植物遗传资源学报 2010,11(6):659-665
Journal of Plant Genetic Resources

植物 DNA 甲基化与作物种质资源保存

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摘要:DNA 甲基化是真核生物基因表达调控的重要机制之一。甲基化 DNA 与甲基特异结合蛋白结合,并作为染色质修饰复合物识别和作用的平台,参与对染色质组织方式的调节,最终影响基因的表达。本文对植物 DNA 甲基化及其生物学功能、检测分析方法以及作物种质资源保存中存在的甲基化现象进行了综述,旨在为深入了解 DNA 甲基化修饰对种质资源的影响,更好地开展作物种质资源保护供参考。

关键词:DNA 甲基化;基因表达调控;逆境胁迫;种质资源保存

Plant DNA Mehtylation and Crop Germplasm Conservation

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Abstract:DNA methylation is one of the important regulation mechanisms for gene expression in eukaryotic genome. Methylated DNA can interact with specific methyl-binding protein,and acts as a platform to facilitate the recognition of chromatin complex,and involves in the organization of chromosome structure,which ultimately determines gene's expression. Here,we reviewed the research progress on plant DNA methylation,summarized its biological functions and detection methods,and introduced the wide occurrence of DNA mehtylation,which might lead to phenotype variation in the process of crop germplasm conservation. The purpose is to provide a clue to understand the DNA mehtylation and explore an approach for the security of conserved crop germplasm.

Keywords:DNA methylation; Gene expression and regulation; Abiotic stress;Germplasm conservation

近年来,表观遗传学(epigenetics)研究成为生物学领域的一个新焦点,但事实上表观遗传学并不是一个新领域。早在 1942 年,Waddington[1]就提出了 Epigenetics 一词,并指出表观遗传与经典遗传的相对性,前者主要研究基因型与表型的关系。1990 年,Holiday[2]对表观遗传学作了较为具体的界定,即生物在不改变基因组序列的前提下,通过 DNA 和组蛋白修饰来调控基因表达。随着生命科学的飞速发展,尤其是基因沉默(gene silencing)和 RNA 干扰(RNA interference)等现象的发现,使表观遗传学的研究范畴进一步扩展。目前表观遗传学研究内容主要包括:DNA 甲基化(DNA methylation)、组蛋白密码(histone codon)、RNA 干扰、基因沉默、基因组印迹(genomic imprinting)、转座子激活(transposon activation)以及 RNA 编辑(RNA editing)等。Bird 等[3-4]认为 DNA 甲基化是表观遗传调控的基础,甲基特异结合蛋白与甲基化 DNA 序列结合,并作为染色质修饰复合物识别、作用的平台,参与对染色质组织方式的调节。

过去的 10 多年间,表观遗传学研究取得了一系列具有里程碑意义的进展。1999 年第 1 个表观基因组研究机构——人类表观基因组协会(human epigenome consortium,HEC)在欧洲成立,2003 年 HEC 率先提出人类表观基因组计划(human epigenome programme,HEP),旨在绘制人类基因组中甲基化位点图谱,以指导和系统地研究 DNA 甲基化在

收稿日期:2010-05-17　　**修回日期**:2010-07-21

基金项目:转基因生物新品种培育科技重大专项(2009ZX08002-012B);中央级公益性科研院所基本科研业务费专项

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人类表观遗传、胚胎发育、基因印迹、等位基因失活及肿瘤发生中的重要作用。2006年，第一张拟南芥全基因组高分辨率甲基化图谱诞生[5]，随后科学家们又绘制了多张拟南芥甲基化图谱，发现甲基化位点的分布决定了基因的表达水平[6-8]。近期，He等[9]绘制整合了表观基因组、mRNA和siRNA转录组等多种信息的水稻表观遗传整合图谱，发现水稻杂交后代甲基化修饰和基因表达存在明显的等位基因偏爱性。不同生物表观遗传图谱的绘制为我们全面深入认识真核生物基因表达调控的机制提供了可能。

鉴于DNA甲基化在表观遗传研究中的地位，本文重点对植物DNA甲基化的研究进展、生物学功能以及作物种质资源保存中的DNA甲基化现象作以综述，为作物种质资源保存提供理论参考。

1 植物DNA甲基化

DNA甲基化主要是指DNA中胞嘧啶第5位碳原子在相关酶的作用下发生甲基化。由于5-甲基胞嘧啶(m^5C)在基因的表达调控方面起着非常重要的作用，因此被称作遗传物质中的第5种核苷酸。DNA甲基化现象在真核生物中广泛存在，它是真核生物基因表达调控的重要机制之一，与生物的生长、发育、分化以及对逆境的适应性息息相关。不同物种的DNA甲基化水平存在差异，高等植物基因组DNA甲基化水平一般介于6% ~25%[10]。

与哺乳动物相比，植物DNA甲基化调控机制也更为复杂。哺乳动物中胞嘧啶甲基化都特异地发生在CG位点，而植物基因组中却存在3种类型的甲基化序列：对称的CG序列、不对称的CNG(N代表任何核苷酸)和CHH(H代表A、C或T)序列。不同序列甲基化的发生、维持以及去甲基化过程是由不同的甲基化酶催化完成[11]。其中，DNA甲基转移酶1(methyltransferase 1，MET1)主要维持CG对称序列甲基化状态[12-13]，染色体甲基化酶(chromomethylase，CMT)维持异染色质中CNG序列甲基化和沉默甲基化位点[14-15]，而结构域重排甲基转移酶(domains-rearranged methyltransferase，DRM)参与对上述3种序列的从头甲基化[16-17]，且这种从头甲基化过程需要小干扰(siRNA)的参与和指导[18-19]。

关于DNA甲基化修饰调控基因表达有2种模型：一种模型认为甲基化DNA特异结合蛋白与基因启动子区结合，导致增强子和基因在空间上“隔离”，引发蛋白质结合区异染色质化，使增强子元件不能正常发挥作用，从而抑制基因的转录表达[4]；另一种模型认为甲基结合蛋白(methyl-binding domain，MBD)与甲基化DNA序列结合，在空间上阻碍了转录因子与基因上游启动子的结合，抑制了基因的表达[4,20]。

2 DNA甲基化的生物学功能

目前，尚未全面揭示植物DNA甲基化的作用，但根据现有的研究结果，可以将DNA甲基化的生物学功能概括为以下几个方面：参与维持基因组的稳定、防御外来DNA的入侵、基因组印迹调节、生长发育和分化调节以及对逆境胁迫的响应等。

2.1 维持基因组稳定

DNA甲基化在维持真核生物基因组稳定性方面发挥着至关重要的作用。植物基因组中存在多种类型的转座子，一般情况下这些转座子都处于无活性的超甲基化状态[21]。转座子的活性取决于染色质状态(异染色质/常染色质)，而异染色质的形成和维持与DNA和组蛋白甲基化状态息息相关[22]，异染色质的改变将会影响转座子的活性[23]。DNA甲基化修饰能有效阻止转座子表达，抑制转座子活性，防止转座子在基因组内或基因组间“跳跃”，减少转座子移动可能带来的危害[21]。Hoekenga等[24]发现玉米Ac转座子的活性与其所处的甲基化状态紧密相关；Hirochika等[25]研究表明，DNA甲基化水平降低导致正常条件下沉默的转座子和高拷贝基因被重新激活。植物通过对转座子甲基化程度的调节，能有效维持基因组的稳定性，成功避免转座带来的有害影响。

2.2 防御外来DNA入侵

作为植物自身防御系统的重要组成部分，抵御外来核酸因子入侵是DNA甲基化修饰的重要生物学功能之一[23,26]。植物DNA甲基化的防御功能可以分为两方面：主动防御和被动防御。主动防御是指植物通过特殊机制识别外来核酸，包括转基因进入体内的DNA和侵染的病原菌DNA，使之发生甲基化而不表达，减少外来DNA表达所造成的危害[26-28]。许多证据表明，DNA甲基化参与调控基因转录沉默(transcription gene silencing，TGS)和转录后沉默(post-transcription gene silencing，PTGS)，其中启动子区DNA甲基化直接抑制基因转录，即TGS，而编码区甲基化状态改变和PTGS密切相关[29]。Wang等[30]将由35S启动子控制的*GUS*基因导入棉花中，发现35S启动子区TATA box DNA

甲基化导致 *GUS* 基因沉默。Meyer 等[31]将玉米 *A*1 基因转到矮牵牛中,发现目标基因在不同转基因株系中表达水平的高低与其整合位点处 DNA 甲基化水平密切相关。Raja 等[28]的研究结果表明,甜菜顶端卷曲病毒(beet curly top virus,BCTV)侵入拟南芥后,BCTV 基因组 DNA 很快被甲基化,导致 BCTV 失活。

同时,植物也可以通过被动防御方式阻止外来核酸入侵。被动防御是指植物通过提高抗病基因的重组率或 DNA 甲基化修饰改变染色体的结构,提高对外来 DNA 的防御能力[32]。受烟草花叶病毒(tobacco mosaic virus,TMV)诱导,烟草病原菌应答基因 *NtAlix*1 和 *NtGPDL* 的 DNA 甲基化状态发生明显改变[33-34]。Boyko 等[32]研究表明,TMV 侵染导致烟草及其后代基因组 DNA 甲基化水平的整体升高,但编码抗病基因 LRR 结构域的区段甲基化水平降低,同时抗病基因的重组率升高。Boyko[32]认为抗病基因重组率增高和特异位点甲基化模式的改变在一定程度上反映了植物对病原菌入侵的适应性。Sha 等[35]发现水稻幼苗接种白叶枯病菌后,其 DNA 甲基化水平明显提高,成株抗病性增强,因此推测 DNA 甲基化与水稻的成株抗性有关。

2.3　调节基因组印迹

哺乳动物和植物继承父本和母本两套染色体组,在子代体内来自双亲的绝大多数基因都能表达,但对于有些基因却只有来自特定亲本的等位基因能够表达,这种表观遗传调控的方式称作基因组印迹[36]。基因组印迹也称亲本印迹,它是一种广泛存在于哺乳动物和植物中的基因表达调控方式。研究表明,在拟南芥种子发育过程中存在广泛的基因组印迹现象[37]。Kinoshita 等[38]发现,在拟南芥胚乳中只有来自母本的 *MEDEA* 基因表达,而在根、茎、叶、胚等器官中可以同时检测到来自双亲的基因表达;Luo 等[39]发现拟南芥 *FIS*2 和 *FIE* 基因的表达也具有类似的基因组印迹特性。Chaudhury 等[40]的研究结果显示,拟南芥 *FIS* 基因可以通过调节染色质的结构,控制下游调节种子发育相关基因的表达,而 *FIS* 自身的表达则受来自亲本特异表达或基因印迹基因的调控,后者的表达受 DNA 甲基化的控制。此外,Lund 等[41]还发现玉米胚乳中种子贮藏蛋白基因(*α-zein*)的高水平表达与其来自母本的 *α-zein* 甲基化水平降低存在明显的相关性,而在胚乳以外的组织器官中并未检测到类似现象。

2.4　调节植物生长发育和分化

许多研究表明,真核生物 DNA 甲基化还参与调控基因的时空表达,与植物的生长、发育、分化和形态建成密切相关,如果 DNA 甲基化水平降低将直接导致植物发育异常[15,23,42]。Finnegan 等[42-43]发现拟南芥 DNA 甲基化水平降低导致其多种表型和发育不正常,如顶端优势消失、植株变小、叶片形状和大小发生改变、育性降低、开花时间改变等。对云兰属植物 *Linaria vulgaris* 的研究表明,*lcyc* 基因甲基化导致其花型由左右对称变为辐射状[44]。Soppe 等[45]发现拟南芥 *FWA* 基因的表达与否决定开花的早晚,序列比较发现野生型和突变体中 *FWA* 的基因序列完全相同,二者的差异在于野生型拟南芥中 *FWA* 基因 5′端两个重复序列处于甲基化状态,因此 *FWA* 基因不表达,而在突变体中 *fwa* 5′端的重复序列发生了去甲基化,*FWA* 基因表达导致开花延迟。DNA 甲基化影响生长发育的另一个经典案例是植物的春化作用。Burn 等[46]用 5 - 氮胞苷(5 - azaC)处理未春化的拟南芥植株,发现处理比对照的开花期明显提前,而对春化作用不敏感的晚开花突变体对 5 - azaC 处理没有任何反应。Finnegan 等[47]利用反义 RNA 技术将拟南芥中甲基转移酶基因(*MET*1)沉默,发现转基因拟南芥基因组 DNA 甲基化水平降低,伴随着转基因植株的提早开花(无需春化),同时还发现低温和去甲基化对开花的诱导作用具有加性效应。此外,许多证据表明,DNA 甲基化还参与对植物的体细胞全能性和细胞分化的调节[4,48-50]。

2.5　应答逆境胁迫

越来越多的实验证据表明,植物 DNA 甲基化水平的动态变化与逆境胁迫密切相关。由于植物的生殖细胞产生于体细胞分化所形成的分生组织,在分生组织形成前产生的表观遗传性状可以直接传给后代[51-52],因此由逆境胁迫引发的 DNA 甲基化也能遗传给下一代[10,53]。

非生物逆境胁迫,如冷、盐、重金属以及渗透胁迫等,均能导致植物 DNA 甲基化水平的改变(表1)。对玉米、烟草、番木瓜和醋栗的研究结果表明,低温诱导或保存会引起 DNA 的甲基化状态改变[10,54-56]。对小麦、烟草、油菜和耐盐植物冰叶日中花的研究显示,盐胁迫导致 DNA 的甲基化水平升高[57-60]。Tan[61]发现盐胁迫导致玉米 ABA 负调节因子 *ZmPP2C* 第一内含子区段发生甲基化,致使 *ZmPP2C* 表达量降低,而参与细胞内活性氧(ROS)

代谢的 *ZmGST* 发生了去甲基化，表达水平升高。重金属离子是导致 DNA 甲基化状态改变的另一重要诱因。重金属胁迫对植物 DNA 甲基化的影响比较复杂，有些植物表现为 DNA 甲基化水平升高，有些则表现为甲基化水平降低，如铝、铬、镉等胁迫导致油菜、萝卜 DNA 甲基化水平升高[33,62-63]；而三叶草和大麻受镍、镉和铬等重金属离子胁迫后，基因组 DNA 甲基化水平降低[64]。葛才林等[65]发现，低浓度重金属（Cu^{2+}、Cd^{2+} 和 Hg^{2+}）胁迫，引起水稻和小麦基因组 DNA 甲基化水平降低，而高浓度则导致甲基化水平提高，因此推测重金属对甲基化水平的影响可能存在剂量效应。此外，来自烟草和豇豆的研究结果表明，渗透胁迫，如 PEG、甘露醇等，也能引发基因组 DNA 特异区段的超甲基化[58,61,66]。

表 1　逆境胁迫与植物 DNA 甲基化水平的关系

Table 1　The relationship bewteen abiotic stress and plant DNA methylation

胁迫类型	物种	效应	参考文献
生物胁迫			
烟草花叶病毒	烟草	NtAlix1 位点甲基化水平降低，表达水平提高	[34]
白叶枯病菌	水稻	DNA 甲基化水平明显提高，成株抗病性增强，DNA 甲基化可能与成株抗性有关	[35]
非生物胁迫			
冷胁迫	玉米	根中 DNA 甲基化水平明显降低，Ac/Ds 转座子区甲基化水平下降；*ZmMI1* 特异表达	[10,55]
	番木瓜	冷储存导致 DNA 甲基化水平提高 0.52-6.62%	[56]
	醋栗	耐冷品种 DNA 甲基化程度提高，冷敏感品种甲基化水平降低	[54]
盐胁迫	小麦	盐胁迫早期，甲基化水平降低，10 天后甲基化程度提高，且耐盐品种甲基化水平比盐敏感品种高	[60]
	冰叶日中花	微卫星 DNA 超甲基化，引起光合作用从 C3 途径转换为 C4 景天酸代谢途径	[57]
	玉米	ABA 负调节因子 *ZmPP2C* 第一内含子甲基化，表达量降低；*ZmGST* 去甲基化，表达量升高	[61]
	油菜	基因组 CCGG 序列甲基化水平提高 0.2-7.6%	[59]
	烟草	基因组 DNA 重复序列甲基化水平提高（从头开始甲基化）	[58]
重金属			
铝	烟草	*NtGPDL* 位点甲基化水平降低，表达水平提高	[33]
镉	萝卜	基因组甲基水平提高，随胁迫强度增加而增加	[62]
铬	油菜	引发基因组 DNA 甲基化从头合成，导致甲基化水平升高，且与胁迫剂量呈正相关	[63]
铬	三叶草、大麻	DNA 甲基化水平升高	[64]
Cu^{2+}、Cd^{2+}、Hg^{2+}	小麦、水稻	低浓度胁迫 DNA 甲基化水平升高，高浓度导致甲基化水平降低	[65]
渗透胁迫			
PEG	豇豆	豇豆根尖基因组 DNA 的 CCGG 位点超甲基化	[66]
D-Manitol	烟草	异染色质特异位点超甲基化	[58]
其他胁迫			
Space flight	水稻	DNA 甲基化模式改变，基因表达模式改变	[67]

3　DNA 甲基化修饰的检测方法

随着表观遗传学研究的热点化，DNA 甲基化修饰检测分析方法也不断涌现。根据 DNA 样品前处理方法不同，DNA 甲基化检测方法可分为 4 大类：色谱法、限制性内切酶消化法、亲和层析或免疫沉淀法及重亚硫酸盐转化法（表 2）。

色谱法首先将 DNA 大分子水解成单核苷酸，然后利用高效液相色谱（HPLC）或毛细管电泳（HPCE）检测核苷酸中 5 - mC 的含量，从而确定 DNA 甲基化的水平，该方法最大的缺陷在于无法获得甲基化位点的信息[68]。限制性内切酶消化法是利用不同限制性内切酶对甲基化位点的敏感性差异特点，先对 DNA 进行酶切，然后结合 PCR 或其他方法检测基因组或特定位点甲基化状态的变化，这类方法仅限于对限制性内切酶的酶切序列进行分析[69-70]。亲和层析和免疫沉淀法则是利用甲基胞嘧啶抗体或结合蛋白分离、富集甲基化的 DNA，然后结合芯片或测序等技术，检测 DNA 的甲基化状态，这类方法对胞嘧啶甲基化程度要求较高[71]。重亚硫酸盐转化法则是用重亚硫酸盐处理 DNA 样品，未甲基化的胞嘧啶经处理后转化为尿嘧啶，而甲基胞嘧啶不被转化，然后通过测序或 PCR，确定甲基化位点[72]。目前，上述 4 类技术都已比较成熟，在实际研究中需要根据研究目的选择适当的检测方法。

表 2　DNA 甲基化检测方法比较

Table 2　Comparison of various DNA methylation detection methods

前处理方法	原理	分辨率	优点	缺点	参考文献
色谱法	高氯酸钾水解 DNA 为单核苷酸，用 HPLC 或 HPCE 检测单核苷酸中甲基胞嘧啶的含量	低	比较简单	无法确定甲基化位点	[68]
限制性酶切法					
甲基化敏感扩增多态性（MASP）	DNA 经甲基化敏感的限制性内切酶消化后，通过 PCR 扩增，电泳等方法富集甲基化 DNA 片段	中等	比较简单	仅限于对酶切位点甲基化的分析	[69,73]
McrBC 消化法	DNA 经特异的甲基化限制性内切酶 McrBC 消化后，通过 PCR 扩增，电泳等方法富集未甲基化的 DNA 片段	中等	DNA 消化效率高	仅限于对酶切位点甲基化的分析	[70,74,75]
亲和层析纯化法					
甲基化 DNA 免疫沉淀（MedIP）	利用单克隆抗体沉淀含有甲基化胞嘧啶的 DNA	中等	有商业化的抗体，可以沉淀所有甲基化胞嘧啶	对胞嘧啶甲基化程度要求高	[5,6,76-78]
MBD 亲和纯化（MAP）	利用 MBD 柱分离含有甲基化胞嘧啶的 DNA	中等	只能回收甲基化的 CpG	对 CpG 甲基化程度要求高	[5,71,76,79]
CXXC 亲和纯化（CAP）*	利用 CXXC 柱分离含有未甲基化胞嘧啶的 DNA	中等	可以直接提取未甲基化的 DNA	对 CpG 甲基化程度要求高	[71]
重亚硫酸盐转化	未甲基化的胞嘧啶经重亚硫酸盐处理后转化为尿嘧啶，而甲基化胞嘧啶则不被转化	高，可达单个碱基	适用于所有样品	甲基化胞嘧啶完全转化很重要	[80]

4　DNA 甲基化修饰与作物种质资源保存

作物种质资源是在不同生态条件下经过长期的自然演变和人工选择形成的，妥善保存作物种质资源对于深入研究和利用其中的优异基因至关重要。对于绝大多数种子植物，一般采取低温干燥的方式进行保存，然而有许多种质资源，如产生顽拗种子且不耐干燥脱水和低温贮藏的芒果、椰子、油棕、咖啡等；不产生种子的脐橙、香蕉等；无性繁殖的苹果、柑橘、甘薯、马铃薯、芋头、生姜等，则需要采用种质圃或组织培养（包括常温和冷冻方式）的保存方式进行保存。对于自然条件下在种质圃中保存的种质而言，必然会受到各种逆境，如干旱、极端温度、各种病害等的胁迫。由于逆境胁迫引发的 DNA 甲基化能遗传给下一代[10,53]，所以采用种质圃方式保存的种质资源其后代表型可能会发生变异。

作物种质资源组织培养保存包括对愈伤组织和再生植株的保存。人工建立的组织培养条件对植物而言也是一种逆境胁迫[81]，因此组织培养物的表型可能会受到影响。许多研究表明，组织培养过程中可产生广泛的 DNA 甲基化变异。人们在水稻、大麦、玉米、大豆等多种粮食作物的组织培养物中均发现了 DNA 甲基化现象[82-86]，而且不同植物 DNA 甲基化变异的趋势和模式存在明显差异，如玉米[86]、油棕[87]、大豆[84]、水稻[83]、香蕉[88]和玫瑰[89]等的愈伤组织或再生植株 DNA 甲基化水平呈下降趋势，而在番茄愈伤组织和豌豆再生植株中 DNA 甲基化水平则呈上升趋势[85,90]。由于 DNA 甲基化水平的降低可能导致转座元件的激活[83]，从而影响植物基因组的稳定性，所以 Phillips 等[81]认为 DNA 甲基化是导致植物组织培养遗传变异的一个根本原因。此外，低温冷冻保存也会对植物种质资源产生一定的影响。Johnston 等[54]发现，低温保存导致耐冷醋栗品种芽分生组织 DNA 甲基化水平升高，而冷冻敏感品种甲基化水平降低；而番木瓜芽尖经低温保存后，其再生苗 DNA 甲基化水平升高约 0.52% ~6.2%，这种由于低温保存产生的 DNA 甲基化变化很可能会导致体细胞变异[56,91]。目前，虽然有不少证据表明作物种质资源保存过程中存在广泛的 DNA 甲基

化修饰现象，但绝大多数研究还局限于对种质资源DNA甲基化状态变化的层面，罕有DNA甲基化修饰导致种质资源发生表型变异的直接证据，这可能有两方面的原因：一方面DNA甲基化研究本身比较复杂；另一方面针对作物种植资源的表观遗传学研究起步较晚。

由于组织培养或种质圃保存、低温保存过程中可能造成种质资源DNA甲基化状态的改变，影响种质资源的基因表达，并可能进一步引发后代表型发生变化，因此应该利用表观遗传学的理论与方法，研究影响作物种质资源DNA甲基化变异的条件和应对措施，提高种质资源保存质量，为深入研究和广泛利用种质资源中的优异基因资源奠定基础。

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植物DNA甲基化与作物种质资源保存

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刊名： 植物遗传资源学报 ISTIC PKU
英文刊名： JOURNAL OF PLANT GENETIC RESOURCES
年，卷(期)： 2010,11(6)

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