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植物茸毛形成的分子机制及其生理功能

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摘要 在植物体生长发育过程中, 茸毛作为植物抵御自然灾害的一道天然屏障, 对于抵御紫外线辐射、病原菌侵袭、食草动物取食及水分过度蒸腾等方面起着不可或缺的作用. 目前的研究表明, 不同植物体茸毛的形成受多类型、多基因共同调控构成一个复杂的网络系统, 在拟南芥中茸毛的形成调控还存在一系列的竞争机制对基因的活性进行促进和抑制. 茸毛在发育过程中还能够与周围环境相互作用, 如对光的反射和光量子辐射拦截, 叶片的热量平衡, 水分蒸发和气体交换等. 而且茸毛对农作物种植和生产利用都具有重要的经济价值和参考意义. 本文综述并分析了近年来植物体茸毛形成相关基因调控以及茸毛生理特性等方面的研究进展, 旨在阐明茸毛形成相关基因调控植物体茸毛形成的机制以及茸毛在环境相互交互过程中各种生理生化特点, 为进一步开展茸毛基因挖掘及其功能特性的相关研究提供重要的理论依据.

关键词 植物, 茸毛, 水分蒸腾, 热量平衡, 气体交换

茸毛是一种植物体形态多样的表皮附属物, 其主要分布于植物体地上部的茎秆、叶片及花器官中, 并且不同植物体中茸毛特征不尽相同. 茸毛结构可以由单细胞构成, 也可以是由多细胞构成; 有些植物体茸毛还可能具有分支, 如拟南芥. 根据有无腺体划分, 还有腺毛和非腺毛结构^[1]. 腺毛可以积累和分泌一些生物碱类, 如尼古丁和萜类生物碱, 这些化学物质能够抵抗昆虫; 而非腺毛可以通过加强在非生物胁迫过程中的抗逆性, 如极端高温和低温、干旱及紫外线辐射, 从而促进植物的正常生长^[2]. 茸毛的起始和时空分布也是研究细胞分化、命运决定以及形态发生机制的模式材料, 并且在植物器官发生时, 茸毛就

开始发育, 其形态发生过程与植物体分化能力、激素水平和环境密切相关^[3]. 随着近年来对植物体茸毛研究的不断深入, 特别是在基因的挖掘上, 此前一些未被阐明的机制逐渐被揭开了其神秘的面纱.

1 茸毛结构特征及分布特点

茸毛是一种适合于细胞分化、细胞周期调控、细胞极性和细胞扩张研究的模式系统. 根据在叶片上的不同分布, 茸毛可分成3类: 大茸毛、小茸毛和腺毛^[4]. 大茸毛通常位于背面, 维管束上方及叶边缘处; 小茸毛在气孔细胞旁; 而腺毛几乎规则地处于叶表面的表皮组织中^[5]. 茸毛在水稻早期发育过程中

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并不明显,直至三叶期才可以明显观察到.以单细胞非腺毛的茸毛为例,茸毛的形态发生大致可以分成5个阶段:(1)在叶面上茸毛的前期细胞径向增大,其中茸毛形成相关基因参与调控,如*GL1*, *MYB23*, *TTG1*, *GL3*, *EGL3*, *TRY*, *CPC*, *ETC1*, *ETC2*, *GL2*, *SAD2*; (2)茸毛细胞杆状结构的出现和增大,一系列相关基因参与核内复制阶段,如*SIM*, *KAK*, *SPY*, *CPR5*, *ICK/KPR*, *RHL2*, *HYP6*; (3)一系列分支基因参与分支结构的形成,如*AN*, *STI*, *FRC*, *TFCA*, *TFCC*, *ZWI*等; (4)分支生长方向基因进一步调控茸毛生长,杆状结构和分支的进一步增大,并且此时分支的尖端呈钝状,如*GRL*, *KLK*, *BRICK1*, *ROP2*, *DIS1*, *DIS2*, *WRM*, *CRK*; (5)随着茸毛的进一步发育,杆状结构和分支继续扩张,此时的分支顶端变尖,并且发育成为表面具有乳状突起的成熟表皮毛(图1)^[6,7].

茸毛的分布和形态与地理位置、气候等自然因素在内的很多因素有关,如番茄的茸毛在茎秆上具有两种不同的分布特点,其茎秆被茸毛覆盖,而在茎的顶端,茸毛分布却非常稀少^[8].此外,茸毛密度的大小在不同的植物器官中也呈不同的分布特点,例如,茶树嫩梢茸毛以芽最密,并伴随幼叶成熟而自行脱

落,同一品种的叶背上茸毛长度依叶序而异,不同嫩叶的茸毛密度依叶片生长次序的不同而有显著差异^[9].Brewer和Smith^[10]发现不同类型的叶片茸毛密度不同,例如,在大豆叶片中,叶片面上茸毛的密度较背部稠密.

2 茸毛发育形成相关的分子机制

随着研究的不断深入,越来越多茸毛发育相关的基因被定位和克隆.在双子叶模式植物拟南芥中,研究人员已经发现一系列与茸毛形成和发育相关的基因,如*GIS*^[11], *MYB23*^[12], *GL3/EGL3*^[13,14], *TTG1*^[15], *GLI*^[16], *GL2*^[17],并且相关网络调控方式也逐渐被认知.但在单子叶植物中,茸毛的分子作用机制仍然不是很清楚,如水稻(*Oryza sativa*)作为一种重要的粮食作物和单子叶模式植物,其农艺性状也会受到茸毛的影响.近年来很多与茸毛相关的基因已被相继定位,如基因*OsGLR1*和*OsGL6*分别定位在第5和6号染色体上^[18,19].此外,一些同源基因,如拟南芥中的*TCL1*基因与水稻中对应的同源基因*OsTCL1/OsTCL2*也被证明能够调控茸毛的生长^[20](表1).

在拟南芥中,茸毛的生长和发育是由一系列复

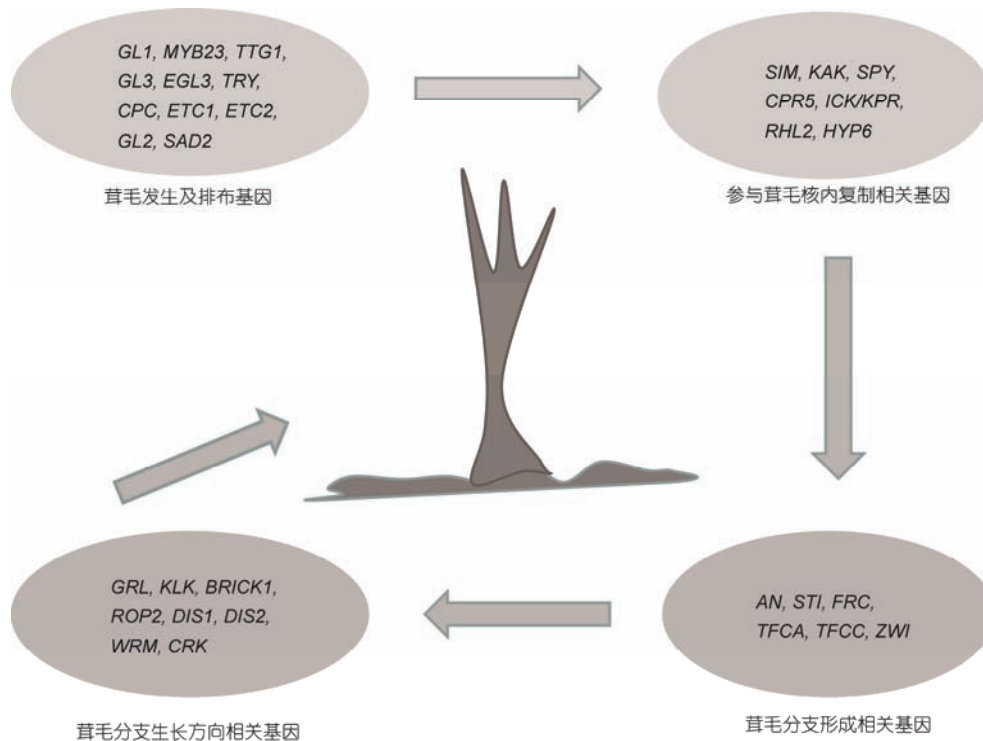


图1 (网络版彩色)植物叶片表面茸毛的形态发生生长过程

Figure 1 (Color online) The process of trichomes formation on the surface of plant leaves

表 1 植物中克隆的茸毛相关基因及其功能

Table 1 The cloned genes and their functions of trichomes in plants

基因(Chr.)	功能	物种	参考文献
<i>AtGL1(Chr.3)</i>	叶片茸毛分化所需的MYB相关基因	拟南芥	[16]
<i>AtGL2(Chr.1)</i>	具有脂质结合START结合域的HD-Zip蛋白	拟南芥	[17]
<i>AtGL3(Chr.5)</i>	bHLH结构的DNA结合超家族蛋白	拟南芥	[13]
<i>AtTTG1(Chr.5)</i>	转导素/WD40重复超家族蛋白	拟南芥	[15]
<i>AtTRY(Chr.5)</i>	同源结构域样超家族蛋白	拟南芥	[21]
<i>AtCPC(Chr.2)</i>	同源结构域样超家族蛋白	拟南芥	[22]
<i>AtTCL1(Chr.1)</i>	同源结构域样超家族蛋白	拟南芥	[11]
<i>AtTCL2(Chr.2)</i>	同源结构域样超家族蛋白	拟南芥	[23]
<i>AtETC1(Chr.1)</i>	同源结构域样超家族蛋白	拟南芥	[24]
<i>AtETC2(Chr.2)</i>	同源结构域样超家族蛋白	拟南芥	[25]
<i>OsGL1(Chr.5)</i>	含有WOX基序的同源结构域蛋白	水稻	[18]
<i>OsGL6(Chr.6)</i>	未知	水稻	[19]
<i>OsHLA/HLb(Chr.9/11)</i>	叶片长软毛互补基因	水稻	[26]
<i>Wo(Chr.1)</i>	含有bZIP基序和START结构域的同源结构域蛋白	水稻	[27]
<i>SlCycB2(Chr.2)</i>	由Wo调控并参与茸毛形成	水稻	[27]
<i>GaHOX1(Chr.7)</i>	HD-Zip IV基因	水稻	[28]
<i>GhMYBs</i>	调节早期纤维和茸毛发育	水稻	[29]
<i>QLP1(Chr.6)</i>	仅减少幼叶茸毛	水稻	[30]
<i>QLP2(Chr.25)</i>	增加成熟叶片的茸毛	水稻	[30]
<i>RDLI(Chr.4)</i>	棉花纤维发育的调控子	水稻	[31]
<i>OCL4(Chr.1)</i>	HD-ZIP IV转录因子	玉米	[32]
<i>MHL1(Chr.3)</i>	应答于调控叶片识别因子	玉米	[33]

杂的基因协同进行网络调控(图2)。其中已报道的与茸毛相关的突变体多达80多个, 40多个相关基因已被克隆, 这些基因一般都是属于转录因子类基因, 包括MYB类, bHLH类和TTG类转录因子, 如GIS亚家族基因(*ZFP5*^[34], *ZFP6*^[35], *GIS3*^[36]等)、转录激活子*GL2*、*GLABRA1(GL1)*、WD40重复蛋白TRANSPARENT TESTA *GLABRA1(TTG1)*以及茸毛起始的关键因子bHLH转录因子*GLABRA3/GLABRA3*增强子(*GL3/ EGL3*)。MYB转录因子家族是植物中最大的转录因子家族之一, 根据N端DNA结构域重复数(DNA-binding domain repeats, R)可分成4大亚类: 4R-MYB, 3R-MYB, R2R3-MYB和1R-MYB, 其分别含有4, 3, 2, 1个DNA结构域重复数^[37]。有研究证明, *GL1*, *TTG1*和*GL3/EGL3*能形成*GL1-GL3/EGL3-TTG1*激活复合体, 触发*GL2*的表达, 进而促进茸毛的形成^[17]。有趣的是, 同样的激活复合体同样能够诱导某些单重复序列R3-MYB基因, 如*TRY*, *CPC*, *ETC*, *TCL*等的表达,

这些R3-MYB基因反过来能从茸毛的前体细胞进入到其相邻的细胞中, 并与*GL1*竞争结合*GL3*或*EGL3*阻断激活复合体的结合, 从而抑制*GL1-GL3/EGL3-TTG1*激活复合体并抑制茸毛的形成^[38]。此外, 有研究表明, *GL3*能够激活*FRC4*影响茸毛的分支^[22]。*KAKTUS(KAK)*和*POLYCHOME(PYM)*被认为是调控茸毛分支的负反馈子, *ANGUSTIFOLIA(AM)*能够通过MYB转录因子*NOEK(NOK)*负调控促进茸毛分支的形成, 而当赤霉素信号受体*SPY*基因缺失突变时则能增加茸毛的分支^[22]。

虽然有证据表明双子叶植物具有相似的控制茸毛形成机制, 但是在单子叶植物中并不适用^[20]。Zheng等人^[20]利用拟南芥R3-MYB转录因子*TRICHOM-ELESS1(TCL1)*的完整氨基酸序列通过BLAST水稻参考基因组得到两个基因*OsTCL1*和*OsTCL2*, 用转化拟南芥原生质体的方法转化*OsTCL1*基因后, 发现*OsTCL1*并不能改变转基因水稻植株的表型, 即通过

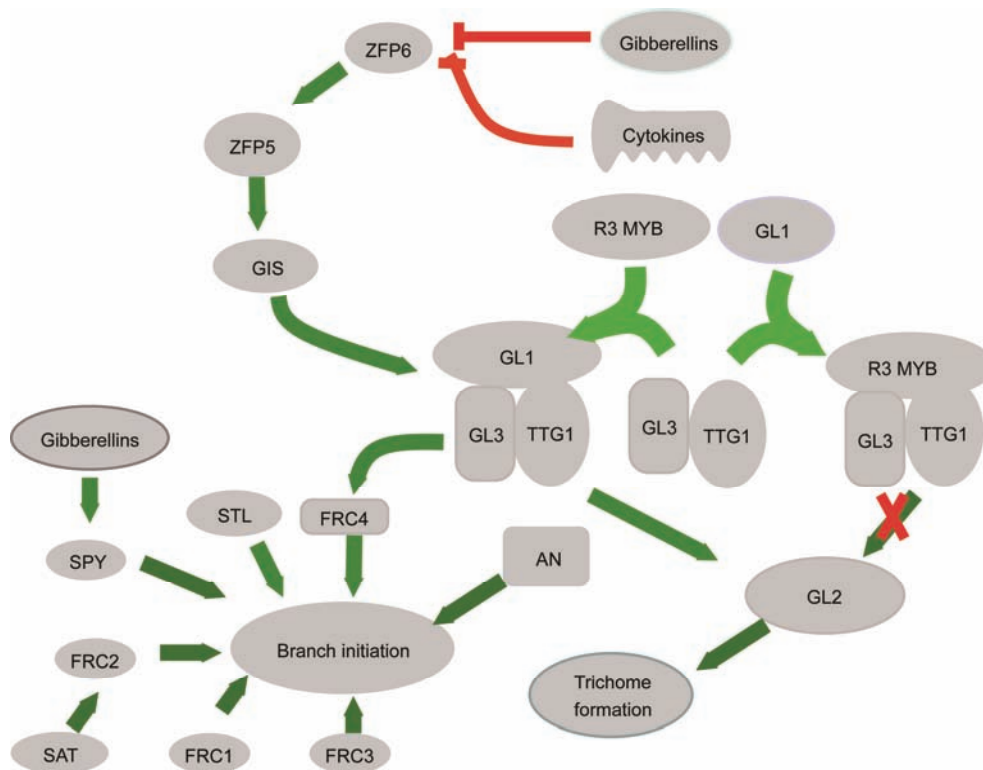


图 2 (网络版彩色)拟南芥茸毛形成信号调控通路^[39]。茸毛形成的复杂网络调控: (1) *GL1*, *GL3/EGL3* 和 *TTG1* 形成三联体MBW激活复合体 (MYB-bHLH-WD40), 触发 *GL2* 的表达, 导致茸毛的产生; (2) 某些单重复 *R3-MYB* 基因能与 *GL1* 竞争结合 *GL3/EGL3*, 抑制三联体MBW激活复合体的形成, 从而抑制茸毛的形成; (3) *GL3* 能够激活 *FRC4* 基因从而影响茸毛的分支, 除此之外, 还有很多基因参与对茸毛分支的调控, 包括 *FRC1-3*, *SPY*, *STL* 等; (4) 赤霉素和细胞分裂素能够通过调控 *ZFP6*, *ZFP5*, *GIS* 等基因参与调控茸毛的形成, 从而进一步调控MBW激活复合体的形成来诱导 *GL2* 的表达从而促进茸毛的形成

Figure 2 (Color online) Signaling pathway for the regulation of the trichomes in *Arabidopsis thaliana*^[39]. The complex network regulation of trichomes formation: (1) *GL1*, *GL3/EGL3* and *TTG1* form triplex MBW activation complex (MYB-bHLH-WD40), triggering *GL2* expression, leading to the formation of trichomes. (2) Some single-repeat *R3-MYB* genes compete with *GL1* for *GL3/EGL3*, inhibit the formation of MBW activation complex and inhibiting the formation of trichomes. (3) *GL3* can activate the *FRC4* gene and thus affect the branch of the trichome, there are many genes involved in the regulation of trichome branch, including *FRC1-3*, *SPY*, *STL*, etc. (4) Gibberellin and cytokinin can be involved in the formation of trichomes by regulating *ZFP6*, *ZFP5*, *GIS* and other genes, and further regulate the formation of MBW-activated complex to induce the expression of *GL2* thereby promoting the formation

过表达 *OsTCL1* 不能影响茸毛的形成, 这表明调控拟南芥茸毛形成的机制在水稻中并不适用. 到目前为止, 除了同源基因外, 在水稻茸毛定位研究中已克隆的基因只有 *OsGLI*^[18], 但其作用机制尚不清楚.

除了拟南芥和水稻外, 在其他植物中也有很多基因参与茸毛的形成, 如已被克隆分别位于4BL和7BS染色体上的小麦 *HI2* 和 *HI2Aesp* 基因^[40]; 在玉米中, 一系列 GLOSSY 家族基因被克隆, 结果证明这些基因能够影响茸毛形态、茸毛的生长及表皮蜡质物质的生物合成^[41]; 在烟草中, 过表达 *MIXTA* 基因能够使植株的子叶、叶片和茎干上形成大量的茸毛. 同时, 另一个基因 *CotMYBA* 还可能影响玉米叶片的生长^[42]; 在马铃薯中, 编码 HD-ZIP 蛋白的 *WO* 基因, 能够与细

胞周期调控因子 *B2* 互作, 在茸毛形成和胚胎发育过程中起到非常重要的作用^[27]. 在棉花中, 与拟南芥茸毛形成相关基因 *GL1* 同源的 miR828 和 miR858 靶向的 MYB2 基因 *GhMYB2D*, 编码 bHLH 结构域的转录因子 *GoPGF* 在纤维发育和形成中都能够促进和抑制茸毛纤维的形成^[43-45]. 在黄瓜中, 茸毛主要是多细胞和非腺毛结构. 有研究表明, 很多已经被定位和克隆的基因与拟南芥调控茸毛的基因同源, 并且具有类似的调控方式, 主要有 *csGLI*^[46], *csGL3*^[47], *CUC3* 和 *STM* 等^[43]. 番茄中, 根据茸毛是否含有或分泌对昆虫或病原体具有抗性的化合物, 将多细胞茸毛分为 I ~ VII 种类型, 分别是 I, IV, VI 和 VII 型的腺体和 II, III 型的非腺体^[48]. 有研究表明, *ShMYB1*, *Tm-2nv*, *BAHD*

等基因参与茸毛的形成调控。

3 茸毛的生理功能

近10年来,很多研究已证明茸毛在植物体与环境相互作用中具有非常广泛的作用。其中,茸毛的密度和长度是重要的影响因素。茸毛长度决定了叶片表面被茸毛遮挡的厚度^[49],并且随着叶片个体差异而有所变化^[50],而茸毛长度增加会导致叶片对光的吸收率下降。致密的茸毛能够调节叶片的热量平衡,并且拦截光量子,从而影响植物体的气体交换,在强光时具有保护作用^[51]。有研究表明,叶片茸毛的密度是可变的,并且受遗传和环境因素决定^[1],当土壤水分不足,高温,蒸气压亏缺(vapour pressure deficit, VPD)时能增加叶片茸毛密度^[52,53]。此外,有茸毛的植株还具有抗虫和抗病等特点,郭香墨和汪若海^[54]利用植物体棉花对不同抗性品系在虫害胁迫下的抗性进行了初步研究,结果表明,多茸毛性状抗棉蚜性最好,光滑叶抗性较差。因此,茸毛的生理特性对植物体自身的生长具有非常重要的作用。我们将通过光反射与能量平衡、紫外辐射的防护、抗旱性、叶肉细胞的气体交换、抗虫性及抗病性六个方面进行阐述。

3.1 光反射与能量平衡

研究表明茸毛是一个具有广谱辐射特性的反射体,其在调节植物能量平衡中具有显著作用。当叶片暴露在环境中时,叶片可以通过蒸腾冷却作用来调节热量的平衡,其中需要足够的水分供应或者叶片吸收水分来供给^[55]。在一些叶片较薄的植物中,叶片表面的反射率会随着季节变化而变化。在冬季,茸毛能够吸收80%的辐射从而使叶片温度稍高于周围环境,而在夏季雨天条件下,茸毛对入射辐射的吸收则降低到30%~40%左右,从而使叶片温度低于周围环境温度,并且茸毛这种降温作用可以增加固碳作用并减少水分20%~25%的损失^[56]。然而,关于茸毛对叶片温度影响的生理生态意义还需要进一步的研究来证明其在与环境互作过程中的作用机制。

3.2 紫外辐射的防护

许多研究证明,茸毛可以吸收紫外线的辐射,从而减少紫外线UV-B对光合系统II光化学活性的损伤并防止气孔关闭。因此,茸毛对UV-B辐射损伤在叶

片发育过程中具有显著的保护作用^[57,58]。最近,Yan等人^[57]发现拟南芥暴露在UV-B中可以诱导茸毛的形成,这可能是由于茸毛细胞壁中存在黄酮类和表皮蜡质物质。茸毛分泌的黄酮类物质主要是以水溶性糖苷形式存在于叶片表皮细胞的液泡中,该物质的积累能够降低表皮层UV-B辐射的透过率,从而减少对植物器官和组织的伤害^[57]。其原因可能是由于黄酮类物质对O-甲基化非常敏感,因此使对紫外吸收的特性向较短的波长扩展,从而更有效地吸收250~320 nm的紫外辐射,降低对植物的紫外UV-B损伤^[58]。黄酮类化合物能吸收并减少植物组织的UV-B辐射量,在植物体中起到“内部过滤器”的功能^[58],因此在植物生化调节中起到重要作用。

3.3 抗旱性

根据植物形态结构特点可以缓解水分供给与需求之间的矛盾,从而增强抗旱性。尚宏芹和刘建萍^[59]发现,植物耐旱的一个可能因素是致密茸毛的存在,空气滞留在茸毛中,降低植物的蒸腾速率而且不影响周围CO₂的交换。此外,茸毛能够隐藏部分孔洞,从而减少水分散失,这在水分保持与缓解叶片温度中起非常重要的作用^[60]。研究表明,茸毛在近端与远端(相对于叶片)对水分保持及水滴的滞留能力具有不同的特点。Fernández等人^[60]通过检测叶片近端与远端茸毛的理化性质,发现与靠近叶片的近端相比,远端的茸毛具有较低的湿度和更高的疏水性。而这种疏水性与远端茸毛的化学特性与结构差异具有很大的关联。然而他们分析后发现这种表面化学特性增加了表面的粗糙度,并且影响叶片的湿度,是这种水分-叶片相互作用的驱动力来源。虽然茸毛近端和远端的许多理化差异和它们各自的叶表面差异尚不清楚,但这些实验数据能够表明茸毛在不同端可能发挥不同的功能。

3.4 叶肉细胞的气体交换

植物体在水生到陆生演化过程中,出现了角质层等保护层以防止水分的过度蒸腾,并出现了气孔,该结构是集中进行气体交换的场所。气孔和角质层在不同的生长环境中,形成各不相同的特点,如旱生植物夹竹桃^[61],为防止水分的过度蒸腾其叶下表面特化出了气孔窝,气孔窝内着生若干气孔,并被茸毛所覆盖,这样既保证了高效率的气体交换,同时也防

止了通过气孔造成的水分过度丢失^[62]。气孔和边界层的阻碍是植物与大气之间进行气体交换的两个主要阻力。Benz和Martin^[63]检测了12种铁兰中的H₂O与CO₂气体交换因素和叶片茸毛覆盖的关系,发现铁兰中的茸毛对增强边界层的气体交换影响可以忽略不计,并且得出结论表示茸毛并不能显著减少水分的蒸腾散失,但能够增加边界层的厚度。蔡水花等人^[64]发现,较高的净光合速率与较高的气孔电导率相关,而后者可能与气孔密度和解剖结构特点相关。

3.5 抗虫性

植物茸毛对昆虫的影响具有双重性,不同的昆虫对茸毛具有不同的反应。茸毛的密度、长度、柔软度或硬度、生长方向和形状可能与抗虫性相关。这种抗虫行为的模式主要是排斥作用,包括栖息排斥(不利于昆虫的附着和运动)和抵制产卵或觅食等行为^[65]。昆虫对植物体茸毛的反应与茸毛的种类有关。一般来说,昆虫对植物体附着和表面的行为、觅食和产卵会受到茸毛和刺的不同程度影响。有研究表明,每单位面积茸毛的数量超过300根时,昆虫就会受到茸毛的影响并死亡^[66]。茸毛还能够影响某些昆虫幼虫的行为,如棉铃虫,茸毛能够阻碍其在棉花叶片和叶柄的初步孵化,并将其暴露于捕食者和高温,最终导致精力衰竭和死亡^[67]。茸毛还会影响具有小咀嚼器昆虫的消化,其原因可能是由于幼虫必须觅食毛状体才能到达表皮,而当消化道积累太多茸毛时则难于被消化^[68]。有研究表明,番茄叶片上的茸毛密度是导致昆虫避开它的主要因素。此外,叶片表面的茸毛还会分泌烷烃、酰基糖、倍半萜烯和一些其他化学物质来杀死或排斥昆虫^[69]。有报道指出,植物体茸毛对抗蚜虫具有重要的作用。尚宏芹等人^[70]利用辣椒体表茸毛与抗蚜虫关系进行研究,辣椒体表茸毛对抗蚜性有关,室内外接种内桃蚜 [*Myzus persicae*(sulzer)] 实验结果表明,茸毛不利于蚜虫侵染,蚜虫在有茸毛植株上的繁殖数最小且主要分布在茸毛密度小的中下部位,在无茸毛植株上主要分

布在中上部位,茸毛不利于蚜虫附着;多茸毛植株上蚜虫的繁殖率、增长倍数显著低于少茸毛植株和无茸毛植株,而且室内自然感染蚜虫实验表明,与有茸毛植株相比,蚜虫更喜欢侵染无茸毛植株。

3.6 抗病性

植物体表面的茸毛在抗病性中也起重要作用。其可以通过将病原菌繁殖体悬浮在叶片的表面来减少接触与入侵的机会,并且有些茸毛可以合成有毒物质来抑制病原菌孢子的入侵和萌发^[71]。Bechmen等人^[72]报道指出酚类物质存在于植物体的叶片中,这些物质是通过茸毛的外部刺激释放。同时,也有研究指出来自茸毛的某些物质可以抑制一些真菌的生长^[73]。有些病毒会以虫体为媒介进行传播,例如玉米矮花叶病(Maize Dwarf Mosaic Virus, MDMV),其能以蚜虫(支二叉蚜、玉米蚜、桃蚜、棉蚜等)为介体传播病毒,通过茸毛的抗虫性进一步抑制其传播^[74]。

4 结语

茸毛广泛存在于植物体的地上部分。近年来,随着对拟南芥以及水稻茸毛基因的挖掘,茸毛相关基因都已被克隆并形成较为清晰的信号通路网络。在单子叶植物水稻中,茸毛的形成机制可能与双子叶植物拟南芥的调控机制不同。同时,一些植物激素还可能参与茸毛的调控,并且在不同的植物中具有不同的调控机制。对于茸毛的生长发育,可能从幼苗起直至死亡整个过程中都具有时空的统一性,此外,植物茸毛的密度、长度和分布等都能发挥相应的生理作用,同时由于特殊的结构特点,赋予了特殊的生理功能。

根据不同地理生态特点以及植物的生长需要,我们可以进一步通过研究茸毛的形成和生理学功能,提高植物体对环境的适应性及产量,通过改变不同植物体茸毛的分布及密度等特点来充分利用其不同的生理特点以促进或抑制茸毛的形成,从而来改变农作物在生活生产中的运用,这对未来的研究与生产都具有重要的理论意义和实际价值。

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Summary for “植物茸毛形成的分子机制及其生理功能”

Molecular mechanism and physiological function of trichome formation in plant

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Trichome, as a protective barrier against natural hazards, plays an indispensable role in resisting ultraviolet radiation, pathogen invasion, herbivores feeding and water excessive transpiration during the process of plant growth and development. Trichomes may be unicellular or multicellular and some plants such as *Arabidopsis thaliana* may also have branches, according to the presence or absence of glands, it can be divided into glandular or non-glandular, the former can accumulate and secrete some alkaloids, such as nicotine and terpenoids, which have an exclusion effect on insects, while the latter can be enhanced the stress resistance during abiotic stress, such as extreme high and low temperatures, ultraviolet radiation, thereby promoting and controlling the normal growth of plants. The current study shows that the formation of trichome is co-regulation by many types and multiple genes, thus form a complex regulation network. The mechanism of the regulation and genes mining of the trichome in the dicotyledonous has made substantial progress in recent years, especially in *Arabidopsis*, Trichome formation in *Athaliana* is thought to be regulated by a competitive system, including the promotion and inhibition of the gene activities. More and more studies have shown that there are a variety of different genes can regulate the trichome formation in different plants. The genes controlling trichome formation are generally a class of MYB transcription factors in *Arabidopsis* [31], whereas a HD-Zip protein, Woolly (Wo) that interacts with Cyclin B2, plays an essential role for trichome formation and embryonic development in tomato. In addition, the Glabrous Rice 1 (GLR1), which encodes a WUS-like homeobox gene (WOX), also regulates the formation of trichomes in rice. It was proposed that Trichome can also interact with the environment under the development process of plants, such as light refraction, light quantum radiation interception, leaf heat balance, wettability, droplet retention, water uptake and gas exchange. Leaf trichome density is variable and determined by genetic and environmental factors, climate drivers such as soil water deficit and high temperature can increase the trichome density. The studies have shown that leaf trichomes can reflect broad-spectrum electromagnetic radiation, and reducing light absorptance and modulating energy balance. Except as described above, trichome can promote gas exchange and limit pathogen growth and spread on leaves. According to the physiological characteristics of the trichome, the crop cultivation, production and utilization have important economic value and significance. In this article, We systematically reviewed and analyzed a series of related studies on the progress and physiological characteristics of genes which related to the regulation of plant trichome formation in recent years, The aim of this review was to elucidate the regulation mechanism of the trichome formation and the physiological and biochemical characteristics, so as to provide an important theoretical basis for further research on the excavation and functional characteristics of the trichome genes.

plant, trichomes, water transpiration, heat balance, gas exchange

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