

# 植物表皮毛发育分子调控机制的研究进展

曹敏<sup>1</sup>, 张璐<sup>1</sup>, 高新梅<sup>1</sup>, 张良邦<sup>1</sup>, 李文强<sup>1</sup>, 郭万里<sup>2\*</sup>

(1. 西北农林科技大学农学院, 陕西杨凌 712100; 2. 浙江大学农业与生物技术学院作物科学研究所, 浙江杭州 310058)

**摘要** 植物表皮毛在环境和植物相互作用中起到缓冲区域的重要作用, 而细胞发育分化的独特性使其成为研究细胞发育调控和细胞命运决定等过程的最佳体系。近年来, 随着分子生物学等技术的快速发展, 植物表皮毛发育分子调控机制的研究发展较快。特别是模式植物拟南芥的部分关键的调控基因已经被克隆并获得其功能信息, 为其他植物复杂表皮毛的研究和农业应用提供了理论指导。该研究主要以表皮毛发育时间的先后顺序综述该领域的研究进展、影响因素和其他植物表皮毛研究的现状, 以为大众和研究者提供比较全面的有关植物非分泌型表皮毛分子调控研究的进展信息。

**关键词** 植物; 表皮毛; 发育; 分子调控

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## Research Progress of Molecular Regulation Mechanism in the Development of Plant Trichomes

CAO Min et al (College of Agronomy, Northwest Agriculture and Forestry University, Yangling, Shaanxi 712100)

**Abstract** The trichome is one of the core factors to protect plant from the environmental stress conditions and acts as buffer zone between plant surface and environment. Furthermore, the specificity of developmental and differentiation of the trichome cell make it one of the optimal system to study the regulation of cell development and cell fate determination. Recently, the development of the molecular regulation mechanism of trichome developed quickly with the improvement of the techniques in life science, specially in Molecular Biology. Some genes related to trichome have been cloned from modern plant *Arabidopsis* and their functions are also known well now. Those results provide the theoretical guidance for complex trichomes in plants and agricultural breeding. In this review, we want to show the molecular regulation of trichome development by its developing time, the factors that effecting trichome development, and the development of the trichome in other plants. Thus we hope this review would offer the recent developmental information of the plant trichome without secretory gland to people and researchers.

**Key words** Plant; Trichome; Development; Molecular regulation

植物表皮毛(Trichome)是地上部分表皮组织所延伸出来的一种毛状结构附属物<sup>[1]</sup>。表皮毛增加了植物表皮层的厚度, 为表皮层和环境间构筑一道天然物理屏障, 减少了植物体内水分的流失和热量的过多积累、消耗, 在一定程度上减轻有害生物的危害、冷冻、紫外线和机械损伤; 另外, 有腺体的表皮毛还可分泌生物碱、芳香油和树脂等化学物质来防御生物和非生物胁迫以及信号传递<sup>[2-4]</sup>。另一方面, 农作物水稻表皮毛缺失的光叶壳表型(光叶稻)有利于作物收获、后续加工, 因而被广泛利用到育种实践中<sup>[5-6]</sup>。例如, 绝大多数美国稻均为光叶稻, 亚洲也有大量种植, 尤其是在我国云南、贵州一带。光叶稻不仅具有高产、优质、抗倒伏等优良特性, 而且具有广亲和性, 因而是开展水稻高产优质育种的重要种质资源<sup>[7-10]</sup>。植物表皮毛发育模式的分子水平研究显得尤为重要, 不仅涉及细胞分化的理论基础, 而且对农业生产具有潜在的指导意义<sup>[11-12]</sup>。

## 1 植物表皮毛研究概况

在植物形态建成中, 主要包括胚胎发育、营养生长、生殖生长3个阶段。在这些阶段中, 人们所关注的一个共同点是分生组织功能转变过程中细胞命运的决定, 而细胞命运则由细胞增殖、分化、细胞间信号传导及细胞形态发生等一系列过程的相互平衡来控制。在植物器官发生时, 表皮毛就开始

发育, 表皮毛的分化与叶片发育、激素水平和生长发育阶段密切相关, 其细胞的分化潜能受到高度协同调控<sup>[13-17]</sup>。

在模式植物拟南芥(*Arabidopsis*)中, 由于表皮毛起源于表皮细胞, 试验操作相对简单, 它成为细胞分化、细胞周期调控、细胞极性、细胞扩展等研究的模式系统<sup>[11, 18-19]</sup>。目前, 拟南芥中已报道的表皮毛突变体有70多个, 其中30多个与表皮毛生长发育相关的基因已被克隆。它们分别控制表皮毛起始、形态发生、分布和数量<sup>[20]</sup>。这些基因大部分编码转录因子, 包括MYB类、bHLH类和TTG类转录因子<sup>[21-25]</sup>。

## 2 植物表皮毛发育的分子调控机制

目前, 人们已经基本阐明表皮毛起始、发育及分化的基本过程<sup>[18]</sup>。这主要得益于对拟南芥各种表皮毛突变体的系统分析。表皮毛细胞的选择、起始以及细胞命运的决定都是由一组表皮毛发育模式基因(Patterning genes)来高度调控的<sup>[26-27]</sup>。在这些基因中, 一些基因会启动相应的细胞信号, 从而控制表皮细胞的分化及表皮毛细胞的决定。与此同时, 核内复制基因(Endoreduplication genes)会专门调控从有丝分裂期到核内DNA复制期的转换以及核内复制的周期数; 一些基因调控表皮毛的分支; 另有一些基因则控制表皮毛的生长方向和体积的变化<sup>[28-29]</sup>。同时, 植物激素合成及其信号途径因子也参与表皮毛的精细调控<sup>[3]</sup>。

**2.1 植物表皮毛起始(Initiation)调控** 拟南芥表皮毛的起始需要不同基因的共同作用。目前已知的主要调控基因都为转录因子, 有GL1(GLABRA1, 属于MYB类因子)、TTG1(WD40)、GL3(GLABRA3, 属于bHLH类因子)、EGL3(ENHANCER of GLABRA3, 也属于bHLH类因子)、GL2(Homologous domain-leucine zipper protein/HD-ZIP IV类家族)、TRY(R3

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**作者简介** 曹敏(1991-), 女, 山西朔州人, 本科生, 专业: 农学。\*通讯作者, 讲师, 从事植物分子逆境生理方面的研究, E-mail: wlguo@zju.edu.cn。

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MYB TRIPTYCHON)、CPC 和 ETC1 等<sup>[2,12,18,23,26,29-30]</sup>。其中, GL1 或 TTG1 突变可引起表皮毛的完全缺失, GL3 的突变可引起表皮毛数量的减少。因此, 这 3 个基因是表皮毛发育的正调控因子<sup>[12]</sup>。另外, GL3 和它的高度同源基因 EGL3 在功能上具有冗余性, 双突变则导致表皮毛完全缺失<sup>[31]</sup>。在表皮毛发育的负调控基因中, TRY 突变引起表皮毛簇生, 表明表皮毛细胞决定的旁侧抑制受到影响; CPC 突变引起表皮毛数量增多; ETC1/ETC2 在功能上与 TRY 和 CPC 具有重叠性, 具有 TRY 和 CPC 的增强子作用。try-cpc 双突变体表现为表皮毛严重簇生, 每簇可多达 40 个表皮毛; 而 try-cpc-etc1 三突变体的表皮毛则完全覆盖整个叶片<sup>[32-33]</sup>。

拟南芥表皮毛的起始主要通过正调控因子 GL1-GL3-TTG1 形成调控复合体, 引起 GL2 在表皮毛细胞中的特异性表达<sup>[22,31,34-36]</sup>。GL2 所编码的 HD-ZIP 转录因子是介导表皮毛发育起始和细胞分化的第 1 个靶基因<sup>[12]</sup>。GL1-GL3-TTG1 复合体同时会激活表皮毛发育的负调控因子, 如 TRY/CPC 和 ETC1 等。这些负调控因子通过细胞间传递到临近细胞, 阻遏该细胞中 GL1-GL3-TTG1 复合体的活性, 从而强烈抑制 GL2 的表达, 使旁侧细胞发育成非表皮毛细胞<sup>[2,18,29,32,36]</sup>, 也说明可传递性转录因子可介导细胞间信号的传导。最新研究表明, GL3 能整合环境信号来调控表皮毛的发育<sup>[4]</sup>。

**2.2 植物表皮毛分支 (Branching) 调控** 植物表皮毛分支的调控主要涉及细胞内微管 (Microtubule; MT) 的排列。在表皮毛发育过程中, 微管的横向排列转向纵向排列的过程是表皮毛分支的重要过程和特征<sup>[37]</sup>。表皮毛细胞经过微管相关药物处理能导致其分支的生长方向性 (Isotropical expansion) 和分支能力丧失。突变体 zwi (zwichel) 表皮毛有很少的分支, 但当采用微管稳定剂紫杉醇 (Taxol) 短暂处理该突变体时能诱导新的表皮毛分支位点<sup>[37-38]</sup>。ZWI 能驱动蛋白类似植物钙调素结合蛋白 (Kinesin-like calmodulin-binding protein) 与微管结合, 并且沿微管正向运动, 说明分支需要沿微管方向的正常运输<sup>[39]</sup>。这些都说明微管在表皮毛分支过程中起着非常重要的作用。有关与形成微管蛋白 ( $\alpha/\beta$ -tubulin) 异源二聚体和微管相关基因的突变能持续性影响表皮毛的分支。显性负向突变体 (Dominant-negative mutations)  $\alpha$ -tubulin 4 和 6 导致微管不稳定, 最终抑制表皮毛的分支<sup>[40]</sup>, 而导致微管稳定的突变体  $\alpha$ -tubulin 6 allele (TUA6D251A/E254A) 能促进表皮毛新分支的形成<sup>[41]</sup>。KIS (KIESEL) 和 POR (PORCINO) 编码微管折叠共同作用因子 A 和 C 的主要功能是完成  $\alpha/\beta$ -tubulin 的组装; KATANIN-p60 是微管切割蛋白 (MT-severing protein)。这些基因的突变导致表皮毛的分支减少<sup>[42-44]</sup>。这些说明微管的重新合成和解聚对表皮毛的分支很关键, 具体的作用机制还有待深入研究。

**2.3 植物表皮毛伸长 (Expansion) 调控** 分支形成后, 表皮毛沿着整个细胞轴线延伸, 而不是通过顶端生长来完成伸长过程<sup>[45]</sup>。表皮毛正向伸长基于机动蛋白骨架 (Actin cytoskeleton) 即微丝。微丝细胞骨架在表皮毛发育早期比较分

散, 而在表皮毛伸长时聚集成厚的束状, 沿着生长轴线一直到表皮毛成熟。采用微丝作用药物处理表皮毛能引起微丝束的非正常组装, 其表型类似于相关突变体的表皮毛表型<sup>[46-47]</sup>, 例如 DISTORTED (Subunits of the actin-related protein2/3) 和 WAVE (Wiskott-Aldrich syndrome protein family verprolin homologous protein) 的突变体<sup>[48]</sup>。器官如高尔基体和过氧化物酶体 (Peroxisomes) 是沿着微丝运动的。Arp2/3 复合体的一个亚单位的基因出现突变, 表皮毛非伸长区域 (F-actin 积累密度较大) 积累了大量的高尔基体, 而过氧化物酶体的移动性降低; 但在表皮毛伸长区域, 高尔基体和过氧化物酶体的移动是正常的<sup>[38]</sup>。微丝也参与内膜的融合, 表皮毛细胞内一般有一个大的液泡, 但突变体 wurm 和 distorted1 (Arp2/3 的亚基) 表皮毛细胞内大液泡附近有很多小的液泡<sup>[49]</sup>, 具体的发生机制不详。

**2.4 植物激素在表皮毛发育中的作用** 近期的研究发现, 次霉素 (GA, Gibberellins)、水杨酸 (SA, Salicylic acid)、茉莉酸 (JA, Jasmonic acid) 和细胞分裂素 (CK, Cytokinin) 的生物合成途径或信号传导途径参与表皮毛发育的起始。植物激素 GA 和 JA 能增加表皮毛的数量和密度, 而 SA 的作用相反<sup>[50]</sup>。主要原因是这些激素影响 WD-repeat/bHLH/MYB 复合体相关基因的表达。其中, GA 和 CK 主要依赖 C2H2 转录因子 (如 GIS1、GIS2、ZFP5、ZFP6 和 ZFP8) 来促进 GL1 的表达, 启动表皮毛的发生<sup>[17,51-54]</sup>。GA 突变体 spy-5 中表皮毛分支增加<sup>[17]</sup>。另外, JA 信号通路 JAZ 因子能与 bHLH 转录因子 (GL3、EGL3 和 TT8) 和 MYB 类转录因子作用 (MYB75 和 GL1), 即 JA 能诱导 JAZ 蛋白降解, 释放 WD-repeat/bHLH/MYB 复合体, 激活下游因子, 从而启动表皮毛的发生<sup>[55]</sup>。另一方面, MicroRNA156 作用蛋白 SPL9 能绕开 GL1, 直接作用于 TCL1 和 TRY 来启动它们的表达<sup>[56]</sup>, 而不是 GA 和 CK 的作用模式<sup>[51,53,57-58]</sup>。另外, 外施乙烯能增加黄瓜的表皮毛分支<sup>[59]</sup>, 增加棉花内乙烯的合成, 增加分支的长度<sup>[60-61]</sup>。乙烯受体 ETR2 通过调控微管的组装来控制表皮毛的分支。最新的研究表明, 番茄中生长素信号通路因子 SIAA15 参与表皮毛的起始调控<sup>[62]</sup>。因此, 植物激素对表皮毛发育调控作用的研究还处在初始阶段, 有待深入的探讨。

**2.5 植物细胞周期调控因子在表皮毛发育中的作用** 一般情况下, 植物表皮毛细胞发育过程中核内 DNA 复制 4 次, 核 DNA 含量达到 32C (1C 等于单倍体核内 DNA 含量)。在此过程中, 前表皮毛细胞形成分支, 并向细胞外延伸<sup>[63]</sup>。因此, 影响细胞有丝分裂进程和核内 DNA 复制 (包括复制次数的调控) 的因子参与细胞表皮毛的起始和发育。

SIM (SIAMESE) 基因抑制有丝分裂循环, 其突变体呈现多细胞表皮毛性, 而其他形态正常<sup>[64]</sup>。SIM 是细胞周期依赖激酶 (CDKs) 的抑制因子, 能与 D-type cyclins (CYCDs) 和 CDKA 相互作用, 而 CYCD-CDKA 复合体被认为在 (G1)/(S) 转换过程中起作用<sup>[65]</sup>。另外, SIM 也是 B-type cyclin (CYCB, (G2)/(M)) 的抑制因子。在正常情况下, CYCB 是不表达的, 但在 sim 中表达<sup>[66]</sup>。最近研究表明, 番茄中一个含有

bZIP 结构和 START 域的 *Wo* (Woolly) 基因调控 B-type cyclin (*SlCycB2*) 的表达,从而参与表皮毛的发育过程<sup>[67]</sup>。这些说明有丝分裂相关因子参与表皮毛的发育,其功能紊乱导致植物表皮毛的非正常发育。

另一方面,细胞核内 DNA 含量和复制频次的非正常变化同样引起植物表皮毛的非正常发育。*GL3* 和 *TRY* 不仅调控表皮毛的启动,而且影响细胞核内复制周期,突变体 *try* 的表皮毛分支明显增加,其核内 DNA 含量也达到 64C,即细胞核内 DNA 复制增加了 1 个周期<sup>[28]</sup>。相反,突变体 *gl3-1* 表皮毛分支明显减少,其核内 DNA 含量降低到 16C<sup>[68]</sup>。次霉素 GA 信号通路不仅影响表皮毛的分支,而且调控核内 DNA 的复制。突变体 *spy-5* 有过量分支的表皮毛和高的 DNA 含量 (64C)<sup>[69]</sup>,相反的是,突变体叶片几乎无毛,很少的二分叉表皮毛<sup>[7]</sup>。*RHL2* 和 *HYP6* 编码与原始细菌同源的拓扑酶 VI (topoVI) 的亚基,而 topoVI 在 DNA 复制过程中解开染色体 (染色体连锁) 中起着重要的作用<sup>[70]</sup>。突变体 *rhl2* (*root hairless2*) 和 *hyp6* (*hypocotyl6*) 有少量的表皮毛分支和核内复制 (8C)。这 2 个突变体核内复制都能正常进行 2 轮,但后期不能正常进行<sup>[71-72]</sup>。突变体 *cpr5* (CPR5: CONSTITUTIVE PATHOGEN RESPONSE 5, 其突变表型模拟细胞程序性死亡) 有少量的表皮毛分支,并且表皮毛体积减小,核内复制循环停留在第 2 循环结束期<sup>[73]</sup>;通过 *GL2* 启动子表达 *ICK1/KRP1* 的转基因植株出现了同样的现象<sup>[74]</sup>。

泛素降解系统调控蛋白可能负向控制表皮毛的分支和核内 DNA 复制<sup>[75-76]</sup>。编码 E6AP C 末端 (HECT) 的泛素连接酶家族基因 *KAK* (*KAKTUS*) 突变后,出现过量分支的表皮毛,同时核内 DNA 含量达到 64C<sup>[69]</sup>。最新的研究表明,*GL3* 和 *EGL3* 都受泛素系统的调节<sup>[77-78]</sup>。然而,这方面的研究进展缓慢,细胞周期相关蛋白参与表皮毛发育的记载还比较零星,并没有形成系统的调控网络。

### 3 拟南芥以外其他植物表皮毛分子调控机制

拟南芥表皮毛结构相对简单,但更多的植物特别是部分作物的表皮毛形态和调控都比较复杂,其分子机理研究也相对滞后。尽管如此,人们还是取得明显的进展。

人们从玉米中分离出多个与表皮毛及表皮蜡质合成相关的 *GLOSSY* 基因<sup>[79-84]</sup>。其中, *GLOSSY1* (*GL1*) 基因编码叶片表皮蜡质层生物合成代谢途径中的关键因子。*GL1* 的突变对表皮细胞的发育具有多效性,不但改变表皮毛的数量,而且损伤表皮角质层的结构。另外,玉米 HD-ZIP 类转录因子 *OCL4* (Outer cell layer 4) 可能参与抑制多毛的分化<sup>[85]</sup>。

水稻中报道的基因主要有 *gl1*、*gl2*、*Hl1*、*Hl2* 和 *Hg*, 其中 *GL1* (Glabrous leaf and hull-1) 基因位于第 5 连锁群 3.8 ~ 24.8 cM。该突变体 *gl1* 表现为叶片和颖壳都光滑无毛,属于单基因隐性突变<sup>[86]</sup>。目前,该位点找到一个与水稻表皮毛发育的基因 *GLR1* (LOC\_Os05g02730), 涉及 DNA 水平的突变<sup>[87]</sup> 以及可能与 DNA 甲基化等表观遗传学的变化有关<sup>[88]</sup>。*gl2* (*glabrous leaf and hull-2*) 突变体的表型与 *gl1* 突变体相同,叶片和颖壳光滑无毛<sup>[86]</sup>; *Hl1* (Hairy leaf-1 或者 Hairy leaf-

*a*, *Hla*) 在经典遗传连锁图中位于第 6 连锁群 118 cM,属于单基因显性突变,表现为叶片表皮毛变粗、变长,当 *gl1* 也存在时其表皮毛长度则会明显变短<sup>[87-88]</sup>; *Hl2* (Hairy leaf-2, Hairy leaf-b, *Hlb*) 与 *Hl1* 等位,也有同样的突变表型, *Hl1* 和 *Hl2* 的表达对表皮毛长度具有一因多效性,花序分枝上的表皮毛长度受到影响,但对颖壳上的表皮毛长度没有明显的影响; *Hg* (Hairy glume) 在经典遗传连锁图中位于第 3 连锁群 29 cM,属于单基因显性突变,表现为颖壳、叶片边缘、花序分枝和外耳上表皮毛变长,该基因的表达分别对叶缘、小穗枝梗和叶耳的表皮毛具有一因多效性。其中大部分基因没有定位到具体基因,对其分子机理也就了解得更少。

在烟草中, *MIXTA* 基因 (来源于 *Antirrhinum majus*, 与棉花 *CotMYBA* 有些同源) 的过量表达使子叶、叶片和茎秆上都产生超量的表皮毛,却不能互补拟南芥突变体 *gl1*。同理,烟草中过量表达拟南芥 *GL1* 也不能改变烟草表皮毛的表型。棉花 *CotMYBA* 基因在烟草中过量表达同样促使表皮毛的起始,产生各种形态的多细胞表皮毛,但不能影响拟南芥的表皮毛形态<sup>[89]</sup>。但是,棉花纤维蛋白 *GaMYB2* 不但能够调控拟南芥 *gl1* 突变体叶片和茎表皮毛的发育,而且诱导种子表皮毛的形成,说明它可能是棉花调控表皮毛发育的关键基因,其作用模式与拟南芥的类似<sup>[90]</sup>。从番茄中克隆到 *CPC-like R3 MYB*, 用 *CPC* 启动子控制该基因的转基因拟南芥中抑制表皮毛的形成而促进根毛的发生,但 *bHLH* 转录因子 *SlGL3* 的转基因植株 (*GL3* 启动子控制) 的表皮毛没有明显的变化<sup>[91]</sup>。

由此可知,尽管植物表皮毛发育分子水平调控机制的研究多集中在模式植物拟南芥中,但其他植物的表皮毛发育调控与拟南芥具有相同的机理,也存在很大的差别,需要进一步的研究来阐明这些植物表皮毛发育分子调控的机理。总之,植物表皮毛的发育调控是一个十分复杂的调控过程,是由环境、植物激素、细胞周期状态、转录因子和细胞骨架等所组成的综合性的调控体系,也覆盖了细胞信号传导和调控的基本过程<sup>[92]</sup>。表面来看,表皮毛细胞的决定和启动似乎是随机发生的,其实是受到正负调控因子的互相平衡和抑制所决定的,即表皮毛细胞分化的潜在命运是受到高度调控的,来源于表皮毛细胞的调制信号在控制细胞命运时潜在地传递了相应的细胞分化信号<sup>[2,29]</sup>。然而,在植物表皮毛发育的各个阶段都还存在很多未阐明的作用机制,特别是农作物和部分经济作物的相关探索还比较少,需要进一步研究。

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