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植物表皮形态建成的分子调控机制

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摘 要 植物表皮细胞在组织器官的生长发育和形态建成中发挥非常重要的作用。植物的表皮是由原表皮发育来的, 表皮包括表皮(扁平)细胞、气孔器和表皮毛等。双子叶植物的表皮由不规则的表皮细胞、气孔器和表皮毛组成; 单子叶植物的表皮由长形的表皮细胞、短形的硅化和栓化表皮细胞、泡状细胞、气孔器和表皮毛等组成。近年来, 随着生物技术的不断提高, 人们对全球淡水资源紧缺的认识加强, 对培育农业抗旱品种的追求, 因此, 对植物表皮形态建成的研究已经成为一大热点。本文综述了目前有关双子叶模式植物拟南芥中气孔及扁平细胞的图式发育及参与调控的分子遗传调控网络, 以及单子叶植物水稻、玉米中参与气孔及表皮细胞图式发育的功能基因。旨在阐明单双子叶模式植物表皮发育调控的分子机制。

关键词 植物表皮; 气孔; 扁平细胞; 形态建成; 网络调控

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植物表皮在组织器官的生长发育和形态建成中发挥非常重要的作用^[1-3]。表皮是植物体内与外界环境的天然保护屏障, 它不仅可以感知外界刺激、传递信号, 吸收营养等, 而且表皮细胞外壁常覆盖一层脂肪性物质, 称角质层, 在植物的地上器官(如茎、叶、花、果实和种子)中具有保护功能^[4-6]。增加表皮层厚度不仅能使植物有效地抵御外界有机胁迫(微生物、病虫害侵袭)和无机胁迫(低温、高盐碱等), 更能减少植物体内热量及水分的散失^[7]; 在地下器官(根)中具有吸收功能。因此, 研究植物表皮的分裂、分化与形态建成对植物的正常生长发育具有非常重要的理论意义。植物叶表皮扁平细胞排列紧密, 细胞边缘凸凹嵌套, 没有细胞间隙(除了气孔)。除一般的表皮扁平细胞外, 叶表皮细胞还包括特化的气孔复合体和表皮毛等附属物, 在禾本科植物叶中还包括泡状细胞、以及由硅质细胞和栓质细胞紧密镶嵌而成的短细胞^[8-10]。近几年来, 随着生物技术的不断提高, 对植物表皮形态建成的研究成为一大热点, 尤其在双子叶模式植物拟南芥中, 取得了一系列的研究成果, 但是在单子叶植物中, 调控气孔及表皮

细胞发育图式的基因及参与分子调控网络的机理研究非常受限, 因此需要更多科技工作者去深入探讨和研究。

1 双子叶植物叶表皮扁平细胞及表皮毛形态建成及分子机制

植物表皮主要作用是增加表皮层的厚度, 减少热量及水分散失, 从而保护表皮层下组织, 以免受到病虫害及机械伤害^[7]。拟南芥(*Arabidopsis thaliana*)作为一种双子叶植物的模式植物, 对其叶表皮的研究已经取得很大的进展。研究证明, 拟南芥叶表皮扁平细胞的发育经历3个阶段: 第1阶段, 表皮原始细胞先沿着叶长轴开始扩展, 形成稍微变长的多变形细胞; 其次, 沿细胞壁的背斜面向邻近细胞侧面延伸, 细胞边缘逐渐形成不规则的锯齿状凸出(lobe); 最后, 细胞凸出进一步向外延伸, 与相邻细胞狭窄的凹陷(neck)处交错相连, 最终形成复杂多变的表皮图式^[11]。拟南芥表皮毛是一种特化的、典型的单细胞结构, 一般有3个分支, 无腺体, 广泛分布于叶、茎、花瓣的表面。其发育过程包括起始发育、分支、延伸和形态建成4个阶段^[12]。叶表皮不规则的齿状凸

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出和颈的形成以及表皮毛的延伸与发育主要受细胞骨架(微管,微丝和中间纤维)的调控。微管主要调控叶扁平细胞延伸与分裂^[1,13]。微管结合蛋白 MAP65 (microtubule associated protein 65) 负责微管稳定以及微管成束^[14];微管切割蛋白 KTN1(katanin 1) 与植物中的小 G 蛋白 ROPs (rho-like small GTPase in plant) 的效应蛋白 RIC1 (ROP-interactive CRIB motif-containing protein 1) 结合,通过切割微管进而调控微管的分布^[15];Rho-GTPase 级联信号通路能调控微管与微丝的排列,从而导致叶扁平细胞形态改变^[11,16]。微丝主要控制表皮细胞边缘的凸出,即 lobe 的形成和图式发育^[2,11,17-18]。微丝结合蛋白 ABPs (Actin binding proteins) 调节微丝的聚合以及微丝动态装配^[19];目前已被证实的拟南芥中微丝结合蛋白主要包括:微丝解聚因子(actin-depolymerizing factors)、前纤维蛋白(profilin)、肌动蛋白(fimbrins)、绒毛蛋白(villin)、肌动蛋白相关蛋白 Arp2/3 (actin-related protein 2/3) 复合体等都参与细胞的形态发生^[20-21]。

在拟南芥中已经证明参与调控扁平细胞及表皮毛发育有多条信号通路,表皮毛的形态和发育的调控均依赖相关基因的精确表达,其中大部分属于 R2R3 类型的 MYB、bHLH (basic helix-loop-helix) 和含 WD40 重复序列的 TTG (TRANS-PARENT TESTA GLABRA1) 类转录因子,表皮毛发育及分子调控目前研究比较清晰^[22-28]。本研究就针对依赖于 SPK1-ROPS-SCAR/WAVE-ARP2/3 这一信号通路进行介绍,该通路基因通过调控微丝核化改变细胞骨架结构,从而导致叶扁平细胞及表皮毛发育过程形态异常,该通路成员有 SPK1 (spike 1), ROPs, 环磷酸腺苷受体结合抑制因子 SCAR/WAVE (suppressor of cAMP receptor/ Wiskott-Aldrich syndrome protein-family verprolin-homologous protein) 复合体, ARP2/3 复合体^[22,29-30]。单突变体 *spk1* 表皮毛分支明显减少,不规则,扭曲延伸,扁平细胞边缘凸出减少^[3,31]。ROP 家族在拟南芥中共有 11 个成员,分别是 ROP1 ~ ROP11, 其中 ROP1 ~ ROP6 主要调控细胞极性生长,参与叶表皮细胞形态建成,组成激活突变体 CA-rop2 扁平细胞显著膨大,非极性分裂生长,表皮毛表现出肿胀表型,分枝不规则,扭曲;而负显性突变体 DN-rop2 扁平细胞狭窄,lobe 变短^[32]。ROP2/4 在扁平细

胞 lobe 顶端质膜上激活,促进 RIC4-依赖的皮层微丝积累,促进了细胞向外凸出生长,控制微丝聚集,而 ROP6 在 neck 区域与 RIC1 结合促进微管的装配,进而抑制细胞凸出形成^[11]。ROPs 信号分子在该通路中起“开关”作用,另一通路就是激活下游 SCAR/WAVE 复合体,继续信号传递^[33-34]。SCAR/WAVE 复合体共包括 5 个亚基,分别是 PIR/SRA1 (PIROGI/Specifically Rac1-associated protein) NAP1/NAP125 (NCK-associated protein), BRICK1/HSPC300 (haematopoietic stem progenitor cell 300), ABI (abl-interactor 2) 和 SCAR/WAVE^[35-37]。研究证明,该复合体中 PIR/SRA1 亚基接收上游 ROPs 的激活信号,SCAR/WAVE 亚基与下游 ARP2/3 复合体直接相互作用并激活下游信号通路^[36-40]。该复合体中单突变体 *pirl*、*nap1*、*brk1*、*wave1* 等都呈现出表皮毛扭曲,分枝不规则表型,并且细胞粘连处有缺口,细胞排列不紧密,brk1 扁平细胞边缘突出变平滑的表型更为明显^[21,37,41-42]。Arp2/3 复合体由 7 个亚基构成,分别是 ARP2、ARP3、ARPC1 — ARPC5^[43-44]。4 种称为“变形 (distorted)”基因分别编码 ARP2、ARP3、ARPC2 以及 ARPC5,单个基因突变同样表现出表皮毛扭曲、肿胀,分枝紊乱,长度减少等表型^[45-47]。大量试验证明编码该信号通路的蛋白功能相对保守,SCAR/WAVE 和 ARP2/3 复合体主要通过调节微丝斑或微丝带的形成来调控细胞极性生长过程,从而改变叶扁平细胞以及表皮毛的形状^[36,48]。目前双子叶植物中,对通过微管和微丝调控拟南芥表皮细胞的图式发育和形态建成的信号通路研究取得较大的成果。

2 双子叶植物中气孔的图式发育及分子机制

气孔是高等植物表皮上的一种特化结构,是蒸腾过程中水蒸气从体内排到体外的主要出口,也是光合作用和呼吸作用与外界气体交换的“大门”,对植物的蒸腾、光合、呼吸等都起着非常重要的作用。气孔在调节植物逆境环境中,常通过其开关来维持体内水分,在维持地球水分平衡、碳氧平衡及植物的生命活动中均发挥着非常重要的作用^[49-50]。当光照、温度、CO₂ 含量、叶片含水量、化学物质等环境因子发生变化时,植物通过调整气孔孔径大小来控制自身与外界的气体交换能

力,以便能更好地适应外界环境^[50-51]。拟南芥的原表皮细胞同时具有发育成扁平细胞、气孔和表皮毛的能力。原表皮细胞逐渐发育成拟分生组织母细胞 MMC(meristemoid mother cell),属于气孔干细胞,并主导气孔系细胞的第 1 次不均等起始分裂,产生 2 个子细胞,小细胞为拟分生组织(meristemoid),继续进行细胞不均等分裂,或者分化为保卫细胞母细胞 GMCs(guard mother cells);其中较大的姊妹细胞称为气孔系基础细胞 SLGC(stomatal lineage ground cell),发育成扁平细胞 PCs(pavement cells),GMCs 再进行一次均等分裂,进而最终分化成 2 个保卫细胞 GCs(guard cells),细胞壁加厚,逐渐形成孔状特化的气孔结构。气孔拟分生组织在发育过程中,经历 1~3 次不均等分裂形成气孔和多个扁平细胞^[49]。把这种经过 1~3 次不均等分裂过程称为气孔系细胞的扩增分裂(amplifying division);把另一种气孔系基础细胞重新获得分裂能力,形成 2 个气孔和 1 个扁平细胞的分裂称为空间分裂(spacing division),这 2 种分裂模式同时调控气孔在表皮层的分布和发育,使气孔分布遵循“一个气孔间隔一个扁平细胞”交错的排列模式^[49,52-53]。

拟南芥中有关气孔发育及调控机理有比较深入的研究,其信号通路主要包括转录因子,配体与受体、MAPK 信号级联等^[54-55]。已经报道了 3 个 bHLH 正调转录因子 SPCH(Speechless)、MUTE 和 FAMA,分别与另 2 种转录因子 SCRM/ICE1(Scream/inducer of cbf expression 1)和 SCRM2(scream 2)形成异二聚体,分别调控由原表皮细胞向拟分生组织,拟分生组织向保卫细胞母细胞,以及保卫细胞母细胞向保卫细胞的分裂与分化 3 个关键过程^[56-59];RNA 聚合酶 II 第 3 大亚基 NRPB3(the third largest subunit of RNA polymerase II)能够与 FAMA 和 ICE1 相互作用,来执行气孔发育和图式分化特异的转录调控,功能缺陷型突变体 *nrpb3-1* 表现出 2 个气孔系细胞簇生的表型,包括簇生拟分生组织、GMCs 和气孔复合体^[60]。另外,MYB 转录因子主要包括 FLP(FOUR LIPS)和 MYB88,编码 2 种 R2R3 类 MYB 蛋白,与 FAMA 独立协同调控 GMCs 向 GCs 的分化和转变,在此过程中,FAMA 须结合另一种叫作 RBR(RETINO BLASTOMA RELATED)蛋白才能行使功能,均在气孔形成晚期发挥重要的调控作用^[56,61-62]。配体主

要包括表皮模式因子 EPFs(epidermal patterning factors)家族 EPF1、EPF2、EPFL5、EPFL6 负调控气孔发育,STOMAGEN/EPFL9 则对气孔发育起正调节作用^[63-65]。受体包括富亮氨酸重复区受体类激酶(LRR-LRK)包括 ERECTA 家族成员[ER、ERL1(ERECTA LIKE 1)和 ERL2],以及 SERK(SOMATIC EMBRYOGENESIS RECEPTOR KINASE)家族成员 SERK1—SERK4,与其共受体富亮氨酸重复的受体类蛋白 TMM(TOO MANY MOUTH)共同调控气孔系前体细胞的不均等分裂;植物促分裂原蛋白活化激酶级联信号 MAPK 信号级联(MAPK signaling cascade)由促分裂原蛋白活化激酶 YODA/MAPKKK、MKK4/MKK5/MKK7/MKK9 和 MPK3/MPK6 构成,YODA-MKK4/5-MPK3/6 信号级联通路中激酶的功能缺失导致叶表皮形成气孔簇,而持续激活将导致叶片没有气孔的形成^[66-68],因此,不同的酶活性水平影响气孔系细胞的正常发育。此外,一个新的受体蛋白 BASL(BREAKING OF ASYMMETRY IN THE STOMATAL LINEAGE)也调控气孔系拟分生组织母细胞和拟分生组织细胞的不均等分裂^[69-70]。枯草杆菌蛋白酶类的丝氨酸蛋白酶 SDD1(STOMATAL DENSITY AND DISTRIBUTION1)作用于 TMM 上游,在拟分生组织细胞和 GMCs 中表达,调控气孔图式发育^[71-72]。

3 单子叶植物气孔及扁平细胞发育图式形成研究进展

虽然有关叶扁平细胞和气孔的研究在拟南芥中取得的进展令人鼓舞,但在玉米(*Zea mays* L.)和水稻(*Oryza sativa* L.)等单子叶植物中,调控气孔及表皮细胞生长发育与形态建成的分子机制研究非常受限,因此亟待研究者去发现和挖掘。

单子叶植物中叶气孔及表皮细胞的生长发育、排列方式等与双子叶植物中截然不同^[73]。在双子叶植物中,虽然 2 个气孔遵循间隔 1 个扁平细胞的排列模式,但是气孔杂乱无章地分布在叶表皮上,并且在成熟叶片中,处于各种分裂与分化状态的气孔和扁平细胞形态随时能被观察到。但是在单子叶禾本科植物中,气孔一列列整齐地排列在叶脉两侧,也遵循 2 个气孔间隔 1 个扁平细胞的排列模式^[8]。早期叶原基形成后,气孔系细胞便开始分裂与分化,并在较短时间内完成发育,

因此在成熟叶片中,几乎观察不到正处于分裂或者分化的气孔系细胞^[73-74]。玉米叶气孔及扁平细胞的发育过程与水稻中基本一致^[75],气孔都是由气孔系原始细胞(也叫保卫细胞母细胞前体细胞)进行第1次不等分裂,产生2个大小不一的子细胞,大细胞直接发育成PCs,而小细胞称为GMCs,GMCs具有气孔系干细胞命运,能继续分裂与分化;当位于GMCs两侧的副卫细胞母细胞SMCs(subsidiary mother cells)接收到GMCs传递的某种信号后,起初在GMCs和SMCs接触的位置形成微丝斑,然后SMCs的细胞核朝GMCs极化进行第2次不均等分裂,形成副卫细胞SCs(subsidiary cells);最后,GMCs再进行1次横向均等分裂,形成对称的2个保卫细胞,随着叶发育成熟,最终形成由2个三角形副卫细胞夹着2个哑铃状的保卫细胞组成的气孔复合体^[76-79]。

目前研究发现,无论在双/单子叶植物中,气孔的分化均受到一类bHLH家族转录因子的调控,主要包括SPCH、MUTE和FAMA^[77]。在水稻中,*OsSPCH2*调控气孔形态及气孔密度,*OsFAMA*主要控制极性分裂及副卫细胞的形态变化,与*ATFAMA*功能保守,调控GMCs向特化GCs分裂。拟南芥中过表达*OsMUTE*气孔缺陷表型得到部分恢复,过表达*ZmMUTE*,也能诱导产生很多的保卫细胞,因此,推测在玉米中,同源蛋白ZmSPCH、ZmMUTE和ZmFAMA都参与调控气孔系细胞发育的信号通路^[77]。玉米中富亮氨酸受体类激酶PAN1(PANGLOSS1)和PAN2作为受体识别来源于GMCs传递的信号,调控SMCs的不均等分裂方向及其子细胞的极性分裂,功能缺失均导致气孔及表皮细胞结构异常,PAN2可能参与微丝极化,影响副卫细胞的形状,基因突变后能引起三角形的副卫细胞变成矩形^[76,80-81]。Rho家族GTPase,ROP2和ROP9与PAN1互作,调控SMCs的极性分裂^[82]。在单子叶植物二穗短柄草中,*STOMATALESS(STL)*基因功能缺失导致叶片中不能形成气孔,并且证明*STL*基因就是拟南芥与水稻中*ICE*的同源基因^[83]。同时他们利用CRISPR-Cas9(clustered, regularly interspaced short palindromic repeats-associated 9)基因编辑技术,分离到*bd-scrn2*突变体,研究表明BdSCRM2功能缺陷,虽然能形成GMCs和SCs,但是GMCs将不能正常分裂,成为开孔。双突变体*bdspch1*、*bdspch2*和

*bdice1*的突变体在气孔发育早期均不能形成GMCs前体细胞,导致气孔密度显著降低,这表明BdSPCHs和BdICE1的功能与拟南芥中的气孔调控比较相似,在调控气孔系细胞早期发育中发挥作用^[83]。因此笔者推测在水稻及玉米等禾谷类作物中,同源蛋白ZmSPCHs(3个)、ZmICE1、ZmICE2、OsICE1和OsSCRM2等也参与气孔系细胞的分裂与分化,这有待更多的学者进行基因功能的研究,以期阐明调控单子叶植物气孔系细胞形态建成的内在基因调控网络。

对玉米及水稻中调控叶扁平细胞形态和表皮毛的基因,推测主要依赖Racs(ROPs)-SCAR/WAVE-ARP2/3复合体这一保守的信号通路^[79]。在玉米中,早期报道了3个*BRK(Brick)*基因通过调控微丝成核,影响微丝排列而导致叶表皮细胞边缘突出(lobe)的缺失,且表皮毛变短、尖端钝化^[84-85]。由于当时基因组信息的不完善,文章没有给出具体的基因座信息,更没有提出这3个基因就是WAVE复合体中的3个亚基,但是笔者通过生物信息学比对和分析,确定BRK1、BRK2和BRK3与拟南芥中HSP300、PIR/SRA1和NAP1就是相互对应的同源蛋白,且进化上功能保守,通过调控微丝成核分别引起叶表皮细胞形态变化^[79,84-85]。在水稻中,表皮毛秃头基因*TUTOUI/ESI*(Early Senescence 1)编码拟南芥及玉米SCAR1同源蛋白,通过控制微丝合成,影响表皮毛的形态发育,表皮毛尖端钝化,并证明功能缺失突变体*esi*对于干旱等逆境胁迫更敏感^[86-87]。ZHOU等^[79]在水稻中克隆了2个调控表皮细胞形态建成基因*LPL2*(less pronounced lobe epidermal cell 2)和*LPL3*,分别是玉米*BRK2*和*BRK3*及拟南芥中*PIR/SRA1*和*NAP1*的同源基因,并证明*LPL2*和*LPL3*在调控水稻叶表皮细胞边缘凸出中发挥不可或缺的功能,同属于水稻SCAR/WAVE复合体的亚基,酵母双杂交试验表明*LPL2*和*LPL3*能够相互作用^[88]。总之,虽然在单子叶植物中,也克隆到少数几个调控叶表皮细胞图式发育的基因,但是离阐明单子叶植物叶表皮形态建成机制仍相差甚远,亟待挖掘。

4 展望

目前,对单子叶植物水稻、玉米叶表皮发育的遗传调控机制还悬而未决,单子叶植物气孔及扁

平细胞的发育机制不等同于双子叶植物,新的分子遗传调控机制方面的许多问题亟待解决:(1)气孔方面:有哪些特异性基因参与调控单子叶植物气孔系细胞的分裂与分化? 气孔发育图式是如何相互调控的?(2)表皮细胞方面:水稻及玉米等单子叶植物中是否存在依赖 ROPs-SCAR/WAVE-ARP2/3 复合体调控表皮细胞形态建成的信号通路? 如果存在,分别由哪些亚基组成? 各自的功能又是什么? 还有哪些信号通路参与其中^[79]? 等等问题亟待探索和研究。

植物表皮细胞发育过程易于显微观察,是研究植物的生长发育、细胞分裂与分化、形态建成和抗逆生理性研究的理想模型^[49]。克隆调控气孔发育相关基因、解析并研究基因功能,增进对水稻玉米等粮食作物气孔和表皮细胞发育机制的认识,可以通过转基因及基因编辑等分子育种手段选育既能节约淡水灌溉,又能促进农作物增产的优良品种的选育,对作物改良具有重大意义。

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Molecular Mechanism for Regulating Epidermal Morphogenesis in Plants

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Abstract The developmental process of epidermal cell was a classical model for studying growth and development, cell division, differentiation and morphogenesis in plant. The epidermis of the plant is developed from the protodermal cells, which includes the epidermal cells, stomatal complex and trichomes. In the model dicot plant *Arabidopsis*, the leaf epidermal cells are mainly composed of irregular pavement cells (PCs), stomata, and trichomes, and they also include long-shaped epidermal cells, short-shaped silicified and suberized cells, vesicular cells and hairs in monocots. It has been a hot area of research about the plant epidermal morphogenesis for the past few years, with the continuous improvement of biotechnology, awareness of the global shortage of fresh water resources, thirst for cultivating agricultural drought resistance varieties. In this review, we summarize the recent advances of the molecular genetic control of plant stomatal and PCs development in *Arabidopsis thaliana*, rice and maize. This paper aims to elucidate the molecular mechanism of epidermal growth and regulation in both model dicot and monocot plants.

Key words Plant epidermis; Stomata; Pavement cell; Morphogenesis; Network regulation

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