



转座元件对植物基因组进化、表观遗传和适应性的作用

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摘要 转座元件是基因组内可移动的DNA序列, 其结构和转座机制具有广泛的多样性. 转座元件普遍存在于植物基因组中, 特别是反转录转座子. 转座元件的扩增、插入可能会改变宿主原本基因组的稳定性, 因此宿主进化出了各种沉默机制防御转座元件的转座. 随着对转座元件研究的不断深入, 越来越多的证据表明, 转座元件的插入所带来的并不完全是破坏, 它们可能是基因组多样性的驱动力, 甚至在作物驯化方面起重要作用. 另外, 转座元件与宿主之间可能相互影响, 尤其是在环境胁迫条件下. 本文概述了植物基因组转座元件的相关研究, 介绍了植物中常见的转座元件, 并探讨了转座元件在植物基因组进化、表观遗传调控中发挥的作用以及在环境胁迫下转座元件与宿主之间存在的合作关系.

关键词 转座元件, 基因组进化, 表观遗传, 环境胁迫, 适应性

转座元件(transposable elements, TEs)又称转座子、跳跃基因, 是可以在基因组内移动到不同位置的DNA序列^[1]. 20世纪40年代末芭芭拉·麦克林托克(Barbara McClintock)^[2]首次提出了TEs的概念, 认为TEs导致了玉米的色素沉着或其他特征的新突变, 并揭示了“Ac/Ds调控系统”, 但这一观念在当时并未被业界学者所接受. 随着测序技术的发展, 曾被视为“垃圾基因”或“自私基因”的TEs已被证实是大多数真核生物基因组的主要组成部分. TEs具有广泛的多样性, 加之具有不同的转座机制, 不仅可以调控临近基因的表达, 同时可以调控整个基因组, 在基因组进化中发挥了重要的作用. 本文将对植物中常见的TEs进行介绍, 并结合一些最新的研究来探讨TEs在植物基因组进化和表观遗传调控中的作用, 还讨论了在环境胁迫下TEs与宿主之间的合作关系.

1 转座元件的分类和结构特征

基于TEs的转座机制和序列相似性, 可将TEs划分为类别I(Class I)和类别II(Class II)两类^[3]. 若根据TEs编码能力的不同, TEs可以分为自主元件和非自主元件, 自主元件能够编码其自身移动所必需的酶, 非自主元件一般需要依赖同源自主元件进行转座^[4,5]. 下面对植物基因组中常见的TEs的分类及结构特征(图1(a))进行简要介绍.

1.1 Class I转座元件

Class I TEs又称反转录转座子(retrotransposons, RTs), 即转座需要RNA介导: 在转座过程中基因首先转录成mRNA, 然后通过TEs编码的反转录酶反转录成cDNA^[6]. RTs转座后原DNA序列仍然保留, 类似于“复制-粘贴”的方式, 因此被认为是基因组大小的主要贡献

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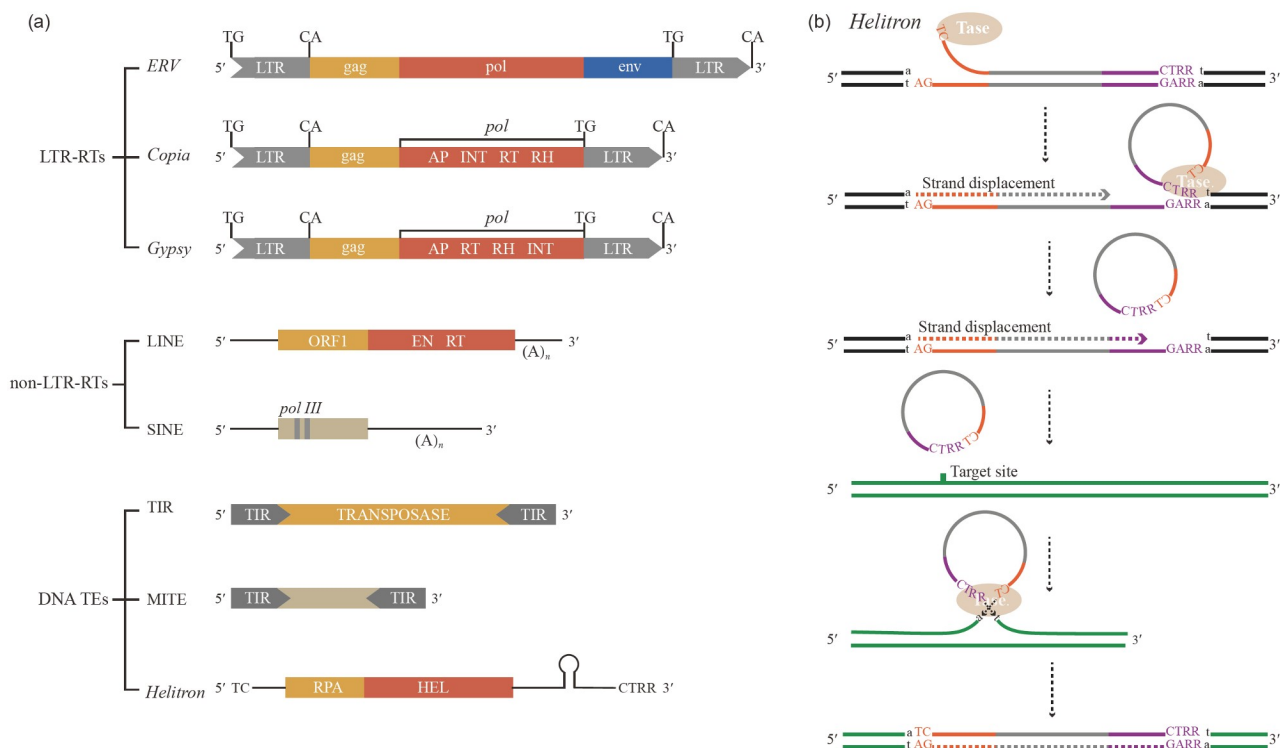


图 1 转座元件的分类和结构特征及Helitron转座方式模型。(a) 转座元件的分类和结构特征。LTR, 长末端重复; TIR, 末端反向重复; ORF1, 未知功能开放阅读框; gag, 衣壳蛋白; pol, 聚合酶类; AP, 天冬氨酸蛋白酶; INT, 整合酶; RT, 逆转录酶; RH, 核糖核酸酶H; env, 包膜蛋白; pol III, 聚合酶III; TRANSPOSASE, 转座酶; REP, 复制起始因子; HEL, 解旋酶; (A)_n, polyA; EN, 核酸内切酶。(b) Helitron转座方式模型。Tase, 转座酶; Strand displacement, 链置换; Target site, 靶位点

Figure 1 Classification and structural characteristics of transposable elements and the model of Helitron transposition. (a) Classification and structural characterization of transposable elements. LTR, long terminal repeat; TIR, terminal inverted repeat; ORF1, open reading frame 1 of unknown function; gag, gagsid protein; pol, polymerase; AP, aspartic proteinase; INT, integrase; RT, reverse transcriptase; RH, RNase H; env, envelope protein; pol III, polymerase III; REP, replication initiator; HEL, helicase; (A)_n, polyA; EN, endonuclease. (b) Helitron transposition model. Tase, Transposase

者^[7]。根据RTs两端侧翼是否存在长末端重复(long terminal repeats, LTRs), 它们可进一步划分为长末端重复反转录转座子(LTR retrotransposons, LTR-RTs)和非长末端重复反转录转座子(non-LTR retrotransposons, non-LTR-RTs)。

(i) LTR反转录转座子。LTR-RTs是大多数植物基因组的主要组成部分^[5], 其在结构和机制上类似逆转录病毒, 两侧末端具有LTRs, 这些LTRs通常是保守的, 并具有2 bp的回文基序(5'-TG...CA-3')^[8]。多数LTR-RTs都包括gag和pol两个开放阅读框(open reading frame, ORF), 其中gag ORF编码病毒样颗粒的结构蛋白; pol ORF编码天冬氨酸蛋白酶(aspartic proteinase, AP)、逆转录酶(reverse transcriptase, RT)、核糖核酸酶H(RNase H, RH)和DDE整合酶(integrase, INT)^[3]。偶尔会在LTR-RTs中发现第3个特别的ORF, 该ORF编码一个包膜基因(env), 说明这种LTR-RTs与逆转录病毒密切相关^[9]。

Copia和Gypsy是植物基因组内常见的两个LTR-RTs超家族, 它们在结构上的区别在于pol ORF内部顺序上INT位置的不同。

(ii) non-LTR反转录转座子。non-LTR-RTs是古老的基因元件, 已经在真核生物基因组中存在数亿年^[10]。non-LTR-RTs主要有长散布核元件(long interspersed nuclear elements, LINEs)和短散布核元件(short interspersed nuclear elements, SINEs)两类, 它们缺乏LTRs, 通常在其3'末端具有poly(A)或简单重复序列。其中, LINEs存在于所有真核生物中, 长度可达几千个碱基对^[3]。完整的LINEs是由一个具有启动子活性的5'非翻译区(untranslated region, UTR)、两个ORFs和一个带有poly(A)尾巴的3'UTR组成^[11]。然而, LINEs的5'端常因不完全反转录而被截断, 因此基因组中大部分的LINEs是以残存序列的形式存在^[10,12]。SINEs均起源于3种pol III转录本中的一种: tRNA、5S rRNA或7SL

RNA^[13]. 它们依赖内部的*Pol III*启动子启动转录, 是非自主元件, 缺乏编码能力, 能够“劫持”LINEs编码的蛋白, 并依赖于LINEs进行转座^[13,14].

1.2 Class II转座元件

Class II TEs为DNA转座子(DNA transposons). 这类TEs转座不需要RNA的介导, 直接通过转座酶将原位点DNA序列切下来插入到新的位点即可发生转座, 类似于“剪切-粘贴”的方式^[6]. 通常TEs插入新的位点会产生靶位点重复(target site duplications, TSDs)^[5], 而DNA链由于发生转座产生的断裂, 会由DNA修复机制修复. DNA转座子依据转座方式可进一步划分为: “剪切-粘贴”模式的DNA转座子、“滚环”模式的*Helitron*超家族和“自合成”模式的*Polintons/Mavericke*超家族, 其中*Polintons/Mavericke*超家族在植物中鲜有报道^[15].

(i) “剪切-粘贴”模式的DNA转座子. 这类DNA转座子起源古老且在真核生物基因组中普遍存在, 其典型特征是存在自主拷贝编码的转座酶和末端反向重复(terminal inverted repeats, TIRs)^[16], 因此又被称为TIR TEs. 它们转座需要剪切DNA双链, 转座酶专门识别某一TE的TIRs, 切除TE, 并将其插入宿主基因组的其他位置. 植物中常见的这类DNA转座子的超家族有*hAT*、*CACTA*、*Mutator*、*PIF/Harbinger*、*Tc1/Mariner*(表1, 结构特征描述见文献^[5]).

(ii) *Helitron*超家族. *Helitron*主要见于植物基因组, 其转座是由Rep/Helicase(RepHel)转座酶催化, 该转座酶通常拥有复制起始因子(replication initiator, Rep)和DNA解旋酶(helicase, Hel)结构域^[17,18]. *Helitron*转座只涉及一条DNA链, 通常携带从宿主基因组中捕获的基因片段^[11], 在转座酶的作用下通过“滚环”的机制进行转座, 即原始元件的一条链被直接复制到靶位点^[19](图1(b)). 它们没有TIRs, 也不产生TSDs, 具有5'端的“TC”基序和3'端的“CTRR”(R=A/G)基序, 以及靠近3'末

端上游可形成16~20 bp的回文序列^[17,20].

(iii) MITE. 微型反向重复转座元件(miniature inverted-repeat transposon elements, MITEs)是一类特殊的非自主转座元件, 广泛存在于动植物基因组中^[20,21]. 它们不具有编码能力, 特征是具有短的TIRs(10~15 bp)、小尺寸(约100~800 bp)、高拷贝数(每个单倍体基因组约有1000~15000个), 并倾向于插入2~3 bp且富含A和T残基的靶位点^[22,23]. 由于其既具备DNA转座子的TIRs和TSDs特征, 又具备RTs高拷贝数的特征, 转座机制也尚不清楚, 因此还无法明确地进行分类. 但由于无法明显地观察到MITEs的转录模式或反转录酶, 目前研究普遍将其归类于DNA转座子^[16,24]. MITEs的进一步分类一直基于TIRs和TSDs的相似性, 它们与能够编码转座酶的自主转座元件共享的TIRs和TSDs序列几乎相同. 目前发现, 植物基因组中MITEs与7个超家族有关: *Tc1/Mariner*、*PIF/Harbinger*、*hAT*、*Mutator*、*CACTA*、*P-element*和*Novosib*^[23].

当非自主元件拷贝数快速增加时, 会使整个家族受到转座酶和抑制机制的限制, 致使自主元件无法正常复制, 最终导致整个家族灭绝, 即“垂直失活”(vertical inactivation)^[16]. MITEs虽然是非自主元件, 无法自主发生转座, 但它们却能够以高拷贝的形式存在于一些植物基因组中, 呈现出“MITE悖论”. 对于出现这种悖论的原因还不清楚, 目前的一些解释是: (1) MITEs倾向插入启动子、内含子和非翻译区, 从而产生了中性的突变; (2) MITEs小尺寸的特点; (3) MITEs可以从宿主监视中逃脱; (4) MITEs可能是由间隙修复失败产生, 当它们原始的自主元件在基因组中丢失或失活时, 一些存活在基因组中的MITEs可能带有序列基序, 可以被相关但非同源的自主元件交叉移位和扩增^[23,25~27].

2 TEs与基因组进化

TEs几乎在所有生物体中都被发现, 并在许多真核

表1 植物TIR TEs的分类及结构特征^[5]

Table 1 Structural features and classification of TIR TEs in plants^[5]

超家族	TSD	元件大小		TIR大小	末端序列(5'→3')
		自主元件	非自主元件		
<i>hAT</i>	8 bp	3~6 kb	3~6 kb	5~22 bp	C/TA...TA/G
<i>CACTA</i>	3 bp	6~21 kb	6~21 kb	12~28 bp	CACTA/G...C/TAGTG
<i>Mutator</i>	7~11 bp, 多数为9 bp	4~16 kb	4~16 kb	0~800 bp	G/C...G/C
<i>PIF/Harbinger</i>	TTA/TAA	3~7 kb	3~7 kb	14~60 bp	GGG/CC...GG/CCCGG/AGCA...TGCT/CC
<i>Tc1/Mariner</i>	TA	3~7 kb	3~7 kb	11~120 bp	CTCCCTCC...GGAGGGAG

生物中积累,以至于它们常常是基因组的主要成分,如玉米、面包小麦基因组中均有大量的TEs^[28,29]。此外,TEs还会对基因组的结构、功能等多方面产生影响,是驱动植物基因组进化的重要角色。

2.1 TEs影响基因表达和基因功能

TEs的插入会以多种方式影响宿主基因的表达。如果TEs插入到顺式调控区,则可能增强基因表达、产生表型差异。例如,对红葡萄、白葡萄和血橙的研究均发现,TEs插入到基因的上游启动子可引起表型的改变^[30,31]。同时,越来越多的研究表明,因TEs插入而引起的表型变异在作物驯化方面起着重要作用^[32-36]。TEs还能够影响宿主基因的转录表达。在番茄(*Solanum lycopersicum*)中,*Copia* LTR-RT的插入消除了MADS-box转录因子*J2(JOINTLESS2)*基因的功能性转录物,导致番茄果柄离区消失^[37]。此外,TEs的插入会对宿主基因功能产生影响。例如,在辣椒(*Capsicum annuum*)的*CaAn2*基因启动子中插入一个non-LTR-RT,可以通过在3'UTR处募集MYB转录因子来激活*CaAn2*的表达,从而可以激活花青素的生物合成^[38]。同样,草莓MYB10启动子中存在的TEs也被证明与花青素的合成有关^[39]。

TEs是非常强大的诱变因子,为了维持正常的基因序列表达,植物基因组进化出了各种沉默机制防御TEs转座。需要注意的是,TEs在宿主基因组的分布并不是随机的,它们对特定的基因组区域表现出了很强的偏好,这种偏好性既可降低对宿主的损害,又能最大限度地提高TEs自身被表达的机会^[12,26,40]。例如,有研究指出,MITEs之所以能在宿主的基因组以极高的拷贝数存在,正是因为它们是特异性地插入启动子、内含子和非翻译区,而非外显子区^[23,27,41]。另外,自然选择、遗传漂变和表观遗传的沉默机制也是影响TEs分布的重要因素。若是TEs的插入太具破坏力,则很容易受到选择压力或引起表观遗传机制的抑制,使含有TEs的等位基因频率降低;与之相对,如果TEs插入内含子或非翻译区,则更容易被容忍^[40,41]。

2.2 TEs介导染色体重排

当TEs作为“控制因子”(controlling elements)被提出时就已经知道它们可以介导染色体的大规模重排^[42],在后人的研究中也得到了证实^[29]。染色体的重排可能发生在TEs切除后双股链断裂的修复过程中,可能

通过同源序列重组发生,或是通过使用异位同源序列作为修复模板的错误修复发生^[43]。如Kreplak等人^[44]在破译豌豆基因组的研究中发现,豌豆基因组的进化速度快于其他已研究的豆科植物基因组,推测可能是因为TEs介导的不平等重组导致基因的获得或丢失,或异位双股链断裂错误修复所导致。

此外,替代转座(alternative transposition)也会导致染色体断裂和各种类型的重排,例如倒位、复制、缺失和易位^[45-47]。这是利用转座酶作用于两个独立、附近的TEs末端,从一个位点释放该元件,并将其插入到另一个位置的过程^[46,48]。例如,玉米*pl*基因的特定等位基因中,完整的*Ac*元件和附近末端缺失的*Ac*元件(*fAc*)可以发生姐妹染色单体转座(sister-chromatid transposition, SCT)事件,从而产生大的侧翼缺失^[49](图2)。同时,因替代转座引起的结构改变可能在重排断点处产生嵌合基因,可能引发新基因的产生^[46,48,50]。

2.3 TEs参与基因组大小进化

基因组大小的差异很大程度上是由于重复序列丰度的差异导致,特别是TEs^[51]。例如LTR-RTs构成基因组中大部分的重复序列,其类似“复制-粘贴”的转座机制可以使不同植物的基因组大小存在巨大差异^[52,53]。近期,对百岁兰(*Welwitschia mirabilis*)的研究发现,该植物在过去1百万~2百万年间曾经历过一次LTR-RTs的急剧扩增,而这些TEs被激活可能是由于百岁兰长期处于极端干旱的环境造成^[54]。澳洲稻(*Oryza australiensis*)在经过3个LTR-RTs家族爆发后,其基因组大小迅速增加了两倍^[55]。同时,棉属^[56]、茶树^[57]等植物的基因组扩增或进化也都与LTR-RTs扩增相关。此外,TEs能够偏好性地插入可能也是宿主基因组扩增的原因之一,这些TEs被宿主基因组所容忍,使它们可以在宿主基因组中逐渐积累。

2.4 TEs的水平转移

水平转移(horizontal transfer, HT)是指两个个体(可能属于不同物种)通过非纵向遗传的方式在基因组之间进行遗传物质的传递^[16]。事实上,大多数已知类型的TEs在其进化历史的某个时刻都是水平传播的,这也是它们能够进化成功的原因之一^[58]。TEs的水平转移(horizontal transfer of transposon, HTT)提供了一种逃避沉默和灭绝的途径,这有助于大多数类型TEs的持久性进化,对它们在植物基因组中的生存至关重要^[58,59]。例如,

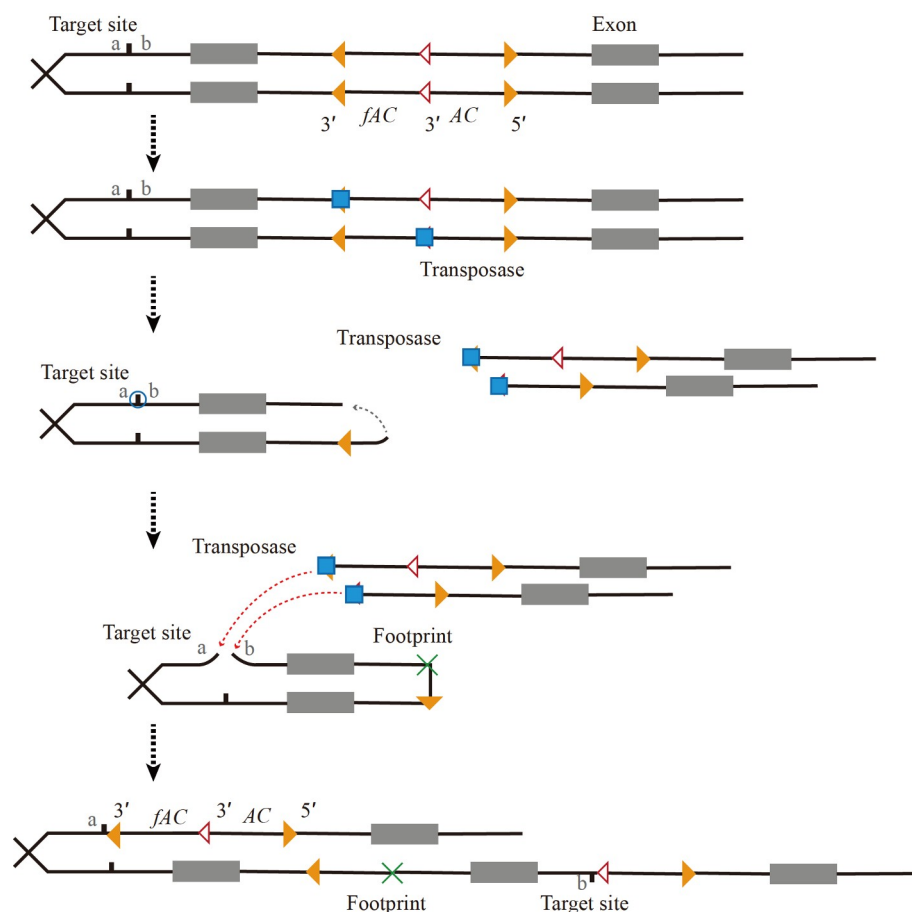


图2 通过姐妹染色单体转座形成序列缺失的模型^[49]. Target site, 靶位点; Exon, 外显子; Transposase, 转座酶; Footprint, 足迹
Figure 2 Model of sequence deletion by sister-chromatid transposition^[49]

在对开花植物进行大规模的比较基因组研究中发现, 预测在过去3百万年里, 单子叶植物和双子叶植物之间发生过数百万例的HTT^[59]. HTT的发生机制尚不清楚, 但它们可以改变基因组的大小和结构, 有助于新基因和基因调控网络的创建, 在驱动基因组进化中发挥重要作用^[60].

3 TEs与表观遗传调控

尽管TEs广泛分布于生物体基因组中, 但大部分TEs是处于休眠或失活状态的^[61]. 也并不是所有的TEs都能转座, 很大一部分TEs是无功能的, 并缓慢地转变为基因组“暗物质”^[62]. 而在某些基因组冲击下可能会触发TEs的激活, 如环境胁迫或杂交事件^[63]. 面对TEs转座为基因组带来的不稳定性, 宿主植物进化出了各种表观遗传调控途径来防御转座事件的发生, 主要包括DNA甲基化和组蛋白尾部修饰.

3.1 DNA胞嘧啶甲基化

DNA甲基化(本文特指胞嘧啶甲基化)是一种进化保守的DNA修饰, 指在细胞核DNA的胞嘧啶环的第五位碳原子上加一个甲基^[64]. 在植物中, DNA甲基化是调控基因表达、沉默TEs和重复序列的重要过程. 大多数已知DNA甲基化的建立、维持和修饰机制已经在模式植物拟南芥中得到了证实^[65~67]. 植物的甲基化在DNA复制后由甲基转移酶1(methyltransferase 1, MET1)与染色质甲基化酶2和3(chromomethylase 2和3, CMT 2和3)维持^[68]. DNA甲基化根据甲基化C(mC)所伴随的序列环境划分为: 对称CG和CHG(H=A、C或T)环境与不对称CHH环境, 其中MET1负责维持CG甲基化(mCG), CMT3是维持CHG甲基化(mCHG)所必需的, CMT2主要维持CHH甲基化(mCHH)^[66,69].

在植物中, TE的沉默主要通过RNA导向的DNA甲基化(RNA directed DNA methylation, RdDM)途径建

立^[70]。siRNA对于维持和建立RdDM十分重要,它们可能来源于RTs序列产生的核双链RNA(dsRNA),由RNase-III-like Dicer酶加工处理^[71]。siRNA可以重新启动完全或不完全互补转录本随后几轮的降解,从而形成一种高效的转录水平的调控机制^[72]。由于植物中的DNA甲基化模式是可遗传的,因此RdDM可以稳定地跨代抑制TEs活性^[73]。RdDM也可能引起附近基因的DNA甲基化,并影响基因的表达;尤其是当这种甲基化“扩散”延伸到附近甲基化水平通常较低的启动子区时,更是会改变基因表达^[64]。例如印记基因*FWA*是负责*fwa-1*和*fwa-2*突变体晚开花表型的基因,*FWA*基因上游是一个类似SINE的串联重复序列^[74]。由于RdDM甲基化,*FWA*的转录被抑制而使宿主表现出正常开花的表型。若甲基化缺失则会重新激活*FWA*的表达,导致宿主表现出晚花表型^[74,75](图3(a))。同样,在对红肉萝卜(*Raphanus sativus*)肉质突变的研究中也有类似的发现。该研究显示,其肉质突变是因*RsMYB1*启动子中*CACTA*

TE的高甲基化所致;甲基化扩散到了*RsMYB1*启动子区,使*RsMYB1*的表达显著下调,进而抑制了花青素的生物合成,导致白肉质突变体^[76]。但甲基化的“扩散”并不是所有TEs的特征^[77]。另外,TEs相关的DNA甲基化有时可以带来有益的调节结果,如*ROS1*基因启动子中的*Helitron*可以负向控制*ROS1*的表达,即*Helitron*的甲基化可以促进*ROS1*表达;而去甲基化则导致*ROS1*无法表达。这说明*ROS1*启动子的功能类似于甲基调节器来感知DNA甲基化水平,并可以通过控制*ROS1*表达来调节DNA甲基化^[78,79](图3(b))。在水稻中,TEs的衍生基因*PANDA*能以表观遗传的方式控制稻穗数目和粒大小,即*PANDA*基因的突变会导致稻穗数目减少而粒大增加;而过表达该基因的转基因植株却表现出相反的表型变化。这为水稻的生产提供了新思路^[80]。

甲基化并不总是维持TEs沉默。少数TEs扩增在植物进化过程中是以爆发的方式发生,例如小麦、玉米、水稻等都经历了一些TE家族的大规模扩增事

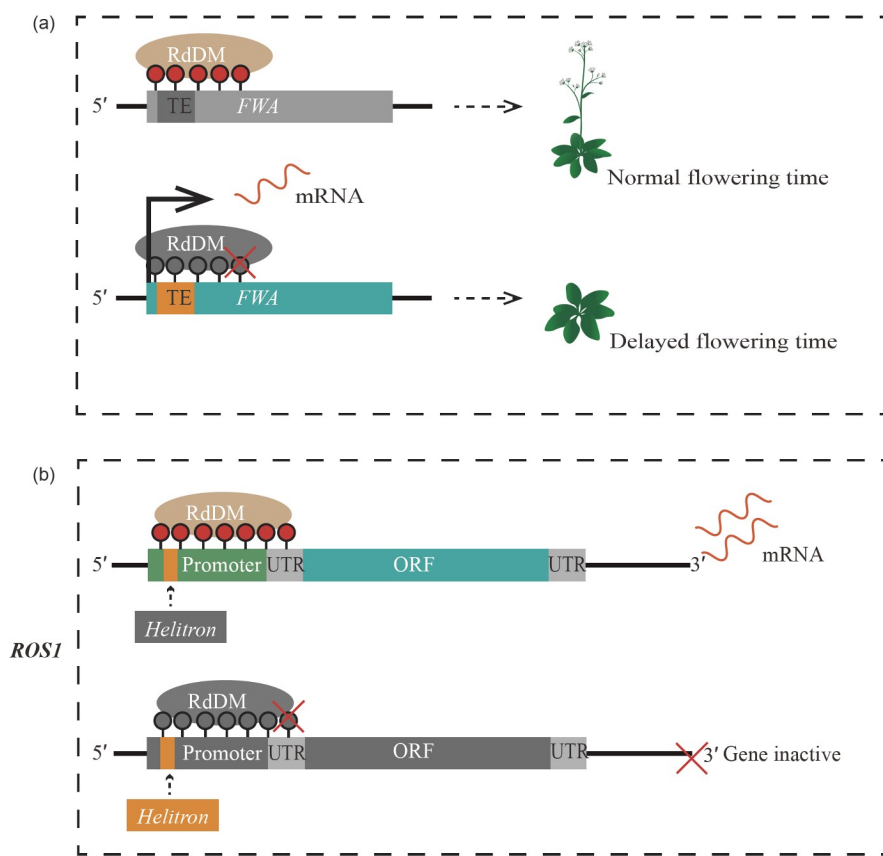


图3 RdDM通过不同方式介导基因表达的模型。(a) RdDM活性与*FWA*基因表达对拟南芥表型的影响。Normal flowering time, 正常花期; Delayed flowering time, 晚花。(b) RdDM活性对*ROS1*基因表达的影响。Promoter: 启动子; UTR, 非翻译区; Gene inactive: 基因失活

Figure 3 A model of RdDM mediating gene expression in different ways. (a) Effects of RdDM activity and *FWA* gene expression on *Arabidopsis thaliana* phenotype. (b) Effect of RdDM activity on *ROS1* gene expression. UTR, untranslated region

件^[27,81,82],说明表观遗传调控的这种沉默机制或自然选择在抑制TEs方面有时也会失败^[69].事实上,TEs可能已经进化出多种方式来避免触发表观遗传沉默.例如*At-Mu1c* TE在拟南芥谱系中发生转座,它们可以通过插入特定的基因组位置(如基因的3'端)来逃避表观遗传沉默^[83].裸子植物挪威云杉(*Picea abies*)TEs拷贝数长期而稳定地增加,可能与TEs沉默相关的siRNA数量减少有关^[84].Sanchez等人^[85]已经初步证明一些RTs可能会进化出与发育相关的逃逸策略,以克服营养组织中转录基因的沉默,为宿主的下一代作出贡献.

3.2 组蛋白修饰

组蛋白修饰和DNA甲基化之间存在广泛的联系和串扰,TEs的有效沉默也需要DNA甲基化和组蛋白修饰之间的协调.其中H3K9和H3K27甲基化是植物转录沉默的两个标志^[86,87].正如上面提及的*PANDA*基因协调稻穗数目和粒大小正是通过调控H3K27甲基化来实现^[80].此外,Guo等人^[87]研究发现,尽管RdDM对玉米*MuDR* TE沉默后DNA甲基化的维持至关重要,但甲基化的缺失并不会使活性恢复.相反,沉默的可遗传维持是通过组蛋白修饰来维持的. Choi等人^[88]认为组蛋白H1和DNA甲基化是联合沉默TEs的. Liu等人^[89]在探究热胁迫对TEs再激活中发现组蛋白H1参与了热激反应,并且调控热胁迫下TEs的激活.总之,表观遗传调控是复杂、多层面的,而DNA甲基化和组蛋白修饰也是一个相互作用的过程.

4 TEs与环境胁迫

TEs也可能在环境适应中发挥作用,因为它们能够产生各种各样的突变,它们对环境变化敏感且具有做出反应的能力^[11].越来越多的证据表明,TEs已经在植物的防御反应中发挥作用.例如,水稻*DEEPER ROOTING 1(DROI)*基因启动子中的*INDITTO2* TE可以传递生长素信号调节*DROI*的转录从而增强水稻避旱性^[90].在大豆中,*GmphyA2*(由负责光周期敏感性的*E4*基因座编码)外显子的*Ty1/copia-like* TE插入破坏与对高纬度的适应有关^[91,92].在对表型与TEs之间联系的探索中发现,TEs的插入可以驱动快速的表型变异,这一现象可能有助于遗传变异有限的物种适应不断变化的环境^[93].同样,在对我我国入侵物种微甘菊(*Mikania micrantha*)的研究中发现,微甘菊基因组的TEs可能增强其变异性,进而增进微甘菊适应环境改变和胁迫的潜能^[94].此外,

环境胁迫会降低DNA甲基化并导致TEs再激活.一个经典的例子是拟南芥中的*ONSEN* TE,含有对热胁迫响应的热激元件.当拟南芥处于高温时,下游的热激转录因子将识别*ONSEN*序列中的热激元件而激活转录^[95].金鱼草(*Antirrhinum majus*)基因组中*Tam3* TE甲基化水平受*Tam3*活性的调节,而*Tam3*的活性取决于*Tam3*转座酶结合DNA的能力并受生长温度的影响^[96].因此,在一些环境胁迫条件下,TEs与宿主之间是相互影响并共同抵御环境胁迫的.

TEs似乎已经进化出与宿主互惠的策略.例如,同样在对热胁迫与*ONSEN* TE的激活机制研究中, Nozawa等人^[97]发现, CMT3可能通过与CMT2竞争性结合H3K9me2,阻止CMT2介导的CHH甲基化和H3K9me2的积累来调节*ONSEN*的转录. *ONSEN*序列中的CHG丰度相较一般TEs降低,而CHH丰度变高,说明*ONSEN*通过减少CHG而逃逸CMT3的甲基化,并利用CMT3来抑制CMT2作用的机制增加表达(图4).同样, MITEs偏向插入基质附着区域(matrix attachment regions),这被认为是为基因和邻近的大量的表观沉默TEs之间提供缓冲^[98].而在像水稻一样的自交植物中,TEs爆发性扩增是一个潜在的有价值的群体多样性来源^[27,99].这些现象说明宿主与TEs之间并非单纯的抑制与被抑制的关系,在面临生存压力时,它们可以进化出互惠的生存策略,提高宿主在胁迫环境中的适应能力.

5 结语

TEs是植物基因组的重要组成部分,它们能对植物基因组的进化产生显著影响. TEs丰度变化可以直接影响基因组大小,即便这可能是一个很漫长的过程. TEs是一把“双刃剑”,它们的插入确实会带来一些破坏,特别是当它们位于一个外显子中时;这可能会导致基因表达的改变,甚至使基因功能丧失.但因表观遗传沉默机制、自然选择和遗传漂变的作用,大多数现存TEs的插入对宿主的影响表现为中性或轻微有害^[100],它们甚至能成为驱动基因组多样性形成的主要动力^[99].另一方面,有越来越多的研究表明,TEs与宿主之间的作用可能是相互影响的,或许TEs与宿主已经逐渐进化出彼此互惠的策略.正如TEs插入在基因组区域的偏好性,以增加表达的机会.在表观遗传调控中,必须通过微调RdDM的活性,从而保持沉默TEs和允许邻近基因表达之间的平衡^[101].或是在一些环境胁迫条件下,一些TEs会被激活并参与到表观遗传调控中,成为宿主适应胁迫

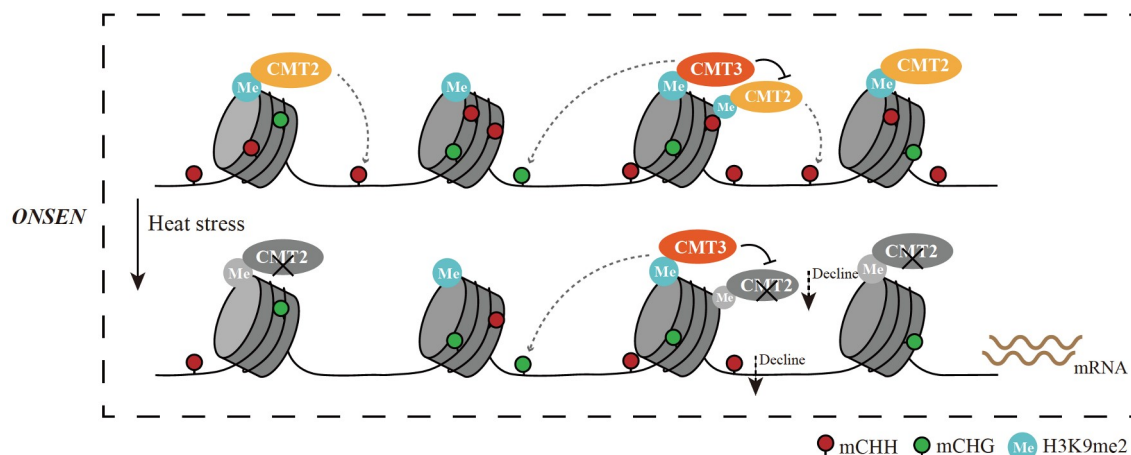


图 4 *ONSEN*在热胁迫下的生存策略

Figure 4 Survival strategies of *ONSEN* under heat stress

迫环境的潜在助手,而这种环境诱导的TEs沉默机制的放松所产生的遗传和表观遗传变异也是植物进化的主要驱动力^[102]。总之,TEs对植物基因组的影响是复杂的,具有双重性。但也很清楚的是,TEs在调控植物基因组进化、胁迫环境适应性以及作物驯化方面都发挥着重要作用。

目前有关植物基因组中TEs的研究越来越多,越来越深入,但仍有很多未知。我们无法完全了解TEs插入

位点到底是其自身的偏好性还是自然选择或基因沉默的结果,也无法清晰地了解HTT发生的机制。而TEs所涉及的表观遗传调控机制的研究也只是初步阶段,还无法确定TEs是如何触发沉默的,这种沉默在不同物种中为什么存在差异,TEs又是如何逃避沉默的,以及TEs爆发是否是宿主基因组的进化策略。因此,关于TEs与植物基因组之间的关系还有很多值得深入研究的方向。

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Summary for “转座元件对植物基因组进化、表观遗传和适应性的作用”

Roles of transposable elements on plant genome evolution, epigenetics and adaptation

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Transposable elements (TEs) are mobile DNA sequences within the genome, and their structure and transposition mechanism are highly diverse. TEs can be divided into retrotransposons (RTs; Class I) and DNA transposons (Class II), depending on whether their transposition intermediate is RNA or DNA. RTs transpose in a “copy-and-paste” manner and are therefore considered to be an essential contributor during genome expansion. RTs can be further divided into long terminal repeat retrotransposons (LTR-RTs) and non-long terminal repeat retrotransposons (non-LTR-RTs). *Copia* and *Gypsy* are two superfamilies of LTR-RTs commonly found in plant genomes, and their structural differences lie in the *INT* positions in the internal sequence of the *pol* open reading frame (ORF). Non-LTR-RTs include long interspersed nuclear elements (LINEs) and short interspersed nuclear elements (SINEs), which lack LTRs and usually have poly(A) or simple repeats at their 3' end. DNA transposons directly cut the DNA sequence at the original site by transposase and insert a new site, similar to “cut-and-paste”. Insertion of DNA transposons into new sites results in target site duplications (TSDs), and DNA strand breaks due to transposition are repaired by DNA repair mechanisms. DNA transposons in plants can be further divided into “cut-and-paste” transposons and *Helitrons* with the “rolling circle” transposition pattern.

TEs play an important role in genome evolution. In the process of their insertion, deletion, and amplification, the host may alter its genome size, gene expression, and gene function. Additionally, TEs may mediate chromosomal rearrangements through homologous recombination or alternative transposition. Overall, TEs are very powerful mutagens that can affect the stability of their host genomes. In order to defend against the transposition of TEs, the host has evolved various silencing mechanisms. In plants, the silencing of TEs is mainly established through RNA-directed DNA methylation (RdDM), which can stably repress the activity of TEs across generations. Methylation not only silences TEs but may also result in DNA methylation of nearby genes and affect expression and function of host genes. Interestingly, the phenotypic differences caused by the insertion of TEs play an important role in crop domestication. Methylation does not always keep TEs silent, such as burst events in some TE families. The evidence for the interaction between TEs and the host is growing, especially under environmental stress conditions, and TEs can be re-activated to help the host survive under stressful conditions. Furthermore, the insertion of TEs is preferred in many cases, and their insertion can be tolerated. Thus, TEs may not be completely inhibited, and they and their hosts may develop a cooperative relationship under environmental stress.

This review summarizes some relevant research on TEs in plant genome evolution, introduces commonly occurring TEs found in plants, and examines how TEs are involved in plant genome evolution, epigenetic regulation, and the symbiotic relationship with the host under cooperative stress.

transposable element, genome evolution, epigenetics, environmental stress, adaption

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