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Advanced Insights into the Role of Enzymes in Plant Pathogenesis

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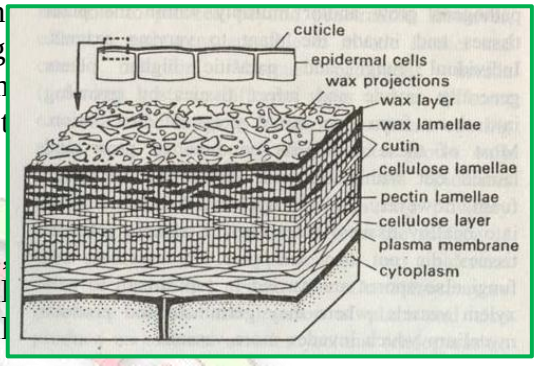
Enzymes are large protein molecules which catalyze all inter-related reactions in the living cell. Most pathogens derive energy principally from enzymatic break down of food materials from host tissue.



Composition of the cell wall

Functionally cell wall is divided into 3 regions, *viz.*, middle lamella (made of pectins), primary wall (cellulose, pectic substances) and secondary cell wall (entirely cellulose).

Middle lamella acts as intercellular cement which binds the cells together in tissue system. Pectin or pectic substances are major chemical constituents of wall layers and entire middle lamella, where as in other layers, cellulose is found in good amounts.

Besides these two major components, other components such as hemicelluloses, lignin and some amount of protein is also present. Main components of cell wall are pectic substances, cellulose, hemicelluloses, lignin and small quantity of protein.

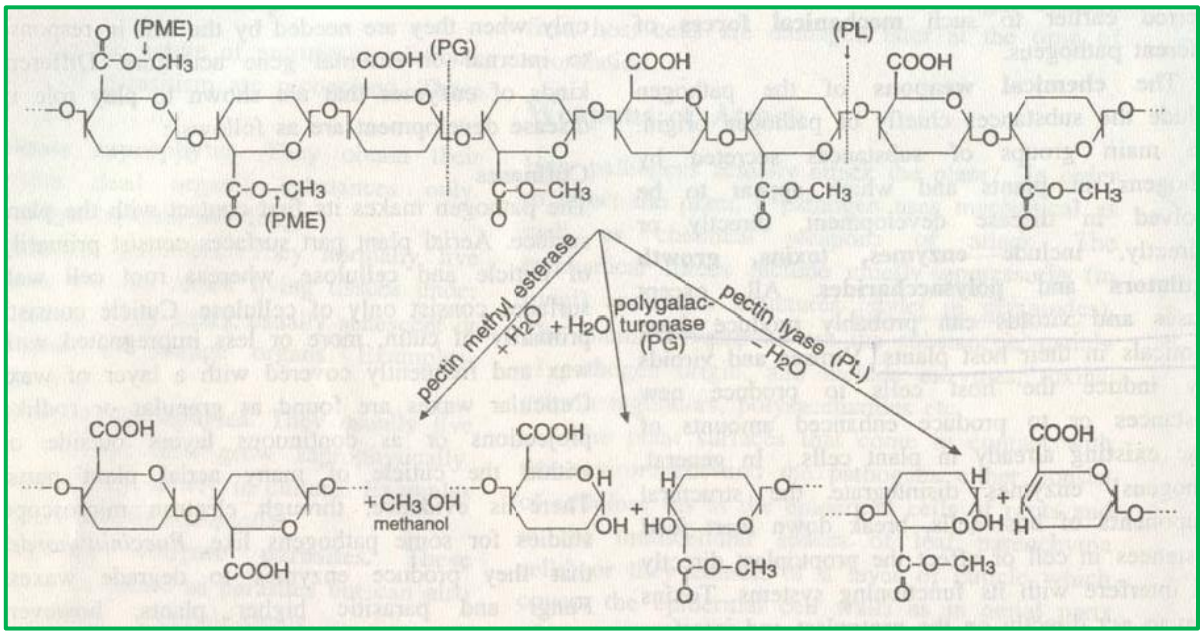
The epidermis of plants is covered by cuticle, whose major chemical substance is cutin in addition to cuticular wax.

Cuticular wax: Plant waxes are found as granular or rod like projections or as a continuous layer outside / within the cuticle. Wax formation is a continuous process and it is not a terminal phase in the development of leaf. Cuticular waxes are made up of long chain molecules of paraffin, hydrocarbons, alcohols, ketones and acids. Most of the fungi and parasitic higher plants penetrate wax layers by means of mechanical force alone.

Cutin: It is an insoluble polyester of unbranched derivatives of **C_{16} and C_{18} hydroxy fatty acids**. Cutin is admixed with waxes on upper side and with pectin and cellulose on the lower side. **Cutinases** break cutin molecules and release monomers as well as oligomers from insoluble cutin polymer. Cutinases reaches its highest concentration at penetrating point of the germ tube and at infection peg of appressorium forming fungi
Ex: *Colletotrichum gloeosporioides, Sphaerotheca pannosa, Venturia inaequalis, Helminthosporium victoriae*.

Pectic substances: These are major components of middle lamella (intercellular cement that holds in place the cells of plant tissues). They also make up a large portion of primary cell wall in which they form an amorphous gel filling the spaces between cellulose microfibrils. Pectic substances are polysaccharides consisting mostly of **d- galactouronic acid** units with **α-1,4-glycosidic bonds**. These chains are esterified with **methyl** groups or linked with other carboxyl groups in calcium and magnesium salt bridges.

Pectic substances are of three types, namely, **pectic acid** (non methylated units), **pectinic acid** (<75% methylated galacturonan units) and **pectin** (>75% methylated units). Term **protopectin** is used to denote substances which are soluble in water and upon restricted hydrolysis yields pectinic acid.



The enzymes that degrade pectic substances are known as **pectinases** or **pectolytic** enzymes. Pectinases and pectolytic enzymes are pectin methyl esterases (PME's), polygalactouronases (PG's) and pectin lyases (PL's).

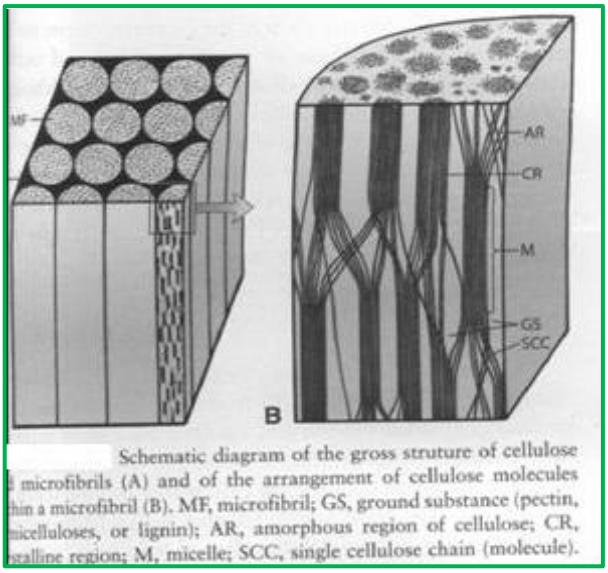
1. **Pectin methyl esterases**: Breaks ester bonds and removes methyl groups from pectin leading to the formation of **pectic acid** and **methanol** (CH_3OH).
2. **Polygalacturonases**: Split pectin chain by adding a molecule of water and breaks the linkage between two galacturonan units. These enzymes catalyze reactions that break α-1,4-glycosidic bonds.
3. **Pectin lyases**: Split pectin chain by removing a molecule of water from the linkage, thereby breaking it and releasing products with unsaturated double bonds.

These pectin enzymes can be **exopectinases** (break only terminal linkage) or **endopectinases** (break pectin chain to random sites). Pectin degradation results in liquefaction of the pectic substances and weakening of cell walls, leading to tissue maceration
Ex: Soft rot bacterium, *Erwinia caratovora* subsp. *caratovora* and other fungi like
Botrytis cinerea, Sclerotium rolfsii, etc.

Cellulose: Cellulose is a polysaccharide, made of chains of **β-D-glucopyranose** units (where C_1 is linked to C_4). Glucose chains are held by **hydrogen** bonds. Cellulose occurs in all higher plants as the skeletal substance of cell walls in the form of microfibrils. Primary and secondary wall consists of a matrix in which a large number of microfibrils are embedded. These microfibrils are like bundles of iron bars in a reinforced concrete building. In some parts of microfibrils the chains are arranged in an orderly fashion attaining crystalline form, when arranged in less orderly fashion, it attains amorphous form. If the proportion of crystalline portion is more, the resistance of the host to pathogen is more. The space between microfibrils and between micelles or cellulose chains is filled with pectins, hemicelluloses and also lignin at maturity.

Cellulose is insoluble in **crystalline** form (native form), and soluble in **amorphous** form (modified cellulose). The enzymatic breakdown of cellulose results in final production of glucose molecules.

Cellulose is degraded by **cellulases**. Cellulase one (C_1) attacks native cellulose by cleaving cross-linkages between chains. A second cellulase (C_2) also attacks native cellulose and breaks into shorter chains. These shorter chains are then attacked by C_x enzyme, which degrade them into disaccharide, **cellobiose**. Finally cellobiose is degraded by the enzyme, **β-glucosidase** into glucose.



Schematic diagram of the gross struture of cellulose microfibrils (A) and of the arrangement of cellulose molecules within a microfibril (B). MF, microfibril; GS, ground substance (pectin, micelluloses, or lignin); AR, amorphous region of cellulose; CR, crystalline region; M, micelle; SCC, single cellulose chain (molecule).

Cellulase degrading enzymes play a role in softening and degradation of cell wall material and facilitate easy penetration and spread of pathogen in the host.
Ex: Basidiomycetes fungi

Hemicellulose: These are the major constituents of **primary cell wall** and also seen in middle lamella and secondary cell wall. The hemicellulose polymers include primarily **xyloglucan** but also glucomannans, galactomannans, arabinogalactans, etc. Hemicelluloses link the ends of pectic polysaccharides and various points of the cellulose microfibrils.
Hemicellulases degrade hemicelluloses and depending on the monomer released from polymer on which they act, they are termed as xylanase, galactanase, glucanase, arabinase, mannose, and so on. Ex: *Sclerotinia sclerotiorum, Sclerotinia fructigena.*

Lignin: Lignin is found in the **middle lamella**, as well as in the secondary cell wall of xylem vessels and the fibres that strengthen plants. It is an amorphous, three-dimensional polymer made up of basic structural unit, **phenylpropanoid**. Lignin forms by oxidative condensation (C-C and C-O bond formation) between phenylpropanoid units or substituted **cinnamyl alcohols** (p-coumaryl alcohol, coniferyl alcohol and sinapyl alcohol). **White rot fungi** (Basidiomecetes) secrete one or more ligninases which enable them to utilize lignin. Ex: *Xylaria, Chaetomium, Alternaria, Cephalosporium*, etc.

Cell wall proteins: Cell wall proteins are similar to other proteins, except that they are rich in aminoacid, **hydroxy proline**. Five classes of structural proteins are found in cell walls: extensins, proline-rich proteins (PRP's), glycine-rich proteins (GRP's), Solanaceous lectins and arabinogalactan proteins (AGP's). Proteins are degraded by means of enzymes, **proteases** or **proteinases** or **peptidases**.

Lipids: Various types of lipids occur in all plant cells. The most important ones are **phospholipids** and **glycolipids**. These lipids contain fatty acids, which may be saturated or unsaturated. Lipolytic enzymes, called **lipases** (phospholipases, glycolipases) hydrolyze lipids and release fatty acids.

Starch: Starch is the main reserve polysaccharide found in plant cells. It is a glucose polymer and exists in two forms: amylose, a linear molecule, and amylopectin, a highly branched molecule. Starch is degraded by enzyme, amylases.