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·专题论坛·

参与木葡聚糖合成的糖基转移酶基因研究进展

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摘要 半纤维素多糖木葡聚糖(XyG)存在于大多数植物的初生细胞壁中，对细胞壁的结构组织和生长发育具有重要的调控作用。XyG在植物进化中存在结构的多样性。该文概述了参与XyG合成的糖基转移酶的最新研究进展，XyG合成需要多种糖基转移酶参与，这些酶类很可能以蛋白酶复合体的形式存在并发挥作用，XyG的结构和组成的改变对植物的生长发育也产生影响。

关键词 木葡聚糖，糖基转移酶，细胞壁，生物合成

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细胞壁是植物细胞最基本的组成结构，对于维持植物机械强度、保持细胞形状、控制细胞生长以及胞间物质的转运和信号转导起着重要作用；同时也是人类生产活动中木材、造纸、纺织、食品、饲料及生物质能源等原材料的主要组成部分(Caffall and Mohnen, 2009; Kong et al., 2009; Pauly and Keegstra, 2010)。植物细胞壁分为初生细胞壁和次生细胞壁。初生细胞壁的主要组分有多糖、蛋白及一些酶类。其中多糖主要包括纤维素(cellulose)、半纤维素(hemicellulose)和果胶质(pectin)。次生细胞壁除含有纤维素和半纤维素以外，还含有木质素(lignin)。其中木葡聚糖是双子叶植物及非禾本科单子叶植物初生细胞壁中含量最丰富的半纤维素多糖，约占初生细胞壁干重的20%以上(Pauly et al., 2013)。木葡聚糖与纤维素、果胶质以及某些伸展蛋白相互交联，形成植物初生细胞壁的主要承载结构(Cosgrove and Jarvis, 2012; Kong et al., 2013)。近年来，许多参与植物木葡聚糖合成的基因陆续被鉴定(Kong et al., 2011; Pauly et al., 2013)。本文主要概述了木葡聚糖的组成、结构及其生物合成的最新研究进展。

1 木葡聚糖的组成与结构

木葡聚糖的主链由β-1,4-D-葡聚糖链(Glc)组成，有典型重复模式的木糖残基(Xyl)连接葡萄糖的O-6位置。这些侧链上的木糖又进一步被不同的单糖、双糖或三糖基所替代。拟南芥(*Arabidopsis thaliana*)中代表性的木葡聚糖亚基的结构如图1A所示(von Schantz et al., 2009)。图1中单个字母分别代表不同的侧链组成。例如，字母G表示无侧链修饰的葡萄糖(Glc)残基，X表示α-D-Xyl*p*-1,6-β- D-Glc*p*基团。Xyl基团可以继续连接β-D-半乳糖基(Gal)，形成β-D-Gal*p*-1,2-α-D-Xyl*p*-1,6-β-D-Glc*p*结构，简称为L。L侧链上的Gal残基可以进一步连接α-L-岩藻糖基(Fuc)，形成α-L-Fuc*p*-1,2-β-D-Gal*p*-1,2-α-D-Xyl*p*-1,6-β-D-Glc*p*,简称为F侧链。在拟南芥中，主要存在的木葡聚糖结构是XLFG、XXXG和XXFG，分别占43%、25%和24% (von Schantz et al., 2009)，还存在少量的XXLG、XLLG和XLXG。同时，我们的研究结果表明，在拟南芥根毛中存在一种木葡聚糖特异结构，即侧链含酸性糖半乳糖醛酸(GalA)的YXXG结构(图1B)，这也更新了传统意义上认为的拟南芥木葡聚糖仅含中性糖侧链的观点(Peña et al., 2012)。植物细胞壁多糖常常会被O-乙酰化，在拟南芥木葡聚糖中，仅有侧链上的半乳糖会被乙酰化，拟南芥叶木葡聚糖侧链含有高达60%的O型乙酰半乳糖(图1A) (Perrin et al., 2003)。而在茄科和禾本科中，木葡聚糖主链上的部分葡萄糖基可以被O-乙酰化(Gibeaut et al., 2005; Jia et

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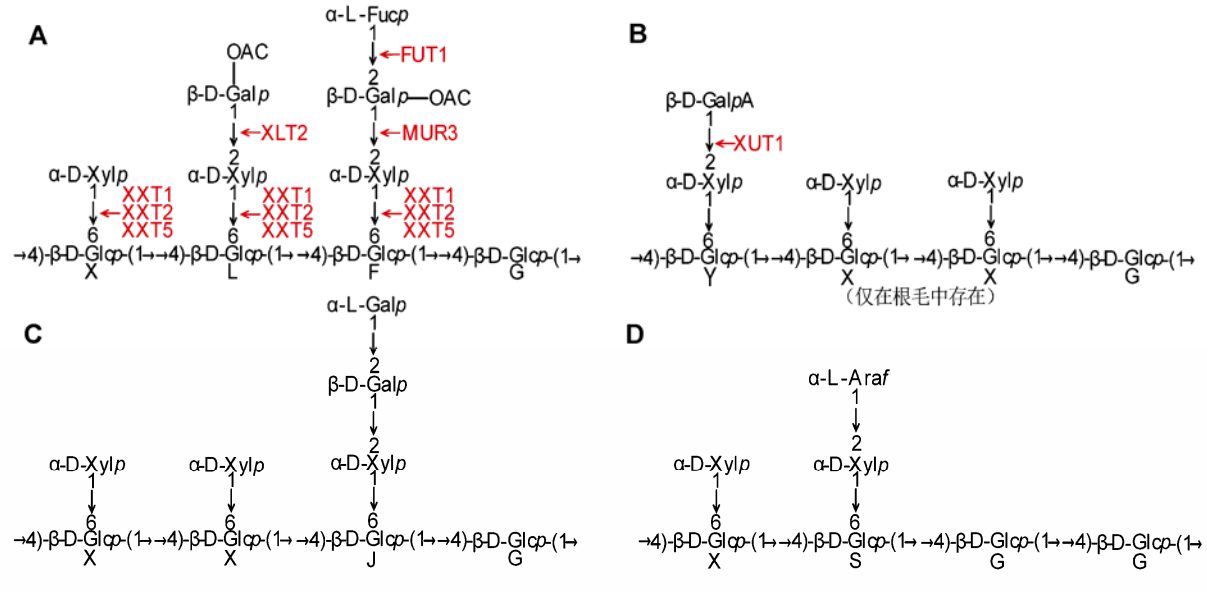

图1 部分陆生植物的代表性木葡聚糖亚基结构及参与其合成的糖基转移酶催化位点

(A) XLFG亚基结构, XXT1、XXT2和XXT5催化木糖基团的转移; **(B)** YXXG亚基结构, XUT1催化半乳糖醛酸基团的转移; **(C)** XXJG亚基结构; **(D)** XSGG亚基结构。Fuc*p*: 岩藻糖; Xyl*p*: 木糖; Gal*p*: 半乳糖; Glc*p*: 葡萄糖; Gal*p*A: 半乳糖醛酸; OAC: 乙酰化基团

Figure 1 Structures of the representative XyGs subunits and glycosyltransferases that involved in xyloglucan biosynthesis

(A) The structure of the XLFG subunit, XXT1, XXT2 and XXT5 are xyloglucan xylosyltransferases that adding xylose residues; **(B)** The structure of the YXXG subunit, XUT1 is a xyloglucan-specific galacturonosyltransferase1; **(C)** The structure of the XXJG subunit; **(D)** The structure of the XSGG subunit. Fuc*p*: Fucose; Xyl*p*: Xylose; Gal*p*: Galactose; Glc*p*: Glucose; Gal*p*A: Galacturonic acid; OAC: Acetylation

al., 2005)。

不同植物中木葡聚糖的葡萄糖主链结构基本相同, 但是在侧链修饰上存在一定的差异, 大部分植物物种都存在XXXG型或XXGG型的木葡聚糖。在希蒙得木(*Simmondsia chinensis*)的木葡聚糖上, L侧链还可以继续连接α-L-半乳糖基(Gal), 形成α-L-Gal*p*-1,2-β-D-Gal*p*-1,2-α-D-Xyl*p*-1,6-β-D-Glc*p* 结构, 称为J (Hantus et al., 1997) (图1C)。在番茄(*Solanum lycopersicum*)木葡聚糖中, Xyl基团还可以连接α-L-阿拉伯糖基(Ara), 形成α-L-Ara*f*-1,2-α-D-Xyl*p*-1,6-β-D-Glc*p*侧链结构, 简称为S (图1D); S侧链上的Ara残基还可以进一步连接β-L-阿拉伯糖基(Ara), 形成β-L-Ara*f*-1,3-α-L-Ara*f*-1,2-α-D-Xyl*p*-1,6-β-D-Glc*p* 侧链, 简称为T (York et al., 1996)。在其它茄科作物如烟草(*Nicotiana tabacum*)中也含有S侧链, 即XSGG结构(Hoffman et al., 2005)。另外, 在苔藓类等维管植物中, Xyl基团可同时在其O-2和O-4位置上连接其它糖基, 如可连接β-D-半乳糖醛酸(GalA)和β-D-半乳糖(Gal), 简称为P; 或连接α-L-阿拉伯糖(Ara)和β-D-半乳糖(Gal), 简称为M; 或连接α-L-阿拉伯糖(Ara)和双糖β-D-Gal*p*-1,6-β-D-Gal*p*, 简称为N (Peña et al., 2008)。不同植物侧链连接的糖基常常会有所差异, 例如番茄中阿拉伯糖基代替了半乳糖基, 并且侧链不含岩藻糖基, 但它们具有类似的功能(Hoffman et al., 2005; Schultink et al., 2013)。这些不同的糖基修饰模式导致了不同植物中木葡聚糖的多样性。

2 木葡聚糖的生物合成

普遍认为木葡聚糖在植物初生细胞壁生长过程中起着重要作用, 因此有关木葡聚糖生物合成酶基因的鉴定已成为重要的研究领域。目前, 拟南芥中大部分参与木葡聚糖及侧链合成的糖基转移酶几乎都已被鉴定, 包括β-1,4-葡萄糖合成酶、α-1,6-木糖基转移酶、

β-1,2半乳糖基转移酶和α-1,2-岩藻糖基转移酶。Cocuron等(2007)研究表明，木葡聚糖的葡聚糖主链是由GT2基因家族的纤维素合成酶类似C基因家族(Cellulose synthase-like C)的3个*CSLC*基因(*CSLC4*、*CSLC5*和*CSLC6*)催化合成(Liepman and Cavalier, 2012)。而CAZy GT34家族的5个基因*XXT1–5* (xyloglucan6-xylosyltran- sferase)编码木糖基转移酶，参与α-d-Xylp-(1→6)-β-d-Glcp的形成，但只有3个*XXT*基因(*XXT1*、*XXT2*和*XXT5*)在木葡聚糖的生物合成中起主要作用(Zabotina et al., 2008, 2012; Vuttipongchaikij et al., 2012)。

5个木葡聚糖木糖基转移酶(*XXT1–5*)基因编码的蛋白参与α-D-Xyl*p*-1,6-β-D-Glc*p*连接的形成(Zabotina et al., 2008, 2012; Vuttipongchaikij et al., 2012)，*XXT1*、*XXT2*和*XXT5*双突变和单突变体表型说明这些基因编码主要的木葡聚糖木糖基转移酶。*XXT2*或*XXT5*的突变导致木葡聚糖合成减少，在它们的单突变体中，木葡聚糖的含量分别下降近30%和50% (Vuttipongchaikij et al., 2012; Zabotina et al., 2012)。与*xxt5*单突变体相比，*xxt1xxt5*和*xxt2xxt5*双突变体中木葡聚糖的含量均略有下降，但在*xx1xxt2*双突变体中，木葡聚糖几乎全部消失，即使用不同的检测方法(如MALDI-TOF和免疫定位等)都检测不到木葡聚糖的存在(Cavalier et al., 2008)，说明XXT1和/或XXT2是木葡聚糖生物合成所必需的。除*xxt5*单突变体和*xxt1xxt2*双突变体根毛形状有异常外，*xxt1xxt2*双突变体地上部分的生长速度比野生型有所减慢，而其它单突变体都没有明显的表型变化，且它们的生长发育也与野生型没有明显的差别(Zabotina et al., 2012)。另有研究表明，水稻(*Oryza sativa*)中*OsXXT1*在维持细胞壁结构和拉伸强度中具有重要作用，该基因突变后水稻细胞壁中木葡聚糖的含量有所下降。水稻*OsXXT1*在拟南芥*xxt1xxt2*双突变体中的过量表达互补了其根毛缺陷、生长缓慢及木葡聚糖的合成下降等表型(Wang et al., 2014)。

木葡聚糖合成酶基本都定位在高尔基体上，很可能通过形成蛋白酶复合体起作用。研究表明，CSLC4酶在XXT1存在下活性有所提高(Cocuron et al., 2007)。Chou等(2012)研究发现XXT1、XXT2和XXT5相互之间可形成复合体行使催化功能，具CSLC4也可能与XXT1、XXT2和XXT5形成复合体共同发挥作用。这3个木葡聚糖转移酶都定位于高尔基体膜上的相同方位，XXT1、XXT2和XXT5蛋白的N端在胞质一侧，而C端位于高尔基体腔内(Søgaard et al., 2012)。CSLC4的催化位点和两端均位于高尔基体膜的胞质一侧(Davis et al., 2010)。是否所有蛋白酶都是多蛋白酶复合体或者在不同情况下有着更动态的结构形式还有待更深入的研究。

拟南芥中有3个参与木葡聚糖侧链合成的基因，即*MUR3* (*MURUS3*)、*XLT2*和*XUT1* (xyloglucan-specific galacturonosyltransferase 1)。进化分析显示这3个基因彼此高度同源，都位于GT47家族的同一个分支上(图2)。它们都转移糖基到木聚糖基的O-2位置，但专一性不同，拟南芥*MUR3*特异地转移半乳糖基到木葡聚糖的第3个木糖基上，分别催化XXXG和XLXG为XXLG和XLLG；而拟南芥*XLT2*特异地转移半乳糖基到木葡聚糖的第2个木糖基上，分别催化XXXG和XXLG为XLXG和XLLG (Madson, 2003; Li et al., 2004; Jensen et al., 2012)。*XUT1*编码的半乳糖醛酸转移酶则催化形成β-D-Gal*p*A-1,2-a-D-Xyl*p*支链，由于*XUT1*仅在根毛中特异表达，因此最早被命名为*ROOT HAIR SPECIFIC8* (*RHS8*)。进一步对*XUT1* T-DNA插入突变体的研究表明，当该基因缺失后，拟南芥根毛的正常伸长受到抑制，表明*XUT1*参与合成的这种酸性木葡聚糖结构Y在根毛细胞的延伸过程中起重要作用(Peña et al., 2012)。

在已研究的木葡聚糖转移酶缺失突变体中，虽然有些突变体有根毛生长等方面的缺陷，但都对植物地上部分的生长影响不大。唯独*MUR3*基因突变的表型比较复杂，并且有多个*MUR3*的突变体被研究和报道(图3)。在对*MUR3*基因突变引起的表型变化研究中，早期获得的*MUR3*基因突变体植株是由EMS诱变获得的点突变，包括*mur3-1*和*mur3-2*，分别在S470L和A290V处发生突变。Madson (2003)在*mur3-1*和*mur3-2*中未检测到*MUR3*参与合成的木葡聚糖F基团的存在，突变体中只存在2种结构，即XXXG和XLXG，但植物能够正常生长(Madson, 2003)。日本Ikuko研究小组在筛选内膜系统紊乱的突变体过程中，发现T-DNA插入突变体*mur3-3*/*kam1-3*植株表型异常，表现为内膜系统紊乱，即内质网系统及部分高尔基体聚合，植株严重矮化，黑暗生长条件下植物的下胚轴不能正常伸长，长度仅为野生型的一半。然而，

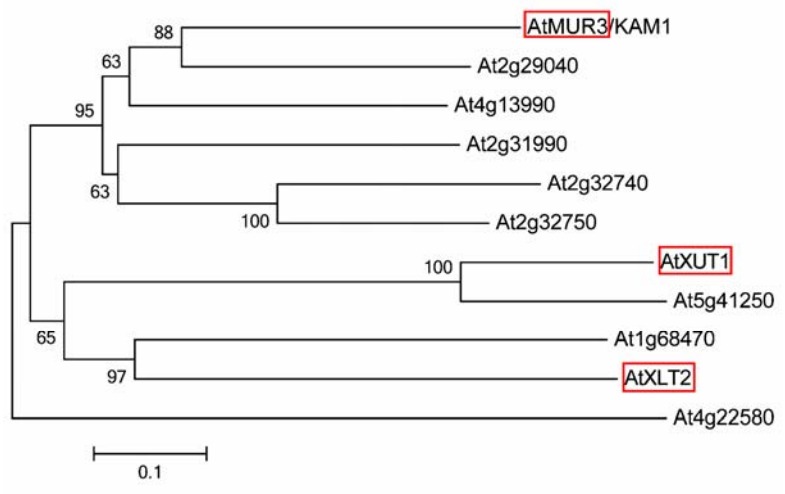

图2 拟南芥*MUR3*同源基因蛋白序列进化树

Figure 2 Phylogenetic tree of *MUR3* homologous genes in *Arabidopsis thaliana*

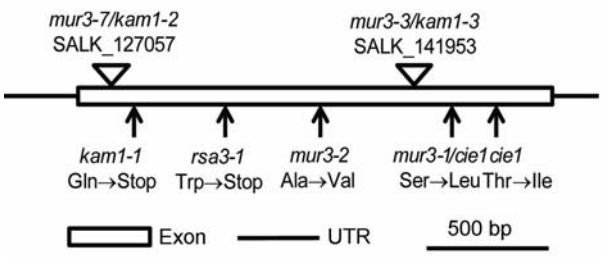

图3 *mur3*突变体突变位点示意图

Figure 3 The schematic diagram of the site of mutation in *MUR3* mutants

*mur3-1*和*mur3-2*的内膜系统仍然正常(Tamura et al., 2005)。蛋白质分析结果显示, *mur3-1*和*mur3-2*是渗漏突变体, 在它们体内仍然有MUR3蛋白的表达, 而*mur3-3*/*kam1*是真正的无义突变。我们对这些突变体木葡聚糖结构的分析也证明了*mur3-1*和*mur3-2*渗漏突变体仍具有微量的MUR3蛋白活性, 突变体除了XXXG和XLXG两种亚基外, 仍含有约占野生型7%–8%的F亚基。而*mur3-3*突变体才是真正的无义突变, 仅含有XXXG和XLXG两种亚基, 无F亚基的存在。我们的研究结果也证实了*mur3-3*中内膜系统紊乱及植株矮化的表型都是由于木葡聚糖结构改变引起的(Kong et al., 2015)。*MUR3*基因的无义突变除引起上述表型外, 对*cie1*/*mur3*突变体的研究显示*MUR3*的缺失还会引起叶柄组织对霜霉菌(*Hyaloperonospora parasitica*)侵染的持续性防御反应(Tedman-Jones et al., 2008); 对*rsa3*/*mur3*突变体的研究显示, RSA3/MUR3及其它细胞壁关联蛋白在抗盐胁迫中起着关键作用, 通过维持肌动蛋白微丝组织来减少由过多的活性氧(ROS)引起的损伤(Li et al., 2013)。但是这些表型是否都与*mur3*突变体中木葡聚糖结构的改变有关还有待进一步研究。

FUT1 (*fucosyltransferase1*)编码岩藻糖基转移酶, 催化岩藻基团转移到半乳糖基或半乳糖醛酸基上, 形成F侧链。*fut1*/*mur2*突变体中拟南芥岩藻糖基化木葡聚糖的完全缺失表明*AtFUT1*是非冗余的(Vanzin et al., 2002; Perrin et al., 2003; Zabotina et al., 2012)。拟南芥中不存在含阿拉伯糖基侧链的木葡聚糖。近来在番茄中鉴定到*MUR3*和*XLT2*的同源基因*XST1*和*XST2*, 采用功能互补的方法, 在半乳糖缺乏的拟南芥*mur3-1 xlt2*突变体中, 过表达*XST1*和*XST2*基因, 结果产生了含阿拉伯糖基侧链的木葡聚糖, 同时互补了*mur3-1xlt2*的生长缺陷, 表明木葡聚糖侧链的糖基在生长、发育及代谢方面的功能具有很高的保守性(Schultink et al., 2013)。

最近发现的*AXY4*和*AXY4L*基因参与了半乳糖的乙酰化, AXY4和AXY4L都属于植物特异TBL蛋白家族(Trichome birefringence-like) (Bischoff et al., 2010; Gille et al., 2011)。有研究显示植物O-乙酰化

在抵抗病原菌侵染方面可能起作用(Manabe et al., 2011)。Pogorelko等(2013)研究显示在拟南芥和二穗短柄草(*Brachypodium distachyon*)的转基因植物体中多糖的乙酰化显著增加了植物对真菌的抵抗作用, 并显示多糖的乙酰化在抵抗真菌侵染中对细胞壁具保护作用。在拟南芥中木葡聚糖是铝主要的结合位点, 木葡聚糖O-乙酰化水平的调节通过影响铝在半纤维素中的结合容量来影响铝的敏感性(Zhu et al., 2014)。

3 木葡聚糖在植物细胞壁网络结构中的作用

近年来, 关于木葡聚糖的结构和生物合成的研究取得了显著进展, 但是人们对于木葡聚糖在初生壁中的功能了解较少。木葡聚糖修饰酶对初生壁机械检测实验的数据揭示了木葡聚糖在壁机械学中的基本结构功能(Park and Cosgrove, 2012b)。木葡聚糖通常融合在细胞壁中, 在壁中木葡聚糖及其寡糖决定了组织张力(Takeda et al., 2002)。植物生长发育包含细胞分裂和细胞形态建成等基本生命过程, 而其中伴随细胞分裂的是细胞壁的不可逆延伸。尽管细胞延伸过程中的内在生物化学过程及生理因子研究还不透彻, 但在所有的模型中都预测细胞的延伸是受纤维素和木葡聚糖等多糖组成的这个网状结构所控制(Cosgrove and Jarvis, 2012)。目前传统的木葡聚糖-纤维素网络结构被广泛接受, 即木葡聚糖将纤维素微纤丝包裹且将它们连接起来, 以形成承载网络结构, 其中果胶作为微纤维间隙的填充基质并增加其延展性(Cosgrove and Jarvis, 2012)。

木葡聚糖结构的改变会影响木葡聚糖自身的特性及其与纤维素等多糖的结合交联, 从而影响细胞壁的张力(Cosgrove, 2005; Park and Cosgrove, 2012b; Wolf et al., 2012)。木葡聚糖在缓冲液中的可溶性及其自我结合能力都与木葡聚糖侧链和结构紧密相关。体外实验证明, 木葡聚糖形成胶的能力受侧链半乳糖基的抑制, 这些半乳糖基侧链显著抑制木葡聚糖的自聚集(self-association); 这种自聚集被认为会影响细胞壁中木葡聚糖与纤维素的结合及相互作用, 从而影响到植物细胞的伸长等发育过程(Shirakawa et al., 1998; Pena et al., 2004; Whitney et al., 2006; Park and Cosgrove, 2012a)。我们最近的研究发现, 通过在*mur3-3*突变体中过表达*XLT2*基因或者引入*XXT2*或*XXT5*突变, 都可以提高木葡聚糖侧链的半乳糖基化, 并且使植株生长表型回复正常。表明半乳糖基化程度的提高对细胞伸长及正常生长具有非常重要的作用(Kong et al., 2015)。

虽然在拟南芥*xxt1xxt2*双突变体中完全检测不到木葡聚糖的存在, 但植物仍能正常生长, 仅仅是生长速度比野生型稍慢些。这不禁使人们怀疑木葡聚糖在维持细胞壁的结构中是否具有重要作用(Cavalier et al., 2008; Zabotina et al., 2012)。进一步分析显示, 果胶和木聚糖在木葡聚糖缺失的植物壁中起着更大的生物力学作用, 木葡聚糖缺失使得植物细胞壁的机械强度降低, 同时不易伸长, 因为他们缺乏α-伸展蛋白的主要靶标(Park and Cosgrove, 2012a)。而且通过^{13}C-NMR检测实验发现, 在完整的拟南芥和绿豆(*Phaseolus radiatus*)细胞壁中包裹在纤维素表面的木葡聚糖少于10%, 这与传统的纤维素-木葡聚糖结构网络模型不一致(Bootten et al., 2004; Dick-Pérez et al., 2011)。因此, 普遍认为的细胞壁中纤维素-木葡聚糖结构网络作为主要承重结构的观点可能需要修正。

4 结语

目前, 有关木葡聚糖结构以及生物合成的研究有了显著进展, 但是有关木葡聚糖的侧链修饰、参与合成的蛋白酶复合体的组成和结构仍需进一步探索。这些研究成果将为揭示植物细胞壁的结构和功能以及通过基因工程技术改变细胞壁多糖成分并应用于工业生产提供理论依据。

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Glycosyltransferase Genes Involved in Xyloglucan Biosynthesis

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Abstract The hemicellulosic polysaccharide xyloglucan (XyG), found in the primary cell walls of most plants, plays important roles in structural organization of plant cell walls and regulation of growth and development. Recent research in structural characterization of XyGs from different plant species revealed the diversification of XyG during plant evolution. This paper reviews progress in studies of glycosyltransferase genes involved in XyG biosynthesis. Most of the XyG-specific glycosyltransferases have been identified, and some of them appear to form a complex for involvement in XyG biosynthesis. We discuss how changes in XyG structure affect plant growth and development.

Key words xyloglucan (XyG), glycosyltransferase, cell wall, biosynthesis

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