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NAAC ACCREDITED ‘A’ GRADE

Topic: The Cell Wall

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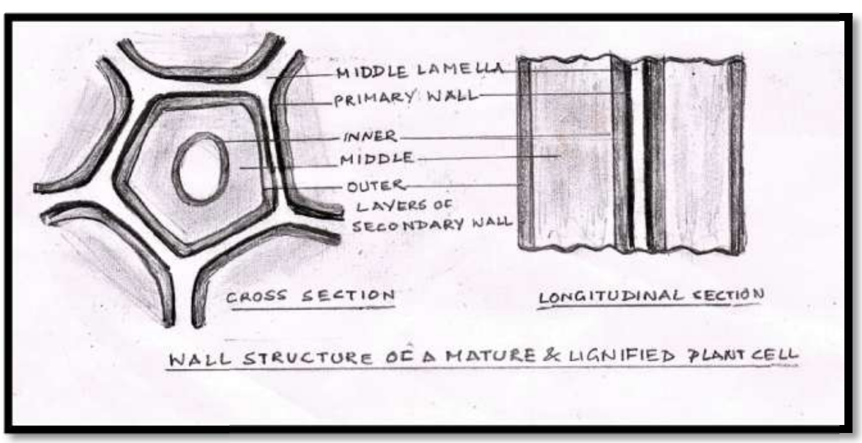
Name of the Department: Department of Botany

THE CELL WALL

Plant cells are different from animal cells in that they are provided with a **tough and rigid** cell wall. The reproductive cells of higher plants lack walls. The cell wall was considered non-living by earlier authors as it was thought to be a product of secretion of the protoplast but later authors have pointed out the intimate relation between the wall and the protoplast. The cell wall delimits the protoplast and protects it from adverse external influences. It gives mechanical support and also imparts shape to the cell.

Formation:

During mitosis, two daughter nuclei are formed through a series of complicated changes. Nuclear division is followed by cytoplasmic division. Protoplasmic matter accumulates in the equatorial region in the form of small droplets which finally cohere to form a continuous plate called the **cell plate**. This plate undergoes physical and chemical changes and is ultimately converted to the intercellular cementing substance called **middle lamella**. The middle lamella is optically inactive and colloidal in nature. It is composed of pectates of calcium and magnesium. Cell wall materials are then deposited over both surfaces of the middle lamella and ultimately a **soft, delicate and plastic primary wall** is formed. This is composed chiefly of cellulose. This primary wall persists as the only wall in many cells, but due to growth sometimes the primary wall gets so much stretched that additional wall material are deposited on both its surfaces to form the **secondary wall**. The main component of the secondary wall is cellulose which may undergo other modifications. In many cells it is usually 3-layered. The layers differ in their physical and chemical properties. While the secondary wall materials are deposited, small unthickened areas are left out. These are called the primary pit fields, through which fine cytoplasmic fibrils called **plasmodesmata** pass from one cell to another establishing an organic continuity of the protoplasm.



WALL STRUCTURE OF A MATURE & LIGNIFIED PLANT CELL

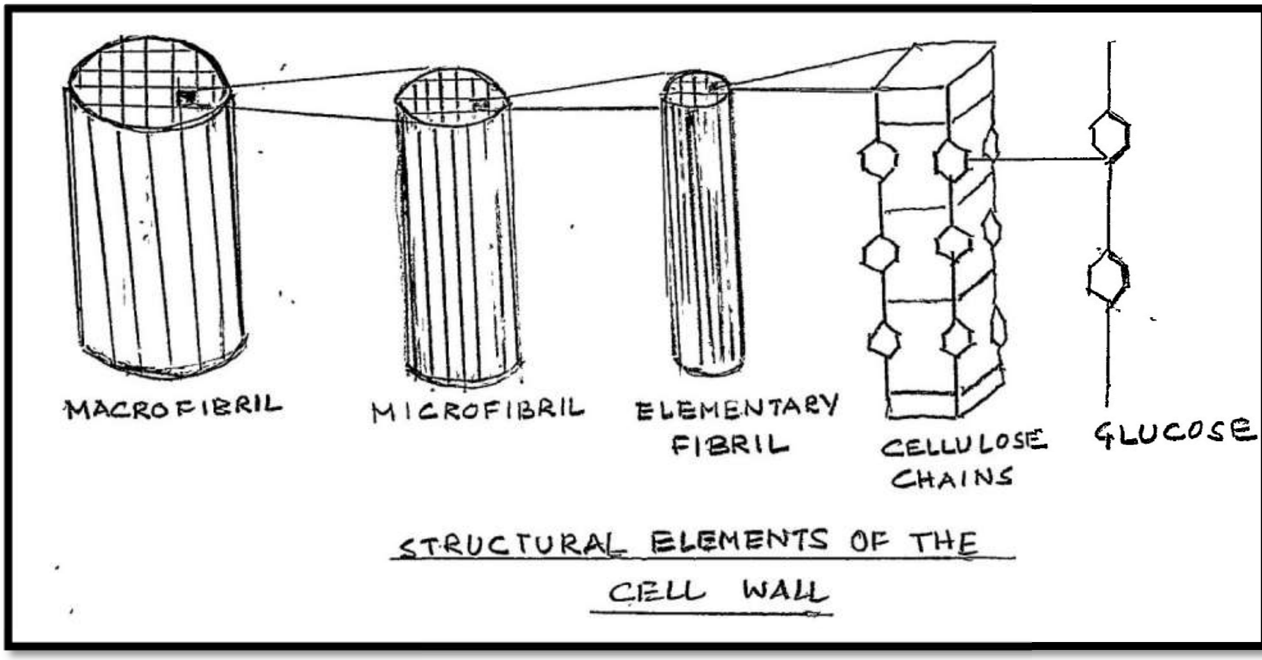
Functions:

- The cell wall protects the living protoplasm from external injury.
- It gives a definite shape to the cell and texture to the tissue.
- It provides mechanical support to the cell.
- Being permeable it allows water and mineral salts to pass through.
- It plays an important role in physiological processes like absorption, translocation, secretion, transpiration etc.
- Cell walls also connect the living protoplasts of adjacent cells through the plasmodesmata.

Ultrastructure:

X-ray diffraction studies, observation with polarized light and electron microscope has revealed that the cell wall is a biphasic structure made up of cellulose fibrils (crystalline phase) embedded in a gel-like non-cellulosic matrix (non-crystalline phase). Under the light microscope the cell wall is observed to contain an array of **macrofibrils (0.5µm in diameter)**. Each macrofibril in turn has been observed to consist of a bundle of **microfibrils (each 250 Å in diameter)**. The microfibrils are only visible under the electron microscope and each of them in turn is made up of a bundle of **micelles or elementary fibrils (each 100 Å in diameter)**. Each micelle is again constituted by **100 cellulose chains** each of which is a **polymer of glucose molecules joined together by β-1-4 glycosidic bonds**. In the primary wall the microfibrils are arranged at random and in the secondary walls they are closely packed and arranged parallel to one another.

The **microfibrils are embedded in a matrix of polysaccharides**. The substances that are present in the matrix, varies with the stage of growth of the plant. In the **early stages of growth pectic substances** and **in the later stages hemicelluloses are predominant**. Xyloglucans, arabinogalactans, rhamnogalacturonans are hemicelluloses that remain linked to each other and to the cellulose microfibrils. A protein called **extensin** is also present.



Chemical constituents of the cell wall:

The major components of the cell wall are the polysaccharides (including cellulose, hemicelluloses and pectin); proteins; lignin; inorganic substances and water. Each type of constituent is described below.

- **Polysaccharides**

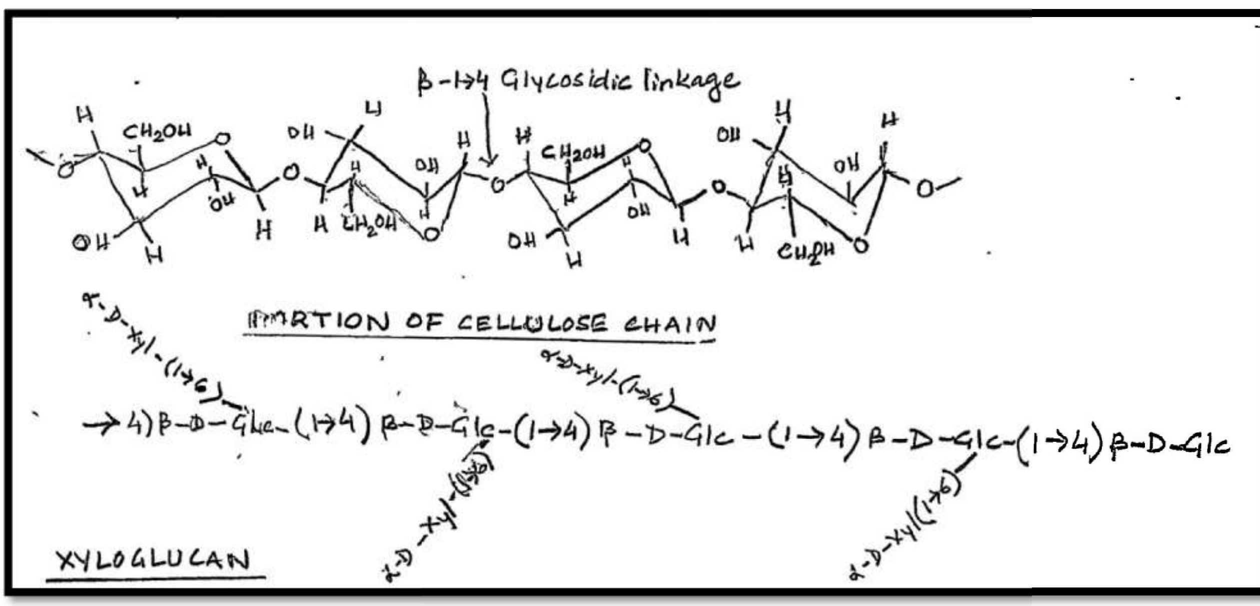
  <u>Celluloses (β-1-4 glucans)</u>-These are the main chemical components of the cell wall comprising 20-90% of it. Cellulose is a polymer consisting of 8000-15000 glucopyranose residues covalently linked by β-1-4 glycosidic bonds, forming a ribbon-like unbranched structure. Intermolecular hydrogen bonds between adjacent cellulose molecules cause them to adhere to one another strongly in an overlapping manner. This gives rise to bundles of 60-70 cellulose chains having same polarity. These bundles are called the microfibrils. These in turn are connected with each other through long hemicelluloses molecules that form hydrogen bonds with the surfaces of the microfibrils.

B-1-4 Mannans-These are unbranched polysaccharides consisting of chains of D-mannopyranose residues linked by β-1-4 glycosidic bonds.

B-1-3 Xylans- These are unbranched polysaccharides consisting of chains of D-xylopyranose residues linked by β-1-3 glycosidic bonds.

Hemiceluloses-These are a heterogeneous group of branched polysaccharides. They are bound to one another and to the cellulose microfibrils forming a complex network. There are many classes of hemicelluloses comprising of a long backbone made up of one type of sugar from which protrude short side chains of other sugars. According to the predominant monosaccharide, hemicelluloses are divided into 3 classes, namely xylans, mannans and galactans. Xylans are composed of linear chains of D-xylopyranose residues linked by β-1-4 glycosidic bonds. Similarly mannans are composed of linear chains of β-D-mannopyranose.

Galactans are made up of chains of β-D-galactopyranose residues linked by β-1-3 glycosidic bonds. Other hemicelluloses are Xyloglucan, galactomannan, glucomannan, arabinogalactan etc.



Pectins-These are a heterogeneous group of branched polysaccharides containing many negatively charge α-D-galacturonic acid and glucuronic acid residues along with rhamnose, arabinose and galactose. As the pectins are negatively charged they are hydrated and remain associated with cations which form cross-links with them. Pectins are found in cell walls in two forms-a linear copolymer of α-(1-4)-linked galacturonic acid forming smooth regions or with α-(1-2)-linked rhamnosyl residues forming hairy regions. They are highly hydrophyllic and the water they introduce into the matrix helps loosen the wall enabling cellulose microfibrils to separate during cell expansion.

- **Lignins**

  These are phenol-derived aromatic polymers which interact with other wall polymers to provide structural integrity and mechanical strength. Lignins are formed by the polymerization of a mixture of 3 subunits namely coumaryl, synapyl and guiacyl propane. Lignin fills up the spaces between the macromolecules of cell walls, thus cementing the components and forming a very strong structure. Thus lignified walls lose plastic extensibility. They are waterproof and resist pathogen attack.

- **Proteins**

  Proteins constitute about 5-10% of the cell wall. They are mostly linked with carbohydrates to form glycoproteins. Glycoproteins like extensin which is responsible for cell wall extension during growth are the structural proteins found in the primary cell walls. Those having high levels of hydroxyproline and serine afford mechanical strength to the wall. Proteins are of two types, **enzymes and structural proteins.** Various enzymes such as invertase, peroxidase, pectinase, cellulose, pectin methylesterase, acid phosphatase and malate dehydrogenase are present in plant cell walls.

- **Incrusting substances**

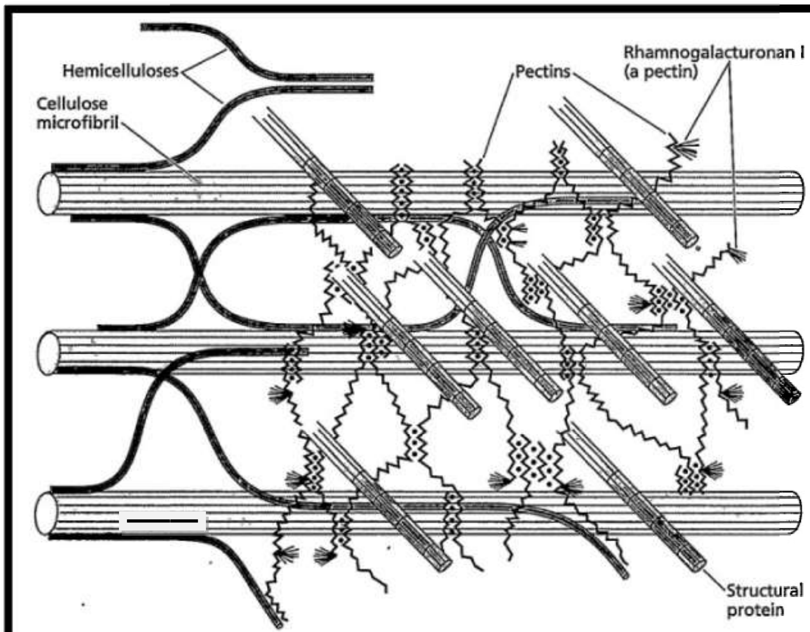
  Cutin and waxes-It forms an impermeable surface coating on the cell walls of epidermal cells called cuticle. Wax is found on the surfaces of some leaves and fruits. Cutin is composed of a complex mixture of hydroxyl fatty acids linked together by ester bonds to form a 3-dimensional network. Cutinized walls contain the phenol, ferulic acid.

Suberin-It is a polymeric substance composed of repeating units of α,ω-unsaturated or monounsaturated dicarboxylic acids ranging from C_{16}-C_{22}. It replaces cutin in cells of submerged plant parts. It is found in seed coats and casparian strips of endodermis.

Inorganic compounds-Calcium carbonate and silicate deposits are the inorganic compounds found on the cell walls of some plants.

- **Water**

  It is an important structural component of the cell wall. By means of sol-gel transformation of pectin it causes reversible changes in the texture of the wall. It increases the permeability to ions and also causes in the hydrolysis of glycosidic bonds during cell growth.



Schematic diagram of the major structural components of the primary cell wall and their likely arrangement. Cellulose microfibrils are coated with hemicelluloses (such as xyloglucan), which may also cross-link the microfibrils to one another. Pectins form an interlocking matrix gel, perhaps interacting with structural proteins. (From Brett and Waldron 1996.)

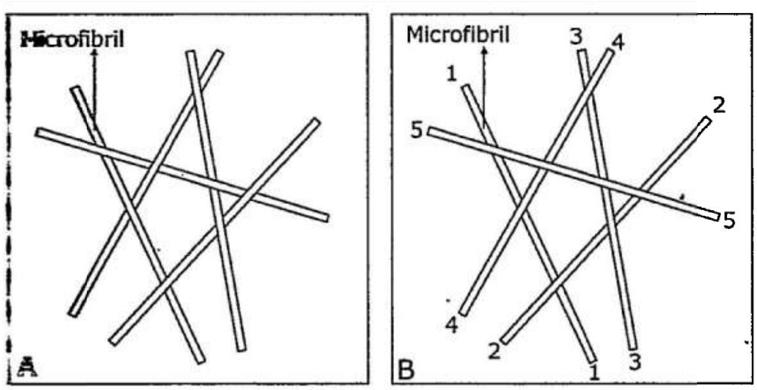
Taken from Plant Physiology by Taiz & Zeiger

Growth of the cell wall:

The cell wall grows in surface area as well as in thickness. Due to stretching of the thin elastic primary wall the cell grows in size. In the early stage the wall is thin and delicate but with growth the wall thickens. There are two classical theories regarding the growth in thickness of the cell wall.

1. **Growth takes place by intussusception**-According to this view, the new wall materials or the new microfibrils are laid down between the existing microfibrils of the expanding wall.
2. **Growth takes place by apposition**-According to this theory, the new microfibrils are laid down on top of the existing ones thus forming a new layer.

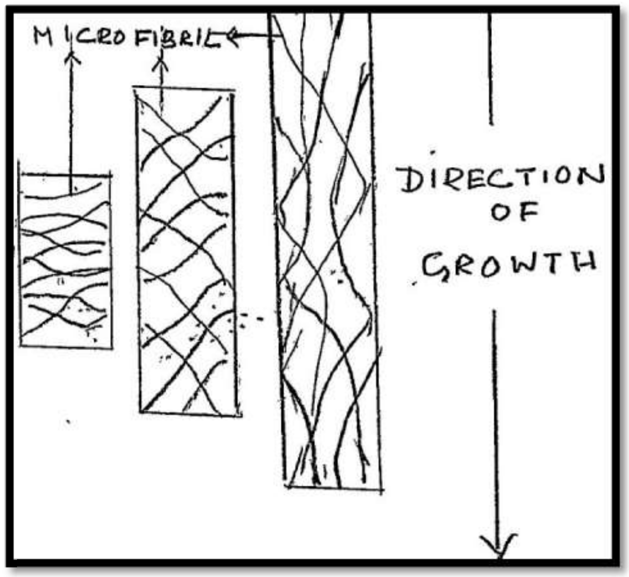
   Most of the recent authors are of the view that although some growth takes place by intussusception, growth of both primary and secondary wall mainly occurs by apposition method.



Diagrammatic representation of the growth of cell wall. A. Intussusception. B. Apposition. The microfibrils are numbered 1-1, 2-2, 3-3, 4-4 & 5-5 according to the sequence of formation. Adapted after Cutter, 1978.

Taken From Plant Anatomy by Pijush Roy

For longitudinal growth, a new theory known as the theory of **multinet growth** is now widely accepted. According to this theory, the orientation of microfibrils, change in successive layers of the wall. According to this theory, at the beginning, the microfibrils are laid down transversely to the long axis of the cell. This layer later on gets pushed outward due to the formation of another layer internal to it. As the cell elongates the first formed layers get stretched and they become oriented gradually along the longitudinal plane.

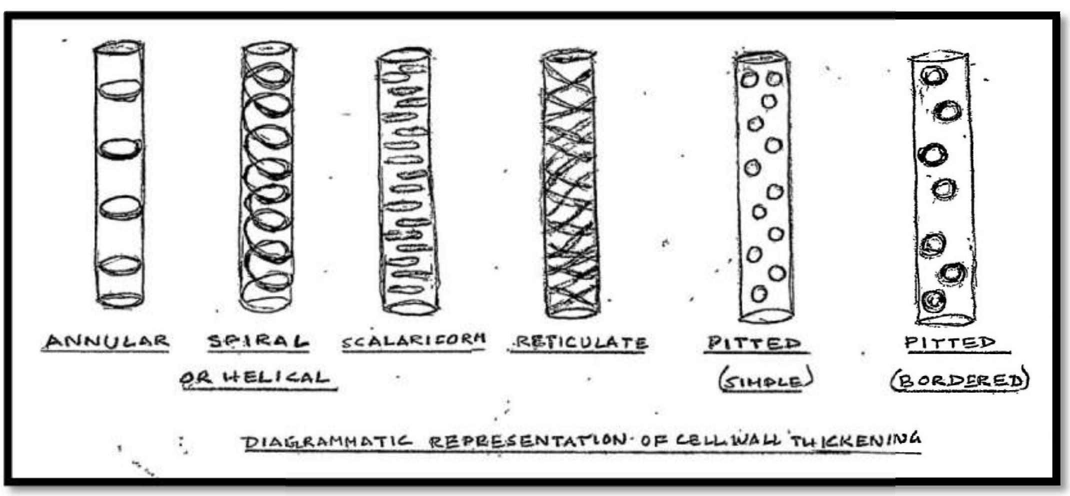


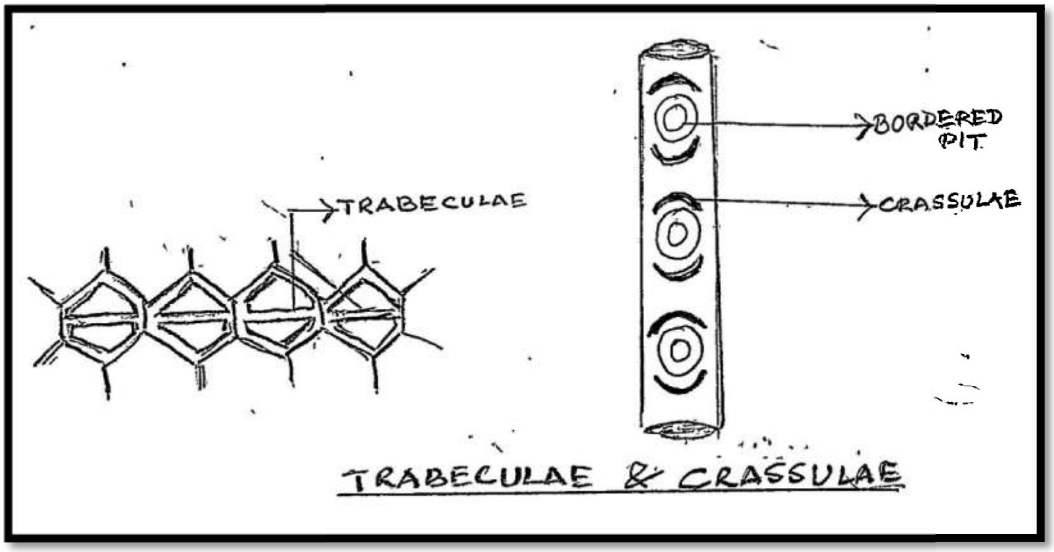
Some authors are of the opinion that the primary wall grows by **mosaic growth**. Their opinion was based on observation under the electron microscope. In this type of growth the thin areas penetrated by the cytoplasm appear in the growing primary wall. In these regions synthesis of cytoplasm occurs thus pushing the microfibrils apart. Enlargement of the cell surface takes place and new microfibrils are woven in to the wall to fill up the thinner areas.

Thickening of the cell wall:

In cells like the fibres, tracheids and vessels secondary wall materials are deposited over the primary wall after wall extension has ceased. They form a rigid secondary wall due to deposition of lignin. The deposition occurs in the form of various patterns which are described below.

1. **Annular**-The deposition is in the form of rings on the inner side of the primary wall, the rest of the wall being thin. Eg. Protoxylem.
2. **Spiral or Helical**-The deposition occurs in the form of one or more helices. Eg. Protoxylem.
3. **Scalariform**-The deposition occurs as parallel bands resembling the rungs of a ladder. Eg. Protoxylem.
4. **Reticulate**- The deposition occurs in the form of a network and the meshes of the network remain thin. Eg. Metaxylem.
5. **Pitted**-Unthickened, circular areas called pits remain in an otherwise thickened wall. Eg. Metaxylem.
6. **Trabeculae**-These are bar or rod-like radial projections of the cell wall extending across the cell lumen. They are found in the tracheids of conifers.
7. **Crassulae**-These are linear or crescent-shaped thickenings over the upper and lower margins of individual or group of bordered pits. They may even encircle the bordered pits. They are the elevated rim of the primary pit fields formed by thickening of the middle lamella and primary wall. They are found in gymnosperm tracheids.





The primary pit fields:

The meristematic cells and their derivatives without secondary walls have some deep depressions on their primary wall which are called the primary pit fields. They are also called primary pits or primordial pits where plasmodesmata exist. The primary pit field areas have a middle lamella and primary wall of both adjacent cells.

Pits:

These are small circular depressions on the secondary wall. A pit comprises of a **pit cavity, pit aperture and pit membrane**. The pit cavity or pit chamber is the interrupted region of the secondary wall. The pit aperture is the mouth or opening of the pit cavity lying towards the cell lumen. The pit membrane or closing membrane consists of the middle lamella and the two thin primary walls of two adjacent cells. Pits on the secondary wall may be of the following types.

- **Simple pit-**Here the secondary wall does not arch over the pit chamber, so the rim of the pit aperture does not have a border. The may be circular, oval or elongated.

- **Ramified pit-**In transverse sections of very thick-walled brachysclereids, simple pits appear as a canal on the wall, often with branches formed by coalescence with neighbouring canals. These branched pits are called ramiform pits.

- **Bordered pit-**These are found in lignified fibres, tracheids and trachea. Here the pit cavity is partly enclosed by the over arching of the secondary wall. In surface view it appears as two concentric circles, the inner circle is the pit aperture and the outer circle is formed by the border (over arching secondary wall). A bordered pit comprises of the pit chamber, pit aperture and the pit membrane. Sometimes the over arching of the secondary wall may be so thick as to form a canal called the **pit canal**. The pit canal has two openings-outer aperture which lies towards the cell wall and the inner aperture which lies towards the cell lumen. Sometimes, the closing membrane between a bordered pit pair may become thickened in the middle to form the **torus**, which remains suspended by microfibrils. Usually the torus is medianly placed to allow movement of water. The pit membrane is flexible and during water movement it swings. Sometimes as it swings it may take a lateral position, thus blocking the pit aperture and stopping the flow of water. Thus the torus acts as a valve.

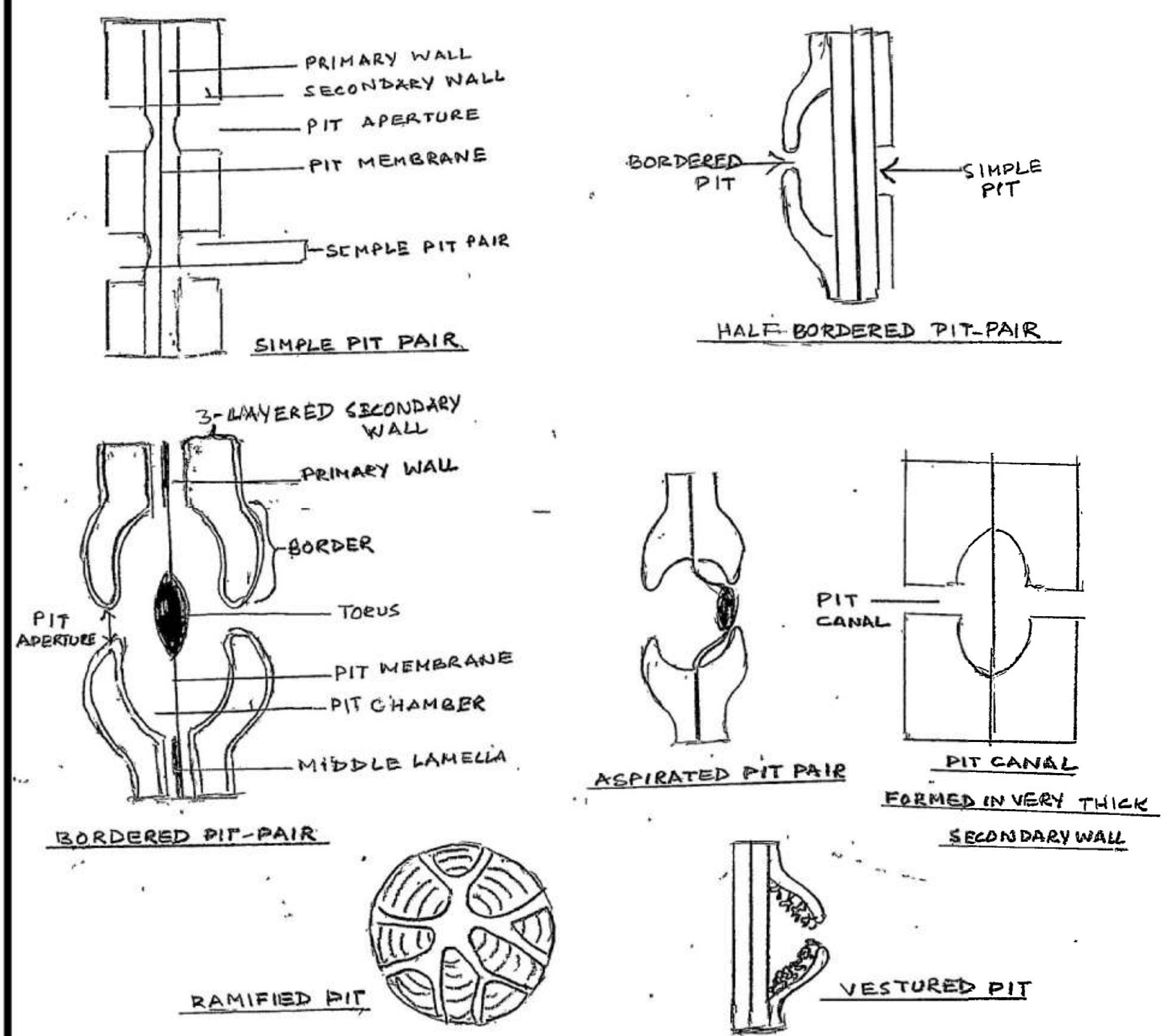
- **Aspirated pit-**Here the torus is laterally placed, blocking the outer aperture of the pit canal. The pit membrane loses flexibility and the pit become non-functional as in the heart wood of *Pinus.*

- **Pit pair-**In a functional pit, a pit on one wall coincides with a pit in the wall of the adjacent cell. These two pits along with the pit membrane in between forms a structural and functional unit called the pit pair. If in a pit pair, the two complementary pits are simple, it forms a <u>simple pit pair</u>. If both are bordered they form a <u>bordered pit pair</u>. If one is simple and one is bordered they form a <u>half-bordered pit pair</u>. If a large pit is complemented by two or more pits it is termed as <u>unilateral compound pitting</u>.

- **Blind pit-**When a pit is not complemented with another pit on the adjacent wall, it is called a blind pit. They are non-functional.

- **Vestured pit-**These pits have minute projections in the pit chamber forming sculptures of various shapes due to accumulation of cytoplasmic materials.

DIFFERENT TYPES OF PITS



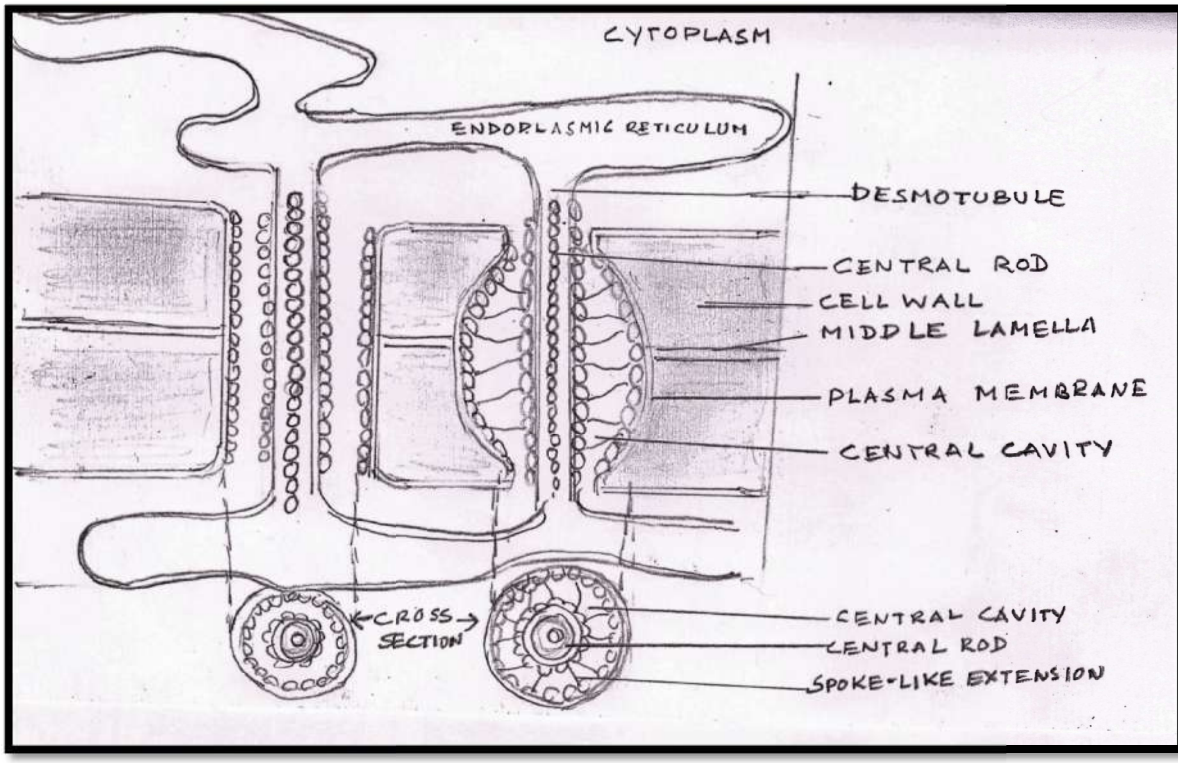
Plasmodesmata:

These are tubular extensions of the plasma membrane (40-50nm in diameter) that traverse the cell wall and connect the cytoplasm of two adjacent cells. During cytokinesis, golgi-derived vesicles containing wall precursors fuse to form the cell plate. However, vesicle fusion is interrupted by the remnants of the spindle apparatus. These channels form primary plasmodesmata that connect clonally related cells. Secondary plasmodesmata are formed either by evaginatio of the plasma membrane at the cell surface or by branching of primary plasmodesmata.

Ultrastructure

Plasmodesmata have a complex structure that controls the macromolecular traffic from cell to cell. Each plasmodesma contains a narrow tubule of endoplasmic reticulum (ER) called **desmotubule**. The desmotubule is continuous with the ER of the adjacent cells. **Globular proteins** are associated with the desmotubule membrane and the plasma membrane within the pore. These globular proteins are interconnected by **spoke-like extensions**, dividing the pore, into 8-10 micro channels through which some molecules can pass from cell to cell.

By following the movement of fluorescent dye molecules of different sizes through plasmodesmata connecting leaf epidermal cells, the limiting molecular mass for transport was determined to be about 700-1000 daltons, which is equivalent to a molecular size of 1.5-2.0 nm. This is the **size exclusion limit (SEL)** of plasmodesmata. The proteins attached to the plasma membrane and the ER within the plasmodesmata, appear to restrict the size of the molecules that can pass through the pore. The SEL of plasmodesmata can be regulated probably by actin and myosin proteins forming the spoke extensions.



Apoplast and symplast:

The apoplast is the continuous system formed by the cell walls and intercellular spaces in plant tissues. In the apoplastic pathway, water moves exclusively through the cell wall without crossing any membranes.

The symplast on the contrary, is the continuous system formed by the cell protoplasts interconnected by the plasmodesmata. In the symplastic pathway, water travels from one cell to another through the plasmodesmata