible even to early microscopists, including Robert Hooke, who originally identified the structures in a sample of cork, and then coined the term **cells** in the 1660s. The thickness, as well as the composition and organization, of cell walls can vary significantly. Many plant cells have both a primary cell wall, which accommodates the cell as it grows, and a secondary cell wall they develop inside the primary wall after the cell has stopped growing. The primary cell wall is thinner and more pliant than the secondary cell wall, and is sometimes retained in an unchanged or slightly modified state without the addition of the secondary wall, even after the growth process has ended.

An ultrastructural model of the plant cell wall

The ultrastructural model presented in recent reviews of wall structure argues for two independent networks within the primary cell wall; the pectin–pectin and xyloglucan–cellulose network. In that model, the polysaccharides of the pectic-network, proteins, and phenolic compounds are organized independently around the framework of the cellulose–xyloglucan network. Such a model utilizes the

well-established models of the pectin–pectin network and XG–cellulose network. However, there is now well-established evidence to show that a covalent pectin–pectin network exists through the linear backbones of the pectic polysaccharides and that the XG polysaccharides have a strong affinity for cellulose and that XG functions, in part, to coat and tether cellulose microfibrils to form the XG–cellulose networks. Furthermore, there is increasing evidence that pectin interacts, perhaps covalently with hemicellulose such as XG or xylan. Realistic wall models, therefore, must integrate the pectic network, the cellulose xyloglucan network and the available knowledge of other wall structural components that have been characterized. A revised wall model that better takes the current structure data into account, would demonstrate the highly crosslinked wall wherein pectin–pectin, pectin–XG, pectin–phenolics, pectin–protein, and XG–cellulose networks provide a cohesive wall network.

The main chemical components of the primary plant cell wall include **cellulose** in the form of organized **microfibrils**; a complex carbohydrate made up of several thousand glucose molecules linked end to end. In addition, the cell wall contains two groups of branched polysaccharides, the **pectins** and **cross-linking glycans**. Organized into a network with the cellulose microfibrils, the cross-linking glycans increase the tensile strength of the cellulose, whereas the coextensive network of pectins provides the cell wall with the ability to resist compression. In addition to these networks, a small amount of protein can be found in all plant primary cell walls. Some of this protein is thought to increase mechanical strength and part of it consists of enzymes, which initiate reactions that form, remodel, or breakdown the structural networks of the wall. Such changes in the cell wall directed by enzymes are particularly important for fruit to ripen and leaves to fall in autumn.

Primary cell walls characteristically extend (grow) by a mechanism called acid growth, which involves turgor-driven movement of the strong cellulose microfibrils within the weaker hemicellulose/pectin matrix, catalyzed by expansin proteins. The outer part of the primary cell wall of the plant epidermis is usually impregnated with cutin and wax, forming a permeability barrier known as the plant cuticle.

The secondary plant cell wall, which is often deposited inside the primary cell wall as a cell matures, sometimes has a composition nearly identical to that of the earlier-developed wall. More commonly, however, additional substances, especially **lignin**, are found in the secondary wall. Lignin is the general name for a group of polymers of aromatic alcohols that are hard and impart considerable strength to the structure of the secondary wall. Lignin is what provides the favorable characteristics of wood to the fiber cells of woody tissues and is also common in the secondary walls of xylem vessels, which are central in providing structural support to plants. Lignin also makes plant cell walls less vulnerable to attack by fungi or bacteria, as do **cutin**, **suberin**, and other waxy materials that are sometimes found in plant cell walls.

Secondary cell walls contain a wide range of additional compounds that modify their mechanical properties and permeability. The major polymers that make up wood (largely secondary cell walls) include:

- cellulose, 35-50%
- xylan, 20-35%, a type of hemicellulose

- lignin, 10-25%, a complex phenolic polymer that penetrates the spaces in the cell wall between cellulose, hemicellulose and pectin components, driving out water and strengthening the wall.

A specialized region associated with the cell walls of plants, and sometimes considered an additional component of them, is the **middle lamella**. Rich in pectins, the middle lamella is shared by neighboring cells and cements them firmly together. Positioned in such a manner, cells are able to communicate with one another and share their contents through special passage termed **plasmodesmata**, these small passages penetrate the middle lamella as well as the primary and secondary cell walls, providing pathways for transporting cytoplasmic molecules from one cell to another.

Additionally, structural proteins (1-5%) are found in most plant cell walls; they are classified as hydroxyproline-rich glycoproteins (HRGP), arabinogalactan proteins (AGP), glycine-rich proteins (GRPs), and proline-rich proteins (PRPs). Each class of glycoprotein is defined by a characteristic, highly repetitive protein sequence. Most are glycosylated, contain hydroxyproline (Hyp) and become cross-linked in the cell wall. These proteins are often concentrated in specialized cells and in cell corners. Cell walls of the epidermis may contain cutin. The Casparian strip in the endodermis roots and cork cells of plant bark contain suberin. Both cutin and suberin are polyesters that function as permeability barriers to the movement of water. The relative composition of carbohydrates, secondary compounds and proteins varies between plants and between the cell type and age. Plant cells walls also contain numerous enzymes, such as hydrolases, esterases, peroxidases, and transglycosylases, that cut, trim and cross-link wall polymers.

Secondary walls - especially in grasses - may also contain microscopic silica crystals, which may strengthen the wall and protect it from herbivores.

Cell walls in some plant tissues also function as storage deposits for carbohydrates that can be broken down and resorbed to supply the metabolic and growth needs of the plant. For example, endosperm cell walls in the seeds of cereal grasses, nasturtium and other species, are rich in glucans and other polysaccharides that are readily digested by enzymes during seed germination to form simple sugars that nourish the growing embryo.

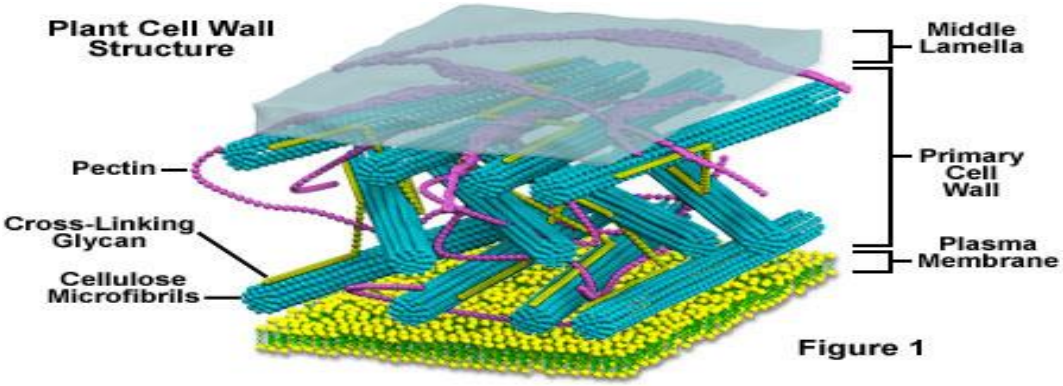
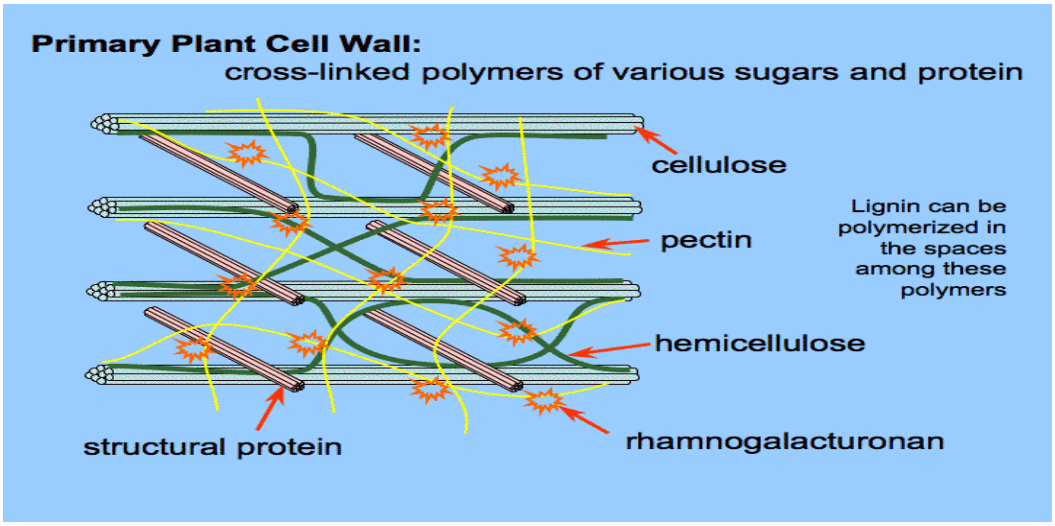
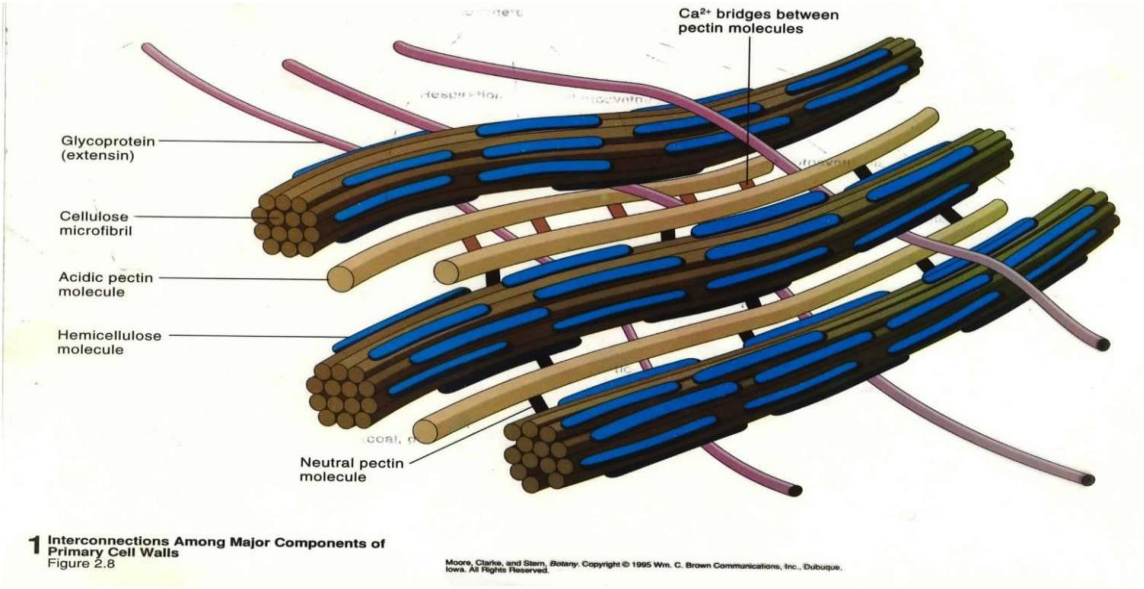


Figure 1





BIOSYNTHESIS OF PLANT CELL WALL

The plant cell wall is a complex macromolecular structure that surrounds and protects the cell, and is a distinguishing characteristic of plants essential to their survival. As a consequence of limited mobility, plants are plastic in their ability to withstand a variety of harsh environmental conditions and to survive attack by pathogens and herbivores. The structure formed by the polysaccharides, proteins, aromatic, and aliphatic compounds of the cell wall enables plants to flourish in diverse environmental niches. Cell wall structure is continually modified to accommodate the developmental stage and the environmental condition. The plant cell lays down the middle lamella and the primary wall during initial growth and expansion of the cell. In many cells, the wall is thickened and further strengthened by the addition of a secondary wall. The primary wall is characterized by less relative cellulose and greater pectin compared to secondary walls. The primary wall is thought to contribute to wall structural integrity, cell adhesion, and signal transduction. The major fraction of primary wall

non-cellulosic polysaccharides in the Type-I walls of dicot and non-graminaceous species are the pectic polysaccharides.

Pectin structure

The pectic polysaccharides comprise a class of GalA-containing polysaccharides that are abundant in the plant cell wall; comprising as much as 30% of dicot, gymnosperm, and non-Poales monocot walls. The structural classes of the pectic polysaccharides include **homogalacturonan (HG), xylogalacturonan (XGA), apiogalacturonan (AGA), rhamnogalacturonan II (RG-II), and rhamnogalacturonan I (RG-I).** The fine structure of the pectic polysaccharides governs the biological role(s) of these molecules within the cell wall.

1. Homogalacturonan

HG is a polymer of a 1,4-linked-D-galacturonic acid that can account for greater than 60% of pectins in the plant cell wall. HG is abundant in potato (Solanum tuberosum) primary walls and, according to immunohistochemical analysis, is particularly dense in the middle lamellae of this species. HG comprises at least 23% of Arabidopsis (Arabidopsis thaliana) leaf walls 6 and 10% of sycamore suspension culture cell walls (Acer pseudoplatanus). The walls of fruits, such as tomato and mango, have up to 35%8 and 52% uronic acid respectively. prepared from orange peel pectin established that the HG backbone has a twofold helical structure, consistent with the egg-box model; however, a small amount of the helical structure also occurs naturally.

HG is covalently crosslinked to RG-I, RG-II, and possibly other wall polymers

The backbone of HG is covalently linked to RG-I and RG-II, and is also hypothesized to be covalently crosslinked to xyloglucan (XG), hemicellulose polysaccharides. It has long been observed that pectic polymers are released from wall preparations by endopolygalacturonase (EPG) treatment that hydrolyzes the glycosidic bonds of the HG backbone to produce monomeric, dimeric, or oligomeric fragments.

Substituted galacturonans: apiogalacturonan and xylogalacturonan

The D-apiose-substituted apiogalacturonan (AGA) is found in the walls of aquatic plants such as the duckweeds (Lemnaceae) and the marine seagrasses (Zosteraceae). Apiose residues are beta-2-linked, 3-linked, as well as 2- and 3-linked to single GalA residues of HG. The characterization of AGA by mild extraction of Lemna walls showed that the substitution of HG can also occur as apibiose, a disaccharide of apiose (Apif-1,30 -Apif-1-). The content of AGA in plant walls appears to fluctuate widely from 0.2% to 20% of non-cellulosic polysaccharides in the dormant buds and the green fronds of giant duckweed, respectively.

Substituted galacturonan: rhamnogalacturonan II

Rhamnogalacturonan II (RG-II) is a substituted galacturonan that is a ubiquitous component of plant walls making up 4% of suspension-cultured sycamore walls and 8% of Arabidopsis leaf walls. An RG-II molecule is recognized as a stretch of HG backbone approximately seven to nine residues long with four well-defined side chain., designated. The structure of RG-II is highly complex with 12 different types of glycosyl residues, including the rare sugar species 2-O-methyl xylose, 2-O-methyl

fucose, aceric acid, 2-keto-3-deoxy-D-lyxo heptulosaric acid (Dha), and 2-keto-3-deoxy-D-manno octulosonic acid (Kdo).

2. Rhamnogalacturonan I

The backbone of the structure of rhamnogalacturonan I (RG-I) has repeating units of [a-D-GalpA-1,2-a-L-Rhap-1,4]n as characterized from suspension-cultured sycamore walls (A. pseudoplatanus) and soybean soluble polysaccharides. Large relative amounts of RG-I are found in the mucilage extruded from the seeds of myxospermous species and in the primary wall and middle lamella of potato (S. tuberosum).

The structure and role of cellulose and hemicellulose in primary walls and the integration of known cellulose, hemicellulose, and pectin structure into a practical three-dimensional model of the primary wall are discussed in the following section:-

A) Cellulose in primary walls

Cellulose is the foremost load bearing network of the primary and secondary wall. The percentage dry weight of cellulose in a dicot such as Arabidopsis ranges from 15% of leaf 6 to 33% of stem walls. The walls of monocot grass species have approximately 6–10% cellulose in leaves and 20–40% in stems. Cellulose is a polymer of b-(1,4)-D-Glc residues that associate with other cellulose chains by hydrogen bonding and Van der Waals forces. The cellulose chains of plant walls are synthesized at the plasma membrane by cellulose synthase complexes that contain multiple cellulose synthase (CesA) subunits which form a rosette structure. The rosettes consist of 6 globular CesA-containing complexes each of which synthesizes growing cellulose chains of 6–10 cellulose molecules which are referred to as 2 nm fibers. Six of the 2- nm fibers then may associate to form microfibrils of approximately 36 glucan chains. The microfibrils average 30 nm in width, a size that may be visualized by spectroscopic methods. The cellulose chains of the primary wall were of low molecular weight compared to cellulose chains of the secondary wall. Cellulose chains may align in parallel (Type I) or antiparallel (Type II) orientation to each other. Only the Type I conformation is known to naturally occur in plants; however, concentrated alkaline treatments may cause Type II cellulose to form during harsh extraction procedures. The cellulose chains may form the Type Ia or Type Ib conformation depending on the extent of staggering of the chains in relation to each other. Type-Ia and Type-Ib are recognized by the triclinic or monoclinic unit cell, respectively, of the crystalline cellulose. Cellulose microfibrils undergo to run parallel with the surface of the plasma membrane after synthesis. It is also thought that the interaction of cellulose microfibils with hemicelluloses may affect the ratio of Type Ia to Type Ib cellulose.

Primary wall cellulose microfibrils are highly crystalline and oriented parallel to the direction of elongation, contrary to the orientation found in secondary walls.

B) Hemicellulose

The hemicelluloses are often described as those wall polymers that (1) are solubilized from the wall by alkaline solvents and (2) are b-(1,4)-linked pyranosyl residues that have the O-4 in the equatorial

position. These are characteristics that result in a cellulose-like conformation and cause a tendency to hydrogen-bond to cellulose chains. Xylans, mannans, and xyloglucan fit this technical definition, but arabinogalactan is also considered a hemicellulose. The hemicelluloses are more abundant in secondary walls than in the primary walls of both dicots and monocot species. Monocot species have significantly more hemicellulose and less pectin than dicots, and also have mixed linkage glucans that make up a major proportion of monocot hemicellulose polysaccharides. Xylan polysaccharides comprise linear chains of b-(1,4)-D-Xylp residues and may be found as arabinoxylan (AX), glucuronoarabinoxylan (GAX), glucuronoxylan (GX), or the unsubstituted homoxylan. Xylans also are decorated by acetyl groups at the O-2 or O-3 position.

The mannans include the galactomannans (GMs) and the galactoglucomannans (GGMs) that are structurally important components of the cell wall as well as an important source of storage polysaccharides. Mannans have a similar three-dimensional structure to cellulose.

Xyloglucan (XG) is the most abundant hemicellulose in dicot primary walls making up 21% of angiosperm and 10% of gymnosperm suspension-cultured cell walls (Pseudotsuga menziesii). The walls of the graminaceous monocots, or grasses, are more than 50% hemicellulosic polysaccharides but only 2–5% of this is xyloglucan. Like cellulose, XG has a core backbone structure of b-(1,4)-D-glucopyranose residues; however, XG is heavily decorated with side chains of a-D-xylose residues linked to the C-6 of backbone glucose residues. The XG is bound to cellulose microfibrils in three distinct domains; (1) XG that is endoglucanase accessible, (2) XG that is solubilized by concentrated alkali, and (3) XG that is neither enzyme accessible nor alkali soluble.

C) The primary cell wall pectic network

The covalent crosslinking of the pectic polysaccharides HG, RG-I, and RG-II has been demonstrated repeatedly in the literature by the EPGase-dependent release of pectic polysaccharides from the wall. The available data suggest that the RG-I and RG-II backbones are continuous with the HG backbone, not that of RG-I sidechains, as suggested by Vincken et al. (2003). If the backbones of the pectins are continuous, the pectic network may be thought of as a macromolecular structure having specific domains of HG, RG-I, and RG-II, however, the arrangement of these domains in vivo is not known. The linkage of HG, RG-I, and RG-II through backbone glycosidic linkages is just one possible way in which the pectins are crosslinked. The pectic network is based on multiple levels of crosslinking that include, but are not limited to, backbone glycosidic linkages, calcium crosslinking, borate ester crosslinking, and covalent linkages to phenolic and possibly other compounds. The HG domains of pectin may self-associate depending on the degree of methylesterification and thus the affinity of HG for calcium ions. RG-I has a unique backbone of alternating 2-linked Rhap and 4-linked GalpA residues. Some rhamnose residues are branched by arabinan, galactan, and/or AG sidechains that may be crosslinked to other wall components such as xylans, xyloglucans, proteins, and lignins. RG-II domains form crosslinks to other RG-II molecules via borate diester linkages, to form RG-II dimers that contribute to wall strength and that affect pore size and flexibility of the pectic network. Greater than 95% of RG-II molecules participate in dimer complexes of RG-II. The linkages that pectic polysaccharides make to other pectins, as well as to other wall molecules, combine to assemble the pectic network of the plant cell wall. The complexity of the pectic network structure and the modulation of the pectic crosslinks contribute strength, flexibility, and functionality to the pectic network, and thus, to the primary cell wall.

D) Pectic crosslinks to hemicelluloses, phenolics, and proteins

There is evidence in the literature to suggest that pectic polysaccharides may also be crosslinked to hemicelluloses, phenolic compounds, and to wall proteins. The crosslinking of pectic polysaccharides to other wall components provides added structural and functional complexity to the wall. Further investigation has suggested that xyloglucan may be linked to the neutral sidechains of RG-I.18 The anionic component of rosa represented up to 30% of the total XG108 and was not separable by HPLC, electrophoresis, 8 M urea, NaOH, or protease treatment. The anionic component and XG was ultimately found to be separable by cellulase, arabinase, galactanase, and endopolygalacturonase treatment, indicating that the anionic component is likely to be RG-I Walls from Arabidopsis cell cultures pulse-labeled with [3 H]arabinose were used to further investigate the stage at which XG becomes linked to the anionic pectic polysaccharide. The release of pectins by protease treatment is likely due to a linkage with the structural protein of the cell wall.

The arabinogalactan proteins (AGPs), proline-rich proteins (PRPs), glycine-rich proteins (GRPs), and wall-associated kinases (WAKs) are wall-associated proteins and are hypothesized to aid in the wall structural reinforcement and regulatory pathways. AGPs are highly glycosylated, similar to animal proteoglycan glycoproteins, and are localized to the cell surface by a glycophosphatidylinositol-lipid anchor at the plasma membrane. AGPs are typically glycosylated by arabinogalactan sidechains that are 3-linked-D-galactan branched at the C-6 by terminal galactose or arabinose residues (Type I arabinogalactan). Potential signaling and/or structural roles have yet to be determined for each specific AGP.

Function of pectic polysaccharide

1. HG–calcium complexes contribute to wall strength
2. RG-II borate complexes contribute to wall strength
3. HG–calcium complexes and RG-I sidechains contribute to cell adhesion
4. HG–calcium complexes and RG-I arabinan affect stomatal function
5. Pectic polysaccharides mediate defense; a barrier and signaling mechanism

Reference:

The structure, function, and biosynthesis of plant cell wall pectic polysaccharides Kerry Hosmer Caffall a , Debra Mohnen a,b,* aUniversity of Georgia, Department of Biochemistry and Molecular Biology and Complex Carbohydrate Research Center, 315 Riverbend Road Athens, GA 30602, United States bDOE BioEnergy Science Center (BESC), 315 Riverbend Road Athens, GA 30602, United States