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How do plants make cell walls?

植物细胞壁研究与生物质改造利用

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摘要 细胞壁是植物细胞区别于动物细胞的重要结构特征之一，在植物细胞生长发育和环境响应中发挥重要作用．同时，地球上陆生植物光合作用产物约70%存于细胞壁中，细胞壁生物质是地球上最丰富的可再生资源．植物如何将光合产物合成为细胞壁成分？人类如何有效利用大量的、可再生的细胞壁生物质资源？这些问题近年来受到了广泛的关注．本文对细胞壁合成、利用生物技术对细胞壁生物质进行改造，以及细胞壁生物质利用等研究进行简要介绍和综述．

关键词 植物细胞壁，纤维素，木质素，半纤维素，纤维生物质

化石能源使用产生的污染和温室气体已使地球环境高度恶化，同时化石能源的不可再生使人类文明可持续发展受到越来越大的挑战．植物通过光合作用利用太阳能将二氧化碳和水合成为有机化合物，全球陆生植物每年生物产量约170×10^9~200×10^9 t，其中约70%转化为高分子聚合物累积在细胞壁中，具有巨大的开发潜力[1]．探索植物如何形成细胞壁以及如何将生物质转化为可利用的能源对人类社会可持续发展具有重要的意义，被*Science*列为人类所面临的需要回答的重要科学问题之一[2~4]．

细胞壁是植物重要的特征性结构，包括中胶层、初生细胞壁和次生细胞壁．前两层普遍存在于所有的植物组织细胞中，由纤维素、半纤维素、果胶质和少量蛋白质组成，与细胞间黏附、细胞扩增及细胞形态的决定有关[5]．次生细胞壁只沉积于特殊类型细胞的初生壁内部，含有纤维素、半纤维素和木质素，赋予细胞壁机械强度以及疏水性，这种物理和化学特性对植物直立生长、水分和营养物质的运输、抵抗外界生物非生物胁迫非常重要[6,7]．自1665年胡克用光学显微镜观察到栓皮栎栓化的次生细胞壁结构，称之为细胞以来，人们对植物细胞壁进行了广泛而深入的观察和研究．从20世纪末至今，细胞壁成分的合成与组装、细胞壁合成调控的分子机制、细胞壁参与环境胁迫等方面都得到了系统解析[8]．同时，细胞壁中所积累的生物高分子聚合物是人类生产生活及生物能源工业的重要原料来源，细胞壁的改造与利用受到越来越多的关注[9]．

1 植物细胞壁的合成与调控

1.1 细胞壁主要成分的合成

纤维素是植物细胞壁的主要成分，约占干重的40%~50%，在细胞壁中以微纤丝的形式存在．葡萄糖以β-(1→4)糖苷键连接而成葡聚糖链，多条葡聚糖链平行排列，糖链间靠氢键连接，形成直径约5~10 nm的结晶态微纤丝[10]．早期使用冰冻蚀刻技术和免疫胶体金标记方法在细胞膜断面上观察到“玫瑰花环”结构的六聚球状蛋白复合体[11,12]．后来的研究表明，

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这种玫瑰花状结构即为纤维素合酶复合体，包括6个亚复合体结构，分别由3~6个纤维素合酶蛋白组成，合成18~36条葡聚糖链构成的微纤丝[13]．纤维素合酶是一类糖基转移酶(glycosyltransferase, GT)，催化二磷酸尿苷葡糖(uridine 5′-diphosphoglucose, UDP-Glucose)形成葡聚糖链．高等植物中纤维素合酶的发现最早基于对细菌纤维素合酶基因的同源克隆，在棉花(*Gossypium hirsutum*)中发现高度同源的基因*GhCesA-1*和*GhCesA-2*[14]．随着测序技术的应用，基因组分析在很多高等植物中鉴定出纤维素合酶家族成员，如拟南芥(*Arabidopsis thaliana*)中10个、毛果杨(*Populus trichocarpa*)中18个、水稻(*Oryza sativa*)中10个以及高粱(*sorghum*)中的12个[15]．

初生细胞壁和次生细胞壁中的纤维素属性有所不同，次生细胞壁中纤维素的结晶度和聚合度都相对较高，且在次生细胞壁的不同层结构中，纤维素的结晶度和聚合度也不同．拟南芥纤维素合酶家族基因的10个成员中除*Ces10*外，一般可分为与初生壁和次生壁相关的两类纤维素合酶基因，各自形成复合体参与纤维素合成，称为拟南芥Ⅰ型纤维素合酶复合体(cellulose synthase complex, AtCSC-I)和Ⅱ型纤维素合酶复合体(AtCSC-II)．木本植物维管系统次生生长过程需要合成大量的纤维素，具有比草本植物更加复杂的纤维素合酶家族．杨树(*Populus*)中的两类纤维素合酶复合体(PtCSC)蛋白种类与AtCSC对应同源，但是数量加倍，并且这两类复合体都参与次生细胞壁的合成，暗示纤维素合酶复合体可能调控不同结晶度纤维素的合成[16,17]．

纤维素在细胞壁内沉积有一定方向性和排列方式，在初生壁中，微纤丝排布方向受皮层维管排列的制约，大多与细胞长轴垂直，而在次生壁中，微纤丝排布方向则复杂化．有很多其他蛋白被发现影响纤维素的合成和沉积过程，但是是否与次生壁纤维素有特异关系还不清楚[18]．

半纤维素是植物初生壁和次生壁中广泛存在的多种单糖形成具有分支结构的多糖，它与细胞壁其他成分纤维素、木质素等相互作用形成网络以加固细胞壁．半纤维素由于骨架及侧链取代的糖分子不同而分为多种类型，包括木葡聚糖、木聚糖、甘露聚糖、葡甘露聚糖以及β-(1→3, 1→4)-葡聚糖．半纤维素是由高尔基体膜上的糖基转移酶来合成的，目前已经鉴定到一些相关酶，但是详细的合成机制还不是非常清楚[19]．

果胶质存在于中胶层和初生壁，是一类富含半乳糖醛酸的多分支复杂多糖，填充在纤维素和半纤维素交联形成的网络中．果胶质的存在能够调节初生壁强度和可塑性，同时在植物对病原菌的响应过程中也起到重要作用[20]．作为最复杂的细胞壁成分，果胶质的合成过程有大量糖基转移酶参与，目前鉴定出参与果胶合成的酶基因很有限[21]．

木质素是植物次生壁特有的一种苯丙烷类多聚物，使其具有很强的机械支撑力，同时帮助抵抗外界昆虫和微生物的入侵，木质素的疏水特性有利于水分从木质部管状分子向上运输[22]．被子植物木质素的组成单体主要有3种类型：对-香豆醇、松柏醇和芥子醇，分别可以聚合形成*H*-木质素(*p*-hydroxyphenyl lignin)、*G*-木质素(guaiacyl lignin)和*S*-木质素(syringyl lignin)．在植物细胞中，木质素的含量和组成随着植物类群不同、组织类型不同、发育阶段不同甚至外界环境的不同都会有所差异，因此木质素的合成途径并不完全相同．随着拟南芥和一些木本植物木质素单体合成基因的克隆和鉴定，对木质素单体合成途径已经有比较完整的认识．木质素单体的合成是在细胞质中进行的，从苯丙氨酸开始，经过去氨基、芳香环羟基化、羟基甲基化、连续的还原等反应合成3种单体，多种酶参与这一过程，并且3种单体的合成途径有所差异[23,24]．木质素单体经过脱氢聚合形成多聚物，近期的研究表明，拟南芥维管组织中漆酶LAC11 (laccases), LAC4和LAC17在催化木质素单体聚合过程中起主要作用，过氧化物酶可能在其他组织木质素沉积中起作用[25,26]．关于木质素单体如何运输到质膜外的细胞壁中目前还没有确定的模型，现在认为木质素单体被转运蛋白运输，但是被哪些蛋白如何运输，还需要更多研究[27]．

1.2　细胞壁合成的调控

植物生长发育过程中细胞壁的合成受到严格调控，特别是只在特殊类型细胞沉积的次生壁，受到多层次的转录网络调控．两类NAC (no apical meristem/*Arabidopsis* transcription activation factor/cup-shaped cotyledon, NAM/ATAF/CUC)家族转录因子被发现作为初级转录因子开启维管组织纤维细胞和导管细胞次生壁合成．一类是NST3/SND1 (NAC secondary wall thickening promoting factor 3/secondary wall-associated NAC domain protein 1)、NST1和NST2，拟南芥中三者的同时突变使得束间纤维和木质部纤维细胞次生壁加厚完全丢失[28]，*nst1nst2*双突变体中，花药药室内壁次生壁加厚受抑制导致花药不能正常开裂[29]．另一类VND (vascular-related NAC domain)基因家族*VND1~7*参与调控导管细胞发育，过表达*VDN6*和*VND7*能诱导百日草(*Zinnia elegans* Jacq.)悬浮细胞系中薄壁细胞转分化为具有环纹和螺纹加厚的原生导管细胞以及具有网纹和孔纹加厚的后生导管细胞，显性抑制这两个基因能抑制拟南芥根中原生导管和后生导管的形成[30]．*VND1~5*在拟南芥花序茎中特异表达在木质部，同*VND6*，*VND7*一起调控导管细胞次生壁加厚[31]．两类NAC转录因子激活很多下游转录因子，包括SND2，MYB46 (v-myb avian myeloblastosis viral oncogene homolog)，MYB85，MYB103和KNAT7 (knotted-like homeobox of *Arabidopsis thaliana* 7)等[32]，也可以直接激活次生壁合成相关酶基因，如纤维素合酶基因*CesA4*，*CesA7*，*CesA8*等，VNDs还调控木质部形成过程中参与细胞程序性死亡的基因*XCP1* (xylem cysteine peptidase 1)和*XCP2*[33~35]．*MYB46*和*MYB83*被NAC转录因子直接调控，遗传学分析发现，*MYB46*和*MYB83*双突变体产生严重的次生壁合成缺陷，过表达*MYB46*和*MYB83*能激活次生壁的各组分合成基因的表达上调[36~38]．*MYB46*和*MYB83*受NAC转录因子调控，二者同时直接激活下游转录因子和部分次生壁合成基因，形成了多级前馈式的转录调控网络对次生壁合成精确调控，同时这种调控网络在不同植物类群中具有保守性[39]．

次生壁合成转录调控网络也受到上游因子调控，目前发现一些激素等信号途径参与其中．对拟南芥下胚轴单独或组合施加外源生长素、细胞分裂素和油菜素内酯，发现*VND6*，*VND7*的表达量产生复杂的变化，其中的调控机制尚不清楚[30]．最近在水稻中研究发现，赤霉素信号途径通过多级转录因子调控次生壁纤维素合酶基因表达[40]．木本植物次生生长过程中维管系统大量沉积次生壁，需要比一年生草本植物更加复杂的调控机制．对毛果杨发育中次生木质部和韧皮部表达的膜蛋白分析鉴定到很多类受体激酶，这类蛋白可能在特定位置的细胞质膜上接受胞外信号调控次生壁成分合成[41]．半乳葡甘露聚糖(galactoglucomannan oligosaccharides, GGMOs)在百日草悬浮细胞体系中可作为外源信号分子诱导管状分子的形成[42]，杨树中内切-1,4-β-甘露聚糖酶PtrMAN6 (endo-1,4-β-mannanase 6)水解甘露聚糖产生GGMOs，可能作为信号抑制次生壁加厚，这些研究结果暗示植物次生壁合成可能受到包括寡糖在内的复杂信号途径调控[43]．

2 植物细胞壁的改造与利用

从最原始的直接燃烧获取热量，人类对细胞壁的利用由来已久，植物为人类提供的能源、纤维、建筑材料、造纸原料等，大部分来源于细胞壁．近几十年来，随着全球能源需求不断增加和温室气体大量排放带来的环境问题日益加剧，寻找可再生绿色能源受到了广泛关注，细胞壁特别是次生细胞壁中的木质纤维素生物质，是获得生物燃料最丰富的可再生原料来源[44]．木质纤维素生物质经过预处理、糖化、发酵3个过程转化为可直接利用的醇类等生物燃料[45]．目前技术成本高、效率低使得纤维素生物质转化利用的市场竞争力不强，利用生物技术手段定向改造生物质，有可能培育高效转化的生物质原料[46]．

细胞壁中纤维素是可被糖化发酵的主要成分，研究表明，增加纤维素总含量以及降低纤维素结晶度可以提高总糖化效率[47,48]．本课题组在研究中发现，调控杨树中纤维素合酶复合体构成，可以改变纤维素结晶度和纤维素水解效率(结果待发表)．有研究表明，在植物中引入高效和耐温型纤维素水解酶的基因，能促进纤维素转化为可发酵的单糖[46]．半纤维素多糖同纤维素微纤丝及木质素交联加固次生壁，阻碍纤维素酶对纤维素的水解作用，因此半纤维素含量与糖化效率呈负相关[49,50]．细胞壁多糖的修饰也会阻碍酶对糖链的降解，如乙酰酯化、甲基酯化等．同时，乙酸基团释放后改变环境的酸碱度影响之后的糖发酵效率[51]，因而半纤维素这些结构的改变可能影响木质纤维生物质的转化效率．虽然果胶质在次生壁的含量非常少，但由于次生壁沉积于富含果胶的初生壁内侧，果胶与初生壁骨架的交联阻碍消化酶对纤维素多糖的降解，因此降低果胶质含量、提高果胶甲基酯化水平有利于提高糖化效率[52]．

木质素是木质纤维生物质转化利用中的主要抑制组分，研究人员试图通过基因工程技术，改变木质素的含量和组成，改进木质纤维生物质的转化利用效率．在杨树中，抑制*4CL* (4-coumarate–CoA ligase)

表达，木质素含量可降低50%，同时，纤维素含量增加[53]．抑制*4CL*表达的同时过表达*CAld5H* (coniferaldehyde 5-hydroxylase)基因，实现了同时降低木质素含量和改变木质素单体组成，木质素含量降低50%，单体组成的S/G (syringyl unit/guaiacyl unit)比率从2增加到6，纤维素含量增加30%[54]，利用木质素含量和单体组成改变的细胞壁生物质材料生产生物乙醇，效率显著提高(结果待发表)．通过抑制*CCR* (cinnamoyl-CoA reductase)基因的表达，木质素含量降低约50%，对5年田间试验种植的转基因杨树分析表明，转基因植物材料的木质素降解效率大为提高[55]．在紫花苜蓿(*Medicago sativa*)中，通过抑制木质素合成代谢基因的表达，使木质素含量降低，基因工程改造的生物质材料转化为糖的效率明显提高[56]．最近，研究报道了在杨树中引入结构改造后的*OMT* (*O*-methyltransferase)基因，显著提高了杨树细胞壁转化为乙醇的效率[57]．另外，在利用生物技术对玉米(*Zea mays*)、柳枝稷(*Panicum virgatum*)和树木进行基因工程改造，对提高生物质的转化效率等方面开展了很多探索研究．基因工程技术可能在培育可高效利用的生物质原料植物方面发挥重要作用．

3 总结与展望

植物细胞壁由多糖聚合物纤维素、半纤维素、果胶质以及苯丙烷类聚合物木质素构成，它们的合成和积累受到植物发育和多种环境因子的调控，虽然在解析纤维素、半纤维素、果胶和木质素的基本合成代谢途径方面取得了一系列进展(图1)，但细胞壁各组分如何与植物生长发育关联、各成分的合成如何调控、细胞壁各成分构成比例如何控制等还很不清楚．这些问题不仅是植物生长发育中的基本科学问题，更对高效转化利用细胞壁生物质具有重要的应用价值．近年来，组学研究技术以及新的细胞壁分析技术的发展有可能为细胞壁合成研究展开新的探索窗口，加速阐明植物如何合成细胞壁这一人类高度关注的科学问题．

目前对木质纤维素生物质进行基因工程改造的很多研究还处于实验室探索阶段，改造细胞壁对植物生长发育会产生非常复杂的影响．如何将多种细胞壁改造方法应用于能源植物，同时不影响其在自然条件下的生长状态是接下来直接面对的问题．

植物细胞壁不仅是植物生命活动中具有关键功能的结构，也是光合作用产物的储存库．细胞壁生物质是地球上最丰富的可再生生物质资源，细胞壁蕴藏着巨大的能源和生物聚合物资源．为了有效开发利用细胞壁，需要了解关于细胞壁合成和调控的新知识，需要利用细胞壁合成的机理来培育可高效转化利用的生物质原料，需要利用细胞壁组成和结构的知识设计高效转化利用的生物质精炼技术．

植物细胞壁是如何合成的？它所蕴藏的能源如何被开发利用？对这些问题的探索和回答才刚起步．

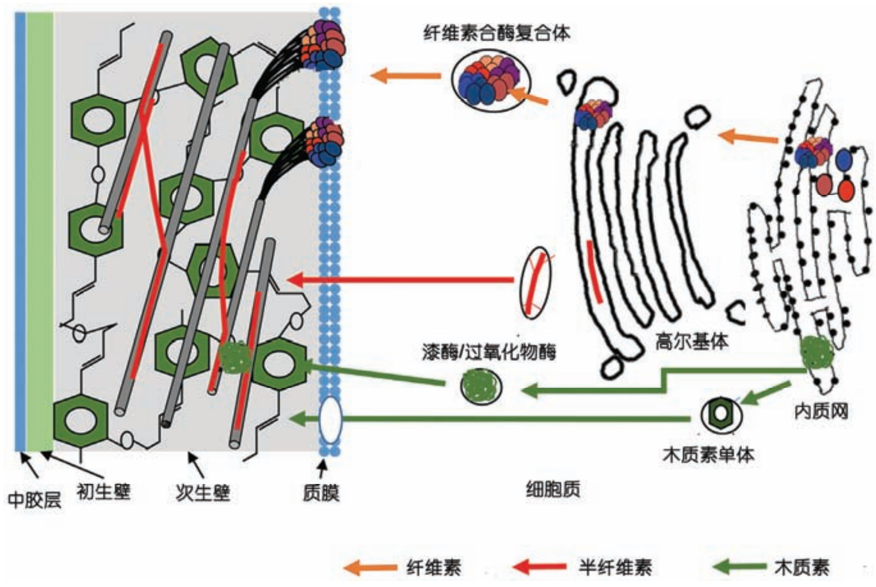

图 1 (网络版彩色)植物细胞壁结构与次生细胞壁合成(修改自[6])

Figure 1 (Color online) Structure of plant cell wall and secondary cell wall synthesis

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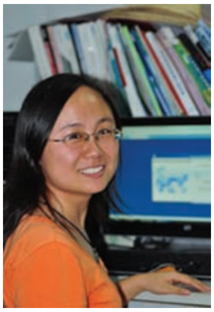

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Understanding of plant cell wall biosynthesis for utilization of lignocellulosic biomass resources

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How do plants make cell walls? How can the cell wall biomass be turned into fuel energy? These questions are still unsolved puzzles that have attracted a great deal of interest in scientific community as well as in industrial and political worlds.

Different from animal cells, plant cells develop characteristic structures of cell walls, which play crucial roles in planting growth and response to environments. As cell walls accumulate approximately seventy percent of the land pant photosynthesized products on the globe, cell wall biomass is the most abundant renewable resource for production of bioenergy and biomaterials. However, only a small portion (~2%) of the plant cell wall resource has been used by human society so far. More efficient utilization of lignocellulosic cell wall biomass is highly desired.

Great effort has been invested in understanding of how cell walls are formed in plant in recent years. Plants cell walls contain cellulose, hemicelluloses, pectic polysaccharides and lignin. These polysaccharides and phenolic polymers are constructed in concrete cell walls for supporting plant growth and development. Cellulose is composed of β-1,4-linked glucose units and a bundle of multiple β-1,4-glucan chains together form microfibrils, providing a skeleton of cell wall structures. Cellulose is synthesized in plants by cellulose synthase (*CesA*) complexes which are integrated and localized in plasma membrane. There are a family of *CesA* genes in plants which direct cellulose synthesis in different layer of cell walls or regulate cellulose microfibril structures. Although cellulose has been used in many aspects of human life, such as fiber cloth, paper, and modified cellulosic products, Cellulose, the most abundant biopolymer on the Earth, promises more utilization in supporting for sustainability of human society development.

Hemicellulose is a group of diverse polysaccharides, such as xyloglucan, heteromannans, heteroxylans and mixed-linkage glucan. Their diverse structure and sugar composition varies in plant species, tissues, even cell types. Hemicellulose polysaccharides, amorphous and soluble in aqueous solutions, are composed of heterogeneous monosaccharide units or linkages in their backbone and branched side chains. Hemicelluloses are usually covalently linked to cellulose and lignin in cell wall matrix. Hemicellulose has been used in many applications such as food products and nutritional supplements. How is hemicellulose synthesized? How do the diverse hemicelluloses function in plant development? How can the abundant hemicellulose sugars be used? Many questions remain to be investigated.

Lignin is polymerized from phenolic monolignols and mainly deposited in the secondary cell walls of vascular plants. Evolved in higher plants, lignin is essential for long distance water transport, mechanical support of up-growth, pathogen defense and for other stress responses. In the cell walls, lignin is usually cross-linked with cellulose and hemicellulose. Although biosynthesis of monolignols including *p*-hydroxyphenyl (*H*), guaiacyl (*G*) and syringyl (*S*) monolignols has been elucidated genetically and biochemically in various plant species, regulation of monolignol formation in different species, tissues and cell types is still unclear. As the second most abundant plant biopolymer after cellulose on the globe, utilization of lignin is highly attended. Lignin is considered as a main recalcitrance during cell wall biomass conversion, therefore modification of lignin biosynthesis is of great interest in engineering plant cell walls for efficient biomass utilization. Laboratory research has showed potential benefits of lignin engineering for lignocellulosic biomass conversion, while application of the technology in the field requires more evaluation.

This review summarizes recent studies of the biosynthesis of plant cell wall components such as cellulose, hemicelluloses and lignin as well as the modification of cell walls for the improvement of lignocellulosic biomass utilization.

plant cell wall, cellulose, lignin, hemicellulose, lignocellulosic biomass

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