Discipline Courses-I

Semester-I

Paper II: Plant Cell Biology

Unit-II

Lesson: Cell Wall

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Introduction

Cell wall is one of the unique features in the plant cell that distinguishes it from the animal cell. The boundary of each cell in plants is, defined by the cell wall. It is made of insoluble structural polysaccharide secreted by the cells. The plasma membrane forms the outermost layer in animal cells where as in plants the plasma membrane lies next to the cell wall, which provides an elaborate extracellular matrix. Plant cell wall can be modified in response to changing environmental conditions.

Importance

Cell wall represents the outer covering of a cell, present outside the cell membrane. Cell wall is present in plants, algae, fungi and bacteria and is absent in animals and protozoans. It has key role in strengthening, plant growth, cell differentiation, water movement and defense.

In plants, cell wall not only provides rigidity and strength but also forms a protective home for the cellular constituents. The definite shape of each plant cell is due to the presence of cell wall. The intact multicellular plant body is formed due to the cementing together of cell wall to that of its neighbors. In addition, direct cell-cell communication is possible through **plasmodesmata**, which are plasma membrane lined channels of cytoplasm that cross the cell wall. Besides protective function, cell wall also plays important role in cellular absorption, secretion, and transport across the cells, and various other functions. Being, the outermost layer in plant cells , it also plays an important role in cellular defense against various pathogens. Unlike animal cells, plant cells are, prevented from swelling and bursting because of osmotic pressure by the presence of cell wall outside. Cell wall also serves to store carbohydrates that can be broken down by enzymes and used by the cell. For e.g. the cell walls in endosperm of cereals are rich in glucans and polysaccharides and nourish the growing embryo during seed germination.

To summarize some of the important functions of cell wall are:

- Gives structural and mechanical support thus determining the overall form and architecture of the plant
- Gives definite shape to the cell
- Prevents cell from bursting by resisting the turgor pressure from inside the cell.
- Regulates exchange of material through the apopalst
- Determines the growth direction and rate
- Protection

- Cell – cell interaction
- Storage in the form of wall carbohydrates
- Source of biological signaling molecules

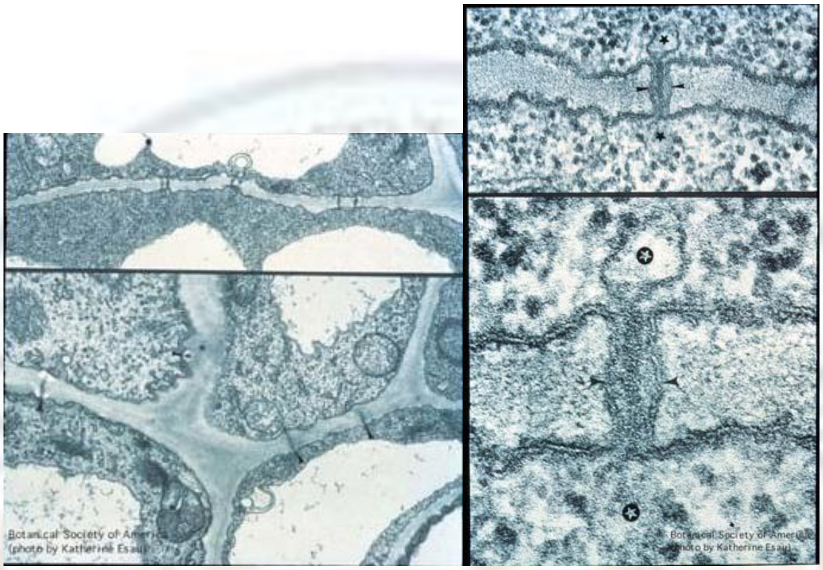

Figure: Electron micrographs showing plasmodesmata (arrow) between two adjacent cells

Source: http://pix.botany.org/set14/14-003h_300.jpg

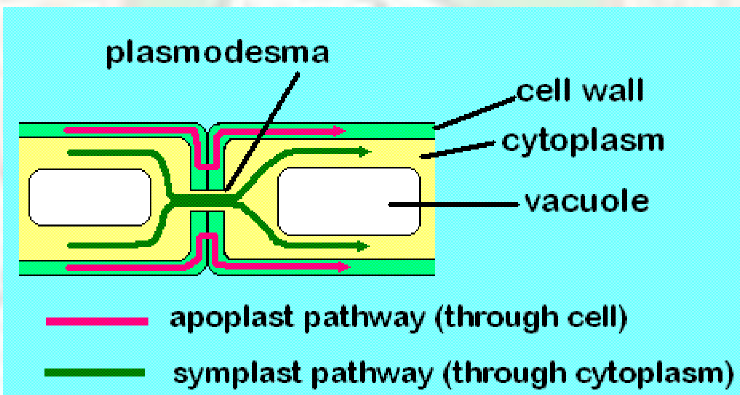

Figure: Diagrammatic representation of Plasmodesmata connecting the two cells via the apoplastic and symplastic pathways.

Source: http://upload.wikimedia.org/wikibooks/en/0/00/Waterpathwaysthroughrootcells.gif

Chemistry of the cell wall

Chemical composition of the cell wall varies within different biological organisms.

Bacterial cell wall

The unicellular prokaryotic bacterial cells are characterized by the presence of cell wall made up of a unique polymer, found nowhere in other living organisms, known as **Peptidoglycan/ Murein**. It is a hetero-polysaccharide consisting of alternating monomers of **N-acetyl glucosamine (NAG)** and **N-acetyl muramic Acid (NAM)** and joined by β 1→4 glycosidic linkage, arranged in parallel chains.

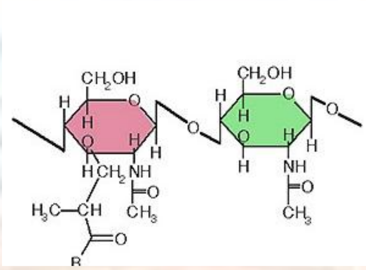

Figure: N-acetyl glucosamine (NAG) and N-acetyl muramic Acid (NAM)

Source: http://www.flickr.com/photos/ajc1/2281351707/

These parallel chains are, cross-linked by tetra-peptide attached to the NAM residues. The amino acids forming the tetra-peptides vary in different species of bacteria.

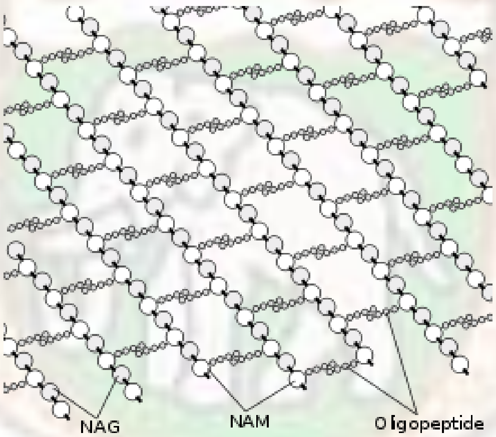

Figure: The chains of N-acetyl glucosamine and N-acetyl muramic acid are joined together by peptide bridges in peptidoglycan

Source: http://upload.wikimedia.org/wikipedia/commons/thumb/2/29/Mureine.svg/271px-Mureine.svg.png

Also visit: http://classes.midlandstech.edu/carterp/Courses/bio225/chap04/04-13a_BactCellWall_1.jpg

Gram positive and Gram negative bacteria

Depending on the cell wall composition, bacteria can be classified into, positive and negative types. This is based on the retention of Gram stain by the bacterial cell wall, the positive bacteria retain the purple crystal violet stain whereas, in the negative bacteria the stain is removed when washed in alcohol.

Animation: Gram staining procedure

Source: http://www.microbelibrary.org/images/shoeb/gram.swf

Animation: Understanding the difference in gram negative and gram positive bacteria

Source: http://www.microbelibrary.org/images/keen/gramstainkeen.htm

The basic difference between the positive and negative bacteria is the presence of a thicker peptidoglycan layer (multi layered) in positive bacteria compared to thin (2-3 layered) wall in the negative bacteria. In positive bacteria, two types of teichoic acids are present. (1) **Lipoteichoic acid,** which spans the peptidoglycan layer and linked to the plasma membrane (2) **Wall teichoic** acid remain linked to peptidoglycan layer. Teichoic acid is absent in negative bacteria, instead the peptidoglycan is bonded to an outer lippolysaccharide (LPS) membrane, known as outer membrane (OM). The Peri-plasmic space (space between OM and plasma membrane) is present in negative bacteria and absent from positive bacteria. In spite of a thinner wall the negative bacteria is more strong and disease causing due to the outer membrane which acts as a barrier to certain antibiotics, lysozyme, detergents, heavy metals, digestive enzymes, bile salts and certain dyes.

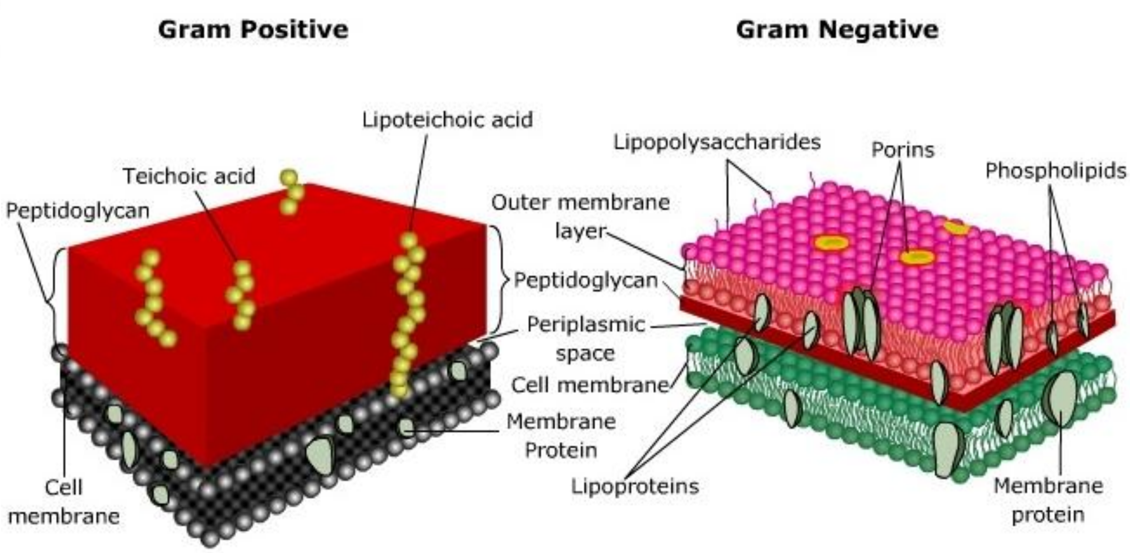

Figure: Difference in cell wall of gram positive and gram-negative bacteria

Source : Author

Differences between gram positive and negative bacteria:

http://classes.midlandstech.edu/carterp/courses/bio225/chap04/table_04_01_labeled.jpg

Cell wall in Archaea

Archaea (single celled microorganisms that inhabit extreme environments) lack peptidoglycan instead their wall is composed of pseudo-peptidoglycan that contains the sugar N-acetyltsalosaminuronic acid (peptidoglycan has the sugar N-acetylmuramic acid instead) and have the crosslinking peptides have L-amino acid rather than D- amino acid as in peptidoglycan. In some groups of archaea the wall contains entirely of polysaccharides (which may be sulfated or negatively charged) or have a layer completely composed of proteins (S layer).

For more information on Archaea visit: http://www.ucmp.berkeley.edu/archaea/archaea.html

Eukaryotic cell wall

Wall layers

The structure and functions of cell wall changes as the cell gradually matures. The property and chemistry of the wall also differs in young and old cells. Three layers of the cell wall can be distinguished:

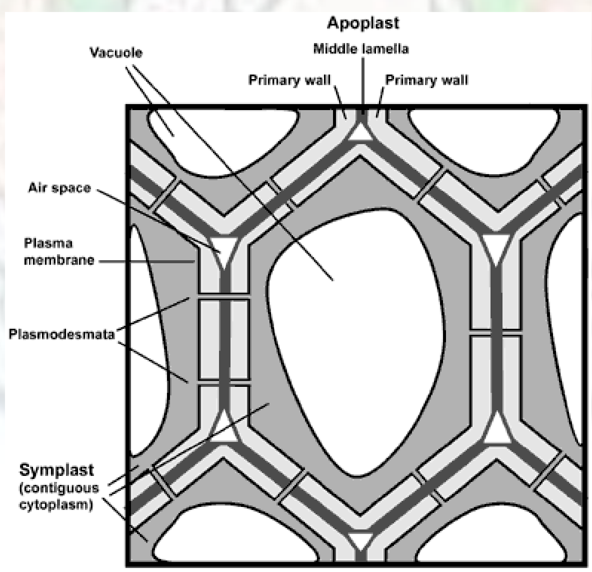

Figure: Wall layers

Source: http://www.ccrc.uga.edu/~mao/intro/apoplas.gif

1. **Middle lamella**- the layer that is present between two adjacent cells and glues them together. It is chiefly composed of pectin.

2. **Primary cell wall (PCW) -** the layer that surrounds a young growing plant cell. It is present on either side of the middle lamella and belongs to adjacent cell. The PCW is relatively thin and flexible which helps the cell to expand in size. It contain approximately equal amount of cellulose, hemicellulose and pectin. The cellulose fibers are, arranged randomly in PCW. It is rich in glycoproteins and devoid of lignin. Primary cell wall grows by a process called as **acid growth**. This involves turgor driven movement of cellulose microfibrils catalyzed by proteins – **expansins**.

3. **Secondary cell wall (SCW)**

It forms when the cell ceased to grow and expand in size. Composed of lignin this layer gives strength and waterproofs the walls. SCW material is, deposited between the plasma membranes and the PCW. As compared to the PCW, it is more rigid and provides mechanical strength to the cell. SCW generally lacks pectin and contain 50-80% cellulose. Some SCW also contain **lignin**, which is a polymer of complex phenolic residues that is responsible for strength and wood density. Unlike PCW, the SCW is, often laid down in layers called S1, S2, and S3. In each layer, the cellulose fibers differ in orientation, which results in a laminated structure that increases the strength of the wall. The lumen of the cell (protoplasm), gradually gets reduced as layers of the SCW are laid.

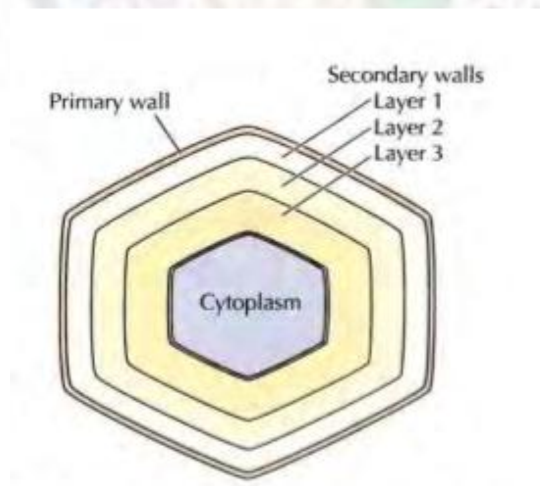

Figure: Successive layers of secondary walls are made inside the previous ones.

Source: Author

Composition

The principal cell wall composition of all eukaryotes (including fungi, algae and higher plants) are polysaccharides. Fungal cell wall and the exoskeleton of crabs and insects are made of a special type of structural polysaccharide called **Chitin,** which is a linear polymer of N-acetyl glucosamine (NAG) residue joined by **β1→4** glycosidic linkages.

Plant cell walls are made of three major polysaccharides- **cellulose**, **hemicellulose** and **pectin**. Cellulose is the most abundant organic biopolymer on the earth. The cellulose fibers are, embedded in a matrix of polymers -**xyloglucan**, **pectin** and **glycoprotein**, which are highly resistant to compression. The cross linking of the cellulose fibers and the matrix by a combination of covalent and non-covalent forces makes the cell wall into a highly complex structure whose composition is usually cell specific.

Cellulose

It is a structural, unbranched, homo-polysaccharide consist of at least of 500 glucose residues arranged in a linear chain, covalently linked to one another by β 1→4 glycosidic linkage.

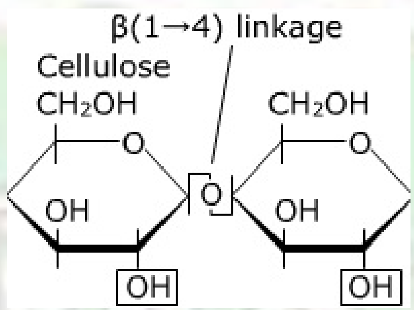

Figure: Cellulose- two adjacent glucose residues joinrd together with β1→4 glycosidic linkage.

Source: Author

Each molecule forms a ribbon like structure that is, stabilized by intermolecular H-bonds, which causes them to adhere strongly to one another in overlapping parallel arrays. A bundle of at least 40-60 such cellulose chains that have the same polarity, form highly crystalline aggregate of 3 nm in diameter and many micrometers in length. These are known as a **microfibrils** which are arranged in layers that are approximately at right angles to each other.

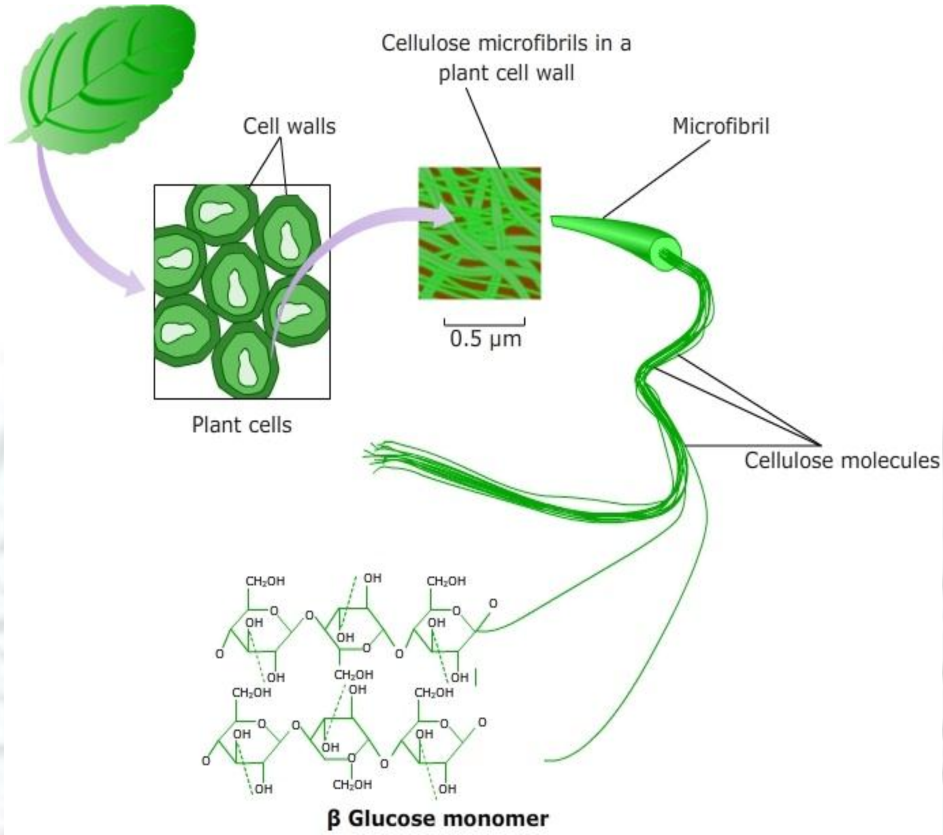

Figure: The association of cellulose molecules into microfibrils and further into a network forming the plant cell wall

Source: Author

Hemicellulose

It is a heterogeneous group of highly branched matrix polysaccharide that binds tightly but non-covalently to the surface of each cellulose microfibrils and, also to one another. The hemicellulose coating on the microfibril helps them to cross-link to one another via H-bonds into a complex network. The extensive network is responsible for the mechanical strength of the plant cell wall.

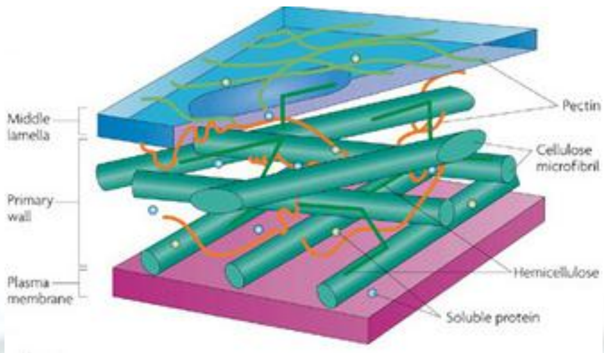

Figure: Hemicellulose crosslinks the cellulose microfibrils adding the strength
Source:
http://www.nature.com/scitable/content/ne0000/ne0000/ne0000/ne0000/14713218/npg_2_1.jpg

There are many classes of hemicellulose; all are branched hetero-polysaccharide having a long β 1→4 linked linear backbone of one type of sugar molecules from which short side chains of other sugar protrude. The backbone sugar molecules form H-bonds along with the outside of the cellulose microfibrils. The sugar of the backbone and the side chains are characteristics of the plant species and its stage of development. **Xyloglucan** and **Xylan** are the two major hemicellulose found in cell wall layers of dicotyledons and monocotyledons respectively. In Xyloglucan, the backbone is of β 1→4 linkage of glucose with the side chains of Xylose, whereas in xylan the backbone is of xylose with side chains of other sugars.

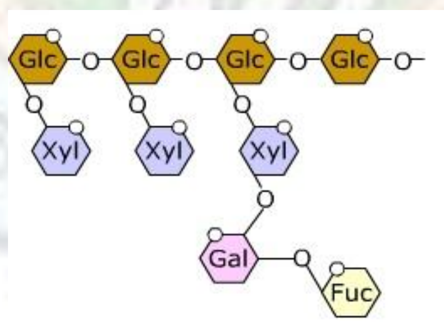

Figure: Hemicellulose -Xyloglucan- having backbone of glucose and side chains of xylose
Source: Author

Pectin

It is the third major type of cell wall polysaccharide. Pectin is a heterogeneous group of branched molecules that contain many negatively charged galacturonic acid residues. These are highly hydrated due to their negative charge and it forms a gel-like network that cross-links the cellulose microfibrils. Being negatively charged, pectin binds positively charged ions such as K^{1+} or Ca^{2+} and traps water molecules to form gel-linked network that is interlocked with the cellulose microfibrils.

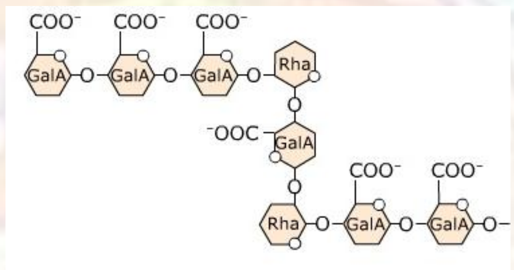

Figure: Pectin
Source: Author

Glycoprotein

In addition to the three major polymers, the matrix of the primary cell wall also contains proteins associated with short chains of carbohydrates called **glycoproteins**. These comprise almost 10% of the dry weight of many primary cell walls. Glycoproteins are both structural and enzymes. **Extensins** are the best-characterized glycoproteins, which are rich in hydroxy-proline. The deposition of extensin makes the cell wall more rigid and less extensible. A large number of enzymes such as peroxidase, phosphatase, cellulase, pectinase etc. have been reported to be present in the first formed cell wall.

Lignin

Lignin is an insoluble polymer of complex phenolic residues, which adds tensile and compressive strength to the cell wall. It is mainly found in mature cell and performs supporting and mechanical functions. Lignin is hydrophobic and replaces water in the cell wall by a process called lignification. It also acts as a barrier to invasion and makes the cell resistant to pathogen attack.

Cutin, Suberin and Waxes

All these are hydrophobic fatty substances commonly found in the wall of outer protective tissues. Cell wall of the epidermal layers is, usually coated with cutin. The secondary protective tissues like cork cells of bark of trees contain suberin or cutin. Both cutin and suberin occur in combination with waxes and reduce the water loss from the surface of the plant.

In roots the endodermal layer contains cells in which suberin is deposited on the transverse and radial walls and is responsible for blocking the passive flow of water and solutes into the vascular tissue.

Algal Cell wall

Algae contain a number of additional polysaccharides. These include- mannans, xylans, alginic acid and sulfonated polysaccharides. Especially of note are a group of algae the **diatoms**- that have a hard cell wall composed of silicic acid.

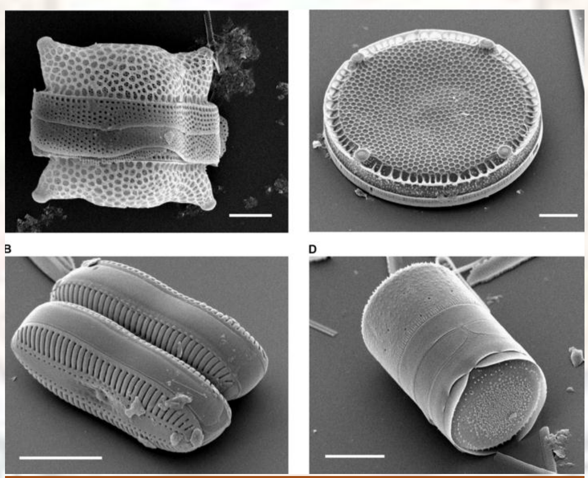

Figure: SEM of Diatoms showing hard siliceous cell wall

Source: http://en.wikipedia.org/wiki/File:Diatoms.png

Fungal cell wall

Fungal cell wall and the exo-skeleton of crabs and insects are made of a special type of structural polysaccharide called **Chitin,** which is a linear polymer of N-acetyl glucosamine (NAG) residue joined by β 1→4 glycosidic linkages.

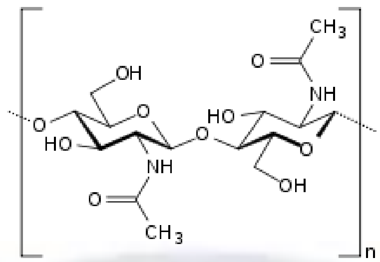

Figure: Chitin

Source: http://upload.wikimedia.org/wikipedia/commons/thumb/1/13/Chitin.svg/220px-Chitin.svg.png

Formation of cell wall

Plant cell divide not by pinching the cytoplasm in half but by assembling a plasma membrane and a cell wall between the two daughter nuclei. A cell wall in the process of formation is called a **cell plate or middle lamella**. The cell plate is formed as small membranous vesicles filled with cell wall precursors released from the Golgi, align themselves along the equatorial plate of the dividing cell, during late anaphase or early telophase. Components of the wall are deposited outside the plasma membrane during the growth of the cell. Various matrix components like hemicellulose and pectin are synthesized in the Golgi apparatus and released in the form of vesicles. During cell division, these vesicles gradually move towards the equatorial plate of the newly divided daughter nuclei. These vesicles appear to be guided to the midplane by microtubules that are derived from the polar microtubules and that are oriented perpendicular to the developing cell plate. The parallel array of microtubules forms the **Phragmoplast,** an open, cylindrical structure restricted initially to the central region of the cell. The phragmoplast guide the vesicles centripetally from the periphery towards the centre of the cell where they fuse to release their contents to form the first formed early cell plate or middle lamella. The microtubules present in the cytoskeleton help in the directional movement of these vesicles. The contents of the vesicles assemble to form the non cellulose components of the primary cell wall, which expands outward as clusters of microtubules and vesicles form at the lateral edges of the advancing cell plate. Eventually, contact is made with the parent cell wall, and the two daughter cells are separated from each other.

An enzyme complex called **cellulose synthase** present as a transmembrane protein in the plasma membrane synthesizes cellulose from UDP-glucose in the cytosol. The cellulose molecules are translocated across the plasma membrane to the exterior of the cell through a pore created by multiple enzyme subunit present in the cell membrane. The **plasmodesmata** that provide channels of continuity between the cytoplasm of adjacent cells are also present in the cell plate and the newly form cell wall.

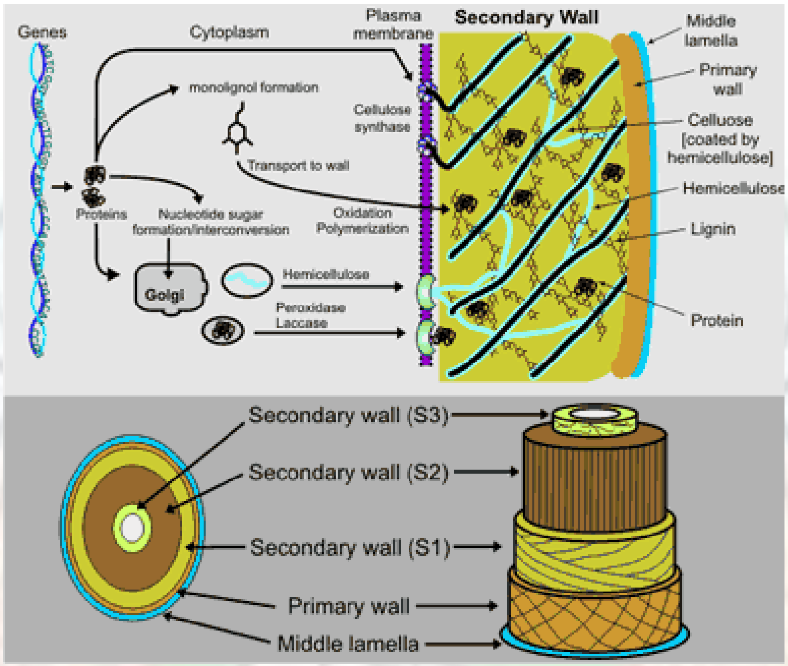

Figure: Cell wall formation

Source: http://www.ccrc.uga.edu/~mao/intro/Secwall.gif

For additional details visit http://www.ccrc.uga.edu/~mao/biosyn/text.htm

Summary

Cell wall forms the boundary of all plant cells. It is universally present in all eukaryotic plant cells as well as in prokaryotic bacterial cells. It is present outside the cell membrane. Animal cell are devoid of cell wall and hence, they are more delicate compared to the plant cells. Besides providing strength, rigidity and definite shape to the cell the wall also participate in various other important cellular functions. The cell wall is composed of cellulose, hemicellulose and pectin in all eukaryotic cells except fungi where chitin forms the principal cell wall component. The cellulose molecules are arranged in the form of microfibril which, are embedded in a matrix of hemicellulose and pectin. In bacteria, cell wall is made of a unique polymer called peptidoglycan. Based on the composition of the cell wall the bacterial cells are classified into two types, Gram positive and Gram negative. The two types of bacteria stain differentially with Gram staining technique.

In all plants depending on the time of formation, there are two types cell wall, namely the primary cell wall and the secondary cell wall. The primary cell was is present in young rapidly growing cells whereas, the secondary cell is present in mature cells. Secondary cell wall contains some special compounds like lignin, suberin, cutin and waxes. Golgi apparatus plays an important role in cell wall development.

Exercises

1. Mention the importance of cell wall in plants.
2. Describe the ultrastructure of cell wall.
3. What are microfibrils?
4. Briefly describe the various chemical components of cell wall.
5. What are the importance of lignin and pectin for the plants?
6. Why the cell lumen (protoplast) get reduced as the SCW is formed?
7. Differentiate between :
    a) PCW and SCW
    b) Cellulose and Hemicellulose
    c) Gram positive and Gram negative bacteria
8. Define the following:
    1. Plasmodesmata
    2. Cutin
    3. Glycoprotein
    4. Extensin
    5. Cellulose
    6. Hemicellulose
    7. Xyloglucan
    8. Cell plate/Middle lamella

Glossary

Archaea: A domain that comprises of single celled microorganisms that inhabit extreme environments such as thermal vents and hypersaline waters.

Apoplast: The pathway through which solutes and water can move through the cell wall and intercellular spaces.

Cell plate: Newly formed cell wall, during cytokinesis in higher plants.

Cellulose: A structural un-branched, polysaccharide of glucose monomers.

Chitin: Polymer of N-acetylglucosamine residues found in fungal cell wall

Extensins: A hydroxyproline–rich glycoprotein that makes the wall less extensible.

Glycoprotein: Proteins associated to oligosaccharides

Gram staining: A staining technique given by Christian Gram (1884)

Lignin: A complex polymer of phenolic residues

Microfibril: Long cellulose chains (40-60) associated parallel to each other to form a crystalline structure(3nm diameter)

Osmotic pressure: Pressure created by the solute molecules in solution inside the cell. It measures the direction of water movement

Pectin: A gel forming polysaccharide containing negatively charged galacturonic acid residues

Peptidoglycan: Component of bacterial cell wall. Linear chains of heteropolysaccharide (NAG+NAM) cross-linked by short peptides.

Plasmodesmata: Intercellular cytoplasmic connection in plant cells through the cell wall

Polysaccharide: Polymer (100-1000) of sugars formed by glycosidic linkage.

Symplast:The pathway through the cytoplasm from which material can move via the plamodesmata from one cell to the other.

Teichoic acid: Present in Gram positive cell wall, being negatively charged (due to PO_4) help in cation intake

Xylan: Principal type of hemicellulose in monocots.

Xyloglucan: Type of hemicelluloses in dicots

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