· 专题论坛 ·

木葡聚糖及其在植物抗逆过程中的功能研究进展

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摘要 木葡聚糖(XyG)是一种存在于所有陆生植物细胞壁中的基质多糖, 是双子叶植物初生细胞壁中含量(20%–25%, w/w)最丰富的半纤维素成分。作为细胞壁的组分, XyG不仅与植物的生长发育密切相关, 还在植物抵抗各种生物和非生物逆境过程中发挥重要作用。XyG代谢相关基因主要通过改变植物细胞壁的组成以及对细胞壁进行重排进而改变细胞壁的弹性/硬度等特性, 影响植物的抗逆性。XyG及其寡糖也可能作为信号分子, 或与其它信号分子协同作用应对逆境胁迫。该文概述了XyG的结构与类型及参与XyG生物合成与降解的相关基因, 重点阐述XyG相关基因应答生物和非生物胁迫的作用机制。

关键词 半纤维素, 木葡聚糖代谢, 生物胁迫, 非生物胁迫, 抗性

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植物细胞壁是围绕在植物原生质体外的一种细胞结构, 由初生细胞壁和次生细胞壁组成。初生细胞壁位于外层, 是由纤维素、半纤维素和果胶等多糖及结构蛋白组成的一种复杂网络结构。次生细胞壁的结构与组成均与初生细胞壁有所不同, 除了纤维素和半纤维素外, 还含有木质素。植物细胞壁除了作为细胞的主要结构成分, 承担机械支撑、维持和决定细胞形态等功能外, 还在植物的生长发育(陈昆松等, 1999)及抵抗各种生物和非生物逆境过程中发挥重要作用(Houston et al., 2016; Vaahtera et al., 2019), 并影响作物的农艺性状(Hu et al., 2017)。

木葡聚糖(XyG)是双子叶植物初生壁中含量最为丰富的半纤维素成分, 约占细胞壁重量的20%–25%, 而禾本科植物中一般仅为2%–10% (Scheller and Ulvskov, 2010)。前人对XyG的结构、分类及参与XyG代谢过程的相关酶基因进行了详细介绍(李雄彪和张金忠, 1994; Del Bem and Vincentz, 2010; 解敏敏等, 2015; Pauly and Keegstra, 2016)。近年来, 随着分子生物学技术的发展, 包括半纤维素在内的细胞壁成分代谢及其在植物生长发育和抗逆过程中的功能研究取得了令人鼓舞的进展。然而, 国内外尚未见关于XyG在植物抗逆过程中的功能及相关机理研究的综述。本文概述XyG结构和类型及参与XyG代谢的相关基因, 并重点介绍这些基因及其产物在植物抗逆过程中的功能及抗性机理。

1 XyG的结构与分类

XyG是一种由D-吡喃葡萄糖残基以β-1→4键相连构成主链的杂多糖, 葡萄糖残基在O-6位上可被D-吡喃木糖残基所取代(Kiefer et al., 1989)。主链上的葡萄糖残基和侧链上的木糖残基都能以特定连接方式在特定位置被各种糖残基取代(Scheller and Ulvskov, 2010)。根据XyG取代基及其连接方式, 目前已鉴定出24种独特结构(Pauly and Keegstra, 2016)。在标准命名法中分别用不同的单个字母代码来命名和区分不同类型的XyG: 如字母G代表主链上的葡萄糖残基未被任何其它糖/非糖基团取代, X代表葡萄糖残基O-6

位被α-D-吡喃木糖基团取代, L代表木糖残基的O-2位被半乳糖基团取代, F代表半乳糖残基的O-2位被岩藻糖基团取代(Fry et al., 1993)。XyG可能含有O-乙酰基取代基, 发生乙酰化(Kiefer et al., 1989)。乙酰基团既可修饰主链的葡萄糖残基, 也可修饰支链半乳糖残基或其它糖残基。这些结构分别用相应字母加下划

线表示。例如, XLFG型XyG表示每4个葡糖残基中前3个被木糖基化, 其中第2个木糖残基被半乳糖基团取代, 第3个被半乳糖基团取代后又进一步被岩藻糖基团修饰, 且半乳糖残基发生乙酰化(图1)。
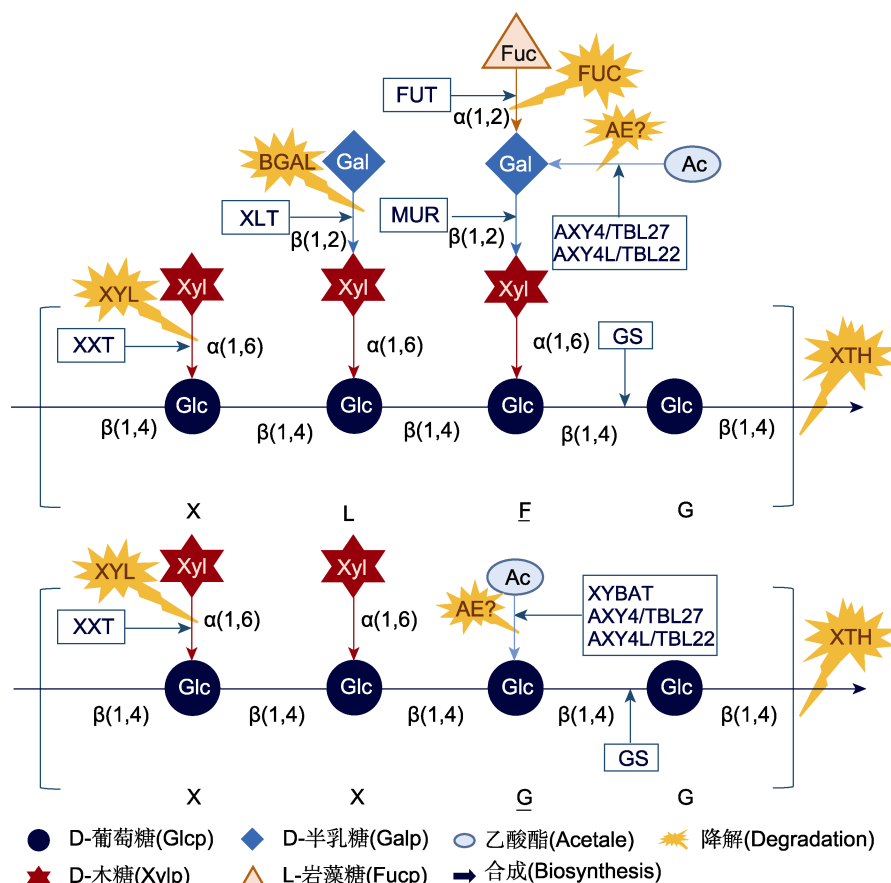
根据寡糖的结构可将XyG分成XXXG和XXGG两种主要类型。双子叶植物的XyG为XXXG型, 而禾本

图1 XLFG型和XXGG型木葡聚糖(XyG)的生物合成与降解示意图
木葡聚糖生物合成酶有FUT (XyG特异岩藻糖基转移酶)、GS (β-1,4-葡聚糖合成酶)、MUR/XLT (XyG特异半乳糖基转移酶)、AXY4L/TBL22和AXY4/TBL27 (XyG特异乙酰基转移酶)、XXT (XyG特异木糖基转移酶)以及XYBAT (XyG葡聚糖骨架乙酰转移酶)。XyG降解酶类有AE (乙酰酯酶)、BGAL (β-半乳糖苷酶)、FUC (α-岩藻糖苷酶)、XTH (XyG内转糖苷酶/水解酶)和XYL (α-木糖苷酶)。图下方为根据XyG命名法获得的相应单字母代码。G: XyG主链葡萄糖残基未连接其它任何糖残基或非糖基团; G: XyG主链葡萄糖残基发生乙酰化; X: XyG主链葡萄糖残基O-6位连接木糖基团; L: X型基团的木糖残基O-2位连接半乳糖基团; F: L型基团的半乳糖残基O-2位连接岩藻糖基团, 且半乳糖残基发生乙酰化。

Figure 1 Schematic of the biosynthesis and degradation of XLFG-type and XXGG-type xyloglucan (XyG)
Enzymes involved in XyG biosynthesis are FUT (XyG: fucosyltransferase), GS (β-1,4-glucan synthase), MUR/XLT (XyG: galactosyltransferase), AXY4L/TBL22 and AXY4/TBL27 (XyG: acetyltransferases), XXT (XyG: xylosyltransferase), and XYBAT (XyG backbone acetyltransferase). Enzymes involved in XyG degradation are AE (acetylesterases), BGAL (β-galactosidase), FUC (α-fucosidase), XTH (XyG endotransglycosylase/hydrolases), and XYL (α-xylosidase). The corresponding one-letter codes from the XyG nomenclature have shown below the pictograms. G: Unsubstituted glucosyl residue of the backbone glucose of XyG; G: Backbone glucose of XyG carries an O-acetyl substituent; X: Xylosyl residue is attached to the glucan backbone of XyG at O-6; L: Galactosyl residue is attached to the xylosyl residue of X group at O-2; F: Fucosyl residue is attached to the galactosyl residue of L group at O-2, and galactosyl residue carries an O-acetyl substituent.

科和茄科植物的XyG为XXGG型。与XXXG型XyG相比, XXGG型XyG的木糖基化程度相对较低, 通常不发生岩藻糖基化(Pauly and Keegstra, 2016)。植物的XyG类型不仅具有物种特异性, 还因不同组织器官及发育阶段而异(Liu et al., 2015)。

　　XyG在结构和生物合成方面都是研究得最清楚的植物细胞壁多糖之一。许多XyG生物合成相关酶已被鉴定。与大多数复杂碳水化合物相同, XyG也在高尔基体中合成。

2　XyG代谢

2.1　XyG的生物合成

2.1.1　主链生物合成
XyG主链骨架的生物合成由XyG特异葡聚糖合成酶, 即β-1,4-葡聚糖合成酶(β-1,4-glucan synthase, GS)负责(Cocuron et al., 2007), 该酶由类纤维素合成酶基因4 (cellulose synthase-like C4, CSLC4)编码, 后者属于碳水化合物活性酶(carbohydrate-active enzymes, CAZy)糖基转移酶2 (glycosyltransferase 2, GT2)家族。

2.1.2　骨架木糖化
所有类型的XyG葡聚糖主链都含有木糖基取代基。XyG特异木糖基转移酶(XyG: xylosyltransferase, XXT)负责将UDP-木糖添加到主链葡萄糖残基O-6位上(Faik et al., 2002)。目前, 已在拟南芥(*Arabidopsis thaliana*)中发现多个GT34基因家族成员编码XXTs (Cavalier et al., 2008)。此外, 在水稻(*Oryza sativa*)、番茄(*Solanum lycopersicum*)和旱金莲(*Tropaeolum majus*)的种子(Wang et al., 2014; Mansoori et al., 2015)中也发现GT34家族的XXT成员。

2.1.3　半乳糖苷化和其它类型的糖基化
大多数XyG木糖残基在GT47家族的一些酶作用下被其它糖基进一步取代, 其中最常见的是D-半乳糖。UDP-半乳糖在β-半乳糖基转移酶(β-galactosyltransferases, β-GAL)的作用下掺入XyG。例如, MUR3专一性负责XXXG第3位木糖残基的半乳糖化, 将XXXG变成XXLG (Kong et al., 2015; Xu et al., 2018), 而XLT2负责XXXG第2位木糖残基的半乳糖

化, 将XXXG变成XLXG (Jensen et al., 2012)。此外, 木糖残基的O-2位也可能被其它糖残基修饰。近年来, 相继鉴定到一些负责糖基转移的酶, 如拟南芥XyG特异半乳糖醛酸基转移酶1 (XyG: galacturonosyltransferase 1, XUT1) (Peña et al., 2012)和番茄XyG特异阿拉伯呋喃糖基转移酶 (SlXST1和SlXST2) (Schultink et al., 2013)。

2.1.4　岩藻糖基化
XXLG型XyG的半乳糖残基通常会被岩藻糖基进一步取代, 形成XXFG。XyG特异岩藻糖基转移酶(XyG: fucosyltransferases 1, FUT1)负责将GDP-岩藻糖添加到XXLG或XLLG的L上(Vanzin et al., 2002)。FUT1属于CAZy家族GT37, 是拟南芥基因组编码的唯一具有FUT活性的酶(Liang et al., 2013)。

2.1.5　骨架及侧链O-乙酰化
XyG的乙酰化主要发生在XXGG型XyG主链的葡萄糖残基及XXXG型XyG侧链的半乳糖残基上(Gille et al., 2011)。植物共有3个蛋白家族参与XyG的乙酰化, 即TBL (trichome birefringence-like)、AXY9 (ALTERED XYLOGLUCAN 9)和RWA (reduced wall acetylation) (Pawar et al., 2017; Pauly and Ramírez, 2018)。植物RWA被认为是乙酰基供体转运蛋白, AXY9蛋白起产生乙酰化中间体的作用(Schultink et al., 2015), 而TBL蛋白是多糖特异性的乙酰基转移酶(Gille et al., 2011; Manabe et al., 2011)。例如, 由TBL基因家族成员编码的 AXY4/TBL27 及 AXY4-like (AXY4L/ TBL22)特异性地乙酰化种子中的XyG (Gille et al., 2011)。在二穗短柄草(*Brachypodium distachyon*)中也鉴定出1种XyG骨架乙酰转移酶(XyG glucan backbone acetyltransferase, XYBAT) (Liu et al., 2016)。

2.1.6　质外沉积与成熟
XyG在高尔基体中合成后, 被囊泡运输到细胞壁。迄今为止, 人们对XyG掺入现有细胞壁的过程知之甚少。已有研究表明, XyG可以通过非酶自组装的方式与现有纤维素微纤维网络结合 (Hayashi et al., 1987)。XyG一旦沉积在壁中, 其结构保持动态, 原因是相关酶的靶标结构域会经历结构成熟和由质外体植物酶降解的周转(Franková and Fry, 2013)。

2.2 XyG的降解

2.2.1 主链降解与重排

植物XyG内转糖苷酶/水解酶(endotransglycosylase/hydrolases, XTHs)基因属于CAZy糖基水解酶16 (glycoside hydrolase 16, GH16)家族基因, 编码的蛋白可能具有2种不同的催化活性, 对XyG的影响不同。其中XyG特异内水解酶(XyG: endohydrolase, XEH)活性在形式上是XyG特异的内切葡聚糖酶(xyloglucan-specific endo-1,4-glucanases, XEGs), 降解XyG主链骨架(Hayashi et al., 1984); 而XyG特异内转糖基酶(XyG: endotransglycosylase, XET)活性则负责XyG网络重塑, 即XyG被降解后再重新连接到其它XyG链上, 从而改变XyG的长度(Franková and Fry, 2013)。XTHs编码的某些蛋白仅具有XEH活性, 从还原端将XyG水解为XyG寡糖(XyG oligosaccharides, XGO) (Shinohara et al., 2017)。此外, Sampedro等(2017)证明, 拟南芥有2个来自GH3家族的β-葡萄糖苷酶(β-GLU)能从非还原端裂解XyG主链骨架未被取代的Glc基团。

2.2.2 支链降解

参与XyG支链降解的糖苷酶主要包括α-木糖苷酶(如AtXYL1/AXY3) (Shigeyama et al., 2016)、β-半乳糖苷酶(如AtBGAL10)和α-岩藻糖苷酶(如AtFUC95A和AXY8) (Günl et al., 2011; Sampedro et al., 2012), 分别降解相应的糖残基。

3 XyG在植物抗逆中的功能

植物在整个生命周期中经常遭受各种生物和非生物逆境胁迫。相应地, 植物采取多种防御策略来应对逆境, 包括改变细胞壁结构与组成、表达包括与木葡聚糖代谢相关基因在内的抗逆基因(Xie et al., 2011; Ma et al., 2013; Yan et al., 2015; Wu et al., 2017; Bacete et al., 2018; Niu et al., 2018), 还可能通过启动抗性相关信号来应对逆境(Engelsdorf et al., 2018)。

3.1 非生物胁迫

3.1.1 低温胁迫

早在20多年前, 拟南芥XyG特异糖基化基因TCH4 (即AtXTH22)就已被证明非常耐(12–18)°C低温(Pu-

rugganan et al., 1997)。近年来, 大量组学研究结果表明多种植物的XyG代谢相关基因(如XTHs)响应低温胁迫, 并可能与植物的抗寒性密切相关(刘静, 2018; Takahashi et al., 2019)。推测低温下植物XTHs等基因表达量的改变影响XyG之间的共价交联以及XyG与纤维素微丝之间的联系, 从而改变细胞壁特性, 增强其抗冻性(Rao and Dixon, 2017)。此外, 研究发现sfr2基因编码的β-GLU是植物抗冻性必不可少的组成型表达蛋白(Thorlby et al., 2004)。鹰嘴豆(Cicer arietinum)在冷驯化过程中, 脱水蛋白和β-glu的表达量以及H_2O_2和丙二醛的含量显著升高, 耐冷能力增强(Khazaei et al., 2015)。

3.1.2 旱涝胁迫

研究表明, 植物XyG降解相关基因参与抗旱/涝过程。Kumar等(2019)发现在聚乙二醇模拟的干旱条件下, 2个耐旱类型鹰嘴豆中的XTH23基因均下调表达, 推测植物通过维持足够的木葡聚糖和纤维素含量来确保保卫细胞对气孔的控制(Rui and Anderson, 2016), 从而抵御逆境。此外, 在涝害条件下10个大豆(Glycine max) GmXTHs的表达量发生显著变化, 过表达拟南芥AtXTH31的大豆耐涝性增强(Song et al., 2018)。

3.1.3 盐胁迫

植物XyG代谢相关基因与其抗盐性的研究多见于XTH基因家族。例如, 转辣椒(Capsicum annuum) CaXTH3的拟南芥耐盐性增强, 推测其通过调节气孔关闭来防止过度失水, 从而提高耐盐性(Cho et al., 2006)。与此类似, 在长期的盐胁迫下, 耐盐植物胡杨(Populus euphratica)叶子发育成肉质叶从而抵御逆境。过表达胡杨PeXTH的烟草(Nicotiana tabacum)耐盐性增强, 叶片肉质化但不膨胀(Han et al., 2013)。相反, 在盐胁迫下, 拟南芥AtXTH30表达量大幅上升, 敲除该基因后其耐盐性增强, 而过表达该基因增加其盐敏感性。盐胁迫引起拟南芥xth30突变体中XGO含量的上升较野生型少, 根部Na^+积累量和H_2O_2含量减少。上述结果表明, XTH30通过调控XyG的侧链合成、改变XLFG的含量和纤维素合成以及皮层维管稳定性负调控植物的耐盐性(Yan et al., 2019)。导致相反结果的可能原因是XTHs的双重酶活

性(Rose et al., 2002)。

3.1.4　铝胁迫

研究表明, 铝毒是由于Al^{3+}与植物的细胞壁结合从而影响根系的伸长, 而XyG被认为是Al主要的结合位点(Zhu et al., 2012)。拟南芥XyG的乙酰基转移酶基因*TBL27*缺失的突变体比野生型植株对Al更敏感, 细胞壁半纤维素中Al积累更多。此外, Al处理可显著降低XyG的*O*-乙酰化水平。研究表明, XyG通过调节*O*-乙酰化水平影响半纤维素中的Al结合能力, 进而影响拟南芥对Al的敏感性(Zhu et al., 2017)。

3.1.5　多重逆境

近年来, 越来越多的研究表明, XyG代谢相关基因能够响应多种逆境或增强植物对多种逆境的抗性。例如, *PeXTH*基因同时具有提高胡杨耐盐及重金属的功能(Han et al., 2013, 2014)。水稻*OsXET9*能够被冷、热和干旱等多种逆境高度诱导表达, 是一个逆境响应标记基因(Dong et al., 2011)。类似地, 辣椒*CaXTH3*也受多种非生物逆境诱导表达, 过表达该基因的拟南芥和番茄表现出对盐和干旱胁迫的耐受性增强(Cho et al., 2006; Choi et al., 2011)。*NtEXGT*是烟草中1个编码XTHs的基因, 该基因不仅受生长素等多种植物生长调节剂诱导, 还在盐、干旱、冷和重金属(如镉)胁迫下上调表达, 但是在低温(0°C)和较高浓度(100 μmol·L^{-1}) ABA处理后表达量却下降, 这表明*NtE-XGT*受ABA调控, 在逆境条件下依赖于ABA信号途径。过表达*NtEXGT*烟草植株具有更强的耐寒性和耐热性(Kuluev et al., 2017)。Iurlaro等(2016)系统研究了硬粒小麦(*Triticum durum*) *XTH*基因家族对脱水和热胁迫的响应, 发现两种逆境对*TdXTHs*表达量的影响因品种的抗逆能力、器官及根的不同区域而异, 脱水时根尖*TdXTHs*表达量及XEG酶活性升高而热处理的效果相反。烟草中的12个*NtXTHs*对盐、碱和冷、热胁迫响应不同(Wang et al., 2018)。上述结果表明, XyG代谢相关基因对逆境的响应可能具有物种、器官及逆境特异性。

3.2　生物胁迫

3.2.1　病害

降解植物XyG是病原菌成功侵染寄主的必要条件

(Choi et al., 2013)。在侵染过程中, 病原菌通过产生各种酶来降解植物细胞壁XyG (DeBoy et al., 2008)。为了应对病原菌的侵染, 植物采取多种措施进行防卫。例如, 表达相应的抑制蛋白抵御病原菌, 植物XyG的降解产物也能诱导抗病性。

3.2.1.1　XyG降解相关基因

质外体组织是植物抵御病原菌的关键战场。病原菌分泌质外体XEGs降解植物XyG的主链, 相应地, 植物通过诱导表达其抑制蛋白(xyloglucan-specific endo-1,4-glucanase inhibitor protein, XEGIP)的方式进行抵抗。这在苹果(*Malus x domestica*)和大豆等多种植物中得到证实。植物XEGIP通过与病原菌XEG结合从而使其失活, 进而抑制病原菌对植物细胞壁XyG的降解(Bai et al., 2015; Ma et al., 2017)。此外, XEGIP还可通过过敏性坏死(Jones et al., 2006)和诱导抗性(Choi et al., 2013)等途径增强植物的抗性。另外, 植物XEGs也可能与感病性有关(Karczmarek et al., 2008)。Li等(2019)发现在接种柑橘溃疡病病原菌(*Xanthomonas citri* subsp. *citri*, Xcc)后, *CsXTH04/21*在感病品种中上调表达而抗病品种正好相反, 并受外源水杨酸和茉莉酸甲酯诱导, 且过表达*CsXTH-04*的甜橙(*Citrus sinensis*)表现感病, 沉默该基因则使甜橙抗病, 表明该基因可能与柑橘对溃疡病的感病性相关。相反, Sharmin等(2012)发现在遭受茎/芽腐病病原菌(*Macrophomina phaseolina*)侵染后, 抗病黄麻(*Corchorus capsularis*)野生种*CtXTH1*基因上调表达而感病栽培种*CoXTH1*下调表达, 表明黄麻*XTHs*表达量可能与其抗病性呈正相关。类似地, *Ma-XTH23*基因在接种香蕉枯萎病菌(*Fusarium oxysporum* f. sp. *cubense*)前后在抗病品种中的表达量均显著高于感病品种, 表明该基因可能与香蕉对枯萎病的抗性有关(Niu et al., 2018)。马铃薯(*Solanum tuberosum*) XTH-Xet5在诱导抗病品种对马铃薯Y病毒(PVY)的过敏性坏死反应过程中起联接不同多糖的作用, 可通过增强细胞壁强度来提高其抗病性(Otulak-Kozieł et al., 2018)。

3.2.1.2　XyG乙酰化

有研究表明, XyG乙酰化程度与植物的抗逆性相关。例如, 将真菌的鼠李糖半乳糖醛酸乙酰酯酶转入拟南

芥后, 植株XyG的乙酰化程度显著降低, 转基因植株对灰葡萄孢菌(*Botrytis cinerea*)等真菌的抗性增强, 但不能增强对病原细菌的抗性(Pogorelko et al., 2013)。拟南芥细胞壁乙酰化程度降低20%的突变体*rwa2*对灰葡萄孢菌的抗性较野生型高(Manabe et al., 2011)。与野生型相比, *rwa2*抗氧化系统酶基因等与植物抗性相关的基因上调表达, 表明降低细胞壁乙酰化程度会导致拟南芥广泛的抗性反应(Nafifisi et al., 2015)。多糖的乙酰化修饰可以保护其不受特定的糖基水解酶水解, 且可与控制细胞延展性的细胞壁成分交联, 从而进一步阻止病原菌的入侵(Gille and Pauly, 2012)。

3.2.1.3　XyG及其降解产物

早期人们发现, XyG降解产生的寡糖片段XGO可抑制烟草坏死病毒, 具有诱导抗性的功能(Subíková et al., 1994)。后来发现用XGO处理烟草BY-2细胞培养物可上调与抗逆相关基因的表达(González-Pérez et al., 2014)。最近, XyG又被证明具有启动葡萄(*Vitis vinifera*)和拟南芥等植物免疫反应的功能(Claverie et al., 2018), 及诱导葡萄细胞悬浮系产生白藜芦醇和拟南芥积累胼胝质等抗性物质。此外, 研究发现纯化的CaXEGIP1蛋白能显著抑制病原菌XEG酶的水解活性, 从而减轻病害(Choi et al., 2013)。Niu等(2018)发现抗枯萎病香蕉品种根毛中识别XXXG型XyG的LM15抗体荧光信号强于感病品种, 且病原菌侵染仅导致抗病品种信号增强, 表明LM15抗原可能与香蕉对枯萎病的抗性呈正相关。

3.2.2　虫害

目前, XyG代谢与植物抗虫性的关系研究较少。芹菜(*Apium graveolens*) *AgXTH1*在桃蚜(*Myzus persicae*)侵染后系统性地在韧皮部中上调表达, 拟南芥中该基因的同源基因*AtXTH33*的突变体比野生型更吸引蚜虫, 表明*AtXTH33*调控拟南芥对蚜虫的抗性(Divol et al., 2007)。Mageroy等(2015)发现, 白云杉(*Picea glauca*) *Pgβglu-1*在抗性品种中的表达量比感病品种高约1 000倍。*Pgβglu-1*表达量、PgβGLU-1酶活性及苯乙酮的含量可作为云杉对食心虫的抗性标记, 而PgβGLU-1酶催化底物后释放的苷元物质对云杉食心虫具有抗性(Delvas et al., 2011)。

4　总结与展望

XyG是双子叶植物初生细胞壁中重要的半纤维素, 根据寡糖的结构可将XyG分成XXXG和XXGG两种主要类型。参与XyG生物合成的主要酶包括GS、XXT、β-GAL、FUT、XUT和TBL, 参与XyG降解的主要酶有XTH、β-GLU、α-木糖苷酶、β-半乳糖苷酶和α-岩藻糖苷酶。虽然近年来有关木葡聚糖代谢方面的研究进展显著, 但有关木葡聚糖的侧链修饰以及参与合成的酶蛋白复合体的组成等仍需进一步探讨。XyG代谢相关基因在植物抵抗各种逆境过程中具有重要作用, 尤其是XyG降解相关基因。关于XyG在植物抗逆过程中的作用机理, 目前普遍认为XyG代谢相关基因通过改变细胞壁的组成及XyG之间或XyG与其它细胞壁成分之间的交联从而改变细胞壁的弹性或硬度, 进而影响植物对非生物胁迫的抗性。也有证据表明, XyG和XGO可作为植物信号分子激发植物的防卫反应, 还可能与其它信号分子协同作用, 共同应对逆境胁迫。随着遗传学、生物化学和分子生物学等多种技术的发展及先进仪器设备的应用, 人们将最终解析XyG在植物抗逆过程中的功能及作用机理。

参考文献

陈昆松, 李方, 张上隆 (1999). 猕猴桃果实成熟进程中木葡聚糖内糖基转移酶mRNA水平的变化. 植物学报 **41**, 1231–1234.

李雄彪, 张金忠 (1994). 半纤维素的化学结构和生理功能. 植物学通报 **11**, 27–33.

刘静 (2018). 低温胁迫对香蕉(*Musa* spp.)细胞壁半纤维素代谢的影响. 硕士论文. 广州: 华南农业大学. pp. 1–47.

解敏敏, 晁江涛, 孔英珍 (2015). 参与木葡聚糖合成的糖基转移酶基因研究进展. 植物学报 **50**, 644–651.

Bacete L, Mélida H, Miedes E, Molina A (2018). Plant cell wall-mediated immunity: cell wall changes trigger disease resistance responses. *Plant J* **93**, 614–636.

Bai S, Dong CH, Zhu J, Zhang YG, Dai HY (2015). Identification of a xyloglucan-specific endo-(1-4)-beta-D-glucanase inhibitor protein from apple (*Malus × domestica* Borkh.) as a potential defense gene against *Botryosphaeria dothidea*. *Plant Sci* **231**, 11–19.

Cavalier DM, Lerouxel O, Neumetzler L, Yamauchi K, Reinecke A, Freshour G, Zabotina OA, Hahn MG, Burgert I, Pauly M, Raikhel NV, Keegstra K (2008).

Disrupting two *Arabidopsis thaliana* xylosyltransferase genes results in plants deficient in xyloglucan, a major primary cell wall component. *Plant Cell* **20**, 1519–1537.

Cho SK, Kim JE, Park JA, Eom TJ, Kim WT (2006). Constitutive expression of abiotic stress-inducible hot pepper *CaXTH3*, which encodes a xyloglucan endotransglucosylase/hydrolase homolog, improves drought and salt tolerance in transgenic *Arabidopsis* plants. *FEBS Lett* **580**, 3136–3144.

Choi HW, Kim NH, Lee YK, Hwang BK (2013). The pepper extracellular xyloglucan-specific endo-β-1,4-glucanase inhibitor protein gene, *CaXEGIP1*, is required for plant cell death and defense responses. *Plant Physiol* **161**, 384–396.

Choi JY, Seo YS, Kim SJ, Kim WT, Shin JS (2011). Constitutive expression of CaXTH3, a hot pepper xyloglucan endotransglucosylase/hydrolase, enhanced tolerance to salt and drought stresses without phenotypic defects in tomato plants (*Solanum lycopersicum* cv. Dotaerang). *Plant Cell Rep* **30**, 867–877.

Claverie J, Balacey S, Lemaître-Guillier C, Brulé D, Chiltz A, Granet L, Noirot E, Daire X, Darblade B, Héloir M, Poinssot B (2018). The cell wall-derived xyloglucan is a new DAMP triggering plant immunity in *Vitis vinifera* and *Arabidopsis thaliana*. *Front Plant Sci* **9**, 1725.

Cocuron JC, Lerouxel O, Drakakaki G, Alonso AP, Liepman AH, Keegstra K, Raikhel N, Wilkerson CG (2007). A gene from the cellulose synthase-like C family encodes a β-1,4-glucan synthase. *Proc Natl Acad Sci USA* **104**, 8550–8555.

DeBoy RT, Mongodin EF, Fouts DE, Tailford LE, Khouri H, Emerson JB, Mohamoud Y, Watkins K, Henrissat B, Gilbert HJ, Nelson KE (2008). Insights into plant cell wall degradation from the genome sequence of the soil bacterium *Cellvibrio japonicus*. *J Bacteriol* **190**, 5455–5463.

Del Bem LEV, Vincentz MG (2010). Evolution of xyloglucan-related genes in green plants. *BMC Evol Biol* **10**, 341.

Delvas N, Bauce E, Labbé C, Ollevier T, Bélanger R (2011). Phenolic compounds that confer resistance to spruce budworm. *Entomol Exp Appl* **141**, 35–44.

Divol F, Vilaine F, Thibivilliers S, Kusiak C, Sauge MH, Dinant S (2007). Involvement of the xyloglucan endotransglycosylase/hydrolases encoded by celery *XTH1* and *Arabidopsis XTH33* in the phloem response to aphids. *Plant Cell Environ* **30**, 187–201.

Dong JL, Jiang YY, Chen RJ, Xu ZJ, Gao XL (2011). Isolation of a novel xyloglucan endotransglucosylase (*Os-XET9*) gene from rice and analysis of the response of this gene to abiotic stresses. *Afr J Biotechnol* **10**, 17424–17434.

Engelsdorf T, Gigli-Bisceglia N, Veerabagu M, McKenna JF, Vaahtera L, Augstein F, Van der Dose D, Zipfel C, Hamann T (2018). The plant cell wall integrity maintenance and immune signaling systems cooperate to control stress responses in *Arabidopsis thaliana*. *Sci Signal* **11**, eaao3070.

Faik A, Price NJ, Raikhel NV, Keegstra K (2002). An *Arabidopsis* gene encoding an α-xylosyltransferase involved in xyloglucan biosynthesis. *Proc Natl Acad Sci USA* **99**, 7797–7802.

Franková L, Fry SC (2013). Biochemistry and physiological roles of enzymes that 'cut and paste' plant cell-wall polysaccharides. *J Exp Bot* **64**, 3519–3550.

Fry SC, York WS, Albersheim P, Darvill A, Hayashi T, Joseleau JP, Kato Y, Lorences EP, Maclachlan GA, McNeil M, Mort AJ, Reid JSG, Seitz HU, Selvendran RR, Voragen AGJ, White AR (1993). An unambiguous nomenclature for xyloglucan-derived oligosaccharides. *Physiol Plant* **89**, 1–3.

Gille S, de Souza A, Xiong GY, Benz M, Cheng K, Schultink A, Reca IB, Pauly M (2011). *O*-acetylation of *Arabidopsis* hemicellulose xyloglucan requires AXY4 or AXY-4L, proteins with a TBL and DUF231 domain. *Plant Cell* **23**, 4041–4053.

Gille S, Pauly M (2012). *O*-acetylation of plant cell wall polysaccharides. *Front Plant Sci* **3**, 12.

González-Pérez L, Perrotta L, Acosta A, Orellana E, Spadafora N, Bruno L, Bitonti BM, Albani D, Cabrera JC, Francis D, Rogers HJ (2014). In tobacco BY-2 cells xyloglucan oligosaccharides alter the expression of genes involved in cell wall metabolism, signaling, stress responses, cell division and transcriptional control. *Mol Biol Rep* **41**, 6803–6816.

Günl M, Neumetzler L, Kraemer F, de Souza A, Schultink A, Pena M, York WS, Pauly M (2011). AXY8 encodes an α-fucosidase, underscoring the importance of apoplastic metabolism on the fine structure of *Arabidopsis* cell wall polysaccharides. *Plant Cell* **23**, 4025–4040.

Han YS, Sa G, Sun J, Shen ZD, Zhao R, Ding MQ, Deng SR, Lu YJ, Zhang YH, Shen X, Chen SL (2014). Overexpression of *Populus euphratica* xyloglucan endotransglucosylase/hydrolase gene confers enhanced cadmium tolerance by the restriction of root cadmium uptake in transgenic tobacco. *Environ Exp Bot* **100**, 74–83.

Han YS, Wang W, Sun J, Ding MQ, Zhao R, Deng SR, Wang FF, Hu Y, Wang Y, Lu YJ, Du LP, Hu ZM, Diekmann H, Shen X, Polle A, Chen SL (2013). *Populus euphratica* XTH overexpression enhances salinity tolerance by the development of leaf succulence in transgenic tobacco plants. *J Exp Bot* **64**, 4225–4238.

Hayashi T, Marsden MPF, Delmer DP (1987). Pea xyloglucan and cellulose: VI. Xyloglucan-cellulose interactions *in vitro* and *in vivo*. *Plant Physiol* **83**, 384–389.

Hayashi T, Wong YS, Maclachlan G (1984). Pea xyloglucan and cellulose: II. Hydrolysis by pea endo-1,4-β-glucanases. *Plant Physiol* **75**, 605–610.

Houston K, Tucker MR, Chowdhury J, Shirley N, Little A (2016). The plant cell wall: a complex and dynamic structure as revealed by the responses of genes under stress conditions. *Front Plant Sci* **7**, 984.

Hu KM, Cao JB, Zhang J, Xia F, Ke YG, Zhang HT, Xie WY, Liu HB, Cui Y, Cao YL, Sun XL, Xiao JH, Li XH, Zhang QL, Wang SP (2017). Improvement of multiple agronomic traits by a disease resistance gene via cell wall reinforcement. *Nat Plants* **3**, 17009.

Iurlaro A, De Caroli M, Sabella E, De Pascali M, Rampino P, De Bellis L, Perrotta C, Dalessandro G, Piro G, Fry SC, Lenucci MS (2016). Drought and heat differentially affect XTH expression and XET activity and action in 3-day-old seedlings of durum wheat cultivars with different stress susceptibility. *Front Plant Sci* **7**, 1686.

Jensen JK, Schultink A, Keegstra K, Wilkerson CG, Pauly M (2012). RNA-Seq analysis of developing nasturtium seeds (*Tropaeolum majus*): identification and characterization of an additional galactosyltransferase involved in xyloglucan biosynthesis. *Mol Plant* **5**, 984–992.

Jones RW, Ospina-Giraldo M, Deahl K (2006). Gene silencing indicates a role for potato endoglucanase inhibitor protein in germplasm resistance to late blight. *Am J Potato Res* **83**, 41–46.

Karczmarek A, Fudali S, Lichocka M, Sobczak M, Kurek W, Janakowski S, Roosien J, Golinowski W, Bakker J, Goverse A, Helder J (2008). Expression of two functionally distinct plant endo-β-1,4-glucanases is essential for the compatible interaction between potato cyst nematode and its hosts. *Mol Plant Microbe Interact* **21**, 791–798.

Khazaei M, Maali-Amiri R, Talei AR, Ramezanpour S (2015). Differential transcript accumulation of *dhydrin* and *beta-glucosidase* genes to cold-induced oxidative stress in chickpea. *J Agric Sci Technol* **17**, 725–734.

Kiefer LL, York WS, Darvill AG, Albersheim P (1989).
Xyloglucan isolated from suspension-cultured sycamore cell walls is *O*-acetylated. *Phytochemistry* **28**, 2105–2107.

Kong YZ, Peña MJ, Renna L, Avci U, Pattathil S, Tuomivaara ST, Li XM, Reiter WD, Brandizzi F, Hahn MG, Darvill AG, York WS, O'Neill MA (2015). Galactose-depleted xyloglucan is dysfunctional and leads to dwarfism in *Arabidopsis*. *Plant Physiol* **167**, 1296–1306.

Kuluev B, Mikhaylova E, Berezhneva Z, Nikonorov Y, Postrigan B, Kudoyarova G, Chemeris A (2017). Expression profiles and hormonal regulation of tobacco *NtEXGT* gene and its involvement in abiotic stress response. *Plant Physiol Biochem* **111**, 203–215.

Kumar M, Chauhan AS, Kumar M, Yusuf MA, Sanyal I, Chauhan PS (2019). Transcriptome sequencing of chickpea (*Cicer arietinum* L.) genotypes for identification of drought-responsive genes under drought stress condition. *Plant Mol Biol Rep* **37**, 186–203.

Li Q, Hu AH, Dou WF, Qi JJ, Long Q, Zou XP, Lei TG, Yao LX, He YR, Chen SC (2019). Systematic analysis and functional validation of citrus *XTH* genes reveal the role of Csxth04 in citrus bacterial canker resistance and tolerance. *Front Plant Sci* **10**, 1109.

Liang Y, Basu D, Pattathil S, Xu WL, Venetos A, Martin SL, Faik A, Hahn MG, Showalter AM (2013). Biochemical and physiological characterization of *fut4* and *fut6* mutants defective in arabinogalactan-protein fucosylation in *Arabidopsis*. *J Exp Bot* **64**, 5537–5551.

Liu LF, Hsia MM, Dama M, Vogel J, Pauly M (2016). A xyloglucan backbone 6-*O*-acetyltransferase from *Brachypodium distachyon* modulates xyloglucan xylosylation. *Mol Plant* **9**, 615–617.

Liu LF, Paulitz J, Pauly M (2015). The presence of fucogalactoxyloglucan and its synthesis in rice indicates conserved functional importance in plants. *Plant Physiol* **168**, 549–560.

Ma L, Jiang S, Lin GM, Cai JH, Ye XX, Chen HB, Li MH, Li HP, Takáč T, Šamaj J, Xu CX (2013). Wound-induced pectin methylesterases enhance banana (*Musa* spp. AAA) susceptibility to *Fusarium oxysporum* f. sp. *cubense*. *J Exp Bot* **64**, 2219–2229.

Ma ZC, Zhu L, Song TQ, Wang Y, Zhang Q, Xia YQ, Qiu M, Lin YC, Li HY, Kong L, Fang YF, Ye WW, Wang Y, Dong SM, Zheng XB, Tyler BM, Wang YC (2017). A paralogous decoy protects *Phytophthora sojae* apoplastic effector *PsXEG1* from a host inhibitor. *Science* **355**, 710–714.

Mageroy MH, Parent G, Germanos G, Giguère I, Delvas

N, Maaroufi H, Bauce É, Bohlmann J, Mackay JJ (2015). Expression of the β-glucosidase gene *Pgβglu-1* underpins natural resistance of white spruce against spruce budworm. *Plant J* **81**, 68–80.

Manabe Y, Nafisi M, Verhertbruggen Y, Orfila C, Gille S, Rautengarten C, Cherk C, Marcus SE, Somerville S, Pauly M, Knox JP, Sakuragi Y, Scheller HV (2011). Loss-of-function mutation of *REDUCED WALL ACETY-LATION 2* in *Arabidopsis* leads to reduced cell wall acetylation and increased resistance to *Botrytis cinerea*. *Plant Physiol* **155**, 1068–1078.

Mansoori N, Schultink A, Schubert J, Pauly M (2015). Expression of heterologous xyloglucan xylosyltransferases in *Arabidopsis* to investigate their role in determi- ning xyloglucan xylosylation substitution patterns. *Planta* **241**, 1145–1158.

Nafisi M, Stranne M, Fimognari L, Atwell S, Martens HJ, Pedas PR, Hansen SF, Nawrath C, Scheller HV, Kliebenstein DJ, Sakuragi Y (2015). Acetylation of cell wall is required for structural integrity of the leaf surface and exerts a global impact on plant stress responses. *Front Plant Sci* **6**, 550.

Niu YQ, Hu B, Li XQ, Chen HB, Takáč T, Šamaj J, Xu CX (2018). Comparative digital gene expression analysis of tissue-cultured plantlets of highly resistant and susceptible banana cultivars in response to *Fusarium oxysporum*. *Int J Mol Sci* **19**, 350.

Otulak-Kozieł K, Kozieł E, Bujarski JJ (2018). Spatiotemporal changes in xylan-1/xyloglucan and xyloglucan xyloglucosyl transferase (XTH-Xet5) as a step-in of ultrastructural cell wall remodelling in potato-potato virus Y (PVY^NTN) hypersensitive and susceptible reaction. *Int J Mol Sci* **19**, 2287.

Pauly M, Keegstra K (2016). Biosynthesis of the plant cell wall matrix polysaccharide xyloglucan. *Annu Rev Plant Biol* **67**, 235–259.

Pauly M, Ramírez V (2018). New insights into wall polysaccharide *O*-acetylation. *Front Plant Sci* **9**, 1210.

Pawar PMA, Ratke C, Balasubramanian VK, Chong SL, Gandla ML, Adriasola M, Sparrman T, Hedenström M, Szwaj K, Derba-Maceluch M, Gaertner C, Mouille G, Ezcurra I, Tenkanen M, Jönsson LJ, Mellerowicz EJ (2017). Downregulation of RWA genes in hybrid aspen affects xylan acetylation and wood saccharification. *New Phytol* **214**, 1491–1505.

Peña MJ, Kong YZ, York WS, O'Neill MA (2012). A galacturonic acid-containing xyloglucan is involved in *Arabi-*

dopsis root hair tip growth. *Plant Cell* **24**, 4511–4524.

Pogorelko G, Lionetti V, Fursova O, Sundaram RM, Qi MS, Whitham SA, Bogdanove AJ, Bellincampi D, Zabotina OA (2013). *Arabidopsis* and *Brachypodium distachyon* transgenic plants expressing *Aspergillus nidulans* acetylesterases have decreased degree of polysaccharide acetylation and increased resistance to pathogens. *Plant Physiol* **162**, 9–23.

Purugganan MM, Braam J, Fry SC (1997). The *Arabidopsis* TCH4 xyloglucan endotransglycosylase: substrate specificity, pH optimum, and cold tolerance. *Plant Physiol* **115**, 181–190.

Rao XL, Dixon RA (2017). Brassinosteroid mediated cell wall remodeling in grasses under abiotic stress. *Front Plant Sci* **8**, 806.

Rose JKC, Braam J, Fry SC, Nishitani K (2002). The XTH family of enzymes involved in xyloglucan endotransglycosylation and endohydrolysis: current perspectives and a new unifying nomenclature. *Plant Cell Physiol* **43**, 1421–1435.

Rui Y, Anderson CT (2016). Functional analysis of cellulose and xyloglucan in the walls of stomatal guard cells of *Arabidopsis*. *Plant Physiol* **170**, 1398–1419.

Sampedro J, Gianzo C, Iglesias N, Guitián E, Revilla G, Zarra I (2012). AtBGAL10 is the main xyloglucan β-galactosidase in *Arabidopsis*, and its absence results in unusual xyloglucan subunits and growth defects. *Plant Physiol* **158**, 1146–1157.

Sampedro J, Valdivia ER, Fraga P, Iglesias N, Revilla G, Zarra I (2017). Soluble and membrane-bound β-glucosidases are involved in trimming the xyloglucan backbone. *Plant Physiol* **173**, 1017–1030.

Scheller HV, Ulvskov P (2010). Hemicelluloses. *Annu Rev Plant Biol* **61**, 263–289.

Schultink A, Cheng K, Park YB, Cosgrove DJ, Pauly M (2013). The identification of two arabinosyltransferases from tomato reveals functional equivalency of xyloglucan side chain substituents. *Plant Physiol* **163**, 86–94.

Schultink A, Naylor D, Dama M, Pauly M (2015). The role of the plant-specific ALTERED XYLOGLU-CAN 9 protein in *Arabidopsis* cell wall polysaccharide *O*-acetylation. *Plant Physiol* **167**, 1271–1283.

Sharmin S, Azam MS, Islam MS, Sajib AA, Mahmood N, Hasan AMM, Ahmed R, Sultana K, Khan H (2012). Xyloglucan endotransglycosylase/hydrolase genes from a susceptible and resistant jute species show opposite expression pattern following *Macrophomina phaseolina* infec-

tion. *Commun Integr Biol* **5**, 598–606.

Shigeyama T, Watanabe A, Tokuchi K, Toh S, Sakurai N, Shibuya N, Kawakami N (2016). α-xylosidase plays essential roles in xyloglucan remodelling, maintenance of cell wall integrity, and seed germination in *Arabidopsis thaliana*. *J Exp Bot* **67**, 5615–5629.

Shinohara N, Sunagawa N, Tamura S, Yokoyama R, Ueda M, Igarashi K, Nishitani K (2017). The plant cell-wall enzyme AtXTH3 catalyses covalent cross-linking between cellulose and cello-oligosaccharide. *Sci Rep* **7**, 46099.

Song L, Valliyodan B, Prince S, Wan JR, Nguyen HT (2018). Characterization of the *XTH* gene family: new insight to the roles in soybean flooding tolerance. *Int J Mol Sci* **19**, 2705.

Subíková V, Slovakova L, Farkas V (1994). Inhibition of tobacco necrosis virus infection by xyloglucan fragments. *Z Pflanzenk Pflanzen* **101**, 128–131.

Takahashi D, Gorka M, Erban A, Graf A, Kopka J, Zuther E, Hincha DK (2019). Both cold and sub-zero acclimation induce cell wall modification and changes in the extracellular proteome in *Arabidopsis thaliana*. *Sci Rep* **9**, 2289.

Thorlby G, Fourrier N, Warren G (2004). The *SENSITIVE TO FREEZING 2* gene, required for freezing tolerance in *Arabidopsis thaliana*, encodes a β-glucosidase. *Plant Cell* **16**, 2192–2203.

Vaahtera L, Schulz J, Hamann T (2019). Cell wall integrity maintenance during plant development and interaction with the environment. *Nat Plants* **5**, 924–932.

Vanzin GF, Madson M, Carpita NC, Raikhel NV, Keegstra K, Reiter WD (2002). The *mur2* mutant of *Arabidopsis thaliana* lacks fucosylated xyloglucan because of a lesion in fucosyltransferase AtFUT1. *Proc Natl Acad Sci USA* **99**, 3340–3345.

Wang C, Li S, Ng S, Zhang BC, Zhou YH, Whelan J, Wu P, Shou HX (2014). Mutation in xyloglucan 6-xylosytransferase results in abnormal root hair development in *Oryza sativa*. *J Exp Bot* **65**, 4149–4157.

Wang M, Xu ZC, Ding AM, Kong YZ (2018). Genome-wide identification and expression profiling analysis of the xy-

loglucan endotransglucosylase/hydrolase gene family in tobacco (*Nicotiana tabacum* L.). *Genes* **9**, 273.

Wu YL, Fan W, Li XQ, Chen HB, Takáč T, Šamajová O, Fabrice MR, Xie L, Ma J, Šamaj J, Xu CX (2017). Expression and distribution of extensins and AGPs in susceptible and resistant banana cultivars in response to wounding and *Fusarium oxysporum*. *Sci Rep* **7**, 42400.

Xie DS, Ma L, Šamaj J, Xu CX (2011). Immunohistochemical analysis of cell wall hydroxyproline-rich glycoproteins in the roots of resistant and susceptible wax gourd cultivars in response to *Fusarium oxysporum* f. sp. *benincasae* infection and fusaric acid treatment. *Plant Cell Rep* **30**, 1555–1569.

Xu H, Ding AM, Chen SH, Marowa P, Wang D, Chen M, Hu RB, Kong YZ, O'Neill M, Chai GH, Zhou GK (2018). Genome-wide analysis of *Sorghum* GT47 family reveals functional divergences of *MUR3-like* genes. *Front Plant Sci* **9**, 1773.

Yan JW, Huang Y, He H, Han T, Di PC, Sechet J, Fang L, Liang Y, Scheller HV, Mortimer JC, Ni L, Jiang MY, Hou XL, Zhang AY (2019). Xyloglucan endotransglucosylase-hydrolase 30 negatively affects salt tolerance in *Arabidopsis*. *J Exp Bot* **70**, 5495–5506.

Yan YL, Takáč T, Li XQ, Chen HB, Wang YY, Xu EF, Xie L, Su ZH, Šamaj J, Xu CX (2015). Variable content and distribution of arabinogalactan proteins in banana (*Musa* spp.) under low temperature stress. *Front Plant Sci* **6**, 353.

Zhu WJ, Ronen M, Gur Y, Minz-Dub A, Masrati G, Ben-Tal N, Savidor A, Sharon I, Eizner E, Valerius O, Braus GH, Bowler K, Bar-Peled M, Sharon A (2017). BcXYG1, a secreted xyloglucanase from *Botrytis cinerea*, triggers both cell death and plant immune responses. *Plant Physiol* **175**, 438–456.

Zhu XF, Shi YZ, Lei GJ, Fry SC, Zhang BC, Zhuo YH, Braam J, Jiang T, Xu XY, Mao CZ, Pan YJ, Yang JL, Wu P, Zheng SJ (2012). *XTH31*, encoding an *in vitro* XEH/XET-active enzyme, regulates aluminum sensitivity by modulating *in vivo* XET action, cell wall xyloglucan content, and aluminum binding capacity in *Arabidopsis*. *Plant Cell* **24**, 4731–4747.

Xyloglucan and the Advances in Its Roles in Plant Tolerance to Stresses

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Abstract　Xyloglucan (XyG) is a matrix polysaccharide present in the cell wall of all land plants. It is the most abundant hemicellulose in the primary cell walls of dicots (20%–25%, w/w). As a very important plant cell wall component, XyG is not only involved in plant growth and development, but also plays important roles in responses of plants to various abiotic and biotic stresses. The use of genes involved in XyG biosynthesis and degradation possibly improve the tolerance of plants to stresses through influencing the cell wall structure (remodelling) and compositions. In addition, XyG and XyG oligosaccharides likely act as signaling molecules or cooperate with other signaling molecules to induce plant resistance. Here, we review the structure and variety of XyG, the genes involved in XyG biosynthesis and degradation, and advances in potential roles of XyG and XyG-related genes in responses to biotic and abiotic stresses.

Key words　hemicellulose, xyloglucan metabolism, biotic stress, abiotic stress, resistance

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