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核糖体介导的翻译调控与植物环境温度适应

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摘要 基因表达是生物体内至关重要的过程, 主要涉及DNA转录为RNA, 再进一步翻译为蛋白质. 这一过程复杂而精细, 涵盖了转录及转录后调控、翻译调控及翻译后修饰等多个环节. 核糖体作为细胞内的翻译机器, 承担着解码信使RNA(mRNA)上的遗传信息, 并将其翻译成多肽链, 最终形成功能性蛋白质的功能. 翻译调控在动植物的生长发育及逆境适应中起着至关重要的作用. 作为固着生长的生物, 植物为了应对外部环境的复杂温度变化, 进化出一系列精细的调控机制. 虽然在转录调控方面的研究相对成熟, 但在翻译层面的探索仍显不足. 本综述旨在总结核糖体介导的翻译调控在植物环境温度适应过程中的研究进展, 帮助我们更深入地理解翻译调控在植物生理和环境适应中的关键作用.

关键词 植物, 温度响应, 翻译调控, 核糖体质量控制

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由于植物固着生长的特性, 其生命活动易受各种外界环境变化的影响. 温度是制约植物生长发育和地理分布的重要环境因子. 在农业生产中, 异常温度严重影响作物品质和产量, 为农业生产和粮食安全带来巨大挑战[1,2]. 因此, 深入解析植物对环境温度变化的响应机制, 对实现分子育种和保障粮食安全具有重要意义. 本文主要从核糖体生物合成, 翻译调控以及核糖体质量控制系统层面综述其调控植物环境适应的研究进展.

1 核糖体生物合成

核糖体是细胞中负责蛋白质翻译的分子机器, 真核生物80S核糖体由60S大亚基和40S小亚基组成. 大小亚基均由核糖体RNA(ribosomal RNA, rRNA)与核糖体蛋白(ribosomal protein, r-protein)构成. 小亚基包含了18S rRNA和33种核糖体蛋白, 大亚基包含了5S rRNA、5.8S rRNA、28S rRNA和47种核糖体蛋白[3]. 核糖体生物合成是细胞内最复杂和耗能的过程之一, 该过程主要包括核糖体RNA前体的转录、加工、修饰, 以及与

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核糖体蛋白组装成核糖体大小亚基前体, 随后这些亚基前体从细胞核运输至细胞质完成成熟过程, 最终形成一个功能完整核糖体以执行翻译功能[4]. 除了核糖体RNA和核糖体蛋白以外, 还有超过200种核糖体组装因子和核仁小RNA(small nucleolar RNAs, snoRNAs)在核糖体生物合成过程的不同阶段发挥着重要功能[3].

异常的核糖体生物合成会对生物体的正常生长发育造成巨大影响. 例如, 在人类中, 核糖体蛋白或核糖体组装因子的突变经常会导致各种疾病的产生, 称作“Ribosomopathies”[5]. 在植物拟南芥中, 严重的核糖体相关突变会导致胚胎致死, 而非致死植株通常表现出生长迟缓、植株矮小、根长变短和真叶变尖等表型[6]. 拟南芥蛋白质精氨酸甲基转移酶(protein arginine methyltransferase)PRMT3是核糖体生物合成的重要调控因子. PRMT3通过与核糖体小亚基蛋白RPS2B的相互作用, 协同调控细胞核内核糖体前体的组装过程; 当两者功能异常时, 导致异常的核糖体生物合成, 并引发核仁胁迫[7,8]. 此外, 核糖体还可以作为生物体应对外界环境变化的重要枢纽[9]. 研究发现, AtPRMT3-RPS2B在翻译层面平衡植物苗期生长发育及低温适应相关基因的表达, 当其发生突变后促进冷响应相关基因翻译, 从而赋予拟南芥抗冷冻表型[10]. 核糖体加工蛋白STCH4 (sensitive to chilling 4)/REIL2通过在低温下维持核仁中rRNA前体加工, 增强低温下冷响应关键转录因子CBFs(C-repeat-binding factors)蛋白翻译, 进而促进植物低温耐受性[11]. 在水稻中研究发现, 低温能够抑制rRNA前体的加工[12]. 水稻中细胞核定位的DEAD-box RNA解旋酶TOGR1(thermotolerant growth required 1)能够帮助稳定pre-rRNA构象, 高温下其酶活性增强, 保证了高温下rRNA的正确加工, 从而赋予水稻耐热性[13]. 综上所述, 植物在应对不同环境温度时通过核糖体生物合成调控机制展现出复杂的适应策略.

2 翻译调控的影响因素

近年来, 随着高通量测序技术的发展, 研究者发现mRNA转录水平与最终蛋白质水平之间并未完全呈现相关性, 越来越多的证据表明翻译调控在这一过程中发挥着重要作用[14,15]. mRNA的5′ UTR(untranslated region, 起始密码子之前)、3′ UTR(终止密码子之后)和末端的poly(A)尾中的非编码序列通常包含多种翻译调控元件. 例如, 5′ UTR中包含上游开放阅读框(upstream open reading frame, uORF)、内部核糖体进入位点(internal ribosome entry site, IRES)以及复杂的RNA二级结构等; 3′ UTR中含有miRNA结合位点等; 此外, RNA修饰的存在也对翻译调控产生影响(图1)[16,17]. 这些元件对mRNA稳定性、翻译调控和亚细胞定位等具有重要调控功能[18].

2.1 上游开放阅读框

上游开放阅读框是存在于5′ UTR的一段短的碱基序列. 研究发现, uORF在多种生物(如人类、小鼠、果蝇、酵母和拟南芥等)中广泛存在, 但仅有少数被鉴定并进行功能研究[19]. 根据uORF终止密码子的位置, uORF可分为3种类型: 与mORF(main ORF)不重叠的uORF、与mORF部分重叠的uORF以及包含mORF的uORF[20,21]. uORF的起始密码子首先由43S预起始复合物识别, 随后与60S核糖体亚基组装为80S核糖体以进行uORF的翻译, uORF上的核糖体通常会对下游mORF的翻译起始产生抑制[22]. 然而, 下游mORF仍然会通过核糖体泄漏扫描(leaky scanning), 或翻译重新起始的方

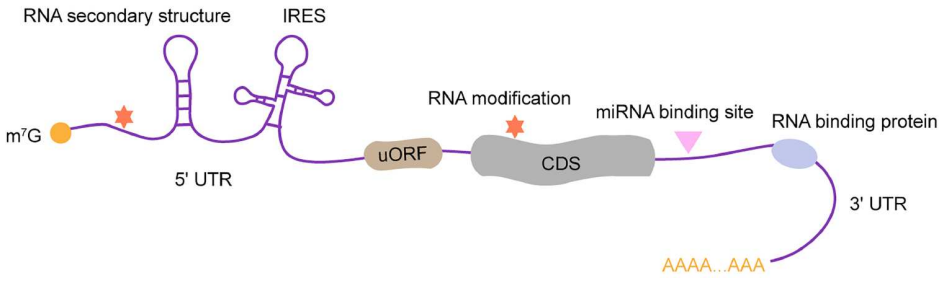

图 1 影响mRNA翻译效率的调控元件. 这些元件包括5′帽子(m7GpppN)、RNA二级结构、内部核糖体进入位点、上游开放阅读框、RNA修饰、miRNA结合位点、RNA结合蛋白和poly(A)尾巴等

Figure 1 Regulatory elements contributing to translational control in mRNAs. These elements include 5′ Cap (m7GpppN), RNA secondary structure, internal ribosomal entry sites (IRESs), upstream open reading frames (uORFs), RNA modification, miRNA binding site, RNA binding protein, and poly (A) tail, etc

式被翻译[18]. 含有uORF的转录本在生物体逆境适应过程中具有重要功能. 例如, 拟南芥*HEAT SHOCK FACTOR B1*(*HSFB1*)上游包含一段保守的uORF, 在正常环境温度下, 该uORF抑制下游*HSFB1*的翻译; 而在高温下其抑制作用减弱, 导致*HSFB1*表达增加[23]. 通过转录组RNA-seq和翻译组Ribo-seq技术的研究发现, 在茶树中, 低温胁迫降低了基因的翻译效率, 但提高了uORFs的翻译效率, 表明冷胁迫通过促进uORFs的翻译来抑制下游基因的翻译[24].

2.2 RNA二级结构

RNA分子的一级序列通过碱基配对形成特定的二级结构, 如RNA双链和发卡结构等. 这些复杂的结构使RNA在调节和催化功能中发挥作用. 然而, 由于RNA结构的动态变化, 且极易受到内部或外部环境变化的影响, 其检测面临巨大困难. 近年来, 结合化学标记方法(如SHAPE和DMS)与高通量测序技术, 研究者能够在全基因组水平上系统鉴定更多RNA二级结构, 这些结构在RNA转录、拼接、翻译、降解和定位等过程中具有重要功能[25]. 例如, 作为异源多倍体物种的小麦, 其转录水平和翻译水平仅部分相关. 通过RNA二级结构组和核糖体分析技术发现小麦体内的mRNA二级结构表现出亚基因组不对称性, 这种不对称性是造成亚基因组翻译效率差异的重要因素[26].

温度是影响RNA折叠的关键因素. 对水稻全基因组水平RNA二级结构分析表明, 高温能够迅速打开RNA二级结构并影响基因的表达[27]. 5′ UTR中可能形成的二级结构包括发夹结构、核糖开关(riboswitches)和RNA G-四链体(RNA G-quadruplex, rG4s)等[28]. 其中发夹结构是常见的二级结构, 例如, PIF7(phytochrome interacting factor 7)的5′ UTR在正常温度条件下会形成RNA发夹结构, 从而抑制下游mRNA翻译; 而在27°C时, 该结构的构象会发生变化, 对PIF7翻译抑制减弱, 最终造成高低温下不同的表型差异[29]. 在拟南芥中, 调节春化与开花的关键基因*FLC*(*flowering locus C*)和反义长链非编码RNA *COOLAIR*也展示了类似特征. 对*COOLAIR*可变剪切体的单分子RNA二级结构解析发现, 不同的*COOLAIR*可变剪切产物能够动态改变其RNA二级结构以适应环境温度变化[30].

2.3 poly(A)尾

poly(A)尾是mRNA末端的一段长的腺苷酸序列, 普遍存在于大多数真核生物mRNA中. 3′末端poly(A)尾巴可以保护mRNA不被降解, 从而增加mRNA的稳定性, 提高翻译效率, 进而影响和调控mRNA的生命周期[31].

常规转录组难以对poly(A)尾进行测序, 近年来, 结合三代测序技术, 如Nanopore和Pacbio, 一系列对poly(A)尾的精确测序技术被开发, 例如FLEP-Seq和PAIso-seq等[32,33]. 研究发现, 在哺乳动物卵子向早期胚胎转变过程中, poly(A)尾长度是动态变化的; 除了长度, poly(A)尾还可以通过内部或者末端的非A残基影响翻译过程[34]. 对拟南芥中的功能研究发现, poly(A)尾中存在非A核苷酸, 其中G的比例最高, 且G可通过对AtPAB的结合抑制效应下调mRNA的翻译效率[35]. 除了生长发育过程中Poly(A)尾长度发生动态变化以外, 其长度也受到外界温度变化的影响[36].

2.4 RNA结合蛋白

5′ UTR通过与真核生物起始因子(eukaryotic initiation factors, eIFs)结合, 成为翻译起始控制的重要枢纽. 当5′ 帽子结合复合物开始识别帽子结构, 以及poly(A)结合蛋白PABP(poly(A) binding protein)与mRNA poly(A)尾结合时, 翻译开始启动[37]. 在植物中, 帽子结合复合物由翻译起始因子eIF4E和支架蛋白eIF4G组成, 二者与解旋酶eIF4A、PABP以及eIF3一起使mRNA环化, 其中eIF4A作为一种解旋酶, 能够与它的辅助因子eIF4B一起解开mRNA上形成的二级结构, 从而招募预起始复合物(43S pre-initiation complex, 43S PIC), 预起始复合物在mRNA的5′ UTR进行扫描, 直到识别AUG起始密码子[37,38]. 翻译起始是蛋白质翻译的限速步骤, 因此很多翻译起始因子在生物体生长发育和逆境适应过程中均具有重要功能. 例如, 拟南芥中翻译起始因子eIF5B/HOT3突变后造成多效生长发育缺陷, 以及高温下热敏感性的表型, 研究发现eIF5B/HOT3介导的细胞质翻译起始能够促进叶绿体生物发生并优化光合作用[39,40].

此外, 还存在一些其他类型的RNA结合蛋白, 例如拟南芥GLYCINE-RICH RNA-BINDING PROTEIN 7 (GRP7)在温暖环境下能形成凝聚体(condensates), 而较低的温度能逆转这种现象. GRP7在细胞质中的液-液相分离(liquid-liquid phase separation, LLPS)有助于应激颗粒的形成, 该应激颗粒招募RNA及翻译起始因子eIF4E1和冷休克蛋白(COLD SHOCK PROTEIN)CSP1

和CSP3, 最终抑制翻译[41]. 水稻中*AET1*(*adaptation to environmental temperature 1*)基因突变后在高温环境下表现为矮秆、小穗和结实率低的表型, 而在温度较低的条件下却与野生型一致. 进一步研究发现*AET1*编码tRNA^{His}鸟苷转移酶, 一方面能够促进pre-tRNA^{His}的修饰和成熟, 另一方面能够结合生长素响应因子*OsARF19*和*OsARF23*, 并通过翻译过程的调节对高温做出响应[42].

2.5 RNA修饰

RNA上存在超过100种类型的化学修饰, 广泛分布于mRNA、tRNA、rRNA及其他非编码RNA上. 这些修饰类型包括N^6-甲基腺苷(N^6 methyladenosine, m^{6}A), 假尿苷(pseudouridine, Ψ), 5-甲基胞嘧啶(5-methylcytosine, m^{5}C)和2′-O-甲基化(2′-O-methylation, Nm)等. RNA修饰广泛参与RNA剪接、稳定性、二级结构维持, 以及mRNA翻译效率和可变多聚腺苷酸化等多种RNA代谢途径, 从而调控动植物的生长发育及胁迫响应过程[43].

例如, 低温会导致mRNA整体m^{6}A修饰水平降低, m^{6}A甲基转移酶复合体成员的敲低, 会导致基因的翻译效率发生改变, 从而影响植物的低温生长状态[44]. 假尿苷修饰是RNA中丰度最高的修饰, 水稻中叶绿体定位的假尿苷合酶(pseudouridine synthase)PUS1能够与叶绿体rRNA前体结合并催化假尿苷修饰; 低温下, OsPUS1的功能缺失造成叶绿体rRNA前体异常积累和成熟rRNA减少, 导致叶绿体中核糖体生物合成和翻译状态受到干扰, 并影响ROS稳态, 最终使得水稻叶片白化[45]. 水稻中OsNSUN2是mRNA m^{5}C甲基转移酶, OsNSUN2通过调节水稻mRNA的m^{5}C修饰, 主要是叶绿体相关基因mRNA, 以维持水稻在较高温度下的正常生长. 在高温条件下, *osnsnu2*突变体的叶绿体功能紊乱, 并导致光依赖的活性氧积累[46]. NAD$^+$帽子修饰RNA(NAD$^+$-capped RNA)是被鉴定到广泛存在于很多物种中的非典型加帽修饰, 并在RNA代谢和生物个体发育中具有重要功能[47,48].

转运tRNA携带氨基酸进入核糖体, 在mRNA指导下合成蛋白质. 在所有RNA分子中, tRNA含有最为丰富的转录后修饰类型, 这些修饰在确保密码子-反密码子配对精确性、维持tRNA结构稳定性及促进mRNA翻译效率等方面发挥着重要作用[49,50]. 水稻中鉴定到*PLEIOTROPIC DEVELOPMENTAL DEFECTS*(*PDD*), PDD编码tRNA修饰酶参与水稻叶绿体tRNA mnm^{5}s^{2}U修饰, 对于叶绿体和植物生长发育具有重要作用[51]. 水稻中*Slender Guy 1*(*SLG1*)编码tRNA 2-硫化蛋白2(RCTU2), 其功能缺失导致水稻体内tRNA硫醇化水平缺陷, 造成高温敏感表型; 此外, *SLG1*具有粳稻自然变异, 其启动子区和编码区的序列差异共同影响了籼稻和粳稻的耐热性差异[52]. 近年来, 高通量测序技术揭示出细胞内存在大量tRNA衍生片段(tRNA-derived fragments, tRFs)或tRNA衍生的小RNA(tRNA-derived small RNAs, tsRNAs), 植物tRFs在应对环境胁迫、参与植物与病原体的相互作用、调节转录后基因沉默及翻译调控等方面发挥着重要作用[53~55].

3 核糖体质量控制与温敏不育

3.1 温敏不育

基于光/温敏型核雄性不育系(photoperiod/thermosensitive genic male sterile, P/TGMS)建立的两系法杂交水稻技术, 是有效利用水稻杂种优势的途径. 这种技术是利用在低温或短日照条件下表现为雄性可育并进行自我繁殖, 而在高温或长日照条件下表现为雄性不育的现象[56]. 光温敏雄性不育系应用过程中, 最关键的影响因素是控制育性转育起点温度(critical sterility-inducing temperature, CSIT). 如果CSIT偏高或不稳定, 会导致育性波动, 成为制约两系法杂交水稻发展的关键因素. 在全球气候变暖背景下, 极端天气频发, 对光温敏核不育系, 尤其是温敏核不育系的繁殖和制种造成了显著影响, 给两系法杂交水稻制种带来了巨大风险. 因此, 深入解析其调控机制尤为重要.

3.2 核糖体质量控制系统

两系法杂交稻品种中超过95%的母本来源于含温敏雄性不育基因*tms5*的两用核不育系, 凸显了*tms5*在两系法杂交稻育种中的核心地位. 研究发现*TMS5*编码核酸酶RNase Z^{S1}[57], 但是其发挥功能的分子机制仍然未知. 近期的研究通过正向遗传学筛选获得了中高温下可以恢复*tms5*突变体育性的抑制子, 这些抑制子基因分别编码了核糖体质量控制(RQC)通路相关的蛋白质: CSIT1[58]、CSIT2/OsHel2[59,60]和OsRqc2[61], 结果表明RQC通路在TMS5介导的育性调控过程中具有重要功能.

在翻译过程中, 核糖体以mRNA为模板, 携带不同氨基酸的tRNA通过反密码子与mRNA上的密码子配

对，完成肽链合成. 当细胞内发生翻译异常或停滞时，可能会导致不完整或有缺陷多肽生成，进而激活核糖体质量控制(ribosome-associated quality control, RQC)系统. 该系统通过停滞核糖体识别、核糖体大小亚基分离、异常新生肽链泛素化并降解，tRNA修复和循环等步骤，以维持生物体内蛋白稳态[62]. RQC通路是细胞为应对错误或失败的翻译所必需的，以清除异常的新生肽链，并促进核糖体亚基分离和tRNA的循环利用[63].

在水稻中的研究发现，CSIT1编码E3泛素连接酶，负责泛素化翻译错误或未正确折叠的多肽[58]. CSIT2/OsHel2作为E3泛素连接酶，主要在蛋白质翻译出错时泛素化核糖体蛋白，促进核糖体大小亚基解离，从而也进一步促进tRNA的解离[59]. 通过在水稻原生质体中建立的核糖体停滞报告基因系统(ribosome stalling reporter system)发现，抑制子中OsHel2在其N端RING结构域的关键酶活位点发生点突变，导致mRNA上翻译停滞的核糖体通读，从而降低了RQC通路中间产物2′,3′-环磷tRNA的产生[60]. 另一个抑制子中OsRqc2蛋白发生点突变(T552I)导致其结合tRNA的种类和在新生肽链C末端添加氨基酸的速率均发生变化[61].

3.3 tRNA循环

深入研究发现TMS5作为2′,3′-环磷酸酶，能够修复核糖体质量控制RQC通路产生的中间产物2′,3′-环磷-tRNA，从而促进tRNA循环利用. 通过开发的环磷RNA(RcP-RNA-seq)和全长tRNA(FINE-tRNA-seq)高通量测序技术发现，在*tms5*突变体中2′,3′-环磷-tRNA过度积累，高温条件下该积累现象更为严重，最终导致成熟tRNA丰度降低，尤其是丙氨酸tRNA(tRNA-Ala)的丰度显著下降. 进一步在*tms5*突变体中过表达tRNA-Ala能够部分恢复其花粉育性，而敲除RQC通路中产生环磷-tRNA的酶OsVms1，降低环磷-tRNA的产生可以完全恢复高温下*tms5*突变体的花粉育性，表明*TMS5*突变导致环磷tRNA修复失败，从而导致体内成熟tRNA的缺乏，整体翻译水平发生变化，成为导致*tms5*高温不育的重要原因[64,65]. 综上所述，以上研究揭示了TMS5与核糖体质量控制通路成员在协同调控水稻温敏雄性不育中的分子机制和调控网络(图2).

4 总结与展望

植物为了应对外界复杂环境的变化，需要不断平衡生长发育和胁迫响应基因的表达，而翻译调控在这一过程中发挥着重要作用. 当生物体处于变化的环境条件时，核糖体能够迅速激活或抑制相关mRNA的翻译，以满足细胞生命活动需求. 为避免细胞内翻译过程中的错误，生物体也进化出了监管和清除系统，例如核糖体质量控制系统，以维持正常细胞生命活动.

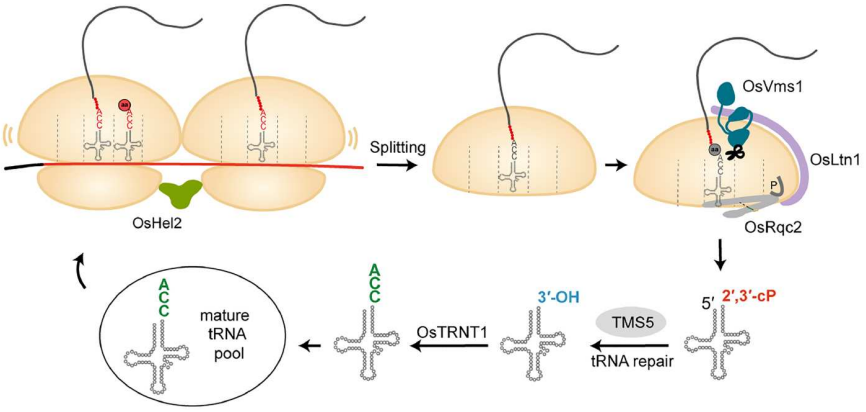

图 2 TMS5和RQC通路在tRNA修复和循环过程中发挥功能的工作模式图. 当核糖体发生碰撞停滞时，OsHel2识别停滞的核糖体并促使大小亚基解离. OsRqc2, OsLtn1和OsVms1依次结合到60S大亚基上形成RQC复合体. OsVms1通过水解异常新生肽链末端的肽酰-tRNA，将新生肽链从核糖体上释放，同时产生2′,3′-环磷-tRNA. 2′,3′-环磷经TMS5修复成3′-OH，然后在OsTRNT1的作用下对tRNA末端添加CCA，形成成熟tRNA，维持体内tRNA稳态

Figure 2 The working model of TMS5 and RQC in tRNA repair and recycling. When ribosome stalling occurs, OsHel2 recognizes the stalled ribosome and promotes the dissociation of the large and small subunits. OsRqc2, OsLtn1, and OsVms1 sequentially bind to the 60S large subunit, forming the RQC complex. OsVms1 releases the nascent peptide chain from the ribosome by hydrolyzing the peptidyl-tRNA at the C-terminus, producing a 2′,3′-cyclic phosphate tRNA. The 2′,3′-cyclic phosphatase is repaired into 3′-OH by TMS5, and then the CCA nucleotides are added to 3′ end of the tRNA by OsTRNT1, forming the mature tRNA, thereby maintaining the intracellular tRNA homeostasis

近年来, 随着技术的发展和研究的深入, 人们对动植物翻译的基本过程和调控机制有了更清晰的认识, 这对于治疗人类疾病和实现作物育种具有重要意义. 例如, 在mRNA序列中存在许多影响翻译的调控元件, 除了阐明其调控机制外, 利用这些机制进行作物改良也成为一个主要目标. 其中, 使用上游开放阅读框(uORF)进行基因编辑以改良作物性状具有重要的应用前景[66,67]. 研究表明, 利用uORF在翻译水平上精准调控抗病蛋白NPR1的表达, 不仅成功赋予水稻出色的抗性特性, 同时确保了其农艺性状不受影响[68]. 随着对调控元件功能研究的不断深化, 未来将有更多类似的元件被应用, 为分子育种进程加速提供支持.

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Summary for “核糖体介导的翻译调控与植物环境温度适应”

Ribosome-mediated translational regulation and environmental temperature adaptation in plants

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The regulation of gene expression is a multifaced process that encompasses transcription from DNA to RNA, and translation from RNA to protein. This intricate system involves multiple layers of regulation, including transcriptional, post-transcriptional, translational, and post-translational mechanisms. Plants, as sessile organisms, are particularly vulnerable to fluctuations in environmental conditions, with temperature being a key factor influencing their growth, development, and geographical distribution. Fluctuating temperature conditions can have a substantial impact on crop quality and yield, thereby posing severe challenges to agricultural production and food security. To cope with these variations, plants have developed sophisticated regulatory mechanisms to adapt to changing temperatures. However, the translational aspects of this process remain less explored. In this review, we summarize recent advancements in our understanding of translational regulation and its role in environmental adaptation in plants.

Ribosome represents a central organelle during this process, essential for decoding the genetic code into functional proteins. Ribosome biogenesis, primarily occurring in the nucleolus, is one of the most complicated and energy-consuming processes within the cell. This process involves the transcription of pre-ribosomal RNAs (pre-rRNAs), and subsequent processing, modification, and assembly with ribosomal proteins, facilitated by numerous assembly factors. Once assembled, ribosomal subunits are transported from the nucleus to the cytoplasm, where they undergo final maturation, a critical step for forming fully functional ribosomes capable of executing translation. During translation, ribosomes utilize mRNA as a template, with transfer RNAs (tRNAs) delivering specific amino acids to the ribosome. There are lots of cis-regulatory elements commonly present in mRNA affecting translation efficiency, including the 5′ untranslated region (5′ UTR), 3′ UTR, 5′ Cap (m7GpppN) at the 5′ end, poly(A) tail at the 3′ end; RNA secondary structure, upstream open reading frames (uORFs), internal ribosomal entry sites (IRESs), etc.

However, when translation mistakenly stalls, it can lead to the generation of incomplete or defective polypeptides. In such cases, the Ribosome-associated Quality Control (RQC) system is activated, playing a crucial role in maintaining protein homeostasis. The RQC system identifies stalled ribosomes, separates ribosomal subunits, ubiquitinates and degrades aberrant nascent peptide chains, repairs and recycles tRNAs. Collectively, these actions prevent the accumulation of faulty proteins and ensure proper cellular function. The accurate orchestration of ribosome biogenesis and translation is vital for the normal growth and development of organisms, as well as for their ability to respond to environmental stresses.

Here, we highlight the essential roles of ribosome translation in stress responses, drawing on numerous studies that have shown how defects in ribosome biogenesis and translation impair responses to extreme temperatures. One notable area of research is the two-line hybrid system, a leading technology in hybrid rice breeding that relies on photo-thermosensitive genic male sterile (P/TGMS) lines, where both temperature and photoperiod influence plant fertility. Recent advances in understanding thermo-sensitive genic male sterility in rice have identified TMS5 as a major gene regulating current TGMS lines. Forward genetic screens have revealed several suppressors encoding components of the RQC, and subsequent experimental evidence has highlighted the importance of RQC and tRNA recycling in TMS5-mediated TGMS in rice. This offers valuable insights for improving TGMS in hybrid crop development. The interplay between ribosome function, translation regulation, and environmental response underscores the significance of this research. This review aims to provide a comprehensive overview of the ribosomal translation process while emphasizing the regulatory roles of the ribosome in plant growth, development, and stress responses.

translational regulation, ribosome-associated quality control, plants, temperature response

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