

植物次生细胞壁加厚过程的转录调控

朱晓博, 张贵粉, 陈鹏*

华中农业大学植物科学技术学院, 生物质与生物能源研究中心, 武汉430070

摘要: 双子叶植物次生木质部中的导管和管胞、单子叶植物初生木质部的导管对于植物体的水分运输至关重要。厚壁组织对植物的机械强度起到主要的支撑作用, 其中双子叶植物是由皮层的厚角组织和维管束提供, 单子叶植物由机械组织和维管束提供。这些行使特殊功能的组织细胞都能发生次生细胞壁加厚, 加厚的细胞类型有管状细胞、纤维细胞、厚壁细胞等。次生细胞壁合成是一个复杂的生物学过程, 本文围绕次生细胞壁加厚发生的主要组织——维管束厚壁组织, 总结了调控次生壁加厚的转录因子, 以便读者能够更加深入地理解复杂的次生壁调控网络。

关键词: 维管束; 次生细胞壁; 转录因子; 调控网络

植物细胞壁中的纤维素是地球上含量最为丰富的生物大分子, 纤维素的生物合成在基础研究方面可以加深对植物生长发育过程调控的认识, 在应用研究方面可以为纤维素类生物质材料降解性改造提供理论基础。植物不同组织的细胞具有不同类型的细胞壁, 次生壁因富含木质素, 具有良好的疏水性和机械支撑作用, 保证了植物维管束和茎髓组织对水分和养分的输送。

伴随着植物的生长和组织细胞类型的特化, 不同类型细胞会经历一次到多次的次生壁加厚过程。次生壁的加厚必然伴随初生壁合成的结束和次生壁合成的开启, 这个转换过程需要与植物发育及外界环境信号进行良好的协同。细胞壁加厚过程中的转录调控, 特别是次生壁加厚过程中伴随果胶质合成的结束、纤维素的大量合成、不同亚类半纤维素的合成以及木质素的合成。以NAC

(NAM、ATAF1/2、CUC2)和MYB类为核心成员的转录因子参与到不同细胞壁组分的合成、糖类不同主链及支链的加工及修饰以及不同大分子之间的交联或解聚等过程。因此, 植物细胞壁合成被认为是最为复杂的生物学过程之一。近20年来, 对于植物细胞壁合成的转录调控过程的认知发生了很大的飞跃, 但是仍有很多核心问题未解释清楚。本文综述了以水稻和拟南芥为代表的单子叶和双子叶植物中细胞壁合成转录调控的研究进展, 并针对次生壁加厚过程中的转录因子及其在调控网络中的层级关系进行了总结, 旨在加深对于次生壁加厚过程转录调控网络的整体认识。

1 单子叶和双子叶植物茎维管束中的细胞构成

单子叶植物水分运输主要通过茎秆的维管束完成, 维管束主要由初生木质部、初生韧皮部和维管束鞘组成(表1)。初生韧皮部在茎发育过程中

表1 单子叶植物茎的结构
Table 1 Structure definition in stem cross section of monocot plants

表皮	机械组织	维管束					基本组织
		初生木质部		维管束鞘	初生韧皮部		
		原生	后生		原生	后生	
最外围一层细胞	厚壁细胞和纤维细胞	原生导管(V型基部)	后生导管(V型两臂)	厚壁细胞	筛管细胞和伴胞细胞	薄壁细胞	

原生韧皮部常被挤毁, 后生韧皮部由方形或者三角形的伴胞(图1, a)和细胞形状大的筛管细胞构成(图1, b)。由图1可见, 单子叶植物初生木质部整体像一个V型, V型基部为原生导管(图1, c), 主要是少量的木薄壁组织; 两臂为后生导管(图1, d), 后生导管之间为管胞或厚壁细胞(图1, e)。维管束鞘由

厚壁细胞构成(图1, f), 这些细胞经历了次生细胞壁加厚过程。导管细胞的次生细胞壁发生了异常加

收稿 2017-06-05 修定 2017-09-13
资助 中央高校基本科研业务费专项资金项目(52902-0900202688)。
* 通讯作者(E-mail: chenpeng@mail.hzau.edu.cn)。

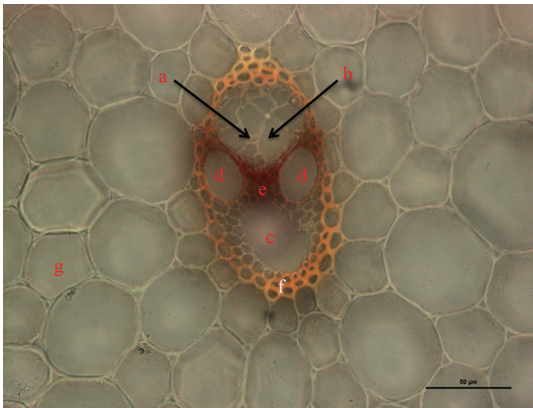


图1 水稻茎秆横切面的间苯三酚染色
Fig.1 Phloroglucinol staining of rice stem transverse section
a: 伴胞; b: 筛管; c: 原生导管; d: 后生导管; e: 管胞或厚壁细胞; f: 维管束鞘; g: 薄壁细胞。标尺=50 μm。

厚, 在提高机械强度的同时也降低了亲水性, 有利于水分的长距离运输。

双子叶植物中负责物质运输的组织为维管柱, 由维管束、髓和髓射线组成(表2)。由图2可见, 在表皮和皮层下的维管束间为厚壁组织(图2, d), 维管柱内为髓和髓射线(图2, e和f), 髓和髓射线由薄壁细胞构成。维管束则由木质部、韧皮部和形成层构成(表2)。形成层由薄壁细胞构成。木质部和韧皮部各包含初生和次生两个部分: 其中次生木质部由导管、管胞、木质部纤维细胞和木质部薄壁细胞构成; 次生韧皮部由筛管、伴胞、韧皮部纤维细胞和韧皮部薄壁细胞构成(表2)。导管细胞、管胞细胞、木质部和韧皮部纤维细胞都会发生次生细胞壁加厚, 筛管细胞和伴胞细胞的细胞壁不加厚为初生壁。

表2 双子叶植物茎的结构

Table 2 Structure definition in stem cross section of dicot plants

表皮	皮层	维管柱					髓	髓射线
		维管束						
		初生木质部	次生木质部	形成层	次生韧皮部	初生韧皮部		
外围单层细胞	厚角组织		导管、管胞、纤维细胞、薄壁细胞	薄壁细胞	筛管、伴胞、纤维细胞、薄壁细胞		薄壁细胞	薄壁细胞

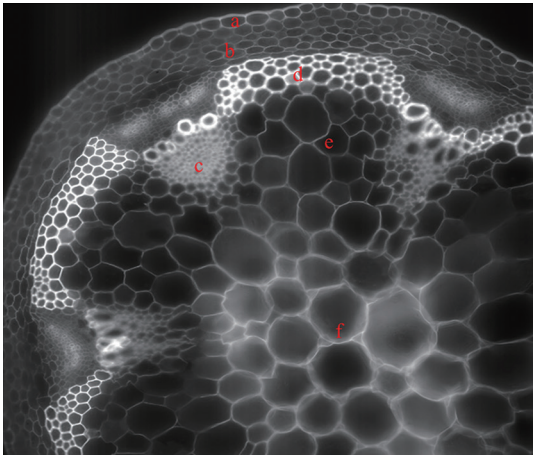


图2 拟南芥茎秆横切面的Calcofluor染色
Fig.2 Calcofluor staining of *Arabidopsis* stem transverse section
a: 表皮; b: 皮层; c: 维管束; d: 厚壁组织; e: 髓射线; f: 髓。放大倍数为20。

用于次生细胞, 使细胞进行次生细胞壁的合成及加厚(Zhong和Ye 2014)。次生壁加厚的调控过程已经研究得相当清楚(Li等2016a, b), 但哪些基因的表达能刺激细胞开始进行次生细胞壁的合成仍不清楚。次生壁加厚发生于细胞停止生长后, 究竟是细胞生长的停止启动了次生壁加厚, 还是次生壁加厚抑制了细胞生长, 这一问题还未有定论(黄成和李来庚2016)。

次生细胞壁加厚过程包含纤维素、半纤维素和木质素的合成基因(McFarlane等2014)。拟南芥纤维素合酶复合体(cellulose synthase complex, CSC)包含10个cellulose synthase (CesA)亚基, 它们的编码基因均属于GT2基因家族(McFarlane等2014; 张保才和周奕华2015)。拟南芥初生壁和次生壁CSC组成有所不同, 次生壁CSC成员为CesA4、CesA7和CesA8 (Taylor等1999, 2000, 2003), 而初生壁成员则是CesA1、CesA3和CesA6, 除此之外还有与CesA6功能冗余的CesA2、CesA5、CesA9, 可能参与初生壁CSC中(Taylor等2003; Desprez等2007;

2 木质部导管次生壁加厚过程的调控

木质部导管的形成伴随着次生细胞壁的加厚。在细胞分裂结束之后, 部分相关的催化酶作

Persson等2007; McFarlane等2014)。拟南芥中KORRIGN1 (KOR1)蛋白与CesA1, 3, 6蛋白互作, 因此也可看作初生壁CSC的成员(Vain等2014); KOR1也可与次生壁的CesA4和CesA8蛋白互作, 辅助次生壁CSC合成纤维素(Mansoori等2014)。

植物细胞的细胞壁分为初生壁和次生壁, 而合成初生壁和次生壁纤维素的CSC并不相同, 那么, 形成CSC的基因表达是如何被调控的呢? Kubo等(2005)通过拟南芥木质部导管分化过程中的微阵列分析发现, 在次生壁合成起始过程中有156个基因发生表达上调, 其中有包括*VASCULAR-RELATED NAC-DOMAIN (VND)*, 包括*VND1~7*等16个转录因子。*VND6*和*VND7*是调控木质部导管形成的核心开关, 它们分别在后生木质部和原生木质部中特异表达: *VND6*超表达引起后生木质部加厚, 而*VND7*超表达则导致原生木质部加厚(Kubo等2005)。研究同时发现, 在*VND7*超表达植株中, 半纤维素合成基因*xylanase 3 (Xyn3)*和纤维素合成基因*irregular xylem 3 (IRX3)*的表达升高, 但*VND6*或*VND7*的RNAi和T-DNA突变体无明显表型。通过显性抑制手段, 作者发现*VND6*显性抑制植株的后生木质部形成受到抑制, *VND7*显性抑制植株的原生木质部形成受到抑制(Kubo等2005)。该研究首次揭示了*VND6*和*VND7*转录因子在后生木质部和原生木质部发育中的作用, 同时研究中所采用的显性抑制方法在后期转录因子功能的研究中也得到广泛应用。显性抑制相比RNAi能更好地解释转录因子在调控网络中的作用。

*VND6/VND7*诱导型材料在次生壁合成调控中被广泛使用, 例如, 研究次生壁启动后短时间内植物体内的表达谱和代谢组的变化(Ohashi-Ito等2010; Li等2016b)。Ohashi-Ito等(2010)通过对悬浮细胞的诱导表达系统进行研究发现, *VND6*的表达可以诱导次生壁纤维素合成基因*CESA4/IRX5*、*CESA7/IRX3*和*CESA8/IRX1*的表达。通过2',7'-bis-(2-carboxyethyl)-5-(and-6)-carboxyfluorescein (BCECF)染色发现, *VND6*诱导表达一定时间后, 次生壁加厚了的木质部细胞全部死亡。Yamaguchi等(2010a)利用类似诱导系统在植物中研究了*VND6*和*VND7*的功能: 当诱导表达含有VP16激活域的*VND6*和*VND7*蛋白时, 木质部导管分化出凹痕和环状两种细胞

壁结构, 其表型类似于*VND6*和*VND7*的超表达植株(Kudo等2005)。有研究表明, *VND7*蛋白的C端对于该蛋白的调控功能至关重要, 缺失C端的*VND7*蛋白不能促进原生木质部和后生木质部的分化(Yamaguchi等2008)。*VND6*和*VND7*除了能直接调控纤维素合成基因*CESA4*、*CESA7*和*CESA8*之外, 也能直接调控纤维素合成基因*IRX8*和*IRX10*、木质素合成基因*caffeoyl coenzyme A ester O-methyltransferase 7 (CCoAOMT7)*和*IRX2/LAC4*以及细胞程序性死亡基因*xylem cysteine protease 1 (XCP1)*等(Kudo等2005; Ohashi-Ito等2010; Yamaguchi等2010a)。*XCP1*和*XCP2*基因促进细胞程序性死亡, 对于木质部导管形成过程有重要作用(Zhao等2000; Avci等2008)。McCarthy等(2011)研究指出*XCP1*在木质部导管中特异表达。研究表明*VND6*除了调控*XCP1*和*XCP2*之外, 还调控*xylem serine protease 1 (XSPI)*、*Arabidopsis thaliana metacaspase 9 (AtMC9)*、*ATSBT1.1*、*AT4g18550*、*At1g14240*、*bifunctional nuclease 1 (BFN1)*和*ribonuclease 3 (RNS3)*等细胞程序性死亡相关基因的表达(Ohashi-Ito等2010; Zhong等2010a; Zhong和Ye 2014)。

目前, 受*VND7*直接调控的转录因子有14个, 且不同*VND*基因之间存在一定程度的功能冗余(Endo等2015)。Zhou等(2014)研究发现, *VND1~VND5*在茎木质部导管中特异表达, *VND4*和*VND5*在下胚轴木质部中表达, *VND1~VND5*超表达上调次生壁合成基因, 导致薄壁细胞中发生次生壁的沉积, *VND3*的显性抑制导致次生壁加厚减弱和木质部的塌陷。

*VND6/VND7*基因的表达也受到*lateral organ boundaries domain 18 (LBD18)*和*lateral organ boundaries domain 30 (LBD30)*上游基因的调控。*LBD18/asymmetric leaves 2-like 20 (ASL20)*和*LBD30/ASL19*在幼苗期叶和根的木质部导管中特异表达(Soyano等2008)。*LBD18*的表达受到抑制后, *VND6*和*VND7*表达下降, 木质部导管次生壁加厚减弱; 反之, 在*LBD18*超表达植株中, *VND6*和*VND7*表达水平升高, 导管次生壁加厚增强(Soyano等2008)。同时, Soyano等(2008)发现*VND6*和*VND7*对*LBD18*和*LBD30*的表达存在反馈调节, Zhong等(2010a)的研究表明*LBD30*受*VND7*直接调控。不

同于*LBD*, 在木质部和韧皮部细胞中表达的*VND-INTERACTING 2 (VNI2)*是*VND*的负向调控因子(Yamaguchi等2010b)。*VNI2*超表达抑制*VND7*的表达, 并抑制幼苗期叶和根中木质部导管次生壁的加厚(Yamaguchi等2010b)。有别于*LBD*和*VNI2*, *E2Fc*对于*VND7*的调控具有两面性: 过量和过低水平的*E2Fc*会抑制*VND7*的表达, 只有适量的*E2Fc*可以激活*VND7*的表达(Taylor-Teeple等2015; Teeple等2015)。

*KNAT7*基因在木质部导管和纤维细胞中的作用不同。*knat7*突变体表现出严重的木质部塌陷(Brown等2005), 但木质部纤维细胞的次生壁加厚增强(Li等2012a)。*KNAT7*超表达植株的维管束间纤维细胞次生壁没有显著加厚(Li等2012a)。有研究证明*KNAT7*能与*MYB75*和*OFP4*形成功能复合体来调控次生壁的加厚(Li等2011; Bhargava等2013; Liu和Douglas 2015)。*XND1*是NAC类转录因子, 在木质部导管中高量表达, *XND1*超表达植株矮小, 木质部导管细胞的次生壁沉积受到抑制(Zhao等2008)。

3 木质部和韧皮部纤维细胞、厚壁组织中纤维细胞的次生细胞壁加厚调控

植物茎秆中纤维细胞主要分布于木质部、韧皮部和厚壁组织中, 也需要次生细胞壁加厚。拟南芥*NAC SECONDARY WALL THICKENING PROMOTING FACTOR 1*和3 (*NST1*和*NST3/SND1*) 在纤维细胞中特异表达, 是调控木质部纤维细胞次生壁加厚的关键因子(Mitsuda等2007; 王瑞芳等2014), 同时, *NST2*也参与茎秆纤维细胞次生壁合成调控(Zhong和Ye 2015; 黄成和李来庚2016)。*NST1*的T-DNA突变体次生壁加厚减弱, 而*NST1*同源基因*NST3*的T-DNA突变体无明显表型(Zhong和Ye 2015)。Mitsuda等(2007)发现*NST1*和*NST3*在茎秆和下胚轴纤维细胞表达, 且功能冗余, *nst1 nst3*双突变体维管束厚壁组织和木质部纤维细胞次生壁没有加厚, 但是木质部导管的加厚不受影响。在*nst1 nst3*双突变体中, 发现纤维细胞中纤维素合成基因*IRX3*和木质素合成基因*cinnamyl alcohol dehydrogenase-d (CAD-D)*的启动子启动*GUS*报告基因, 但是没有检测到活性; 纤维素合成基因*IRX3*和*IRX5*, 木质素合成基因*IRX4*、*IRX12*和*AtOMT1*, 木聚糖合成基因*fragile fiber 8 (FRA8)*表达大幅度下

调(Mitsuda等2007)。*NST3*超表达植株中, 植物地上组织细胞全部出现次生壁异常加厚(Mitsuda等2007; Zhong等2007a); 纤维细胞中纤维素、半纤维素和木质素合成基因表达上调, 厚壁组织纤维细胞次生壁发生异常加厚(Zhong等2006)。Ohashi-Ito等(2010)研究发现, *SND1*可以直接诱导木质素合成基因*phenylalanine ammonia-lyase 1 (PAL1)*、*CCoAOMT*和*4-coumarate 3 (4CL3)*的表达, 以及半纤维素合成基因*IRX9*、纤维素合酶类基因*cellulose synthase-like B 02 (CSLB02)*、阿拉伯半乳糖蛋白基因*fasciclin-like arabinogalactan-protein 12 (FLA12)*的表达。在转录因子方面, *NST3/SND1*的超表达诱导*MYB63*和*MYB58*的表达(Zhou等2009; Ohashi-Ito等2010), 从而促进木质素的合成(Zhou等2009)。

早期鉴定的*NST3/SND1*下游转录因子包括*SND2*、*SND3*、*MYB103*、*MYB85*、*MYB52*、*MYB54*、*MYB69*、*MYB42*、*MYB43*、*MYB20*和*KNAT7* (Zhong等2006, 2007a, 2008; Ohashi-Ito等2010; Yamaguchi等2010a; Taylor-Teeple等2015)。*SND2*、*SND3*、*MYB103*、*MYB85*、*MYB52*、*MYB54*、*MYB69*和*KNAT7*基因的抑制表达均导致厚壁组织和木质部纤维细胞中次生壁加厚的减少, *MYB85*表达抑制的植株中发生导管变形(Zhong等2008)。此外, 超表达*SND2*、*SND3*和*MYB103*导致纤维细胞次生壁加厚增强, 超表达*MYB85*则引起茎秆表皮和皮层细胞木质素的异常沉积(Zhong等2008)。*SND2*、*SND3*、*MYB103*、*MYB85*、*MYB52*和*MYB54*可以直接调控次生壁合成相关基因, 例如*SND2*、*SND3*和*MYB103*诱导*CESA8*的表达, *MYB85*诱导木质素合成基因*4CL1*的表达, *MYB52*和*MYB54*诱导*CESA8*、*4CL1*以及木聚糖合成基因*IRX9*基因的表达(Zhong等2008)。后续研究发现, *SND1*、*NST1*、*NST2*、*VND6*和*VND7*直接调控*MYB46*、*SND3*、*MYB103*和*KNAT7*等转录因子的表达, 从而构成了现有的三层次生壁合成调控网络的骨架(图3)(Zhong等2007b, 2008; McCarthy等2009; Wang和Dixon 2012; 黄成和李来庚2016)。

以*SND1/NST3*和*NST1*为核心的次生壁加厚的多层转录因子调控网络在其他物种中也相继得到了证实(Li等2012b)。位于调控网络第一层次的*NST1*和*NST2*以及调控导管形成的*VND6*和*VND7*

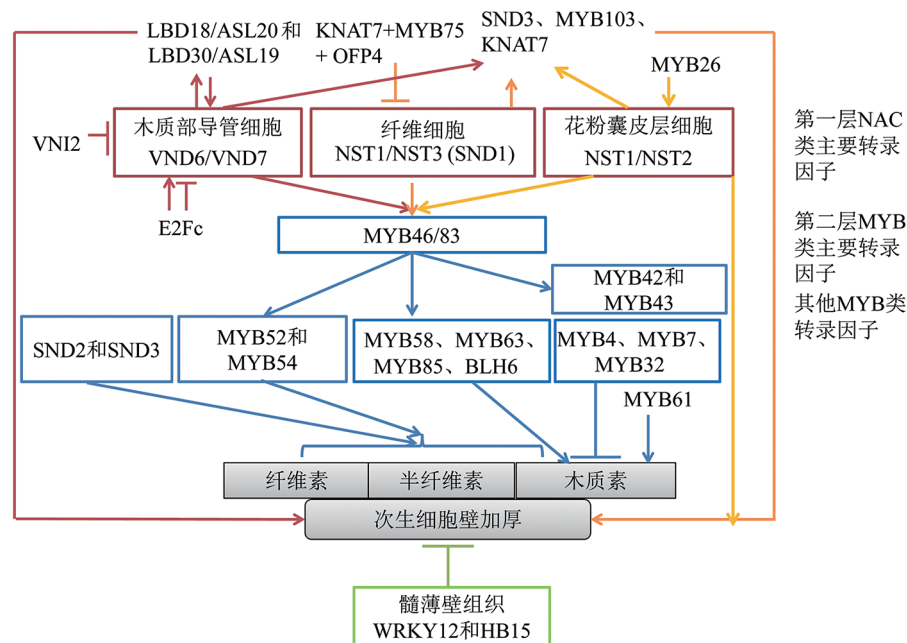


图3 拟南芥次生壁合成调控网络示意图

Fig.3 Transcription regulation network of the secondary wall biosynthesis in *Arabidopsis*

箭头表示正调控; T形线表示负调控。

不仅在蛋白序列上具有同源性,而且对下游的MYB46和MYB83等转录因子均具有调控作用。MYB46在花序茎秆的厚壁组织纤维细胞、木质部纤维细胞和木质部导管细胞中特异表达, *SND1*与MYB46启动子结合并促进其表达(Zhong等2007b)。MYB46的超表达导致MYB85和KNAT7等二级转录因子的表达升高,进而激活*CESA7*和*CESA8*、木聚糖合成基因*FRA8*、木质素合成基因*CCoAOMT*和*4CL1*的表达,从而导致叶表皮细胞、花序茎秆维管组织细胞、茎秆导管细胞的次生壁加厚。反之,MYB46的显性抑制则导致纤维细胞和导管细胞的次生壁加厚显著减弱(Zhong等2007b)。MYB46直接调控MYB43、MYB52、MYB54、MYB58和MYB63转录因子(Zhou等2009; Kim等2014a), Kim等(2012, 2013, 2014a, 2014b)的研究证明MYB46直接调控*CESA4*、*CESA7*、*CESA8*、甘露糖合成基因*cellulose synthase-like A 9 (CSLA9)*,以及其他木质素及木聚糖合成相关基因的表达。MYB83为MYB46的功能性冗余基因,同MYB46一样在茎秆导管和纤维细胞中表达,但根中仅在导管细胞中表达(Zhong等2007b; McCarthy等2009; Zhong和Ye 2011)。MYB46的T-DNA突变体没有明显表型

(Zhong等2007b)。myb83 myb46双突变体中,木质部导管次生壁加厚受阻,植株生长受到抑制(McCarthy等2009; Zhong和Ye 2011)。MYB46/MYB83的显性抑制导致导管和纤维细胞中次生壁加厚的减弱(Zhong等2007b; McCarthy等2009)。同NST1、NST3和VND7一样,MYB46/MYB83的超表达激活二级转录因子MYB42、MYB43、MYB52、MYB54、MYB63和MYB85基因的表达,诱导纤维素、半纤维素和木质素合成基因表达(图3)(Zhong等2007b; McCarthy等2009)。

4 花药皮层及茎髓细胞次生壁加厚的调控

NST1和NST2转录因子调控花药皮层细胞的次生细胞壁加厚过程(Mitsuda等2005)。虽然NST1或NST2单基因的T-DNA突变体没有明显表型(Mitsuda等2005),但是NST1的显性抑制植株中花药不能开裂,并且花药皮层细胞壁木质素含量降低。nst1 nst2双突变体与显性抑制植株表型一致(Mitsuda等2005)。NST1或NST2超表达植株的花药、雄蕊、胚珠、茎秆、叶片和根等组织中的细胞都发生次生壁异常加厚(Zhong和Ye 2015)和次生壁合成基因的上调表达(Mitsuda等2005)。拟南芥MYB26调控NST1和NST2的表达,是花药皮层细胞次生壁

加厚的主要调控因子(Yang等2007)。*myb26*突变体花药皮层细胞次生壁不加厚,花粉有活力但花药不开裂,从而导致雄性不育(Steiner-Lange等2003)。

不同于花药皮层和木质部维管束,在茎髓组织薄壁细胞中,WRKY12是次生壁加厚的主要调控因子(Wang等2010)。*WRKY12*在髓组织中特异表达,*wrky12-1*突变体发生次生壁异常加厚,说明*WRKY12*抑制茎髓组织薄壁细胞次生壁加厚(Wang等2010)。*WRKY12*可结合*NST2*的启动子并抑制其表达,*wrky12*突变体中*NST2*基因表达升高,髓组织薄壁细胞次生壁加厚,且调控次生壁合成的转录因子*AtC3H14*的基因表达量升高(Wang等2010)。

除了众多转录因子之外,microRNA也参与了次生细胞壁加厚的转录调控。我们通过研究发现,*miR165b*超表达造成*HB15*基因的表达量下降,导致髓薄壁细胞次生壁加厚(Du等2015; Du和Wang 2015)。Sun等(2017)发现超表达*miR319*抑制*TEO-SINTE BRANCHED 1/CYCLOIDEA/PCF 4 (TCP4)*的表达,TCP4可以与*VND7*的启动子结合,TCP4的超表达诱导次生壁纤维素合成基因*CESA4*、*CESA7*和*CESA8*,半纤维素合成基因*IRX8*和*IRX10*以及木质素合成基因*laccase 4 (LAC4)*和*laccase 7 (LAC7)*的表达,因此*miR319*通过TCP4间接调控*VND7*开关基因及下游次生壁合成相关基因的表达。

5 其他植物中类似于拟南芥细胞壁加厚的调控网络

现有的拟南芥中次生壁合成的多级调控网络确保对次生壁合成的精确调控(图3),这种调控网络在植物中具有相当高的保守性。由于*VND1*~*VND7*、*NST1*、*NST2*、*SND1*属于NAC类转录因子大家族,所以将其通称为*secondary wall NACs (SWNs)*(Zhong等2010a; Zhong和Ye 2014)。杨树中有6个与*NST*同源的*SWNs*类基因,*PtrWNDs*在木质化细胞中表达(Zhong等2010c, 2011b; Zhong和Ye 2010; Ohtani等2011)。*SWNs*基因在大多数陆地植物,包括被子植物、裸子植物和无维管组织的苔藓类植物中都有发现(Zhong等2010b)。杨树基因*PtrWNDs*在拟南芥中的异源表达可以恢复*snd1 nst1*双突变体的表型,*PtrWNDs*的超表达引起次生壁合成基因的表达上升,说明*PtrWNDs*是拟南芥*SND1/NST1*的直系同源基因(Zhong等2010b, 2011a; Ohtani等2011)。在*PtrWNDs*表达量下降的转基因

杨树中,木质部导管和纤维细胞的次生壁加厚受到抑制(Zhong等2011b)。杨树*SND1*的剪接突变体*PtrSND1-A2IR*发生*SND1*的剪接突变,导致*SND1*基因的表达受到抑制(Li等2012b)。桉树*EgWND1*是*AtSND1/NST1*的直系同源基因(Zhong等2010b)。水稻和玉米中*SND1*的同源基因有7个,分别为*OsSWN1*、*OsSWN3*、*OsSWN7*、*ZmSWN1*、*ZmSWN3*、*ZmSWN6*和*ZmSWN7*(Zhong等2011a)。有研究表明*OsSWN1*和*OsSWN2*参与调控水稻维管束厚壁组织和纤维细胞的次生细胞壁加厚过程(Yoshida等2013)。

同第一层开关基因*SWNs*类似,调控网络的第二层开关*MYB46/MYB83*在维管植物中也是保守的(图3)。目前在拟南芥和水稻之外鉴定的*MYB*类同源基因有*PtMYB4/8*、*EgMYB2*、*PtrMYB2/21*和*PtrMYB3/20*(Patzlaff等2003; Goicoechea等2005; Bomal等2008; McCarthy等2010; Zhong等2013; Zhao等2014; Zhong和Ye 2014)。*OsMYB46*、*ZmMYB46*与拟南芥*MYB46/MYB83*是直系同源基因,在拟南芥中超表达*OsMYB46*或*ZmMYB46*可以激活整个次生壁合成途径(Zhong等2011a)。但水稻和拟南芥*MYB*基因作用方式也存在细微的不同:水稻*OsMYB58/63*调控纤维素合成基因*OsCESA7*的表达,拟南芥中同源*MYB*基因则调控木质素合成基因的表达(Noda等2015)。与拟南芥类似,玉米*ZmMYB42*调控木质素的合成,在拟南芥中超表达*ZmMYB42*引起木质素合成通路基因的上调及木质素单体比例的改变(Sonbol等2009),但是Fornalé等(2010)发现*ZmMYB31*抑制木质素合成基因表达,负向调控木质素的合成。另外,共表达结果显示,*OsMYB55/61*和*OsBLH6*作为第三层次的转录因子,也参与调控次生细胞壁的形成(Zhong等2011a; Hirano等2013)。

6 细胞壁各个主要成分合成基因的调控

次生壁加厚涉及的合成基因主要包括纤维素、半纤维素和木质素合成途径中的基因,关于这些合成基因的表达调控,特别是*NAC*、*MYB*和*VND7*等开关基因对各个次生壁组分合成基因的影响已有很多报道(Mitsuda等2007; Wang和Dixon 2012; Nakano等2015; 黄成和李来庚2016)。目前,拟南芥*MYB58*、*MYB63*、*MYB85*和*BLH6*转录因

子以及其他植物中的直系同源基因被认为是调控网络中第三层的转录因子(图3),较专一地调控木质素的生物合成(Bomal等2008; Zhong等2008; Cassan-Wang等2013; 郭光艳等2015)。MYB58和MYB63是两个紧密相关的转录因子,并且是第二层次转录因子MYB46/83的直接靶标(Zhou等2009)。在MYB58/MYB63基因表达量受到抑制的转基因植株中,木质素的合成减少,导致次生壁加厚减弱,茎秆机械支持能力减弱;在MYB58/MYB63超表达植株中,木质素合成基因表达上调,木质素沉积增多,但是纤维素和半纤维素含量并没有明显变化(Zhou等2009)。BLH6也受到MYB46的直接调控(Zhong和Ye 2014; Liu等2015),在*blh6*突变体中,纤维细胞木质化程度降低(Cassan-Wang等2013)。MYB61的超表达植株的木质素异常沉积(Newman等2004; Romano等2012)。与MYB58/63恰恰相反,同样处于第三层次的MYB4、MYB7和MYB32转录因子以及它们在其他植物中的同源基因,则负向调控木质素的生物合成(Jin等2000; Preston等2004; Sonbol等2009; Fornale等2010; Legay等2010; Shen等2012)。在其他植物中,我们发现纤维素合成基因CESA4和CESA8,木聚糖合成基因IRX14(Lee等2010)、IRX10(Brown等2009)、PARVUS(Lee等2007)、UDP-Xyl Synthase 3 (UXS3)和UXS6(Pattathil等2005)受到第一层次转录因子SWNs基因的直接调控(Zhong和Ye 2014)。水稻MYB103L属于第二至第三层次的转录因子,调控CESA4、CESA7、CESA9和BCI基因的表达(Ye等2015)。

7 展望

维管束组织的木质部导管、纤维细胞和花药皮层次生细胞壁加厚的主要调控网络已经研究得相当清楚(图3)。多个物种中的研究表明,SWNs在次生细胞壁加厚调控网络中执行类似的功能(Zhong和Ye 2010, 2014),例如,在*nst1 nst3*双突变体中,用SND1启动子驱动VND1~VND7基因的表达能恢复突变体的表型(Zhou等2014)。但在不同的细胞类型中,这些SWNs基因又发挥着各自特殊的调控功能。

作为调控网络第二层次的SND3、MYB46、MYB103和KNAT7是SWNs的直接靶标基因(Zhong等2010a)。对SND1和VND7的研究表明,SWNs不仅调控其下游转录因子的表达,而且也直接调控

细胞壁合成、细胞壁修饰以及程序性死亡基因的表达(Ohashi-Ito等2010)。对SWNs直接靶标基因的启动子研究发现,它们都含有SNBE顺式作用元件(Zhong和Ye 2011)。大多纤维素、半纤维素和木质素合成基因的启动子序列中都含有SNBE位点,说明它们可能也受到SWNs的直接调控(Zhong和Ye 2014)。

植物从种子生长发育成一个完整的个体,虽然细胞中存在着同一套基因组,但是不同生长时期、不同的组织部位、不同的细胞类型中,都有自己单独的一套基因表达模式。次生壁加厚现象除了在维管束中的导管和纤维细胞中存在,果实中的石细胞、种皮、树叶、花药的皮层细胞中也有发生(Mitsuda和Ohme-Takagi 2008; Zhong和Ye 2014)。另外,次生壁基因的表达也会受到激素的调控,黄成和李来庚(2016)在综述中做了详尽的描述。同一个基因(如KNAT7转录因子基因)在不同的细胞中起的作用不同(Brown等2005; Zhong等2008)。植物体中存在次生壁加厚的厚壁组织细胞和不加厚的薄壁组织细胞,通过不同的调节机制调控一系列转录因子和细胞壁合成基因的表达,以达到组织细胞分化的目的。随着研究的深入和系统化,我们越来越认识到,单单通过表型分析和单个基因的功能研究不足以解释细胞壁加厚的过程。通过对共表达分析和ChIP结合高通量测序方法、合适的蛋白标记和细胞学方法以及转录组-蛋白组分析等方法的综合运用,将更好地揭示不同层级转录因子在次生壁加厚过程中的功能。

参考文献

- Avci U, Petzold HE, Ismail IO, Beers EP, Haigler CH (2008). Cysteine proteases XCP1 and XCP2 aid micro-autolysis within the intact central vacuole during xylogenesis in *Arabidopsis* roots. *Plant J*, 56 (2): 303–318
- Bhargava A, Ahad A, Wang S, Mansfield SD, Haighn GW, Douglas CJ, Ellis BE (2013). The interacting MYB75 and KNAT7 transcription factors modulate secondary cell wall deposition both in stems and seed coat in *Arabidopsis*. *Planta*, 237 (5): 1199–1211
- Bomal C, Bedon F, Caron S, Mansfield SD, Levasseur C, Cooke JE, Blais S, Tremblay L, Morency MJ, Pavy N, et al (2008). Involvement of *Pinus taeda* MYB1 and MYB8 in phenylpropanoid metabolism and secondary cell wall biogenesis: a comparative *in planta* analysis. *J Exp Bot*, 59 (14): 3925–3939
- Brown DM, Zeef LA, Ellis J, Goodacre R, Turner SR (2005). Identification of novel genes in *Arabidopsis* involved in secondary cell

- wall formation using expression profiling and reverse genetics. *Plant Cell*, 17 (8): 2281–2295
- Brown DM, Zhang Z, Stephens E, Dupree P, Turner SR (2009). Characterization of IRX10 and IRX10-like reveals an essential role in glucuronoxylan biosynthesis in *Arabidopsis*. *Plant J*, 57: 732–746
- Cassan-Wang H, Goué N, Saidi MN, Legay S, Sivadon P, Goffner D, Grima-Pettenati J (2013). Identification of novel transcription factors regulating secondary cell wall formation in *Arabidopsis*. *Front Plant Sci*, 4: 189
- Desprez T, Juraniec M, Crowell EF, Jouy H, Pochylova Z, Parcy F, Hofte H, Gonneau M, Vernhettes S (2007). Organization of cellulose synthase complexes involved in primary cell wall synthesis in *Arabidopsis thaliana*. *Proc Natl Acad Sci USA*, 104: 15572–15577
- Du Q, Avci U, Li S, Galleo-Giraldo L, Pattathil S, Qi L, Hahn MG, Wang H (2015). Activation of *miR165b* represses *AtHB15* expression and induces pith secondary wall development in *Arabidopsis*. *Plant J*, 83 (3): 388–400
- Du Q, Wang H (2015). The role of HD-ZIP III transcription factors and *miR165/166* in vascular development and secondary cell wall formation. *Plant Signal Behav*, 10 (10): e1078955
- Endo H, Yamaguchi M, Tamura T, Nakano Y, Nishikubo N, Yoneda A, Kato K, Kubo M, Kajita S, Katayama Y, et al (2015). Multiple classes of transcription factors regulate the expression of *VASCULAR-RELATED NAC-DOMAIN7*, a master switch of xylem vessel differentiation. *Plant Cell Physiol*, 56 (2): 242–254
- Fornalé S, Shi X, Chai C, Encina A, Irar S, Capellades M, Fuguet E, Torres JL, Rovira P, Puigdomènech P, et al (2010). ZmMYB31 directly represses maize lignin genes and redirects the phenylpropanoid metabolic flux. *Plant J*, 64: 633–644
- Goicoechea M, Lacombe E, Legay S, Mihaljevic S, Rech P, Jauneau A, Lapierre C, Pollet B, Verhaegen D, Chaubet-Gigot N, et al (2005). EgMYB2, a new transcriptional activator from *Eucalyptus* xylem, regulates secondary cell wall formation and lignin biosynthesis. *Plant J*, 43: 553–567
- Guo GY, Bai F, Liu W, Bi CL (2015). Advances in research of the regulation of transcription factors of lignin biosynthesis. *Sci Agric Sin*, 48 (7): 1277–1287 (in Chinese with English abstract) [郭光艳, 柏峰, 刘伟, 秘彩莉(2015). 转录因子对木质素生物合成调控的研究进展. *中国农业科学*, 48 (7): 1277–1287]
- Hirano K, Kondo M, Aya K, Miyao A, Sato Y, Antonio BA, Namiki N, Nagamura Y, Matsuoka M (2013). Identification of transcription factors involved in rice secondary cell wall formation. *Plant Cell Physiol*, 54 (11): 1791–1802
- Huang C, Li LG (2016). Research progress on regulation of plant secondary cell wall thickening. *Plant Physiol J*, 52 (1): 8–18 (in Chinese with English abstract) [黄成, 李来庚(2016). 植物次生细胞壁加厚调控研究进展. *植物生理学报*, 52 (1): 8–18]
- Jin H, Cominelli E, Bailey P, Parr A, Mehrtens F, Jones J, Tonelli C, Weisshaar B, Martin C (2000). Transcriptional repression by AtMYB4 controls production of UV protecting sunscreens in *Arabidopsis*. *EMBO J*, 19 (22): 6150–6161
- Kim WC, Kim JY, Ko JH, Kang H, Han KH (2014a). Identification of direct targets of transcription factor MYB46 provides insights into the transcriptional regulation of secondary wall biosynthesis. *Plant Mol Biol*, 85 (6): 589–599
- Kim WC, Ko JH, Han KH (2012). Identification of a *cis*-acting regulatory motif recognized by MYB46, a master transcriptional regulator of secondary wall biosynthesis. *Plant Mol Biol*, 78 (4-5): 489–501
- Kim WC, Ko JH, Kim JY, Kim J, Bae HJ, Han KH (2013). MYB46 directly regulates the gene expression of secondary wall-associated cellulose synthases in *Arabidopsis*. *Plant J*, 73 (1): 26–36
- Kim WC, Reza IB, Kim Y, Park S, Thomashow MF, Keegstra K, Han KH (2014b). Transcription factors that directly regulate the expression of *CSLA9* encoding mannan synthase in *Arabidopsis thaliana*. *Plant Mol Biol*, 84 (4-5): 577–587
- Kubo M, Udagawa M, Nishikubo N, Horiguchi G, Yamaguchi M, Ito J, Mimura T, Fukuda H, Demura T (2005). Transcription switches for protoxylem and metaxylem vessel formation. *Genes Dev*, 19 (16): 1855–1860
- Lee C, Teng Q, Huang W, Zhong R, Ye ZH (2010). The *Arabidopsis* family GT43 glycosyltransferases form two functionally nonredundant groups essential for the elongation of glucuronoxylan backbone. *Plant Physiol*, 153 (2): 526–541
- Lee C, Zhong R, Richardson EA, Himmelsbach DS, McPhail BT, Ye ZH (2007). The *PARVUS* gene is expressed in cells undergoing secondary wall thickening and is essential for glucuronoxylan biosynthesis. *Plant Cell Physiol*, 48 (12): 1659–1672
- Legay S, Sivadon P, Blervacq AS, Pavy N, Baghdady A, Tremblay L, Levasseur C, Ladouce N, Lapierre C, Séguin A, et al (2010). EgMYB1, an R2R3 MYB transcription factor from eucalyptus negatively regulates secondary cell wall formation in *Arabidopsis* and poplar. *New Phytol*, 188: 774–786
- Li E, Bhargava A, Qiang W, Friedmann MC, Forneris N, Savidge RA, Johnson LA, Mansfield SD, Ellis BE, Douglas CJ (2012a). The Class II *KNOX* gene *KNAT7* negatively regulates secondary wall formation in *Arabidopsis* and is functionally conserved in *Populus*. *New Phytol*, 194 (1): 102–115
- Li E, Wang S, Liu Y, Chen JG, Douglas CJ (2011). OVATE FAMILY PROTEIN4 (OFP4) interaction with KNAT7 regulates secondary cell wall formation in *Arabidopsis thaliana*. *Plant J*, 67 (2): 328–341
- Li Q, Lin YC, Sun YH, Song J, Chen H, Zhang XH, Sederoff RR, Chiang VL (2012b). Splice variant of the SND1 transcription factor is a dominant negative of SND1 members and their regulation in *Populus trichocarpa*. *Proc Natl Acad Sci USA*, 109 (36): 14699–14704
- Li Z, Fernie AR, Persson S (2016a). Transition of primary to secondary cell wall synthesis. *Sci Bull*, 61 (11): 838–846
- Li Z, Omranian N, Neumetzler L, Wang T, Herter T, Usadel B, Demura T, Giavalisco P, Nikoloski Z, Persson S (2016b). A transcriptional and metabolic framework for secondary wall formation in *Arabidopsis*. *Plant Physiol*, 172 (2): 1334–1351
- Liu Y, Douglas CJ (2015). A role for OVATE FAMILY PROTEIN1 (OFP1) and OFP4 in a BLH6-KNAT7 multi-protein complex regulating secondary cell wall formation in *Arabidopsis thaliana*. *Plant Signal Behav*, 10 (7): e1033126
- Mansoori N, Timmers J, Desprez T, Alvim-Kamei CL, Dees DC,

- Vincken JP, Visser RG, Höfte H, Vernhettes S, Trindade LM (2014). KORRIGAN1 interacts specifically with integral components of the cellulose synthase machinery. *PLoS ONE*, 9 (11): e112387
- McCarthy RL, Zhong R, Fowler S, Lyskowski D, Piyasena H, Carleton K, Spicer C, Ye ZH (2010). The poplar MYB transcription factors, PtrMYB3 and PtrMYB20, are involved in the regulation of secondary wall biosynthesis. *Plant Cell Physiol*, 51 (6): 1084–1090
- McCarthy RL, Zhong R, Ye ZH (2009). MYB83 is a direct target of SND1 and acts redundantly with MYB46 in the regulation of secondary cell wall biosynthesis in *Arabidopsis*. *Plant Cell Physiol*, 50 (11): 1950–1964
- McCarthy RL, Zhong R, Ye ZH (2011). Secondary wall NAC binding element (SNBE), a key *cis*-acting element required for target gene activation by secondary wall NAC master switches. *Plant Signal Behav*, 6 (9): 1282–1285
- McFarlane HE, Döring A, Persson S (2014). The cell biology of cellulose synthesis. *Annu Rev Plant Biol*, 65: 69–94
- Mitsuda N, Iwase A, Yamamoto H, Yoshida M, Seki M, Shinozaki K, Ohme-Takagi M (2007). NAC transcription factors, NST1 and NST3, are key regulators of the formation of secondary walls in woody tissues of *Arabidopsis*. *Plant Cell*, 19 (1): 270–280
- Mitsuda N, Ohme-Takagi M (2008). NAC transcription factors NST1 and NST3 regulate pod shattering in a partially redundant manner by promoting secondary wall formation after the establishment of tissue identity. *Plant J*, 56 (5): 768–778
- Mitsuda N, Seki M, Shinozaki K, Ohme-Takagi M (2005). The NAC transcription factors NST1 and NST2 of *Arabidopsis* regulate secondary wall thickenings and are required for anther dehiscence. *Plant Cell*, 17 (11): 2993–3006
- Nakano Y, Yamaguchi M, Endo H, Rejab NA, Ohtani M (2015). NAC-MYB-based transcriptional regulation of secondary cell wall biosynthesis in land plants. *Front Plant Sci*, 6: 288
- Newman LJ, Perazza DE, Juda L, Campbell MM (2004). Involvement of the R2R3-MYB, AtMYB61, in the ectopic lignification and dark-photo morphogenic components of the *det3* mutant phenotype. *Plant J*, 37 (2): 239–250
- Noda S, Koshiha T, Hattori T, Yamaguchi M, Suzuki S, Umezawa T (2015). The expression of a rice secondary wall-specific cellulose synthase gene, *OsCesA7*, is directly regulated by a rice transcription factor, OsMYB58/63. *Planta*, 242 (3): 589–600
- Ohashi-Ito K, Oda Y, Fukuda H (2010). *Arabidopsis* VASCULAR-RELATED NAC-DOMAIN6 directly regulates the genes that govern programmed cell death and secondary wall formation during xylem differentiation. *Plant Cell*, 22 (10): 3461–3473
- Ohtani M, Nishikubo N, Xu B, Yamaguchi M, Mitsuda N, Goué N, Shi F, Ohme-Takagi M, Demura T (2011). A NAC domain protein family contributing to the regulation of wood formation in poplar. *Plant J*, 67 (3): 499–512
- Pattathil S, Harper AD, Bar-Peled M (2005). Biosynthesis of UDP-xyllose: characterization of membrane-bound At *Uxs2*. *Planta*, 221 (4): 538–548
- Patzlaff A, McInnis S, Courtenay A, Surman C, Newman LJ, Smith C, Bevan MW, Mansfield S, Whetten RW, Sederoff RR, et al (2003). Characterization of a pine MYB that regulates lignification. *Plant J*, 36: 743–754
- Persson S, Paredes A, Carroll A, Palsdottir H, Doblin M, Poindexter P, Khitrov N, Auer M, Somerville CR (2007). Genetic evidence for three unique components in primary cell-wall cellulose synthase complexes in *Arabidopsis*. *Proc Natl Acad Sci USA*, 104: 15566–15571
- Preston J, Wheeler J, Heazlewood J, Li SF, Parish RW (2004). *AtMYB32* is required for normal pollen development in *Arabidopsis thaliana*. *Plant J*, 40 (6): 979–995
- Romano JM, Dubos C, Prouse MB, Wilkins O, Hong H, Poole M, Kang KY, Li E, Douglas CJ, Western TL, et al (2012). AtMYB61, an R2R3-MYB transcription factor, functions as a pleiotropic regulator via a small gene network. *New Phytol*, 195 (4): 774–786
- Shen H, He X, Poovaiah CR, Wuddineh WA, Ma J, Mann DG, Wang H, Jackson L, Tang Y, Stewart CN Jr, et al (2012). Functional characterization of the switchgrass (*Panicum virgatum*) R2R3-MYB transcription factor PvMYB4 for improvement of lignocellulosic feedstocks. *New Phytol*, 193: 121–136
- Sonbol FM, Fornalé S, Capellades M, Encina A, Touriño S, Torres JL, Rovira P, Ruel K, Puigdomènech P, Rigau J, et al (2009). The maize ZmMYB42 represses the phenylpropanoid pathway and affects the cell wall structure, composition and degradability in *Arabidopsis thaliana*. *Plant Mol Biol*, 70: 283–296
- Soyano T, Thitamadee S, Machida Y, Chua NH (2008). *ASYMMETRIC LEAVES2-LIKE19/LATERAL ORGAN BOUNDARIES DOMAIN30* and *ASL20/LBD18* regulate tracheary element differentiation in *Arabidopsis*. *Plant Cell*, 20 (12): 3359–3373
- Steiner-Lange S, Unte US, Eckstein L, Yang C, Wilson ZA, Schmelzer E, Dekker K, Saedler H (2003). Disruption of *Arabidopsis thaliana* MYB26 results in male sterility due to non-dehiscent anthers. *Plant J*, 34 (4): 519–547
- Sun X, Wang C, Xiang N, Li X, Yang S, Du J, Yang Y, Yang Y (2017). Activation of secondary cell wall biosynthesis by miR319-targeted *TCP4* transcription factor. *Plant Biotechnol J*, 15 (10): 1284–1294
- Taylor NG, Howells RM, Huttly AK, Vickers K, Turner SR (2003). Interactions among three distinct Cesa proteins essential for cellulose synthesis. *Proc Natl Acad Sci USA*, 100: 1450–1455
- Taylor NG, Laurie S, Turner SR (2000). Multiple cellulose synthase catalytic subunits are required for cellulose synthesis in *Arabidopsis*. *Plant Cell*, 12: 2529–2540
- Taylor NG, Scheible WR, Cutler S, Somerville CR, Turner SR (1999). The *irregular xylem3* locus of *Arabidopsis* encodes a cellulose synthase required for secondary cell wall synthesis. *Plant Cell*, 11: 769–780
- Taylor-Teeple M, Lin L, de Lucas M, Turco G, Toal TW, Gaudinier A, Young NF, Trabucco GM, Veling MT, Lamothe R, et al (2015). An *Arabidopsis* gene regulatory network for secondary cell wall synthesis. *Nature*, 517 (7536): 571–575
- Vain T, Crowell EF, Timpano H, Biot E, Desprez T, Mansoori N, Trindade LM, Pagant S, Robert S, Höfte H, et al (2014). The cellulose KORRIGAN is part of the cellulose synthase complex. *Plant Physiol*, 165 (4): 1521–1532

- Wang H, Avci U, Nakashima J, Hahn MG, Chen F, Dixon RA (2010). Mutation of WRKY transcription factors initiates pith secondary wall formation and increases stem biomass in dicotyledonous plants. *Proc Natl Acad Sci USA*, 107 (51): 22338–22343
- Wang HZ, Dixon RA (2012). On-off switches for secondary cell wall biosynthesis. *Mol Plant*, 5 (2): 297–303
- Wang RF, Hu YS, Gao WH, Zhang YX, Song XS (2014). Functions of NAC transcription factors family in stress responses in plants. *Plant Physiol J*, 50 (10): 1494–1500 (in Chinese with English abstract) [王瑞芳, 胡银松, 高文蕊, 张宜欣, 宋兴舜(2014). 植物NAC转录因子家族在抗逆响应中的功能. *植物生理学报*, 50 (10): 1494–1500]
- Yamaguchi M, Goué N, Igarashi H, Ohtani M, Nakano Y, Mortimer JC, Nishikubo N, Kubo M, Katayama Y, Kakegawa K, et al (2010a). VASCULAR-RELATED NAC-DOMAIN6 and VASCULAR-RELATED NAC-DOMAIN7 effectively induce trans-differentiation into xylem vessel elements under control of an induction system. *Plant Physiol*, 153 (3): 906–914
- Yamaguchi M, Kubo M, Fukuda H, Demura T (2008). VASCULAR-RELATED NAC-DOMAIN7 is involved in the differentiation of all types of xylem vessels in *Arabidopsis* roots and shoots. *Plant J*, 55 (4): 652–664
- Yamaguchi M, Ohtani M, Mitsuda N, Kubo M, Ohme-Takagi M, Fukuda H, Demura T (2010b). VND-INTERACTING2, a NAC domain transcription factor, negatively regulates xylem vessel formation in *Arabidopsis*. *Plant Cell*, 22 (4): 1249–1263
- Yang C, Xu Z, Song J, Conner K, Vizcay Barrena G, Wilson ZA (2007). *Arabidopsis* MYB26/MALE STERILE35 regulates secondary thickening in the endothecium and is essential for anther dehiscence. *Plant Cell*, 19 (2): 534–548
- Ye Y, Liu B, Zhao M, Wu K, Cheng W, Chen X, Liu Q, Liu Z, Fu X, Wu Y (2015). CEF1/OsMYB103L is involved in GA-mediated regulation of secondary wall biosynthesis in rice. *Plant Mol Biol*, 89 (4–5): 385–401
- Yoshida K, Sakamoto S, Kawai T, Kobayashi Y, Sato K, Ichinose Y, Yaoi K, Akiyoshi-Endo M, Sato H, Takamizo T (2013). Engineering the *Oryza sativa* cell wall with rice NAC transcription factors regulating secondary wall formation. *Front Plant Sci*, 4: 383
- Zhang BC, Zhou YH (2015). Plant cell wall formation and regulation. *Sci Sin Vitae*, 45 (6): 544–556 (in Chinese with English abstract) [张保才, 周奕华(2015). 植物细胞壁形成机制的新进展. *中国科学: 生命科学*, 45 (6): 544–556]
- Zhao C, Avci U, Grant EH, Haigler CH, Beers EP (2008). XND1, a member of the NAC domain family in *Arabidopsis thaliana*, negatively regulates lignocellulose synthesis and programmed cell death in xylem. *Plant J*, 53 (3): 425–436
- Zhao C, Johnson BJ, Kositsup B, Beers EP (2000). Exploiting secondary growth in *Arabidopsis*. Construction of xylem and bark cDNA libraries and cloning of three xylem endopeptidases. *Plant Physiol*, 123: 1185–1196
- Zhao Y, Sun J, Xu P, Zhang R, Li L (2014). Intron-mediated alternative splicing of WOOD-ASSOCIATED NAC TRANSCRIPTION FACTOR1B regulates cell wall thickening during fiber development in *Populus* species. *Plant Physiol*, 164 (2): 765–776
- Zhong R, Demura T, Ye ZH (2006). SND1, a NAC domain transcription factor, is a key regulator of secondary wall synthesis in fibers of *Arabidopsis*. *Plant Cell*, 18 (11): 3158–3170
- Zhong R, Lee C, McCarthy RL, Reeves CK, Jones EG, Ye ZH (2011a). Transcriptional activation of secondary wall biosynthesis by rice and maize NAC and MYB transcription factors. *Plant Cell Physiol*, 52 (10): 1856–1871
- Zhong R, Lee C, Ye ZH (2010a). Global analysis of direct targets of secondary wall NAC master switches in *Arabidopsis*. *Mol Plant*, 3 (6): 1087–1103
- Zhong R, Lee C, Ye ZH (2010b). Evolutionary conservation of the transcriptional network regulating secondary cell wall biosynthesis. *Trends Plant Sci*, 15 (11): 625–632
- Zhong R, Lee C, Ye ZH (2010c). Functional characterization of poplar wood-associated NAC domain transcription factors. *Plant Physiol*, 152 (2): 1044–1055
- Zhong R, Lee C, Zhou J, McCarthy RL, Ye ZH (2008). A battery of transcription factors involved in the regulation of secondary cell wall biosynthesis in *Arabidopsis*. *Plant Cell*, 20 (10): 2763–2782
- Zhong R, McCarthy RL, Haghighat M, Ye ZH (2013). The poplar MYB master switches bind to the SMRE site and activate the secondary wall biosynthetic program during wood formation. *PLoS ONE*, 8 (7): e69219
- Zhong R, McCarthy RL, Lee C, Ye ZH (2011b). Dissection of the transcriptional program regulating secondary wall biosynthesis during wood formation in poplar. *Plant Physiol*, 157 (3): 1452–1468
- Zhong R, Richardson EA, Ye ZH (2007a). Two NAC domain transcription factors, SND1 and NST1, function redundantly in regulation of secondary wall synthesis in fibers of *Arabidopsis*. *Planta*, 225 (6): 1603–1611
- Zhong R, Richardson EA, Ye ZH (2007b). The MYB46 transcription factor is a direct target of SND1 and regulates secondary wall biosynthesis in *Arabidopsis*. *Plant Cell*, 19 (9): 2776–2792
- Zhong R, Ye ZH (2010). The poplar PtrWNDs are transcriptional activators of secondary cell wall biosynthesis. *Plant Signal Behav*, 5 (4): 469–472
- Zhong R, Ye ZH (2011). MYB46 and MYB83 bind to the SMRE sites and directly activate a suite of transcription factors and secondary wall biosynthetic genes. *Plant Cell Physiol*, 53 (2): 368–380
- Zhong R, Ye ZH (2014). Complexity of the transcriptional network controlling secondary wall biosynthesis. *Plant Sci*, 229: 193–207
- Zhong R, Ye ZH (2015). The *Arabidopsis* NAC transcription factor NST2 functions together with SND1 and NST1 to regulate secondary wall biosynthesis in fibers of inflorescence stems. *Plant Signal Behav*, 10 (2): e989746
- Zhou J, Lee C, Zhong R, Ye ZH (2009). MYB58 and MYB63 are transcriptional activators of the lignin biosynthetic pathway during secondary cell wall formation in *Arabidopsis*. *Plant Cell*, 21 (1): 248–266
- Zhou J, Zhong R, Ye ZH (2014). *Arabidopsis* NAC domain proteins, VND1 to VND5, are transcriptional regulators of secondary wall biosynthesis in vessels. *PLoS ONE*, 9 (8): e105726

Research progress in the transcriptional regulation of secondary cell wall thickening

ZHU Xiao-Bo, ZHANG Gui-Fen, CHEN Peng*

Biomass and Bioenergy Research Center, Faculty of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, China

Abstract: Vascular bundles in dicot and monocot plants hold vessels that are essential for plants to transport water. Similar to the xylem vessel cells, sclerenchyma and collenchyma cells, which provide mechanical support for the plant body, also undergo substantial secondary cell wall thickening. Biosynthesis of the secondary cell wall is a complex process that needs to be coordinated with plant growth. This review summarizes recent findings for the transcriptional regulation of secondary cell wall biosynthesis to facilitate a comprehensive understanding of how the secondary cell wall thickening is regulated during vascular tissue development.

Key words: vascular bundle; secondary cell wall; transcription factor; regulatory network

Received 2017-06-05 Accepted 2017-09-13

This work was supported by the Fundamental Research Funds for the Central Universities (Grant No. 52902-0900202688).

*Corresponding author (E-mail: chenpeng@mail.hzau.edu.cn).