

根毛的生长发育及其遗传基础

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摘要: 根毛是根系特异化表皮细胞外伸形成的管状凸起物, 是植物吸收矿质养分和水分的重要器官。根毛的发育可分为根毛细胞命运决定、根毛起始、根毛顶端生长和根毛成熟等阶段。本文对根毛发育生长过程中的细胞形态及其生理生化变化进行了综述, 并从根表皮细胞命运决定分子机理, EXPANSIN、bHLH和MYB等转录因子以及小G蛋白和生长素/乙烯等方面简要说明了根毛生长发育的遗传基础。

关键词: 根毛; 发育; 表皮细胞; 扩展蛋白; 转录因子; 小G蛋白; 生长素/乙烯

Root Hair Development and Its Genetic Basis

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Abstract: Root hairs are long tubular outgrowths from specialized epidermal cells of roots. Root hairs can increase the root surface area for aiding plants in nutrient and water acquisition. Development of root hairs includes four phases: root hair cell fate specification, root hair initiation, root hair tip growth and root hair maturation. This review represents cells morphology and the physiochemical changes in four phases of root hairs, followed by discussion about the molecular mechanisms of root hair cell fate specification, the regulatory mechanisms of TFs (EXPANSIN, bHLH and MYB) ROPs and auxin/ethylene on root hairs development.

Key words: root hair; development; epidermal cell; EXPANSIN; transcription factor; ROPs; auxin/ethylene

根毛是植物根系的重要组成部分, 它是植物根表皮细胞凸起形成的组织, 是根的一种特殊结构(Peterson和Farquhar 1996; 严小龙2007)。根毛在生长发育初期含有丰富的果胶物质、原生质等; 其生长发育后期, 由于果胶质钙化等变化, 根毛顶端逐渐变硬; 随着根毛继续发育, 部分细胞质和细胞核逐渐移至根毛顶端, 根毛中间形成大的液泡, 此阶段的根毛顶端富含核蛋白体、线粒体、内质网等(马元喜1999; 张均2008)。成熟的根毛细胞壁由2层构成, 外层呈明胶状, 有粘性, 含有纤维素、果胶质和角质等; 内层具有致密的微纤维状结构(马元喜1999; 张均2008)。根毛不仅能有效地扩大根系表面积以利于根系对水分和矿质养分的吸收利用, 而且还有助于植物根的固定以及与土壤微生物间的互作等(Grierson和Schiefelbein 2002; 张德健等2011; 曹秀等2013; Tanaka等2014)。深入研究植物根毛, 不仅对提高作物养分和水分的吸收利用、增加作物产量、改善作物品质等具有重要的理论和实践意义, 而且对深入探索细胞分化决定、细胞发育以及细胞程序化死亡等机理也有重要意义(Zhang等2013a; Cao等2013; Li等2014;

Kacprzyk等2014)。近年来的研究表明, 根毛发育大致分为4个阶段, 相关转录因子以及特异基因调控其生长发育(Lee和Cho 2013; Vandamme等2013)。本文拟对根毛发育不同阶段以及根表皮细胞命运决定, EXPANSIN、bHLH和MYB转录因子以及小G蛋白和生长素/乙烯等对根毛发育调控的分子机理等方面进行综述, 为深入研究植物根毛的生长发育以及其遗传基础提供参考。

1 根毛的生长发育

根毛是由根系特化的表皮细胞生长而来, 其发育大致可分为4个阶段, 即根毛细胞命运决定(root hair cell fate specification)、根毛起始(root hair initiation)、根毛顶端生长(root hair tip growth)和根毛成熟(root hair maturation) (Gilroy和Jones 2000; 何晓薇2008; Lee和Cho 2013)。

1.1 根毛细胞命运决定

根毛细胞来源于根系的表皮细胞, 然而不是

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所有的表皮细胞都能够发育成根毛。如在拟南芥 (*Arabidopsis thaliana*) 的表皮细胞中, 只有位于两个皮层细胞上方的表皮细胞才能够发育成根毛, 该表皮细胞称作为生毛细胞(Duckett等1994)。生毛细胞具有显著特点: 分裂速率较快, 细胞长度及细胞化程度小, 胞质浓厚, 细胞核及核仁较大, 且细胞表面形成独特的纹饰结构(Galway等1997; Berger等1998)。

植物表皮细胞特化成为根毛的方式主要有三类: 第一类是随机方式, 即任何一个表皮细胞都有可能发育成为根毛, 大多数双子叶植物、很多单子叶植物和大多数蕨类植物都属于这一类, 例如绿珠草、番茄等(Clowes 2000; Pemberton等2001; Tominaga-Wada等2013; Tominaga-Wada和Wada 2014); 第二类是不对称细胞分化方式, 即表皮干细胞后期分生组织不对称分裂产生2种大小不同的表皮细胞, 只有短表皮细胞才能分化成为根毛, 这种方式主要存在于低等蕨类、一些单子叶植物、原始被子植物以及双子叶家族的莲科植物, 如二穗短柄草、水稻、玉米、大麦等(孟繁静和高美须 1985; Kim等2006; Kim和Dolan 2011); 第三类是位置方式, 即位于两个皮层细胞之间的表皮细胞能够发育成为根毛, 而位于一个皮层细胞上方的表皮细胞不能发育成为根毛, 此类方式主要存在于十字花科植物以及真双子叶植物当中, 如拟南芥等(Dolan等1993; Duckett等1994; Galway等1994; Clowes 2000; Kim等2006; Tominaga-Wada等2013)。

以拟南芥为模式植物的第三类根毛发育方式研究较为透彻。拟南芥根的皮层一般有8个细胞, 大约有8个生毛细胞和14个非生毛细胞, 在一些特殊情况下, 非生毛细胞也可能转化成为根毛细胞, 这类细胞称作异位根毛细胞(ectopic root hair cell) (Duckett等1994; Galway等1994)。表皮细胞能否分化形成根毛的决定因素是细胞所处的位置, 而不是细胞的最初来源。正在分化的拟南芥根毛细胞若被激光杀死, 临近的非根毛细胞因为受到挤压产生移动, 并占据原来根毛细胞的位置, 并最终能够分化成为根毛(Berger等1998)。这种细胞位置和细胞类型的联系表明细胞与细胞之间的信息交换对于根表皮细胞的命运决定十分重要。

1.2 根毛起始

根毛的起始是指命运特化的根表皮细胞的细胞壁一侧开始膨胀, 细胞逐渐变宽、变长至形成一个管状凸起的过程(Schiefelbein和Somerville 1990; Bibikova等1999; Gilroy和Jones 2000)。

根毛起始过程中伴随着根毛细胞的细胞壁酸化。在根毛凸起的位点, 根毛细胞的细胞质中会形成一个局部的碱性区域, 该区域的细胞壁呈现酸性, 从而产生了一个局部的pH梯度(Bibikova等1998)。生毛细胞的细胞壁pH值的下降活化了扩张蛋白(EXPANSIN), 进而催化了细胞壁的松弛导致该位点进一步扩张和膨胀, 此过程还伴随着内质网和肌动蛋白在周围的聚集(Bibikova等1998; Ridge等1999; Baluška等2000)。人为抑制细胞壁酸化能够抑制根毛起始, 当恢复到酸性条件时, 抑制效应消失(Gilroy和Jones 2000)。然而整个生毛细胞的细胞壁被人为酸化后, 根毛起始的位置并没有被改变, 因此可认为除了细胞壁附近形成的pH浓度梯度外, 还有其他因素参与调控根毛起始。例如生长素和乙烯也参与了根毛起始: 如拟南芥生长素不敏感突变体*auxin resistant 2 (axr2)*和乙烯响应突变体*ethylene response 1 (etr1)*只有少数根毛发生, 且主要位于细胞的基部(远离根分生组织), 这表明生长素和乙烯既参与调控根毛起始的数量又调控根毛在细胞中凸起的位置(Masucci和Schiefelbein 1994, 1996)。

1.3 根毛顶端生长

根毛细胞完成凸起过程之后, 进入顶端生长阶段。根毛顶端生长伴随着复杂的组装、运输等生化反应。该阶段的根毛顶端会形成一个主要由分泌小泡构成的细胞致密区域, 并伴随着合成新的质膜和细胞壁物质(Gilroy和Jones 2000; Emily等2014; Larson等2014)。这些新合成的细胞壁物质由根毛细胞中的平滑内质网、粗面内质网和高尔基体产生的分泌囊泡, 经过微丝系统运输到根毛顶端, 微丝系统遭到破坏会阻止根毛的顶端生长(Bibikova等1999; Ichikawa等2014)。有研究发现 *ROOT HAIR DEFECTIVE3* 参与调控内质网融合, 该基因突变后, 内质网融合受阻, 根毛顶端生长被终止(Zhang等2013b)。顶端生长的细胞是高度动态的, 大量的细胞成分在内部快速移动, 细胞核也

移至管中并滑动到顶端附近,但始终和伸长生长的尖端保持一定的距离(Galway等1997)。顶端积累大量的质膜和细胞壁物质将进行装配和交联,使凸起部位继续向外延伸直至成为成熟的根毛(Gilroy和Jones 2000)。肌凝蛋白因为具有沿着细胞骨架运输细胞器、囊泡、蛋白复合物等细胞组分并能维持细胞极性的作用,因此肌凝蛋白XIK突变后,根毛的顶端生长被终止(Park和Nebenführ 2013)。

根毛起始需要凸起位点呈碱性的细胞质和酸性的细胞壁之间形成局部pH梯度,然而随着进入到顶端生长阶段,这种pH梯度随之消失。细胞质pH较高会抑制根毛顶端生长,细胞外pH较低更会引起生长中的根毛破裂(Carol和Dolan 2002)。

影响根毛顶端生长的因素有细胞壁、肌动蛋白、脂类信号通路、离子转运和GTP酶等。在拟南芥中细胞壁扩展蛋白家族中有2个成员(*EXP7*和*EXP18*)在顶端生长中的根毛表达,其功能型突变体的根毛长度显著降低(Cho和Cosgrove 2002)。水稻中最近的研究发现编码木葡聚糖木糖基转移酶*XXT1*突变后,根系细胞壁抗张强度下降,细胞壁结构破坏,从而抑制根毛生长发育(Wang等2014a)。肌动蛋白在根毛伸长过程中始终位于根毛细胞尖端,*DER1*编码了植物组织中主要的肌动蛋白ACTIN2,其突变体的根毛密度和长度受到显著抑制,因此可证实ACTIN2参与根毛细胞起始和顶端生长(Ringli等2002)。另有研究表明肌动蛋白聚合对维持根毛顶端生长也十分重要(Vazquez等2014)。根毛顶端生长需要脂类信号通路的参与:*CAN OF WORMS1* (*COW1*)基因编码的是一个磷脂酰肌醇转移蛋白,其在根毛中表达,降低它的活性将影响根毛顶端生长(Böhme等2004);*TIP GROWTH DEFECTIVE 1*基因编码一个S-酰基转移酶,其功能缺失突变体的表型为根毛分叉(Hemsley等2005);植物磷脂酰肌醇(PI)途径中一些关键酶,如磷脂酰肌醇-4-羟基激酶(*PI4Kβ*)、多磷酸肌醇激酶(*IP-K2α*)、磷脂酰肌醇-4-磷酸磷酸酶(*RHD4*)、磷脂酰肌醇-4-磷酸-5-激酶(*PIP5K3*)和磷脂酰肌醇-3-激酶(*PI3K*)等都是根毛细胞顶端正常生长所必需的(Xu等2005; Preuss等2006; Lee等2008; Stenzel等2008; Thole等2008)。最近克隆了特异编码单子叶植物

NADPH氧化酶基因*RTH5*,该基因突变体或采用NADPH氧化酶抑制剂处理,根毛凸起和伸长生长均受到抑制(Nestler等2014; Lin等2014)。植物根毛顶端生长需要离子通道和转运体的参与。拟南芥钾离子转运突变体*Arabidopsis K transporter1*和*Tiny root hair1*的根毛伸长都受到不同程度的抑制(Rigas等2001; Desbrosses等2003);通过质膜上钙离子通道的Ca²⁺流入是根毛顶端正常生长所必需的,若用细胞膜钙离子通道转运体抑制剂处理将导致胞外Ca²⁺浓度梯度的消失,这也将抑制根毛生长(Schiefelbein等1992)。GTP酶对根毛顶端生长也十分重要:一个编码GTP酶的ADP核糖基化因子*ARF1*是细胞膜转运所必需的,它定位于根表皮细胞的高尔基体中,参与根毛的内吞作用;Rab蛋白是另一类GTP酶,*RabA4b*定位于根毛尖端,调控根毛细胞中的液泡运输;还有两个编码ARF-GTP酶激活蛋白的基因*AGD1*和*RPA*也是维持根毛顶端正常生长所不可缺少的(Song等2006; Yoo等2008)。

1.4 根毛成熟

当根毛顶端生长到一定程度,根毛就会停止生长,进入成熟阶段,此时其尖端形成对称的圆顶性末端。此阶段,根毛顶端的细胞质分散,且含有囊泡的胞质逐渐消失,液泡扩大进入根毛顶端,同时钙离子浓度梯度和钙离子通道随之消失,细胞壁中会形成β纤维素层,内质网会变得更松散(Galway等1997, 1999; Ridge等1999; Véry和Davies 2000; Molendijk等2001)。

2 根毛生长发育的遗传基础

2.1 表皮细胞命运决定

前文述及在拟南芥根系中,位于一个皮层细胞上方的表皮细胞不能发育成为根毛,称作非生毛细胞(N);位于两个皮层细胞之间的表皮细胞能够发育成为根毛,称为生毛细胞(H) (Grierson和Schiefelbein 2002)。在N细胞中特异表达的基因有:*TTG* (*TRANSPARENT TESTA GLABRA*)、*GL3* (*GLABRA3*)、*EGL3* (*ENHANCER OF GLABRA3*)和*WER* (*WEREWOLF*)。TTG含有WD40重复序列的小蛋白,GL3和EGL3是bHLH转录因子,WER是R2R3 MYB转录因子。它们形成转录复合物WER-GL3/EGL3-TTG,该复合物在N细胞中大量积累与表达,并且正调控一个编码同源域亮氨酸拉链转

录因子 *GLABRA2* (*GL2*) 的表达 (Rerie 等 1994; Masucci 和 Schiefelbein 1996; Walker 等 1999; Lee 和 Schiefelbein 1999; Bernhardt 等 2003; Schiefelbein 2003; Pesch 和 Hulskamp 2004; Ueda 等 2005)。 *GL2* 是根毛生长发育负调控因子, 其主要通过磷脂信号途径调节根毛发育, 目前已克隆其直接下游靶基因 *PLD1* (Ohashi 等 2003)。 H 细胞中特异表达的基因有: *CAPRICE* (*CPC*)、 *TRIPTYCHON* (*TRY*) 和 *ENHANCER OF TRY AND CPCs* (*ETCs*)。 单突变或者多突变这些基因, 将抑制根毛生长 (Wada 等 1997; Schellmann 等 2002; Kirik 等 2004a, b; Simon 等 2007)。 *CPC/TRY* 通过抑制表皮细胞中 *GL2* 的表达, 从而决定该细胞发育成 H 细胞 (Schellmann 等 2002; Tominaga 等 2008)。

2.2 扩展蛋白与根毛生长发育

扩展蛋白 (EXPANSIN) 是一种引起植物细胞壁松弛的蛋白质, 在植物细胞伸展以及一系列涉及细胞壁修饰的生命活动中起着关键作用 (Cosgrove 1997, 2000; Lee 等 2001)。 EXPANSIN 分布较广, 覆盖了几乎所有植物。 EXPANSIN (EXPs) 主要分 2 类, 即 α -EXPANSIN (EXP) 和 β -EXPANSIN (EXPB), 它们在进化、 结构和功能上相当保守 (Lee 和 Kende 2001, 2002; Cosgrove 2000; Lee 和 Schiefelbein 2002; 何晓薇 2008)。

空间调节细胞壁扩张对植物细胞形态发生至关重要, 如根毛生长发育 (Fowler 和 Quatrano 1997; 何晓薇 2008)。 大麦 (*Hordeum vulgare*) 突变体 *expl* 因该基因的表达被抑制从而导致无根毛表型 (Kwasniewski 和 Szarejko 2006)。 在根毛起始阶段, 凸起位点的细胞壁的 pH 开始下降, 这将激活 EXPs 以水解断裂细胞壁的主要结构, 从而催化细胞壁松弛为根毛凸起做铺垫 (Bibikova 等 1998)。 目前在拟南芥中发现 *AtEXP7* 和 *AtEXP18* 参与调控根毛生长发育, 并认为生长调节抑制剂 (如乙烯作用抑制剂 1-MCP) 调控根毛发育是通过下调它们的表达, 从而抑制生毛细胞细胞壁松弛, 进而阻碍根毛凸起 (Cho 和 Cosgrove 2002)。 拟南芥 *rh6* 突变体的根毛生长受到显著抑制时, 发现该突变体显著降低了 *AtEXP7* 和 *AtEXP18* 的表达 (Cho 和 Cosgrove 2002)。 也有研究发现 EXPs 不仅大量积累于生毛细胞的凸起位点, 根毛伸长生长过程也伴随着其

大量表达, 因此认为 EXPs 对于根毛凸起和顶端生长同样重要 (Baluška 等 2000)。

通过 EMS 诱变水稻得到一个短根毛突变体, 该突变体的第 6 号染色体上的 *EXP17* 的一个点突变造成催化域第 104 位的谷氨酸发生突变成为精氨酸, 该突变破坏了高度保守的二硫键, 造成该蛋白功能丧失 (Yu 等 2011)。 缺磷和激素处理能够部分诱导 *exp17* 根毛伸长生长, 但不能回复至野生型水平, 因此推测 *EXP17* 处于根毛形态发生调控路径比较下游的位置, 并与根毛发生和顶端生长时细胞壁的变化直接相关联 (何晓薇 2008)。 缺磷处理也能诱导大豆 (*Glycine max*) *GmEXPB2* 上调表达进而促进根毛伸长生长, 超表达该基因能够显著提高根毛长度及磷吸收 (Guo 等 2011)。

2.3 bHLH 转录因子与根毛生长发育

bHLH (basic helix-loop-helix, 碱性螺旋-环-螺旋) 转录因子, 是一个大类转录因子家族, 在拟南芥中有 162 个成员, 在水稻中有 167 个成员 (刘晓月等 2011)。 bHLH 转录因子的结构包括两个保守区域: 一是碱性区域, 分布在多肽链的 N 端, 含有 10~15 个碱性氨基酸, 具有 DNA 识别和结合位点; 另一为 HLH 区域, 分布在 C 端, 主要由约 40 个疏水氨基酸残基构成, 利于 HLH 之间相互作用形成二聚体 (刘文文和李文学 2013)。 已报道与根毛发育相关的 bHLH 转录因子有 3 类。

GLABRA3 (*GL3*) 和 *ENHANCER OF GLABRA3* (*EGL3*) 属于拟南芥 bHLH 转录因子家族的亚组 III f。 *GL3* 和 *EGL3* 这两个基因单突变体的根毛数目有一定的增加, 双突变体中根毛数目则显著增加, 表明这两个转录因子负调控根毛生长发育, 并且它们之间部分功能冗余 (Payne 等 2000; Bernhardt 等 2003)。

ROOT HAIR DEFECTIVE 6 (*RHD6*) 和 *ROOT HAIR DEFECTIVE SIX LIKE 1* (*RSL1*) 属于 bHLH 基因家族的亚组 VIII c。 在拟南芥中, *rh6* 有少量的根毛发生, *rsl1* 根毛表现正常, 而这两个基因的双突变后则无根毛, 表明这两个转录因子正调控根毛发育, 并且也存在部分功能冗余 (Menand 等 2007)。 研究表明 *RHD6* 和 *RSL1* 在拟南芥决定表皮细胞命运的转录调控复合体的下游调控根毛细胞的发育 (Menand 等 2007)。

*ROOT HAIRLESS 1 (RHL1)*在百脉根(*Lotus japonicus*)中被克隆到, 其突变体*rhl-1*表现为无根毛, 另外一个等位突变体*rhl-2*有少量根毛发生(Karas等2009)。

2.4 MYB转录因子与根毛生长发育

MYB类转录因子家族是指含有MYB结构域的一类转录因子。MYB结构域是一段约51~52个氨基酸的肽段, 包含一系列高度保守的氨基酸残基和间隔序列(陈俊和王宗阳 2002)。

研究表明MYB类转录因子*WER* (R2R3 MYB)和*CPC* (R3 MYB)参与根毛生长发育的遗传调控。*WER*通过激活*GL2*的表达抑制根毛的发生, 而*CPC*通过抑制*GL2*的表达从而使根毛得以发生(Lee和Schiefelbein 2002; 牛耀芳2013)。Ryu等(2005)发现*WER*能够直接调控*CPC*的转录及表达, 从而间接影响根毛细胞的发生发育。已报道调控根毛发育的MYB转录因子中与*CPC*同源基因有*TRYPTICHO* (*TRY*), *ENHANCER OF TRY AND CPC1*, *2 (ETC1、ETC2)*, *ENHANCER OF TRY AND CPC3/CPC-LIKE MYB3 (ETC3/CPL3)*, *TRICHOMELESS1、2/CPC-LIKE MYB4 (TCL1、TCL2/CPL4)*; 与*WER*同源基因有*GLABRA1 (GL1)* (Lee和Schiefelbein 2001; Simon等2007; Wang等2007; Tominaga等2008; Gan等2011; Tominaga-Wada和Nukumizu 2012; Tominaga-Wada等2013; Tominaga-Wada和Wada 2014)。目前调控根表皮细胞命运的网络系统越来越清晰: *WER*和*CPC*能竞争结合*GL3/EGL3-TTG*形成复合物, 再作用于*GL2*基因(Libault等2010); *CPC*蛋白只产生于非根毛细胞, 通过转运子转移到相邻的生毛细胞, 形成*CPC-GL3/EGL3-TTG*复合物, 该复合物抑制*GL2*表达以促进根毛凸起; 生毛细胞中*GL3/EGL3*被转运到相邻非生毛细胞, 再作用于*WER*和*TTG*, 形成*WER-GL3/EGL3-TTG*复合物, 从而促进*GL2*表达, 进而抑制根毛形成, 同时该蛋白复合物正调控*CPC*, *CPC*可通过转运子运输到相邻的生毛细胞形成反馈抑制循环圈(Lee和Schiefelbein 2002; Wang等2007; Libault等2010)。正是由于该反馈抑制循环的形成, 决定了表皮细胞命运, 精准调控着复杂的根毛凸起。

2.5 小G蛋白与根毛生长发育

G蛋白是普遍存在于真核生物细胞中的一个

GTP结合蛋白家族, 其中一类蛋白称作小G蛋白 (small GTPases), 其分子量约为21~30 kDa (Cherfils和Zeghouf 2013; Hobbs等2014)。研究发现一种特殊的小G蛋白ROP (Rho-related GTPase from plants)在根毛生长发育过程中具有重要调控作用(Wang等2002; 朱昌华2006; Huang等2013)。与根毛生长发育密切相关的ROPs主要有*ROP2*、*ROP4*和*ROP6*。过量表达拟南芥*ROP2*可提高根毛数量和密度; 过量表达*ROP2*激活型突变体, 也可促进根毛顶端生长; 过量表达其非激活型突变体, 则显著抑制根毛伸长生长(Jones等2002; Molendijk等2001, 2004; Feijo等2001; Fu和Yang 2001)。

ROPs能够影响细胞内肌动蛋白、活性氧含量和钙离子浓度梯度, 而它们均参与了根毛伸长生长(Foreman等2003; Samaj等2004; Voigt等2005; Jones等2007; Lavy等2007; Takeda等2008; Kwasniewski等2013; Ketelaar 2013; Nestler等2014; Lin等2014)。ROPs能够促进钙离子浓度梯度的形成和稳定, 若破坏ROP4蛋白的活性, 则引起根毛顶端钙离子浓度梯度消失及微管结构变化, 进而导致根毛的肿胀(Molendijk等2001)。钙离子通道活化时间仅有0.7 s, 而钙离子浓度梯度和与之有关的顶端生长能持续数分钟, 这可能的机理正是ROPs蛋白参与形成并稳定钙离子浓度梯度, 进而促使泡状物在根毛顶端融合, 这些泡状分泌物又有利于向根毛顶端传输钙离子流和ROPs, 因此它们的相互作用形成一个正反馈调控循环, 从而使根毛可以稳定进行顶端生长(朱昌华 2006)。

2.6 生长素和乙烯与根毛生长发育

生长素和乙烯作为调控植物生长发育的主要激素, 参与调控植物根毛凸起和伸长生长。拟南芥生长素响应突变体*axr1*的根毛伸长生长受到了显著抑制, 外源添加合适浓度的萘乙酸(NAA)和吲哚丁酸(IBA)则显著促进了根毛的生长发育(Delbarre等1996; Pitts等1998; Marchant等1999; Niu等2011; 张德健等2011; Zhang等2013a)。拟南芥乙烯不敏感突变体*etr1*的根毛数量和长度则受到了显著抑制, 1-氨基环丙烷-1-羧酸(ACC)作为乙烯合成前体能够显著提高野生型拟南芥根毛的长度和密度(Masucci和Schiefelbein 1994; Tanimoto等1995)。有意思的是生长素和乙烯不是孤立影响根

毛生长, 而是以交互作用调控根毛发育: 拟南芥生长素响应突变体 $axr1$ 根毛生长受到显著抑制, 外源添加ACC能回复其根毛生长; 拟南芥乙烯信号传导突变体 $ein2-1$ 的根毛伸长生长受到阻碍, 而NAA能够有效缓解此阻碍作用(Pitts等1998; Rahman等2002; Muday等2012)。研究者采用转录组技术分析认为生长素和乙烯均能够使90%与根毛生长发育相关的基因表达上调, 这充分证明了生长素和乙烯以交互作用参与调控根毛的生长发育(Bruex等2012)。值得注意的是, 在植物根毛发育研究结果中曾有人提出“乙烯中心”假说, 即土壤环境、生长调节剂、矿质养分等能影响根系生毛细胞中乙烯的浓度, 进而调控根毛的生长发育(Michael 2001)。

前文已述拟南芥生毛细胞的分化是由包括CPC、WER、GL3/EGL3、TTG和GL2蛋白构成的一个转录因子级联引起的, 然而在生长素和乙烯调控根毛发育的过程中, 这些基因的表达未受到影响(Masucci和Schiefelbein 1996; Dolan 2001; Rigas等2013)。在拟南芥生长素响应基因突变体 $axr1$ 中的观察发现其根毛数量未受到影响, 但其长度受到了显著抑制(Pitts等1998)。因此可认为生长

素和乙烯主要影响根毛的伸长生长。然而采用生长素类似物NAA处理拟南芥能使其根毛发育正调控基因CPC、TRY等上调表达, 从而促进更多根毛的产生, 而生长素运输抑制剂1-N-naphthylphthalamic acid (NPA)能够提高根毛凸起负调控基因WER、TTG和GL2的表达量, 进而抑制根毛的发生(Niu等2011; 牛耀芳2013)。更多的研究已证实生长素和乙烯能够通过EXPs调控根毛生长发育: NAA和ACC在一定程度上诱导水稻 $exp17$ 突变体根毛生长, 但不能回复到野生型表型(何晓薇2008)。这可能因为EXPs在根毛的发生和伸长生长过程中可能处于较下游的位置, 其能直接作用于生毛细胞细胞壁, 激素或上游基因的改变都无法使突变体的根毛表型得到回复。

3 结语

植物表皮细胞特化成为根毛的方式主要有三种。拟南芥作为第三种方式的模式植物, 其根毛生长发育遗传调控研究较清楚。如图1所示, 有2条路径参与调控根表皮细胞分化: 一是TTG/WER/GL2路径, 该路径在非生毛细胞中表达, 促使该细胞特化成非根毛细胞; 二是CPC/TRY路径, 该路径在生毛细胞中表达, 促使其命运特化成根毛细胞

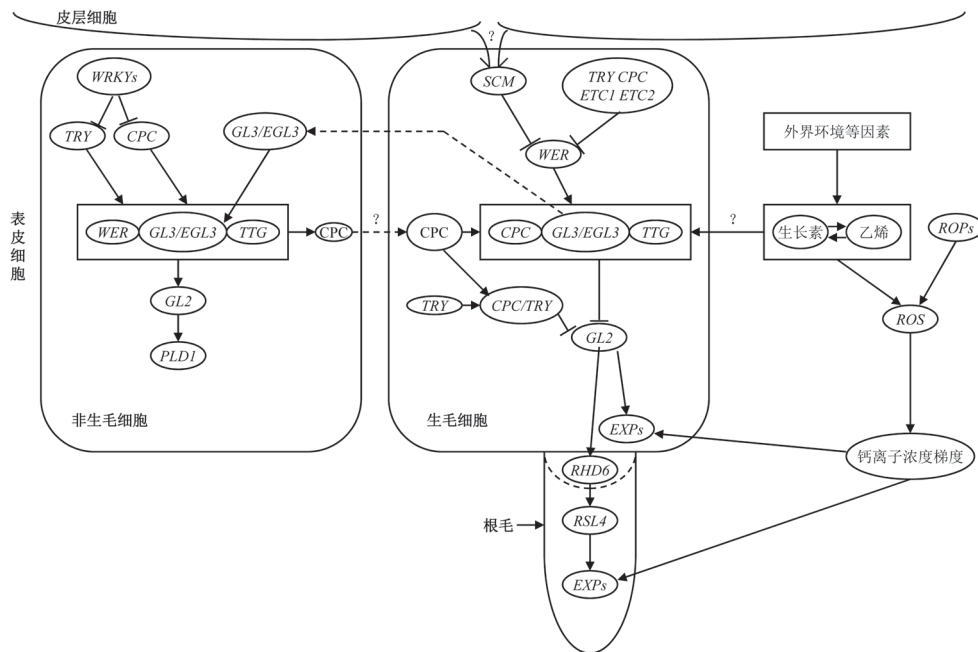


图1 拟南芥根毛生长发育模式图

Fig. 1 A model of root hair development in *Arabidopsis*

参考Libault等(2010)并作补充; 其中“ \longrightarrow ”代表正调控, “ $\longrightarrow|$ ”代表负调控, “ \dashrightarrow ”代表跨膜转运, “ \cdots ”代表根毛凸起。

(Schellmann等2002; Schiefelbein 2003; Savage等2008; Libault等2010)。CPC基因在生毛细胞中表达, 其蛋白却在非生毛细胞中表达(Tominaga-Wada和Wada 2014)。CPC是如何被靶定并通过胞间连丝运输到生毛细胞从而决定根毛细胞命运, 目前并不清楚。已报道一个受体蛋白激酶SCRAMBLED (SCM)参与了位置方式中表皮细胞的命运决定: SCM是位于表皮细胞的富含亮氨酸的受体类蛋白, 可能通过其配基在表皮细胞中不连续分布来决定细胞分化(Kwak等2005)。进一步研究该受体蛋白激酶, 可能对探析皮层细胞与表皮细胞之间信号传递的过程更有帮助。番茄(*Lycopersicon esculentum*)根毛发育方式与拟南芥不同, 然而最近在番茄中发现了与拟南芥TRY高度同源基因SITRY, 它正调控根毛凸起(Tominaga-Wada和Nukumizu 2012; Tominaga-Wada等2013; Tominaga-Wada和Wada 2014)。虽然不同种类植物其根毛发育方式不同, 但它们是否有共同发育途径及机制还值得探讨。

TTG/WER/GL2路径的上游调控网络近些年有了新的进展, 研究认为WRKY转录因子作为根毛发育负调控因子在非生毛细胞中抑制根毛发育的正调控转录因子TRY和CPC的表达, 从而提高了WER和GL2的蛋白活性, 进而阻碍根毛凸起(Rishmawi等2014)。研究报道了拟南芥WRKY75在缺磷、病原菌侵入、衰老等过程中表达上调, 然而干涉该基因, 却能促进根毛生长发育(Dong等2003; Devaiah等2007; Encinas-Villarejo等2009; Rishmawi等2014)。从WRKY角度深入探析环境胁迫调控根表皮细胞命运决定的分子机理可能是一个较好的途径。

CPC/TRY路径的下游调控网络较清楚的是RHD6。一般认为RHD6作为根毛凸起和伸长生长的一个关键调控因素受CPC/TRY/GL2和CPC/TTG/GL2调控, 而RHD6通过RSL4调控EXPs的表达, 最终影响根毛的生长发育(Masucci和Schiefelbein 1996; Cho和Cosgrove 2002; 何晓薇2008; Won等2009; Yi等2010; Lee和Cho 2013; Rigas等2013)。然而生长素和乙烯能够回复拟南芥rhd6突变体无根毛表型, 说明激素调控根毛生长发育或许独立于TTG/CPC/TRY/GL2/RHD6路径(Masucci和Schiefelbein 1996; Pitts等1998; Cho和Cosgrove

2002; Jang等2011; Rigas等2013)。然而Niu等(2011)认为生长素部分通过该路径影响根毛生长发育。生长素和乙烯是否依赖TTG/GL2途径调控根毛细胞的分化有待于深入研究。

EXPs也参与根毛命运决定, 然而它可能也位于CPC/GL2路径的下游调控生毛细胞细胞壁软化直至凸起成为根毛(Cho和Cosgrove 2002; Won等2009; Lee和Cho 2013)。一般认为外界环境通过EXPs以另一条途径影响根毛生长发育: 如镁胁迫能够促进根系活性氧(ROS)产生并促进其在根毛尖富集, 而ROS通过激活细胞膜上的钙离子通道来调节细胞内钙离子信号, 这些信号途径调控根毛特异性表达基因EXPs, 从而影响细胞壁软化, 最终影响根毛凸起和伸长生长(Carol和Dolan 2002; 牛耀芳2013)。目前已在水稻、拟南芥中克隆了调控根毛发育的EXPs, 然而其他植物中该基因参与根毛发育罕有报道。因此可进一步研究其他植物中调控根毛生长发育的EXPs, 并深入挖掘这些基因调控根毛发育的共同作用元件。最近在水稻中克隆了EXPA8, 缺磷等非生物胁迫能显著降低该基因表达量, 进而调控细胞壁松弛以增强植物根系适应胁迫环境能力, 如促进根毛生长发育(Wang等2014b)。EXPs不仅参与了磷和生长调节剂对根毛生长的影响, 也涉及缺Fe、适度干旱等对根毛发育的影响(Cho和Cosgrove 2002)。有研究认为激素、矿质养分、逆境等环境条件以及根毛发育相关基因可能都是通过EXPs最终影响根毛生长发育(Cho和Cosgrove 2002)。然而该结论缺乏直接证据, 因此可进一步从非生物胁迫方面深入挖掘EXPs与其他因子(如磷、铁、生长素、乙烯、ROS、钙离子信号等)在根毛生长发育过程中的调控机理。

ROS同时也受ROPs的调节影响根毛伸长生长。然而ROPs或许与磷、生长素等环境因素以不同机理参与根毛生长发育(Shin等2005, 2010; Huang等2013; Sundaravelpandian等2013; Nestler等2014; Lin等2014)。ROP2、ROP4和ROP6在根毛发育过程中都有积累, 然而根毛的顶端只有ROP2和ROP4的积累(Molendijk等2001; Jones等2002)。ROPs调控根毛起始可能与调节根毛顶端伸长生长是两个不同的机制。

最近Szarejko课题组收集了大麦19种根毛突变体, 每一个突变体都是单基因或隐性突变体, 这对未来鉴定基因调控根毛发育提供了较好的试材(Chmielewska等2014)。

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