植物学报 *Chinese Bulletin of Botany* 2024, **59** (3): 355–372, www.chinbullbotany.com
doi: 10.11983/CBB24006

·特邀综述·

重要的种子储存物质长寿命mRNA

朱晓博[1,2], 董张[1,2], 祝梦瑾[1,2], 胡晋[1,2], 林程[3], 陈敏[2], 关亚静[1,2*]

[1]浙江大学海南研究院, 三亚 572000; [2]浙江大学农业与生物技术学院现代种业研究所, 杭州 310058
[3]苏州农业职业技术学院, 苏州 215008

摘要 高等植物通常从种子萌发开始, 经过营养生长和生殖发育后重新形成种子, 由此完成世代更迭。种子中积累的碳水化合物、脂质、蛋白质及mRNA等大分子物质对于维持其发芽潜力至关重要, 其中部分mRNA可长期保存而不被降解, 被称为长寿命mRNA (即long-lived mRNA)。在水稻(*Oryza sativa*)中, 与萌发相关的long-lived mRNA在花后10–20天开始转录积累, 花后20天至种子完全成熟期间, 一些与休眠和胁迫响应相关的long-lived mRNA转录并保存在细胞中。Long-lived mRNA种类繁多, 主要包括蛋白质合成类mRNA、能量代谢类mRNA、细胞骨架类mRNA及逆境响应相关的mRNA, 如小热激蛋白和LEA家族蛋白。Long-lived mRNA的转录组分析表明, 很多基因的启动子区域都包含脱落酸(ABA)或赤霉素(GA)相关的顺式作用元件, 拟南芥(*Arabidopsis thaliana*) *atabi5*突变体种子中约有500个不同于野生型的差异表达long-lived mRNA, 暗示ABA和GA是影响long-lived mRNA种类的关键激素。Long-lived mRNA通常与单核糖体和RBP蛋白交联在一起, 以PBs (P-bodies)形式存在于细胞中, 保护mRNA不被降解。与种子休眠相关的long-lived mRNA在种子后熟过程中逐渐被降解, 而且一些特定long-lived mRNA的氧化修饰是种子打破休眠的一种生物现象。在种子长期贮藏过程中, long-lived mRNA的随机降解直接关系到种子的寿命和活力, 保留下来的mRNA在种子吸胀初期被翻译成蛋白质, 促进种子在吸胀早期快速萌发。该文综述了种子重要储存物质long-lived mRNA的特征和功能, 并提出了本领域需要进一步研究的科学问题, 以期为深入理解种子休眠、萌发与寿命的分子机制提供参考。

关键词 长寿命mRNA, 种子休眠, 种子萌发, 种子贮藏

朱晓博, **董张**, **祝梦瑾**, **胡晋**, **林程**, **陈敏**, **关亚静** (2024). 重要的种子储存物质长寿命mRNA. 植物学报 **59**, 355–372.

种子作为特殊的植物器官, 能够在含水量很低的情况下保持活性。在种子发育成熟过程中, 各种大分子物质合成并积累, 如糖类、脂质和蛋白质, 同时转录并积累了大量mRNA。通常情况下, mRNA的寿命只有几分钟到十几分钟, 但是种子积累的部分mRNA却可以保存几周甚至几年, 因此也被称为长寿命mRNA (long-lived mRNA) (Narsai et al., 2007; Sano et al., 2015)。1965年, Dure和Waters利用转录抑制剂Act D (actinomycin D)处理棉花(*Gossypium* spp.)种子, 发现其能够正常伸出胚根, 推测种子本身含有一些能够保证其正常发芽的mRNA, 这些mRNA在种子发育成熟过程中未被降解而保留下来, 由此学者们在棉花种子中确认了long-lived mRNA的存在(Dure and Waters, 1965; Harris and Dure, 1978)。后续又在玉米(*Zea mays*) (Villa-Hernández et al., 2013)、大麦(*Hordeum vulgare*) (Sreenivasulu et al., 2008)、小麦(*Triticum aestivum*) (Zhao et al., 2020a)、水稻(*Oryza sativa*) (Howell et al., 2009)、芸薹(*Brassica rapa* var. *oleifera*) (Zhao et al., 2020a)及豌豆(*Pisum sativum*) (Nomura et al., 2007)、向日葵(*Helianthus annuus*) (Bazin et al., 2011)和拟南芥(*Arabidopsis thaliana*) (Nakabayashi et al., 2005)等物种中验证了long-lived mRNA的存在。通过分析转录组数据, 发现水稻种子包含17 000多个long-lived mRNA (Howell et al., 2009), 拟南芥和大麦种子中各有12 000多个long-lived mRNA (Na-

收稿日期: 2024-01-10; 接受日期: 2024-03-30
基金项目: 海南省科技计划三亚崖州科技城联合项目(No.320LH032)、海南省自然科学基金(No.322CXTD522)、浙江省“三农九方”科技协作计划(No.2023SNJF04302)、苏州市农业科技创新项目(No.SNG2022063)和江苏省“双创博士“项目(No.JSSCBS20221012)
* 通讯作者。E-mail: vcguan@zju.edu.cn

kabayashi et al., 2005; Sreenivasulu et al., 2008)。

1 Long-lived mRNA的转录积累及种类

Long-lived mRNA在种子发育过程中转录积累，并与核糖体和RBP (RNA binding protein)蛋白等形成PBs (P-bodies)，从而防止其被快速降解，因此可以保存较长时间。在种子吸胀初期，long-lived mRNA作为模板被翻译成蛋白质，以确保种子发芽前期所需的物质和能量代谢(Sajeev et al., 2019)。

1.1 Long-lived mRNA的转录积累

研究人员利用蛋白抑制剂(cycloheximide)处理拟南芥种子，发现其均不能萌发，但用转录抑制剂Act D处理后种子可正常萌发，暗示long-lived mRNA对种子萌发起重要作用(Rajjou et al., 2004)。种子在发育过程中积累long-lived mRNA，研究发现水稻的种胚在花后10天已完成分化，且能够正常发芽。但经Act D处理后，花后10天的胚不能正常发芽，说明此时胚中积累的mRNA不足以满足种子萌发的需求(Sano et al., 2015, 2019)。而用Act D处理花后20–40天的种胚，其均可以正常萌发，暗示有助于种子萌发的long-lived mRNA可能在花后10–20天开始积累，并且能够满足种子萌发起始的需求(Sano et al., 2015) (图1)。此外，花后10天种胚的正常萌发速率远远慢于20–40天种胚(Sano et al., 2015)，推测long-lived mRNA在保证种子快速发芽方面发挥重要作用(Rajjou et al., 2004; Itoh et al., 2005; Matilla, 2022)。在豇豆(*Vigna unguiculata*)种子中也发现了类似的规律，long-lived mRNA(如*pSAS10*)的转录在花后10–15天开始积累，并在干种子中长期保存(Ishibashi

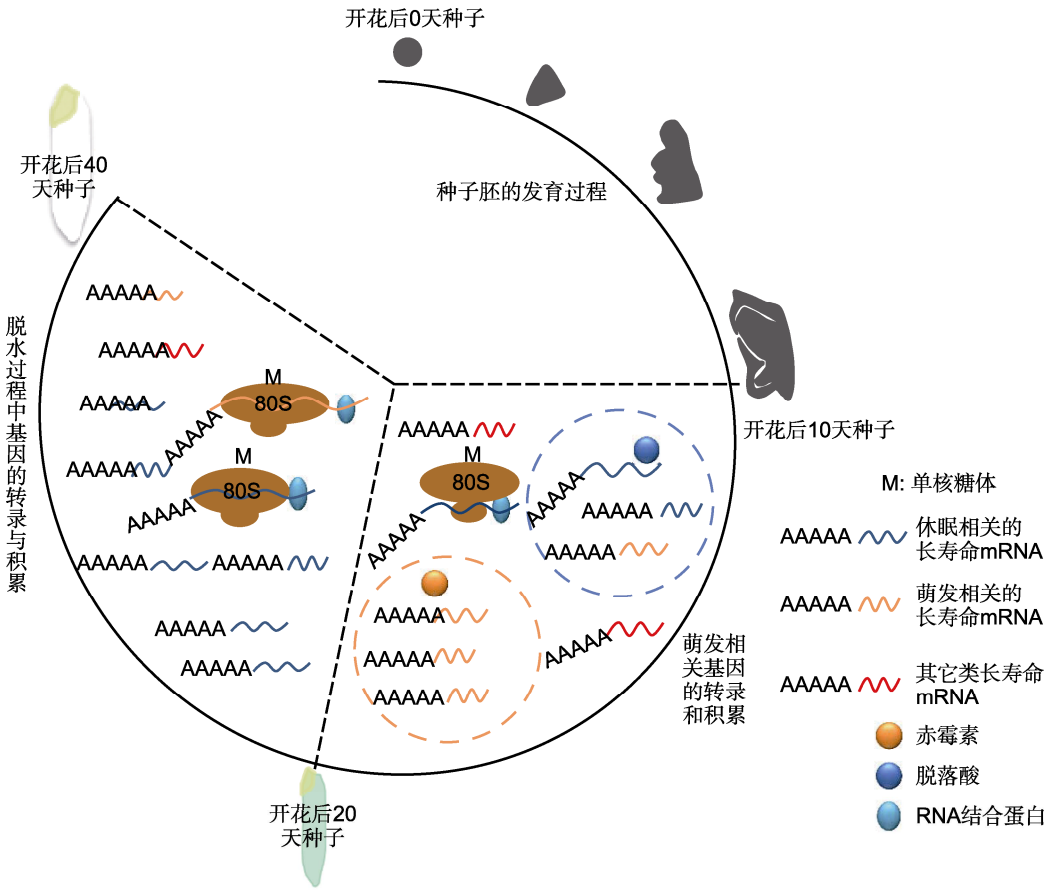

图1 长寿命mRNA在水稻种子发育成熟期的变化(种子胚发育过程参考Sano et al., 2015)

Figure 1 The changes of long-lived mRNAs during rice seed development (the development of seed embryo process refer to Sano et al., 2015)

et al., 1990)。

大多数正常植物种子成熟干燥后的含水量很低, 但仍然具有高萌发率, 这与体内储存的long-lived mRNA有密切关系, 而这些mRNA之所以未被降解, 主要是由于大部分mRNA与单核糖体和RBP蛋白交联在一起, 以PBs蛋白形式存在于细胞中, 为mRNA提供保护(图1) (Standart and weil, 2018; Sano et al., 2019; Matilla, 2022; Kearly et al., 2024)。研究表明, 水稻种子中大约有17%的mRNA交联在单核糖体上, 并在种子吸胀过程中被翻译成蛋白质(Sano et al., 2019)。蛋白质组学分析发现, 种子中包含RBP蛋白(RNA-binding proteins) RZ-1A 和 GRP1A (glycine-rich RBP), 且都含有1个K结构域(K domain) (Masaki et al., 2008), 起到稳定mRNA的作用(Sano et al., 2013; Sajeev et al., 2019)。在拟南芥种子胚根伸出的过程中,有30个种子特异的RBP参与其中(Sajeev et al., 2022)。但是哪些类型的long-lived mRNA易与核糖体复合体结合, 哪些RBP在种子发育过程中调控mRNA的功能及如何调控尚需进一步研究。

1.2 Long-lived mRNA的种类

Sano等(2012)分析对照和Act D转录抑制剂处理后的种子发芽时期的蛋白质组数据, 发现与萌发相关的109个蛋白质翻译于long-lived mRNA, 222个蛋白质翻译于吸胀过程中新转录的mRNA。GO (Gene Ontology)和KEGG (Kyoto Encyclopedia of Genes and Genomes)分析发现, 109个蛋白质主要参与能量的合成代谢, 如糖酵解、核苷酸结合蛋白和细胞骨架形成, 222个蛋白质主要涉及丙酮酸代谢和TCA循环。通过RNA-sequencing分析花后10–20天的种子胚, 结果显示long-lived mRNA涉及能量代谢、蛋白代谢和转运、非生物胁迫响应以及胚发育等共529个基因的转录(Sano et al., 2015)。在非生物胁迫响应方面包含LEA (late embryogenesis abundant)蛋白和热激蛋白(heat shock protein)的long-lived mRNA。但在种子吸胀7小时后, 这两类mRNA水平降低(Sano et al., 2015), 推测其可能是为响应种子脱水耐性进行的转录积累, 对种子萌发并无直接作用(Sano et al., 2013)。

在拟南芥中, 编码LEA蛋白的基因有51个(Wise, 2003; Hundertmark and Hincha, 2008), 种子中包含17个LEA蛋白的long-lived mRNA (Kimura and Nambara, 2010)。从向日葵种子中也克隆出2个LEA蛋白D-113和Emb-1的编码基因(Almoguera and Jordano, 1992), 暗示干种子中积累的LEA蛋白的mRNA可能在环境胁迫中发挥作用, 如抵抗冷或干旱等非生物胁迫(Mertens et al., 2018)。脂质代谢相关的long-lived mRNA, 如油脂蛋白(oleosin)转录本(Sreenivasulu et al., 2008; Kimura et al., 2010), 在油体(oil body)代谢中发挥重要作用, 为种子发芽提供能量(Siloto et al., 2006)。乙醛酸循环相关酶的mRNA, 如PED1/KAT2催化3-keto-acyl-CoA成为acyl-CoA, 再进入乙醛酸循环进行能量代谢(Kimura and Nambara, 2010)。Long-lived mRNA还包含*NAC* (如*RD26*)、*AP2-EREBP* (*RAP2*和*DREB2A*)、锌指蛋白类的转录因子基因(*ABI5*), 其中表达量最高的是NAC家族转录因子基因*ATAF1* (Kimura and Nambara, 2010), 其参与DNA修复(Yoshiyama et al., 2009)。在大麦种子中鉴定到337个转录因子转录本可能为long-lived mRNA, 其中74个转录因子在胚乳成熟过程中高表达, 但在萌发时表达量降低(Sreenivasulu et al., 2008)。在转录抑制剂的作用下, RBs (ribosomal proteins)蛋白仍然在种子吸胀过程中被翻译合成, 表明long-lived mRNA中包含核糖体蛋白的mRNA, 并在发芽过程中发挥重要作用(Beltrán-Peña et al., 1995; Sánchez-de-Jiménez et al., 1997; Montoya-García et al., 2002; Villa-Hernández et al., 2013)。在大麦种子中还鉴定出一些与贮藏时间长短相关的mRNA, 如半胱氨酸合酶和丝氨酸羧肽酶转录本(Sreenivasulu et al., 2008)。

在种子吸胀萌发阶段, long-lived mRNA可保障初始能量代谢(如糖酵解和乙醛酸循环)所需的蛋白质和酶类, 之后体内新合成的mRNA有助于快速提供大量的能量, 如三羧酸循环的激活。因此, long-lived mRNA和吸胀过程新合成的mRNA共同促进种子萌发(Aspart et al., 1984; Suzuki and Minamikawa,1985; He et al., 2011; Sano et al., 2019)。

1.3 脱落酸和赤霉素影响long-lived mRNA的种类和积累

Long-lived mRNA的转录积累受植物激素调节, 其中

主要是赤霉素(gibberellin, GA)和脱落酸(abscisic acid, ABA) (Kimura and Nambara, 2010; Sano et al., 2019)。GA和ABA的合成及信号通路相关基因在种子成熟和萌发早期均有表达，而乙烯(ethylene, ET)、油菜素内酯(brassinosteroid, BR)、生长素(indole-3-acetic acid, IAA)和茉莉酸(jasmonic acid, JA)合成基因只在种子萌发时表达(Sreenivasulu et al., 2008)。GA合成相关基因*GA2* (编码*ent*-kaurene synthase A)、*GA3* (编码*ent*-kaurene oxidase)、*KAO1* (编码*ent*-kaurenoic acid oxidase)、*GA20OX1*、*GA20OX2*、*GA20OX3* (编码GA20-oxidases)、*GA3-OX* (编码GA3 oxidase)和*GA2OX1*、*GA2OX2* (编码GA2-oxidases)等在种子成熟和萌发早期保持高表达(Jacobsen et al., 2002; Sreenivasulu et al., 2008)。同样，在种子成熟过程中维持高表达的还有ABA结合蛋白(ABA binding protein)、磷酸酶2C (ABI2)、ABA信号响应结合蛋白(ABA-responsive element binding protein)和ABA不敏感蛋白(ABA-insensitive protein 3, ABI3)等ABA合成代谢通路相关蛋白(Sreenivasulu et al., 2008)。通过分析大麦种子成熟过程中糊粉层细胞的转录组数据(Chen and An, 2006)，发现在表达的基因启动子顺式作用元件中，有69个基因可能响应GA信号，主要涉及细胞壁合酶降解及多糖、核酸和脂质类的合成代谢，其中60个基因的启动子上也含有响应ABA信号的ABRE顺式作用元件。此外，有32个转录因子也可能响应GA和ABA的调控(Sreenivasulu et al., 2008)。大麦种子糊粉层积累的油脂蛋白Ole1和Ole2的转录受GA_3抑制，α-淀粉酶受GA_3诱导，ABA则拮抗GA_3的抑制和诱导作用(Aalen et al., 2001)。在豌豆种子发育过程中，BRs的两类活性物质BL (brassinolide)和CS (castasterone)被合成并积累，且2个氧化酶BR C-6 oxidase (CYP85A1和CYP85-A6)的转录水平显著升高，推测BL和CS可能在豌豆种子发育过程中发挥作用(Nomura et al., 2007)。

对比分析拟南芥ABA合成缺失突变体*aba2*和ABA代谢缺失三突突变体*cyp707a1*/*a2*/*a3*干种子long-lived mRNA的转录组数据，发现体内ABA的含量并不影响long-lived mRNA的转录积累，只对吸胀萌发过程中的基因转录产生影响(Okamoto et al., 2010)。而在ABA不敏感突变体*abi5* (*ABA-insensitive 5*)的干种子中，发现约500个基因的表达受到影响(Nakabayashi et al., 2005)。此外，水稻中长距离运输ABA的蛋白DG1 (defective grain-filling 1)帮助叶片中合成的ABA转运至种子中积累，保证种子发育过程中淀粉相关基因的正常表达和发育(Qin et al., 2021)。

2 Long-lived mRNA与种子休眠

种子本身未完全通过生理成熟或存在发芽障碍，即使给予适当的发芽条件但仍不能萌发的现象被称为种子休眠(关亚静和胡晋, 2020)。种子收获后在贮藏过程中逐渐达到生理成熟、打破休眠称为后熟(Bazin et al., 2011; Nelson et al., 2017)。对比拟南芥休眠种子和后熟种子的转录组数据，通过分析主成分(principal component analysis, PCA)，发现处于休眠状态的种子比后熟阶段的种子多了442个高表达的基因，其中转录因子有57个，另有一些为胁迫响应蛋白，如LEA蛋白、过氧化物酶和小热激蛋白。后熟阶段有779个基因的表达高于休眠状态的种子，其中包含40个转录因子基因。7 545个基因在休眠和后熟状态下的表达量无差异(Cadman et al., 2006)。RNA聚合酶(RNA polymerases)的表达在这两个阶段无差异，说明休眠种子并非处于静止状态(Sano et al., 2019)。SIGA和SIGD (sigma cofactors)是定位于质体的蛋白并参与质体蛋白的起始转录，这2个蛋白质编码基因表达量在后熟阶段显著高于休眠阶段(Tiller et al., 1991; Isono et al., 1997; Cadman et al., 2006)，暗示其可作为种子休眠解除的指标之一。

拟南芥休眠种子的442个高表达基因中，43%的基因启动子区域有2–3个ABRE顺式作用元件，推测与ABA相关(Cadman et al., 2006)。GA3OX2 (GA3-beta-dioxygenase)可将无活性的GA前体物质催化为有活性的GA_1和GA_4，其在后熟种子中的表达量是休眠状态下的40倍；而将有活性的GA转变为无活性前体物质的*GA2OX1*在休眠期高表达。GA信号的响应基因*GASA4*在后熟阶段的表达量是休眠阶段的120倍(Cadman et al., 2006)。ABA相关基因在后熟过程中被逐渐降解，这对于种子休眠解除并顺利萌发是重要的先决条件之一(Ingle and Hageman, 1965; Howell et al., 2009; Nelson et al., 2017)。

氧气可以在低含水量种子细胞中扩散，因此mRNA

的鸟嘌呤极易被氧化修饰, 从而阻止基因组DNA被氧化破坏(Martinet et al., 2005; Oracz et al., 2007; Kong and Lin, 2010)。而特定的long-lived mRNA的氧化修饰是种子打破休眠的一种重要方式, 通过分析向日葵后熟阶段种子的转录组数据, 发现有24个long-lived mRNA被氧化修饰, 且其翻译蛋白大多参与细胞信号通路, 包含2C蛋白磷酸酶PPH1 (protein phosphatase 2C PPH1)、促丝裂原活化蛋白激酶磷酸化酶1 (mitogen-activated protein kinase phosphatase 1)及苯胺裂解酶1 (phenyl ammonia lyase 1) (Bazin et al., 2011)。小麦种子中被氧化修饰的long-lived mRNA种类有氧化磷酸化(oxidative phosphorylation)、核糖体合成(ribosome biogenesis)和α-淀粉酶抑制(α-amylase inhibitor activities) (Gao et al., 2013)。

拟南芥*SLY1* (*SLEEPY1*)负调控种子的休眠能力(Ariizumi and Steber, 2007), 其*sly1-2*突变体对GA信号不敏感, 种子的休眠能力增强, 需要经过2年的后熟过程才能解除休眠(Ariizumi and Steber, 2007; Ariizumi et al., 2013)。Nelson等(2017)对比*sly1-2*及开花相关突变体*ft1-1* (*flowering locus t-1*)与L*er* (WT)的干种子转录组数据, 发现*ft1-1*与L*er*无显著差异, 但*sly1-2*有794个基因的表达量与L*er*不同, 且前50个高表达基因与DELLA转录相关, 说明这些基因的表达差异可能在种子发育成熟过程中产生。AtrbohB是NADPH氧化酶, 参与蛋白质和long-lived mRNA的氧化修饰(Oracz et al., 2007), 其mRNA有2个剪切状态AtrbohB-α和AtrbohB-β, 均存在于干种子中, 而后熟种子中只有AtrbohB-β的转录本, 推测long-lived mRNA可通过转录后剪切形式的变化调控种子的休眠状态(Müller et al., 2009)。AtAIL6 (AINTEGUMENTA-like 6)是在种子中高表达的转录因子, 且在种子发育过程中也维持高表达, 将其超表达后种子的发芽率只有12%, 但经过长时间的贮藏后熟处理, 种子的萌发率达到40%, 说明AtAIL6作为long-lived mRNA参与调控种子休眠(Liu et al., 2023)。*OsDOG1-3* (编码DOG1-like protein)是拟南芥*DOG1*的同源基因, 其表达模式类似于*AtDOG1*, 在种子成熟过程中表达且表达量逐渐升高, 但在吸胀过程中表达量下降(Nakabayashi et al., 2012; Wang et al., 2020b)。ABA信号通路转录因子OsbZIP75以及OsbZIP78直接调控*OsDOG1-3*的表达, 而OsDOG1-3又正向反馈调节ABA相关基因的表达, 并增加ABA含量, 从而调控种子休眠(Wang et al., 2020b)。WRKY36 (bHLH的转录因子)通过与AFP2 (ABi5-binding protein 2)互作, 直接抑制*DOG1*的表达。同时, TPR2 (topless-related protein 2)通过与AFP2互作, 直接参与并减少*DOG1*位点的乙酰化修饰, 降低其表达, 由此WRKY36-AFP2-TPR2通过影响*DOG1*的表达反向调控种子休眠(Deng et al., 2023)。*OsGLP2-1* (编码Germin-like protein 2-1)在种胚的盾片中表达, 该基因表达受抑制后, 新鲜种子丧失休眠能力, 但超表达该基因可增强种子的休眠能力, 进一步分析发现, *OsGLP2-1*由ABI5直接调控并作为long-lived mRNA参与调控种子休眠(Wang et al., 2020a)。

种子休眠相关基因大多在种子发育成熟过程中表达并积累, 由此推测其可能作为long-lived mRNA储存在种子中发挥作用。表1列举了2010–2024年间研究报道可能作为long-lived mRNA参与调控种子休眠的基因。

3 Long-lived mRNA与种子寿命

种子在贮藏过程中, 会受到外界环境的影响而导致活力下降和寿命缩短(Rajjou and Debeaujon, 2008)。种子中储存的long-lived mRNA对环境胁迫有一定的抵抗作用, 但在种子贮藏过程中, long-lived mRNA被逐渐降解, 并最终丧失抵抗外界不良环境的能力。长片段的long-lived mRNA在贮藏过程中易发生非特异性降解, 而短片段的long-lived mRNA即使经过长时间贮藏仍可保持很高的表达量, 但这些短片段mRNA并不能满足种子快速萌发的需求(Fleming et al., 2018; Sharma et al., 2018; Zhao et al., 2020b)。Zhao等(2020a, 2020b)研究表明, 特定贮藏条件下long-lived mRNA链上每天发生断裂的平均频率为β-value, 反映了mRNA片段的平均降解速率, 且long-lived mRNA的降解程度能够更加精确地指示种子的衰老程度, 并优于现有的根据贮藏种子的萌发率、电导率和根长苗高等判断种子寿命的方法(Zhao et al., 2020b; Niñoles et al., 2022)。太空环境贮藏13个月的水稻种子萌发率仅为同批次地面贮藏种子的一半, 转录组测序发现与萌发相关的基因在太空

表1 可能作为long-lived mRNA参与调控种子休眠的基因

Table 1 The genes regulated seed dormancy may be long-lived mRNA

基因名称	ID	表达特点	功能	分子机制	物种	参考文献
SDR3.1	LOC_Os03g-11550	开花后5天开始表达，15天达到峰值	反向调控种子休眠	与ABI5互作，并抑制*ABI5*的表达	水稻	Guo et al., 2024
SRO1	TraesCS4A-01G321300	在叶片、根和种子中表达	反向调控种子休眠	与TaVP1互作，抑制穗上萌发基因*TaPHS1*和*TaSdr*的表达，且影响TaVP1与TaABI5的互作	小麦	Liu et al., 2024
OsWSD1	LOC_Os03g-24460	在种子发育过程中，其表达量逐渐降低；在种子吸胀前36小时稳定表达	正向调控种子休眠	抑制GA的合成和α-淀粉酶的活性；突变后对ABA不敏感	水稻	Huang et al., 2023
AtAIL6	AT5G10510	在整个种子发育过程中维持高表达	正向调控种子休眠	FUS3直接调控*AtAIL6*的表达	拟南芥	Liu et al., 2023
WRKY36	AT1G69810	在种子中高表达	反向调控种子休眠	WRKY36与AFP2互作，复合体直接抑制*DOG1*的表达	拟南芥	Deng et al., 2023
AFP2	AT1G13740	在种子中高表达	反向调控种子休眠			
OsNAC2	LOC_Os04g-38720	在种子发育和萌发过程中高表达	正向调控种子休眠	直接抑制*OsABAox1*和*OsABAox2*的表达	水稻	Zhao et al., 2023
BG14	AT2G27500	在整个种子发育过程中维持高表达	正向调控种子休眠	降解胚细胞间的胼胝质，调控发育种子中ABA的积累	拟南芥	Wang et al., 2023
SPT	AT4G36930	–	存在正向和反向两种调控种子休眠机制	在Landsberg *erecta*与Columbia中种子休眠的遗传表现相反。直接抑制*RGA*和*MFT*的表达，直接调控*ABI5*的表达	拟南芥	Vaistij et al., 2013
OsDOR1	LOC_Os03g-20770	在种子胚中特异表达	正向调控种子休眠	OsDOR1与OsGID1互作，破坏Os-GID1-OsSLR1复合体的形成，影响GA信号转导	水稻	Kim et al., 2023
FIP1	AT5G58040	在干种子中表达	正向调控种子休眠	FIP1是一个加工pre-mRNA 3'端的蛋白，*Abi5*、*DOG1*和*PYL12*在突变体*fip1*中表达量下降	拟南芥	Li et al., 2023
OsNCED3	LOC_Os03g-44380	在种子胚发育过程中高表达	反向调控种子休眠	突变后，种子胚的ABA含量降低，GA含量升高；而超表达植株中，种子胚的ABA/GA比例关系到种子的休眠性	水稻	Chen et al., 2023
SFL1	AT1G27461	在种子发育过程中表达量逐渐升高	反向调控种子休眠	*OsSdr4*的同源基因，且功能相同	拟南芥	Zheng et al., 2022
AtMLP329	AT2G01530	在种子胚的胚根中表达	正向调控种子的初级休眠	DOF6直接调控*MLP329*的表达；突变后，GA合成酶基因*GA1*表达量升高，ABA合成酶基因*ZEP*表达量下降	拟南芥	Chong et al., 2022
TaETR1	TraesCS4A-02G274300	在所有组织中都有表达，在根中表达量最高	正向调控种子休眠	超表达植株的种子对乙烯不敏感	小麦	Wei et al., 2023
AtAAH	AT4G20070	在发育中的角果、根和干种子及萌发期的种子中高表达	反向调控种子休眠	外施硝酸钾可部分恢复*ataah*种子的高休眠性表型	拟南芥	Yazdan-panah et al., 2022
OsABA8ox1	LOC_Os02g-47470	在种子中表达	反向调控种子休眠	降低ABA含量	水稻	Fu et al., 2022
OsABA8ox2	LOC_Os08g-36860					
OsABA8ox3	LOC_Os09g-28390					

表1 (续)
Table 1 (continued)

基因名称	ID	表达特点	功能	分子机制	物种	参考文献
KCS12	Mtr.49305.1.-S1_at	在种皮中表达	正向调控种子休眠	控制种皮细胞中长链脂肪酸的合成	蒺藜苜蓿	Chai et al., 2021
FHY3	AT3G22170	随着角果的发育，表达量逐渐升高，在干种子中表达量达到峰值	反向调控种子休眠	白光促进FHY3蛋白积累；FHY3与phyB互作，直接调控*RVE2*和*RVE7*的表达，直接抑制SPT的表达	拟南芥	Liu et al., 2021
FT	AT1G65480		正向调控种子休眠	在种子中特异表达FT或者TFL1，GA含量降低	拟南芥	Chen et al., 2021
TFL1	AT5G03840					
OsbZIP09	LOC_Os01g-59760	ABA处理15分钟可诱导*OsbZIP09*的表达	反向调控种子休眠	利用RNA-seq和DAP-seq分析了52个OsbZIP09直接调控的基因，包括休眠相关基因*OsLOX2*和*LEA*家族	水稻	Zhu et al., 2021
TaAMY2	TraesCS7D-02G380400	开花后5天高表达，之后表达量逐渐降低	反向调控种子休眠	在超表达*TaAmy2*植株中，α-淀粉酶的活性升高，导致可溶性糖含量升高，新鲜种子没有休眠性，对ABA不敏感	小麦	Zhang et al., 2021
OsGLP2-1	LOC_Os02g-29000	在种子盾片中特异表达	正向调控种子休眠	受ABA诱导表达，GA抑制其表达；ABI5和GAMYB拮抗地调控*GLP2-1*的表达	水稻	Wang et al., 2020a
REF6	AT3G48430	在发育中的角果表达	反向调控种子休眠	在角果发育过程中，REF6结合*CYP-707A1*和*CYP707A3*，并负责这2个基因的H3K27me3修饰	拟南芥	Chen et al., 2020b
HSFA9	Medtr4g126-070	在种子中特异表达	反向调控种子休眠	调控ABA代谢和信号通路	蒺藜苜蓿	Zinsmeis-ter et al., 2020
SD6	LOC_Os06g-06900	在种子发育过程中表达量逐渐降低	反向调控种子休眠	与OsICE2互作，直接促进*ABAOX3*的表达	水稻	Xu et al., 2022
OsICE2	LOC_Os01g-70310	在种子发育过程中表达量逐渐升高	正向调控种子休眠	与SD6互作，直接抑制*ABAOX3*的表达	水稻	
OsDOG1L-3	LOC_Os01g-20030	在开花后15天的种子中表达量达到最大值，后逐渐下降	正向调控种子休眠	正反馈影响ABA合成基因的表达，增加种子中ABA含量	水稻	Wang et al., 2020b
OsbZIP75	LOC_Os09g-34060	在种子中高表达	正向调控种子休眠	OsbZIP75直接调控*OsDOG1L-3*	水稻	
OsbZIP78	LOC_Os10g-38820	在种子中高表达	正向调控种子休眠	同OsbZIP75	水稻	
OsBT1	LOC_Os02g-10800	在种子中特异表达，开花后21天达到峰值；在茎、叶、叶鞘和穗中几乎不表达	正向调控种子休眠	–	水稻	Song et al., 2020
AtPER1	AT1G48130	在种子中特异表达	正向调控种子的初级休眠	清除种子中的活性氧，抑制ABA降解和促进GA合成	拟南芥	Chen et al., 2020a
ETR1/*RDO3*	AT1G66340	–	正向调控种子休眠	ERF12与TPL相互作用，直接抑制*DOG1*的表达，而*ETR1*是*ERF12*的上游基因，参与调控*ERF12*的表达	拟南芥	Li et al., 2019
DOGL4	At4g18650	在新鲜种子和干种子中都有高表达；在开花后6天胚乳中、开花后8天胚中开始表达	反向调控种子休眠	在F_1代种子的胚乳细胞中，来自父本的基因甲基化*DOG4*的启动子，降低其表达；纯合突变体种子的休眠能力增强	拟南芥	Zhu et al., 2018
ROS1	AT2G36490	在干种子中表达	反向调控种子休眠	在F_1代种子的胚乳细胞中，ROS1调控父本的*DOGL4*启动子区的去甲基化，促进*DOG4*的表达		

表1 (续)
Table 1 (continued)

基因名称	ID	表达特点	功能	分子机制	物种	参考文献
GHNAC83	GlaUn0572-12	在叶片、花和根中高表达; 在球茎中低表达	正向调控种子休眠	GHNAC83直接抑制*GHPP2C1*的表达，影响ABA信号；直接结合*GHIPT*的启动子，负调控CK的合成	唐菖蒲	Wu et al., 2019
GHPP2C	GlaUn0788-52	在根、叶、球茎、雄蕊、雌蕊和花瓣中都有表达	反向调控种子休眠	PP2C家族蛋白, ABA信号通路蛋白, 识别ABA分子		
ASPG1	AT3G18490	在圆锥花序及萌发的种子中表达	反向调控种子休眠	可能通过影响GA信号通路，影响种子休眠及萌发	拟南芥	Shen et al., 2018
EBS	AT4G22140	在种子发育早期及吸胀前24小时的种子中表达	正向调控种子休眠	植物特有的一类转录调节蛋白，与SHL在调控种子休眠上功能冗余，并且与AGL67互作	拟南芥	Narro-Diego et al., 2017
GATA12	AT5G25830	在新鲜种子中表达量最高，在干种子中也有表达	正向调控种子休眠	RGL12与DOF6互作，直接调控*GATA12*的表达	拟南芥	Ravindran et al., 2017
KNOX4	Medtr5g011-070	在种皮细胞中显著表达	反向调控种子休眠	突变体种子的种皮角质层发生变化，直接调控角质层合成基因的表达	蒺藜苜蓿	Chai et al., 2016
OsGA20ox2	LOC_Os01g-66100	在发育中的种子和胚细胞中表达	反向调控种子休眠	影响发育中种子的GA合成基因表达	水稻	Ye et al., 2015
RDO5	AT4G11040	在种子中特异表达，在干种子中表达量最高	正向调控种子休眠	RDO5编码一个PP2C磷酸酶，通过抑制RNA结合蛋白APUM9的表达调控种子休眠	拟南芥	Xiang et al., 2014
APUM9	AT1G35730	在开花后16天的种子中高表达，之后表达量逐渐降低	反向调控种子休眠			
WRKY41	AT4g11070	在成熟种子、种子胚、叶脉和下胚轴中表达	正向调控种子休眠	WRKY14直接调控*ABI3*的表达，但与ABA通路无关联	拟南芥	Ding et al., 2014
HON	AT1g07430	在开花后9天的种子中表达，开花后12天表达量达到峰值	反向调控种子休眠	是PP2C家族蛋白，在ABA存在时，与PYR1/RCAR11互作；抑制ABA信号而激活GA信号	拟南芥	Kim et al., 2013
ABI4	AT2G40220	在种子中高表达	反向调控种子休眠	ABI4直接抑制*CYP707A1*和*CYO-707A2*的表达；突变体中ABA含量降低, GA含量升高, *abi4*突变体可以恢复*ga1-t*不发芽的表型	拟南芥	Shu et al., 2013
SNL1 *SNL2*	AT3G01320 AT5G15020	随着种子成熟，表达量逐渐升高	正向调控种子休眠	SNL1与SNL2形成组蛋白去乙酰化复合体，SNL1与组蛋白去乙酰化酶HDA19互作，调控乙烯合成基因及ABA合成、降解基因的乙酰化水平	拟南芥	Wang et al., 2013
AtDOF6	AT3G45610	在新鲜种子中表达，在后熟过程和吸胀时期逐渐降低	正向调控种子休眠	与TCP14互作，TCP14反向调控种子休眠	拟南芥	Rueda-Romero et al., 2012
AtET2	AT5G56780	在成熟的种子胚中表达	正向调控种子休眠	FUS3直接抑制*AtET2*的表达	拟南芥	Ivanov et al., 2012
FUS3	AT3G26790	在种子胚发育过程中持续表达，在成熟种子中高表达	反向调控种子休眠			
KYP/*SUVH4*	AT5G13960	在吸胀种子中表达量最高	反向调控种子休眠	突变体中，*DOG1*和*ABI3*的表达量升高	拟南芥	Zheng et al., 2012

表1 (续)
Table 1 (continued)

基因名称	ID	表达特点	功能	分子机制	物种	参考文献
AMP1	AT3G54720	在种子发育过程中表达，在开花后8天的种子中表达量最高	反向调控种子休眠	在不同背景的拟南芥中，突变后的种子休眠表型不一致，初步鉴定突变后影响ABA含量	拟南芥	Griffiths et al., 2011
TaMFT	AB456688	在不成熟胚的盾片和胚芽鞘中表达；在种子发育过程中保持高表达	正向调控种子休眠	*AtMFT*的同源基因	小麦	Nakamura et al., 2011
NCED6	AT3G24220	在发育中的种子胚乳中表达	正向调控种子休眠	在种子中诱导表达*NCED6*后，种子中的ABA含量升高，萌发率下降，新鲜种子的休眠率升高	拟南芥	Martínez-Andújar et al., 2011
DOG1	AT5G45830	仅在种子中表达，且在开花后9天表达量最高	正向调控种子休眠	–	拟南芥	Bentsink et al., 2006

–: 未知 –: Unknown

环境贮藏种子中的表达量比地面种子降低了2倍(Sugimoto et al., 2016)。

相同植物不同品种种子的long-lived mRNA种类有所不同，使得不同品种的种子寿命存在很大差异。Niñoles等(2022)比较了具有长寿命种子的拟南芥品种Da-1和短寿命种子的品种Ors-1的干种子转录组数据，发现热激响应转录因子HSF1A和HSF1B在Da-1中的表达量是Ors-1中的50余倍，并且双突变体*hsf1a*/*hsf1b*经过人工老化21天后，发芽率显著低于野生型，说明HSF1A和HSF1B作为long-lived mRNA可能正向调控种子寿命(Niñoles et al., 2022)。水稻种子长寿命品种NX32的long-lived mRNA包含脂质贮藏(lipid storage)、种子油体合成(seed oil body biogenesis)、负调控种子休眠(negative regulation of the seed dormancy process)、解除种子休眠(release of seeds from dormancy)和正调控种子萌发(positive regulation of seed germination)等生物过程相关基因的转录，而种子低寿命品种YZX的long-lived mRNA主要包含种子成熟(seed maturation)、ABA信号响应(cellular response to abscisic acid stimulus)、细胞水分平衡(cellular water homeostasis)和响应脱水干燥(response to desiccation)等生物过程相关基因的转录(Wang et al., 2022)。

E3泛素连接酶AtATL5 (ARABIDOPSIS TOXICOS EN LEVADURA 5)在拟南芥种胚中高表达，且受加速老化诱导表达。*atatl5*的种子寿命变短，而与其互作的RNA结合蛋白ABT1 (ACTIVATOR OF BASAL TRANSCRIPTION 1)突变后，种子寿命变长，显示AtATL5通过泛素化ABT1蛋白并使其降解来调控种子寿命(He et al., 2023)。葡聚糖酶BG14 (GLICOSYLPHOSPHATIDYLINOSITOL-ANCHORED B-1,3-GLUCANASE)参与降解种子胚中的胼胝质，正常收获的突变体*bg14*种子的发芽率与野生型无显著差异，但经加速老化之后，*bg14*在吸胀3天时停止萌发，而野生型的种子萌发率达84.7% (Wang et al., 2023)。DNA/RNA结合蛋白家族WHY (WHLRLYBG-14)的WHY1和WHY3功能冗余地调控种子寿命，双突变体材料的种子发芽率与野生型无显著差异，但在35°C、83%的相对湿度条件下加速老化处理7天后，种子萌发率显著低于野生型(Taylor et al., 2023)。MSR (METHIONINE SULFOXIDE REDUCTASE)蛋白参与调控甲硫氨酸的去氧化修饰，种子中特异表达*OsMSR5*对于维持种子寿命非常重要。经过人工加速老化处理，*MSR5*的RNAi种子发芽率仅有8%，显著低于野生型，而超表达种子发芽率达65%，显著高于野生型(Hazra et al., 2022)。*AtATL5*、*AtBG14*和*OsMSR5*在种子发育过程中表达，并在种子成熟期达到峰值，且其mRNA均定位于种胚中(Hazra et al., 2022; He et al., 2023; Wang et al., 2023)，推测这些基因可能作为long-lived mRNA参与调控种子寿命。图2显示在种子后熟和长时间贮藏过程中long-lived mRNA的变化。

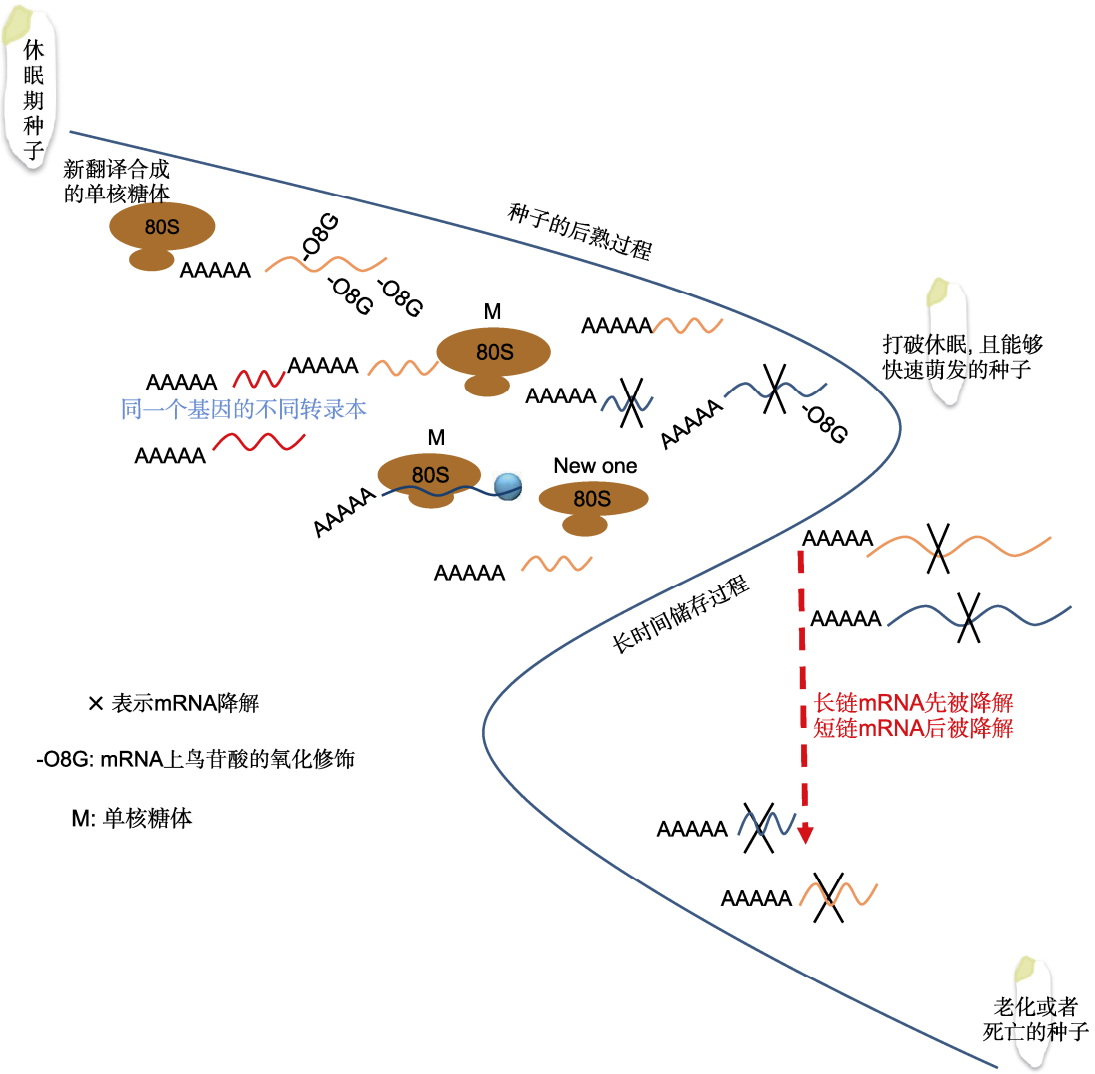

图2 长寿命mRNA在种子后熟和长时间贮藏阶段的变化

Figure 2 The changes of long-lived mRNA during seed after-ripening and long-term storage stage

4 研究展望

Long-lived mRNA赋予每颗种子独有的特点，且母株受到特异环境因素引起特异基因的转录积累也会以long-lived mRNA的形式保留在种子中，并在后代种子休眠和发芽等特性中表现出来(Cadman et al., 2006; Iwasaki et al., 2019; Suriyasak et al., 2020)。种子在发育过程中遭遇低温后，*DOG1*在种子中的表达量显著升高，增强了种子的休眠能力(Deng et al., 2023)。粳稻和籼稻种子的不同休眠性和萌发率，以及拟南芥不同亚型种子之间在休眠和寿命上的差异，均与种子体内保存的long-lived mRNA有一定关系。通过对低GI (glycemic index)和高GI水稻品种种子进行转录组分析,发现两者的淀粉代谢存在很大的差异，尤其种子中储存的long-lived mRNA的种类对于淀粉的可消化性至关重要(De Guzman et al., 2017)。灌浆期高温会使ABA相关基因启动子区域的甲基化修饰减少，造成*OsNCED*s基因在种子中的表达量升高，而α-淀粉酶基因启动子区域的甲基化修饰增多，表达量降低，最终导致收获后的种子萌发率下降(Huh et al., 2007; Suriyasak et al., 2020)。当母株受到冷胁迫，使得负调控休眠的基因*ALN* (*ALLANTOINASE*)启动子区域的甲基化修饰增多，进一步加深了种子休眠(Iwasaki et al., 2019)。

综上, long-lived mRNA包含与种子休眠、萌发和

寿命特性相关的转录组, 推测种子在后熟阶段, 与休眠相关的转录组缓慢降解或维持低表达(Nakabayashi et al., 2005), 休眠打破后, 种子呈现出高的活力和萌发率。在贮藏过程中, 与萌发及寿命相关的mRNA逐渐降解, 致使种子活力下降、寿命缩短。目前, 有关种子中的long-lived mRNA尚存在很多科学问题需要进一步探究。例如, 萌发过程中long-lived mRNA的翻译非常关键, 但哪些mRNA被优先翻译及其筛选机制尚不清楚, 优先参与翻译的mRNA是否存在表观修饰特征? 种子发育成熟过程中选择mRNA作为long-lived mRNA的信号或者调控机制是什么? 是否存在关键的转录调控因子? long-lived mRNA在种子贮藏过程中的降解机制是什么? 目前已报道与种子萌发速率、休眠及寿命相关基因的mRNA是否属于long-lived mRNA? long-lived mRNA随着储存时间的延长有降解趋势, 导致建库测序得到的RNA完整性不高, 可能会影响long-lived mRNA种类和数量的判断。可否通过Act D处理后的种子萌发表型筛选调控long-lived mRNA的关键基因?

基于此, 我们尝试利用Act D筛选可能有功能的long-lived mRNA。采用人工老化(温度45°C、相对湿度90%)处理日本晴种子3天后, 发现其萌发速率与未老化种子的萌发速率一致(附图1A, B); 但在Act D溶液中发芽时, 老化后种子的萌发率在吸胀3天时低于未老化种子(附图1A, B), 表明Act D处理将long-lived mRNA的变化在萌发速率上表现出来。将Act D处理下未萌发的老化种子转移至水中, 种子能重新萌发并长成正常幼苗(附图1C, D), 说明该方法有望将筛选到的种质保留下来。因此, 我们推测如果利用Act D筛选水稻或拟南芥的突变体库, 筛选出不能萌发的种子, 该种子中可能包含关键long-lived mRNA (可能是同时调控多个基因转录的关键转录因子)的突变, 从而导致没有足够的long-lived mRNA保证种子萌发, 再将不萌发的种子转移至正常条件下培养, 就可能得到调控种子萌发的关键long-lived mRNA的突变材料。

作者贡献声明

朱晓博: 构思并撰写文章; 董张、祝梦瑾和胡晋: 论文修改; 陈敏和林程: 修改图片; 关亚静: 指导撰写并修改文章。

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Indispensable Material for Germination: Long-lived mRNAs of Plant Seed

Xiaobo Zhu[1, 2], Zhang Dong[1, 2], Mengjin Zhu[1, 2], Jin Hu[1, 2], Cheng Lin[3], Min Chen[2], Yajing Guan[1, 2*]

[1]Hainan Institute, Zhejiang University, Sanya 572000, China; [2]The Advanced Seed Institute, College of Agriculture and Biotechnology, Zhejiang University, Hangzhou 310058, China; [3]Suzhou Polytechnic Institute of Agriculture, Suzhou 215008, China

Abstract Higher plants usually start from seed germination and re-form seeds after vegetative growth and reproductive development, thus completing the life cycle. Carbohydrates, lipids, proteins, mRNA and other macromolecular substances accumulated in seeds are crucial to maintain the germination potential of seeds, some of mRNA can be preserved for a long time without degradation, known as long-lived mRNA. In rice, long-lived mRNA associated with germination began to be transcribed and accumulated 10 to 20 days after flowering, and some long-lived mRNA associated with dormancy and stress response were transcribed and preserved in cells from 20 days after flowering to seed maturity. There are many kinds of long-lived mRNA, mainly including some protein synthesis mRNA, energy metabolism mRNA, cytoskeleton mRNA and some stress response related mRNA, such as small heat shock protein, LEA (late embryogenesis abundant) family proteins. Transcriptomic analysis found that the promoter regions of many genes contain ABA- or GA-associated *cis*-acting elements, and there are about 500 differentially expressed long-lived mRNAs in the *Arabidopsis atabi5* (*ABA-insensitive 5*) mutant seeds that differ from the wild type, suggesting that abscisic acid (ABA) and gibberellin (GA) are the key hormones that influence the type of long-lived mRNA. Long-lived mRNAs are usually cross-linked with a single ribosome, RNA binding protein, which exists in cells in the form of P-bodies (PBs) to protect the mRNA from degradation. However, long-lived mRNAs associated with seed dormancy are gradually degraded during seed post-ripening, and the oxidative modification of some specific long-lived mRNAs is also a biological phenomenon to break seed dormancy. During the long-term storage of seeds, the random degradation of long-lived mRNA is directly related to the life and vitality of seeds, and the retained mRNA is translated into protein to help the rapid germination of seeds in the early stage of imbibition. In this paper, the characteristics and functions of long-lived mRNA are reviewed, and some future scientific issues are discussed to provide a reference for further understanding of the molecular mechanisms of seed dormancy, germination and longevity.

Key words long-lived mRNAs, seed dormancy, seed germination, seed storage

Zhu XB, Dong Z, Zhu MJ, Hu J, Lin C, Chen M, Guan YJ (2024). Indispensable material for germination: long-lived mRNAs of plant seed. *Chin Bull Bot* **59**, 355–372.

* Author for correspondence. E-mail: vcguan@zju.edu.cn

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附图1 Act D处理下水稻日本晴种子萌发情况

Appendix figure1 The seed germination of rice *Nipponbare* under Act D treatment

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通讯作者/团队简介

关亚静，博士，教授、博导，浙江大学“求是”青年学者，农业与生物技术学院现代种业研究所种子科学与工程中心主任，浙江大学海南研究院种子工程与检验检疫团队方向负责人，中国作物学会种子专业委员会副会长，中国植物学会种子与技术专业委员会副主任。主要从事种子发育成熟和活力分子机理、多功能种子丸化及种子增值技术研究。