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Impact of Lignification on Secondary Cell Wall Development: A Review

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ABSTRACT

Plants are comprised of different particular cell types that contrast in their cell wall arrangement and structure. The cell walls of specific tissues like xylem sclerenchyma are portrayed by the occurrence of cellulose and the heterogeneous lignin polymer all of which assumes a noteworthy role in the physiology plant growth and for the sustainable economic purposes like bioethanol production. By far most of plant biomass comprises of various cell wall polymers created by living plant cells. The greater part of these polymers are vitality rich connected sugars that shape the major auxiliary system in plant cell walls, especially in the thick secondary cell wall describing certain tissues. Notwithstanding cell wall polysaccharides, another critical cell wall biopolymer is lignin restricting the access to cell wall sugars Because of its huge financial effect and pivotal job in vascular plant advancement; lignification is an imperative topic in plant biochemistry. So it is really important to understand the intricate network of secondary cell wall components and their biosynthesis which will be the major highlights for discussion in this review.

Keywords: *Arabidopsis thaliana, Lignin, Cellulose, Matrix polysaccharides, Secondary cell wall, Saccharification, Transcription factors, Biofuel production*

INTRODUCTION

Plants are comprised of different particular cell types that contrast in their cell wall arrangement and structure. The cell walls of specific tissues like xylem sclerenchyma are portrayed by the occurrence of cellulose and the heterogeneous lignin polymer all of which assumes a noteworthy role in the physiology plant growth and for the sustainable economic purposes like bioethanol production. By far most of plant biomass comprises of various cell wall polymers created by living plant cells. The greater part of these polymers are vitality rich connected sugars that shape the major auxiliary system in plant cell walls, especially in the thick secondary cell wall describing certain tissues. Notwithstanding cell wall polysaccharides another critical cell wall biopolymer is lignin restricting the access to cell wall sugars Because of its huge financial effect and pivotal job in vascular plant advancement lignification is an imperative topic in plant biochemistry. Lignin is a polyphenolic polymer kept in particular cell kinds of vascular plants. It is an imperative segment of plant woody tissues and the second richest biopolymer after cellulose on earth. The insolubility and crystalline nature of cellulose alongside its relationship in secondary cell wall with a lignin framework makes it an essential basic polymer in plant cell walls.It assumes noteworthy job in the load bearing system of primary cell wall in view of its physical properties is critical in deciding the introduction of cell extension. After a time of development a few cells make a thick auxiliary cell wall inside the primary wall. The secondary cell wall gives the mechanical solidarity to plants that enable them to stand upright and is an essential part in well working xylem vessels. Cellulose is exceedingly plenteous in the secondary cell wall. Cellulose is a basic polymer of unbranched β-1,4-connected glucan chains (Figure 1).

Progressive glucose buildups are rearranged 180 framing a level strip in which the rehashing unit is cellobiose. These parallel chains are then ready to shape broad hydrogen bonds between individual cellulose chains. This outcome in crystallization of various cellulose chains into microfibrils-insoluble link like structures presenting the physical properties required for their job in the cell wall. The P,S and G wall layers of cell wall have a wide range of polymers (Table 1).

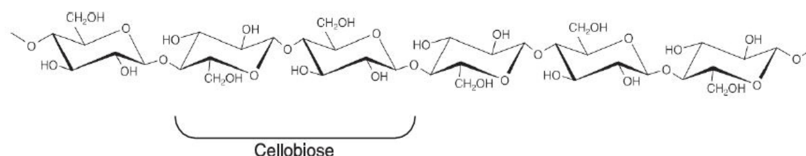

Figure 1: A fragment of -1,4-glucan and the repeating unit cellobiose is marked

Layer	Polymer (% d.w. AIR)
P- Layer	Cellulose (30–40%) Homogalacturonan (up to 40%BL) RG I (lower than that of homogalacturonan) Type II arabinogalactan (?) Rhamnogalacturonan II (?)structure Xyloglucan (=20% BL) Xylan (=5% BL) (Darvill et al., 1980). Mannan (=3% BL) (Marcus et al., 2010). Lignin (60–70% AL^y) (Donaldson et al., 2001).
S-Layer	Cellulose (50%) Xylan (20-30%) Glucomannan (=5%) Type II arabinogalactans Lignin (10-20%)
G-Layer	Cellulose (=75%) Xyloglucan (=15%) Fibres of poplar. RG I (?–8%) Mannan (=2%) Type II arabinogalactans (=2%)

The cellulose fibrils were reported in all three wall layers [1-4]. The main non cellulosic polysaccharide such as xylan was reported in S layers [5,6]. While the study on sugar proportions indicate that xylose and xyloglucan is the most abundant non cellulosic component of G layers in Populus alba [7-9].

Lignin formation is an important adaptation in vascular plants while evolution from aquatic plants. Plant annually fixed about 50 million tons of carbon in the form of lignin. In contrast to cellulose, lignin arrangement is cell specific and displays sub-cell confinement with various monomeric organizations. The lignin monomers called as monolignols differ in the degree of methoxylation. The three monomers are in particular, non-methoxylated p-coumaryl alcohol, monomethoxylated conferyl alcohol and dimethoxylated sinapyl alcohol (Figure 2).

Which individually offers ascend to H, G and S lignin. When the lignin monomers are enacted in the cell wall by phenol-oxidases, they can uproot the extreme charge through their conjugated unsaturation prompting different mesomeric frames. The lignin polymer, at that point frames by the end-wise expansion of new actuated monomers to its developing ends and branches [10]. Elucidating the mechanism of lignification for all cell types is not well understood. So far we understand that lignin forms in spaces between the cellulose microfibrils by the oxidative coupling of monolignols [11]. The way that lignin can't be expelled once it is saved recommending that plants require a particular mechanisms to control lignin biosynthesis. The biosynthesis of monolignols is initiated from phenyl-propanoid pathway [12]. In spite of the fact that tyrosine was viewed as the beginning stage of phenyl-propanoid digestion in a few plants for example grasses [13,14]. It has been seen that monolignols are gotten from phenylalanine by means of number of enzymatic responses catalyzed by the accompanying proteins: Phenylalanine ammonia lyase (PAL), Cinnamate 4-hydroxylase (C_4H), 4-coumarate coenzyme A ligase (4CL), Ferulate 5-hydroxylase (F_5H), p-coumarate 3-hydroxylase (C_3H). The polyphenolic polymer is made up of monomeric units that are connected

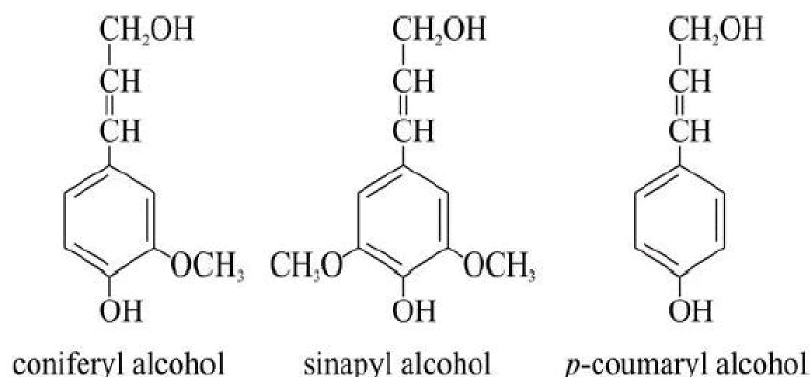

Figure 2: Chemical structures of the phenylpropanoid alcohols used to construct the lignin polymer

together by covalent bonds. Studies have demonstrated that monolignol biosynthesis and polymerization to frame lignin are firmly controlled in various cell types and tissues. However, our insight about the hereditary control of monolignols biosynthesis and transport and lignin polymerization is partly known with some promising results. It turns out to be increasingly troublesome when we realize that monolignols are delivered in non-lignified tissues as well. The situation becomes more complicated since we realize that monolignols or related compounds are some of the time created in non-lignified tissues.

LIGNIFICATION IN SPECIALIZED PLANT-CELL

Lignification happens amid the separation of particular cell types alongside various stress signals. The timing and differentiation of lignification in different cell types varies according to different stress signals. The deposition of lignin in each cell type ensures proper adaptation of plants to the changing environment. The cell which shows lignin deposition during their differentiation is tracheary elements and fibers. Tracheary components are an essential segment of the Xylem components. A specialized type of the vascular tissue system responsible for the water and mineral ascent of sap which provides mechanical resistance to plants from gravitational pull [15]. TEs act as cylindrically shaped elements in plants which undergo programmed cell death removing their cell content and thus fortify the cell wall by reinforcement by forming lignified secondary cell wall [16]. Genetic expulsion of TE lignification in entire plants results in crumbled TEs because of the failure of the cell to withstand the negative pressure related with the ascending of the sap [17,18]. Sclerenchyma cells incorporates fibres and sclereids in charge of secondary cell wall development found in a wide range of plant tissues for example xylem, phloem, epidermis and cortex in grasses and grains and in natural product plump tissues (for example stone cells in pear fruit [19]. Lignification can be actuated in light of any stress for example any wound [20] pathogen assault [21], dry season [22] UV radiation [23] low temperature [24] decreased supplement accessibility [25] CO_2 and ozone hazard [26,27]. These stress invigorated lignins more often surfaced the secondary cell wall of plants that are ordinarily not lignified for example leaf epidermal or stem pith parenchyma cells.

However confirmations have demonstrated the association of laccase in this procedure. In vitro tries were performed in P. taeda 20 years prior to relate laccase with lignification. Three antisense poplar lines, lac3AS, lac90AS and lac110AS were created yet no huge change in lignin substance and structure was observed. Be that as it may lac3AS displayed a two-triple increment in total phenolic content and demonstrated a change of xylem fiber cell walls. The outcomes demonstrated that LAC3 is basic for ordinary cell wall structure and unity of poplar xylem strands. Substance part examination of the Arabidopsis lac15 mutant seeds uncovered almost 30% decline in lignin content contrasted with wild-type columbia. This was the main direct proof for conceivable job of laccase in lignin synthesis.

LACCASES AND PEROXIDASES – MONOLIGNOLS TO LIGNIN

Plant Laccases are an important class of oxido-reductase and shares the homology with fungal laccase. However there is distinction in the reduction potential and diverse pH necessity, which may halfway record for its role in lignin biosynthesis, in spite of the lignolytic activity of fungal laccase. Plant laccase is coded by multigene family, the articulation in particular tissues can be controlled by certain interpretation factor by MYB and NAC families, miRNA and different sorts of abiotic and biotic anxieties. Laccases, class of multi-copper glycoprotein oxidases, catalyzes oxidation of a wide scope of substrates, for example phenols and amines in spite of the fact that their exact biochemical jobs in higher plants is to a great extent indistinct for e.g., Arabidopsis thaliana contains 17 laccases with just a single having a known physiological function. Out of 17 laccases 9 are xylem specific showing their transcript

expression in internodal inflorescence axis resulting in maximum lignin deposition. If we compare the roles of laccases in Arabidopsis we can look at spatial and temporal expression petterns of Arabidopsis laccases and differentiated in various tissues at different development stages utilizing RT-PCR and promotor-GUS combinations. Primer research dependent on bioinformatics investigations, proposes that most laccases may likewise be firmly controlled at both transcriptional (antisense transcripts, histone and DNA-methylation) and post-transcriptional (microRNAs) level.

Laccase genes (AtLAC2, AtLAC4, AtLAC11 and AtLAC17) that are highly expressed in Arabidopsis stems were studied intensively for lignin research. AtLAC17 was specifically expressed in the interfascicular fibers while AtLAC4 was expressed in interfascicular fibers. Arabidopsis t-DNA insertion mutants were oppressed for examination in plant development and described for secondary cell wall. Two double mutants were gotten by intersection the AtLAC17 (LAC 17) mutant with two AtLAC4 mutants (lac4-1 and lac4-2). The single and double mutants indicated typical development, with the exception of the lac4-2 lac17 mutant had a semi-dwarf phenotype and crumbled vessels. The single mutants had decreased lignin levels, the stems of lac4-1, lac17 and lac4-2 lac17 had lignin content diminished by 20% and 40%, individually, while triple mutant of lac4, lac11, lac17 captured the plant growth totally [28].

Peroxidase work in plants is so mind boggling to comprehend due to the absence of substrate particularity different restricting sites the high number of genes their assorted variety in structure and our constrained learning of peroxidases transcription and translation. Class III peroxidases are generally attentive about lignin biosynthesis encoding around 73 peroxidases [29] out of which transcripts of 58 of these genes have now been observed. It was affirmed that 71 genes could yield stable proteins folded comparatively to horseradish peroxidase (HRP). The putative developed peroxidases got from these genes indicated 28-94% amino acid sequence similarity and were altogether focused to the endoplasmic reticulum by N-terminal signal peptides. Cell wall polymerization occurs by type III and Laccase in development stage of cell wall where they cause the monolignol oxidation and lignification. Peroxidases requires Hydrogen Peroxide as the substrate whereas laccases needs oxygen to catalyze. It has been observed that out of 73 PRX, PRX 2, 25, 71contribute to lignification of Arabidopsis thaliana stem. Recombinant forms of proteins of these three plant peroxidases, AtPrx-2, 25, and 71, responsible for lignin polymerization in the Arabidopsis stem were produced [30].

Peroxidases are the large multigene families in Arabidopsis and Oryza (73 and 138 respectively), characterizing the biological role of every member is difficult. Clear screening of the role of peroxidases is difficult as they have very low substrate specificities [31]. Studies have shown that PRX are mainly involved the formation of S and G units that explains the plant's lignin monomeric structure. For example a recent study have shown that anti-sense of one PRX suppression resulted to overall reduction of both and S and G subunit in tobacco. Alignment of 73 Arabidopsis peroxidase provided an evidence for the identification of orthologous peroxidases in other plant species and helped in recollecting all the knowledge of peroxidase structure and functional relationships in various species.

TRANSCRIPTION FACTORS REGULATING SECONDARY CELL WALL BIOSYNTHESIS

There are certain transcription factor family related with Primary and Secondary Cell wall biosynthesis. They have been observed to be the master switches of secondary cell wall biosynthesis. These transcription factors can be positive and negative regulators resulting in up-regulating and down-regulating the cell wall biosynthesis. Further examination of the administrative components of cell wall synthesis will encourage the designing of plant feedstocks reasonable for biofuel creation. TFs are potent candidates for improving biomass as they control the biosynthesis of multiple cell wall components. Genetic modification of secondary cell wall components to improve saccharification efficiency will reduce the cost of pretreatment by decreasing the recalcitrance and facilitate subsequent ease in fermentation.

The secondary cell wall associated NAC TFs namely SND1/NST3, NST1, VND6, and VND7 function as the master switches and the MYB TFs act as a secondary master switches to regulate downstream genes in secondary wall formation. Overexpression of MYB46 and MYB83 activates genes of cellulose, xylan and lignin biosynthesis, and causes ectopic deposition on secondary cell walls suggesting that these MYB TFs are also master switches of secondary cell wall formation. NST1 is the master transcriptional switch regulating all transcription factors. A more recently discovered KNAT7 belonging to KNOX family is negatively regulating secondary cell wall formation and functionally conserved in populous [32] and positively up-regulating the secondary cell wall in Arabidopsis MYB family containing and MYB46 and MYB58 is a lignin specific transcription factor positively regulating the secondary cell wall 11 is under the control of NST1 (NAC associated secondary cell wall thickening factor 1) (Figure 3).

DISTURBANCE IN LIGNIN BIOSYNTHESIS AFFECTS SECONDARY CELL WALL FORMATION AND SACCHARIFICATION

Lignin is an imperative polymer giving the quality keeping up the upstanding stance for the plant, decline in lignin

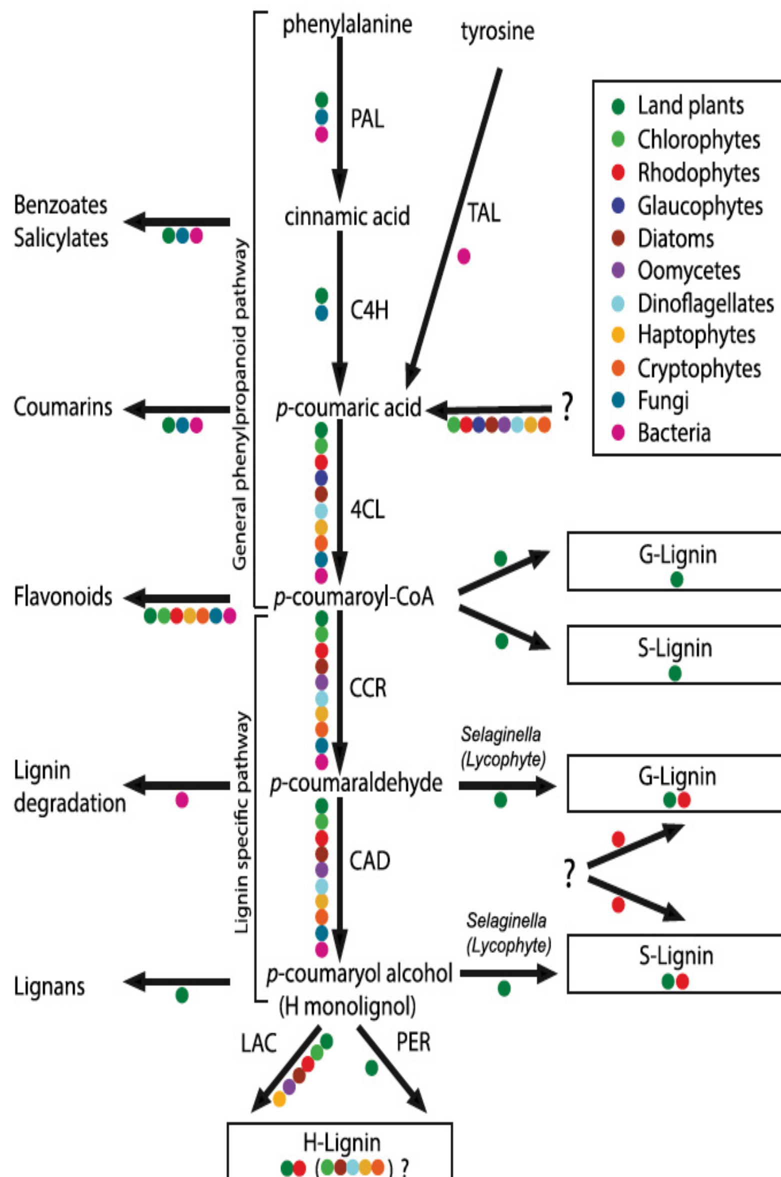

Figure 3: Phenylpropanoid pathway by Labeeuw [40]

substance to about 64% of the wild-type level in *Arabidopsis* was endured with no undeniable growth penalty. Opposite decrease in lignin was not repaid by an expansion in cell wall polysaccharides. In most lignin mutants the saccharification yield was enhanced by up to 88% cellulose [33]. The saccharification procedure showed that lignin content was the fundamental factor deciding saccharification yield.

TRANSPORT

Once the monolignols are formed inside the cytoplasm, they are transported across the plasma membrane to the cell wall for further polymerization into lignin. Mechanism of transport was still unknown for a long time and different hypothesis were exacted (Passive diffusion, exocytosis and passive transport). Very recently, it was postulated that glycosylation status determines their transport. Monolignols are transported through ABC transporter [34]. They are polymerized by laccases and peroxidases. Genetic involvement of ABC transporters was further validated in the cell wall and confirmed that these cassettes are important and necessary for the monolignol [35-40].

APPLICATION

Biofuel has received remarkable progress in terms of research in recent years as an environmental friendly and

economical resource. As the first generation biofuels are derived from food products, the second generation biofuels are usually derived from non-food products such as lignocellulose biomass. There are just two business scale lignocellulosic biofuel offices in the world. A 20 million gallon for every year biorefinery in cresentino, Italy, claimed by beta renewables, uses a steam pretreatment and organic change procedure to deliver lignocellulosic fuel from a varieties of perennial grasses, corn stover, wheat and rice straw and poplar. A facility possessed by kior in columbus, Missouri, is relied upon to create 13 million gallon for each time of gas and diesel by pyrolysis of forest service's buildup. The second generation biomasses are progressing remarkably in terms of research and still lot of work is going on. The processing of second generation biofuel includes pretreatment for the hydrolysis of high molecular mass polysaccharides into low molecular mass sugar monomers on the basis of enzymatic digestion following by fermentation into cellulosic ethanol. Feedstock for lignocellulosic biofuel creation can be non-consumable vitality products, for example, vitality grasses (Miscanthus, switchgrass, sweet sorghum, etc.), farming and modern squanders, which are normally monetarily attainable and not bargaining with sustenance security can be delivered in large amounts. The real segment of the lignocellulosic biomass is the plant cell wall, a heterogeneous complex for the most part comprising of cellulose, hemicellulose and lignin. Lignin is considered as the essential hard-headed segment to saccharification, since it is expected to hinder the movement of cellulosic enzymes keeping the arrival of cellulose. Lignin limits the yield of ethanol production therefore its removal before fermentation is necessary, which is an adding cost to the biofuel production and environment. Genetic engineering is still possible to manipulate the lignin biosynthesis or modification of lignin structure. If we manipulate Laccase and Peroxidase which are responsible for oxidation of monlignols and causes coupling of monomers into lignin polymer will serve as a great approach to lignin production.

CONCLUSION

Clearly biosynthesis and polymerization of monolignols is more perplexing than it is theorized that lignin is connected with a wide range of cells to meet explicit physiological capacities, yet shows different properties for every cell type, which clarifies why no particular component for lignification is characterized. Contingent upon the ideal lignin properties for the cell function, explicit substrates and proteins will be delivered in particular cell types despite the fact that a high utility for the two substrates and enzymes is as yet held. Lignification occurs by itself and works in symbiosis with other cells to ensure full lignification that will better help adapt the cells to the changing environment.

There are vast numbers of regulatory checkpoints involved in the process of lignification allowing plants to respond accordingly to the changing environmental cues. These checkpoints can act as novel targets to optimize lignin production. The checkpoint can resemble, how are glycosylated monolignols discharged from the vacuole? What are their jobs? Are PRX involved and how do they involve in lignification? What is relative contribution of laccase and PRX in lignification? For the most part, the mechanism of lignification has been considered for quite a while at monolignol biosynthetic level, frequently with the objective of diminishing lignin contents. It is currently certain that there might be numerous different checkpoints that will result in novel challenges to increase plant biomass for bioenergy production. We will expect to get the answers of some prospective questions in this decade.

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