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·特邀综述·

PPR蛋白参与细胞器RNA C→U编辑机制研究进展

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摘要 植物体中线粒体和叶绿体是半自主细胞器, 具有自己的基因组。RNA编辑对于细胞器基因的正确表达至关重要, 最常见的RNA编辑是C→U。RNA C→U编辑需要多种编辑因子参与, 其中PPR蛋白中的PPR基序阵列特异性地靶向编辑位点, PPR-DYW蛋白DYW结构域是催化C→U编辑的脱氨酶。该文综述了PPR蛋白参与RNA C→U编辑机制的最新研究进展, 并讨论了人工合成PPR编辑因子的潜在应用价值。

关键词 PPR蛋白, RNA C→U编辑, 线粒体, 叶绿体

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植物的线粒体和叶绿体不仅分别是呼吸作用和光合作用的场所, 还是多种物质代谢的场所, 因此其对植物生长各阶段都至关重要。植物的线粒体和叶绿体分别由α-棒状杆菌和蓝细菌内共生演化而来。在演化过程中, 线粒体和叶绿体中大部分基因已经转移到细胞核, 只有少部分基因仍位于这2个细胞器的基因组中, 因此线粒体和叶绿体为半自主细胞器。线粒体和叶绿体基因组中的基因编码线粒体和叶绿体关键功能蛋白, 线粒体基因主要编码氧化磷酸化呼吸途径中复合物亚基蛋白、核糖体亚基蛋白、核糖体RNA以及一些tRNA; 叶绿体基因编码光合作用复合物亚基蛋白、转录起始因子、RNA聚合酶亚基、核糖体亚基蛋白、核糖体RNA以及tRNA。线粒体和叶绿体基因转录后加工和翻译过程复杂, 包括RNA编辑、内含子剪接、5′和3′末端的成熟、RNA稳定以及蛋白翻译。这些过程需要多种不同核基因编码蛋白的参与, 如参与RNA编辑的PPR (Pentatricopeptide Repeat)蛋白、MORF (Multiple Organelle RNA editing factor)蛋白、ORRM (Organelle RNA Recognition Motif-containing)蛋白以及OZ1 (Sandoval et al., 2019; Small et al., 2020), 参与内含子剪接的PPR蛋白、CRM结构域蛋白、PORR蛋白、RNA解旋酶、mTERF以及成熟酶(Maturase) (Brown et al., 2014)。

RNA C→U编辑是线粒体和叶绿体基因表达的关键过程, RNA编辑通常恢复进化保守的氨基酸、产生起始或终止密码子、调控内含子剪接和促进tRNA成熟等(Kadowaki et al., 1995; Fey et al., 2002; Xu et al., 2020; Wang et al., 2021)。RNA编辑缺陷会严重损害植物的生长发育, 导致植物呈现矮小、黄化或者白化等表型(马艳莉等, 2011; Bentolila et al., 2012; Liu et al., 2021); 抑制种子发育, 导致种子呈现小籽粒(small kernel)、籽粒发育缺陷(defective kernel)、空果皮(empty pericarp)以及胚缺失(embryo defective)等表型(Liu et al., 2013; Li et al., 2014; Yang et al., 2022b) (附表1)。RNA编辑广泛存在于植物线粒体和叶绿体中, 高等植物线粒体中一般有300–600个编辑位点, 而叶绿体中有20–30个编辑位点(Notsu et al., 2002; Mower and Palmer, 2006; 邓李坤等, 2012; Bentolila et al., 2013; Wang et al., 2019; Liu et al., 2021)。编辑位点的数量根据物种不同存在显著差异, 低等植物小立碗藓(*Physcomitrella patens*)线粒体中有11个编辑位点(Rüdinger et al., 2009) , 叶绿体基因组中仅有1个编辑位点(Miyata and Sugita, 2004); 而在睡莲属植物线粒体和叶绿体基因组中分

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别有865和98个RNA C→U编辑位点(He et al., 2021)。此外，地钱纲是苔藓植物中起源古老的一个分支，是复杂复叶状苔类植物，长期以来被认为是陆生植物中唯一缺乏RNA编辑的类群，但是最新研究发现以洞穴为主要生境的地钱纲植物光苔(*Cyathodium cavernarum*)的线粒体和叶绿体中分别有172和129个RNA C→U编辑位点(Shen et al., 2024)。

截至目前，在低等植物小立碗藓中只发现PPR-DYW一种RNA编辑因子，且体外酶活实验表明，PpPPR65和PpPPR56能有效催化*ccmF*$_C$-103和*nad4*-272以及*nad3*-230位点的编辑(Oldenkott et al., 2019; Hayes and Santibanez, 2020)。因此，小立碗藓中RNA编辑可能仅由PPR-DYW蛋白完成。而高等植物中RNA编辑由RNA编辑复合体(editosomes)完成，包含多种RNA编辑因子，如PPR蛋白、MORF蛋白、ORRM蛋白、OZ1和ISE2 (Sandoval et al., 2019; Small et al., 2020)。PPR蛋白是其中非常关键的一种，其PPR基序决定了编辑位点的特异性以及PPR-DYW蛋白DYW结构域催化C→U的脱氨反应。

1 PPR蛋白的分类和结构

PPR蛋白是一个大的蛋白家族，广泛分布在植物中。水稻(*Oryza sativa*)、玉米(*Zea mays*)、拟南芥(*Arabidopsis thaliana*)和小立碗藓基因组中分别有477、521、450和103个PPR蛋白(O'toole et al., 2008; Wei and Han, 2016)。PPR蛋白由2–27个含大约35个低保守氨基酸残基的PPR基序串联重复组成(Small and Peeters, 2000)。根据组成PPR基序的不同，PPR蛋白分为P类和PLS类。P类PPR蛋白完全由35个氨基酸残基组成的P基序串联重复而成，一些P类PPR蛋白的C端具有特殊的结构域，如CC (Coiled-coil)、WQQ repeats和SMR (Small MutS related)。PLS类PPR蛋白由3种PPR基序串联重复而成，包括P基序(35个氨基酸残基)、L基序(35–36个氨基酸残基)以及S基序(31–32个氨基酸残基)。Cheng等(2016)根据组成PPR基序氨基酸的保守性将P、L和S基序分别细分为P1和P2基序、L1和L2基序以及S1、S2和SS基序。PLS类PPR蛋白的3个亚型蛋白PPR-E、PPR-E+和PPR-DYW在其C端分别具有E、E+和DYW结构域(Lurin et al., 2004; Cheng et al., 2016)。PPR蛋白特异地识别和结合单链RNA，即每个PPR基序第一位和最后一位氨基酸组合后共同识别1个碱基，进而特异地识别和结合RNA序列(Barkan et al., 2012; Yin et al., 2013)。

2 PPR-DYW蛋白参与RNA编辑的机制

PPR蛋白是植物RNA编辑过程的核心组分。截至目前，已报道了多个PPR蛋白参与RNA C→U编辑，其中绝大部分是PLS类PPR蛋白，包括PPR-DYW、PPR-E和PPR-E+蛋白(附表1)。PPR-DYW蛋白的PPR基序特异地识别和结合编辑位点上游序列，其DYW结构域催化编辑位点的脱氨反应。通常PPR-DYW蛋白识别的RNA序列位于编辑位点上游–4的位置(Barkan and Small, 2014)，进而确保DYW结构域准确地催化编辑位点进行脱氨反应。多项研究表明，PPR-DYW蛋白的PPR基序特异地识别和结合编辑位点上游的序列(Okuda et al., 2006)。RNA C→U编辑是胞嘧啶脱氨形成尿嘧啶的过程(Blanc et al., 1995; Yu and Schuster, 1995)。据报道，催化该过程的脱氨酶都具有CDAs-like的锌离子结合保守氨基酸(HxE(x)nCxxC)，位于PPR-DYW蛋白C端的DYW结构域具有这些保守的氨基酸。然而，DYW结构域是否具有脱氨酶活性尚未得到实验证实。Oldenkott等(2019)在大肠杆菌(*Escherichia coli*)中异源表达小立碗藓PPR-DYW蛋白PpPPR65和PpPPR56，并分别同时表达这2个蛋白负责编辑的位点*ccmF*$_C$-103和*nad4*-272以及*nad3*-230，发现当2个蛋白在细菌中表达时，对应的位点被有效编辑，而表达去掉DYW结构域或者突变DYW结构域上关键氨基酸的PpPPR65和PpPPR56蛋白均导致对应编辑位点完全缺失或者编辑效率严重降低，特别是当锌离子结合的保守氨基酸突变时，RNA编辑完全缺失。因此，该研究证实位于PPR-DYW蛋白C端的DYW结构域是催化RNA C→U编辑的脱氨酶。随后，Hayes和Santibanez (2020)在体外证实了DYW催化RNA C→U编辑的脱氨酶活性。经体外纯化PpPPR65蛋白，然后与*ccmF*$_C$ RNA孵育，发现*ccmF*$_C$-103可被有效编辑。进一步研究表明，PpPPR65蛋白单体呈现高催化活力，而多聚体导致催化活力降低，并且DYW的催化活力依赖锌离子和ATP。Takenaka等(2021)解析了拟南芥PPR-DYW蛋

白OTP86的DYW结构域晶体结构，发现DYW与细菌脱氨酶EcCD具有类似的蛋白结构，但是也存在不同。相似之处是脱氨酶的核心区域由5个β-折叠和2个α-螺旋组成，其中前2个β-折叠位于PG-box结构域。DYW与EcCD不同之处在于DYW的β2-折叠和β5-折叠之间插入了2个β-折叠(β3，β4)和1个α-螺旋(α1)，该插入被称为Gating domain；另一个显著不同是DYW脱氨酶具有沉默和激活2种状态。不与底物结合时，DYW脱氨酶表现沉默状态；当与底物结合时，Gating domain中的2个β-折叠和1个α-螺旋发生构象改变，使酶的活性中心呈现高效催化活性的构象，进而催化RNA C→U的脱氨反应。此外，DYW脱氨酶的活性与2个锌离子有关，一个位于脱氨酶活性中心，另一个与C端3个高度保守的氨基酸残基DYW中的Y结合，研究表明这些氨基酸突变严重抑制DYW脱氨酶活性(Boussardon et al., 2014; Hayes and Santibanez, 2020; Takenaka et al., 2021)。DYW1是拟南芥中结构特殊的DYW蛋白，该蛋白不具有PPR结构域，仅由N端信号肽和缺少部分N端氨基酸的DYW结构域组成。Toma-Fukai等(2023)解析了该蛋白的晶体结构，与OTP86的DYW结构域不同的是，DYW1中的1个α-螺旋取代了OTP86的DYW结构域Gating domain中的2个β-折叠。

通常结构典型的PPR-DYW蛋白只负责少数几个位点的编辑。例如，玉米中PPR2263只负责*nad5*-1550和*cob*-908位点的编辑(Sosso et al., 2012)；拟南芥中MEF7负责*ccb206*-28、*cob*-325、*nad2*-1433和*nad4L*-41位点的编辑(Zehrmann et al., 2012)。然而在玉米中一些结构典型的PPR-DYW蛋白，除参与识别位点的编辑外，其功能缺失还导致其它多个位点的编辑缺陷。玉米中EMP5是定位于线粒体的PPR-DYW蛋白，*EMP5*基因突变除导致*rpl16*-458位点的编辑完全缺失外，还造成其它9个位点的编辑效率显著降低(Liu et al., 2013)。EMP21也是一个结构典型的PPR-DYW蛋白，预测该蛋白可识别和结合*nad7*-77、*atp1*-1291和*atp8*-437位点上游的RNA序列，EMP21功能缺失导致3个位点的编辑完全缺失。此外，*Emp21*突变导致其它78个位点的编辑缺失或效率严重降低(Wang et al., 2019)。*emp5-4*是*Emp5*基因的一个弱突变体，该突变导致*Emp5-4*编码一个缺失DYW结构域的结构类似于PPR-E+的蛋白，该突变体*rpl16*-458位点的编辑效率下降但并非完全缺失，而*emp21*突变体中该位点的编辑效率也显著降低。遗传分析显示，*emp5-4*/*emp21-1*双突变体中该位点的编辑效率相比单突变体显著降低，且这2个蛋白都与MORF8互作，暗示EMP5-4可能间接招募EMP21，进而EMP21的DYW结构域部分催化*rpl16*-458位点的编辑(Wang et al., 2019)。除这2个蛋白外，PPR27、ZmPPR26和DEK48功能缺失也导致多个位点的编辑缺失或者效率显著降低(Liu et al., 2020, 2021; Yang et al., 2022a)。

高等植物除具有典型的PPR-DYW蛋白外，还具有少数几个非典型的PPR-DYW蛋白，这类蛋白只具有少数几个不太保守的PPR基序和C端的DYW结构域，不具有典型的E1和E2结构。这类蛋白在拟南芥中有5个，分别是DYW2、DYW3、DYW4、MEF8和MEF8S，由于未发现*DYW3*的EST (expressed sequence tag)，推测该基因是一个假基因(Yang et al., 2022b)；玉米中有3个，分别是PCW1、ZmDYW2A和ZmDYW2B；水稻中只有2个，即OsDYW2和OsPCW1 (Wang et al., 2023)。其中，拟南芥中的DYW2、MEF8和MEF8S及玉米中的PCW1、ZmDYW2A和ZmDYW2B功能已被解析。这些基因突变均导致线粒体和叶绿体中大量位点的编辑缺陷，最终导致胚胎致死。DYW2、MEF8/8S、PCW1和ZmDYW2A/2B分别参与392、151、102和108个位点的编辑(Diaz et al., 2017; Guillaumot et al., 2017; Yang et al., 2022b; Wang et al., 2023, 2024)。

3 PPR-E/E+蛋白参与RNA编辑的机制

高等植物中超过一半的PLS类蛋白是PPR-E和PPR-E+蛋白。拟南芥中有200个PLS类PPR蛋白，其中包含47个PPR-E和60个PPR-E+蛋白(Lurin et al., 2004)；玉米中有238个PLS类PPR蛋白，包含76个PPR-E和49个PPR-E+蛋白(Wei and Han, 2016)。几乎所有已报道的PPR-E/E+蛋白都参与RNA C→U编辑。与PPR-DYW蛋白类似，PPR-E/E+蛋白的PPR基序特异地识别和结合编辑位点上游的序列，进而准确识别编辑位点。然而，PPR-E/E+蛋白不具有C端的DYW脱氨酶，需要招募其它脱氨酶完成RNA编辑。CRR4是一个特殊的PPR-E+蛋白，由11个PPR基序、E结构域和部分E+结构域组成，可特异地识别拟南芥

叶绿体*ndhD*-1位点，功能缺失导致该位点的编辑完全缺失(Kotera et al., 2005; Okuda et al., 2006)。拟南芥*dyw1*突变体该位点的编辑完全缺失，研究发现CRR4与DYW1互作，且CRR4-DYW1的融合蛋白可以回补*crr4-3*/*dyw1-1*双突变体中*ndhD*-1的RNA编辑(Boussardon et al., 2012)。这说明PPR-E+蛋白可以招募反式DYW脱氨酶，进而完成RNA编辑。2017年，2个独立的课题组分别以线粒体定位的PPR-E+蛋白SLO2和叶绿体定位的PPR-E+蛋白CLB19为诱饵蛋白进行IP-MS实验，富集到非典型PPR-DYW蛋白DYW2和结构特殊的P型PPR蛋白NUWA，一系列的遗传和分子生物学实验表明，PPR-E+蛋白SLO2以及CLB19在NUWA的辅助下招募DYW2，进而进行RNA编辑(Andrés-Colás et al., 2017; Guillaumot et al., 2017)。最新研究表明，玉米中ZmDYW2A/2B是PPR-E+蛋白招募的脱氨酶，ZmNUWA辅助PPR-E+蛋白对ZmDYW2A/2B的招募(Wang et al., 2024)。与DYW2蛋白不同的是，玉米中PPR-E+蛋白招募ZmDYW2A/2B可能主要通过ZmNUWA辅助，而拟南芥中PPR-E+蛋白招募脱氨酶除需要NUWA以外，可能还需要其它P类PPR蛋白(Wang et al., 2024)。氨基酸序列比对分析发现，DYW2和ZmDYW2A/2B的DYW结构域不具有完整的脱氨酶结构，这2个蛋白丢失了PG-box (DYW脱氨酶中的β1-和β2-折叠)以及Gating domain的N端(Takenaka et al., 2021)。通过分析5 107个PPR-E+蛋白的E+结构域，发现E+结构域具有PG-box以及Gating domain的N端(Wang et al., 2023)。因此，DYW2和ZmDYW2A/2B的DYW结构域中丢失的PG-box和Gating domain的N端被PPR-E+蛋白中E+结构域弥补。PCW1和MEF8/8S具有完整的DYW结构域，遗传和分子生物学证据证实PCW1和MEF8/8S分别是玉米和拟南芥中PPR-E蛋白招募的脱氨酶(Yang et al., 2022b; Wang et al., 2023)。

4 P类PPR蛋白参与RNA编辑的机制

P类PPR蛋白是PPR蛋白中一个大的亚类，主要参与内含子剪接、前体RNA的成熟和翻译起始等。该类蛋白只有少数几个参与RNA C→U的编辑，分别是拟南芥中的NUWA、GRP23和PPME及玉米中的bCCP1和ZmNUWA。其中NUWA、GRP23、bCCP1和ZmNUWA除具有PPR基序以外还具有其它特殊结构域。NUWA、ZmNUWA和bCCP1均由N端bZIP (basic region/nuclear localization signal leucine zipper motif)结构域、中间的PPR基序和C端CC (Coiled- coil)结构域组成(Andrés-Colás et al., 2017; Guillaumot et al., 2017; Wang et al., 2023, 2024)。GRP23包含N端bZIP结构域、中间的PPR基序、截短的CC结构域以及C端WQQ结构域(Ding et al., 2006)。这4个结构特殊的P类PPR蛋白都参与植物细胞器中大量位点的RNA编辑。拟南芥NUWA和GRP23分别调节226和358个位点的编辑；玉米bCCP1和ZmNUWA分别参与66和107个位点的编辑。NUWA、GRP23、bCCP1和ZmNUWA参与RNA编辑并非通过识别和结合RNA，而是通过辅助和促进PPR-E或PPR-E+招募非典型PPR-DYW蛋白参与RNA编辑(Andrés-Colás et al., 2017; Guillaumot et al., 2017; Yang et al., 2022b; Wang et al., 2023, 2024)。Zang等(2024)发现，玉米中ZmGRP23可以辅助PPR-E蛋白DEK56对PCW1的招募。

5 PPR蛋白参与RNA编辑的工作模型

我们根据文献总结出PPR蛋白参与RNA编辑的几种工作模型。(1) 线粒体和叶绿体中PPR-DYW蛋白特异地识别编辑位点上游的序列，C端DYW催化RNA C→U编辑，该过程可能需要其它编辑因子参与，如MORF蛋白(图1A)。研究显示，MORF蛋白可促进PPR蛋白对底物的结合(Yan et al., 2017)。(2) PPR-E+蛋白结合到编辑位点上游的RNA，在P型PPR蛋白(NUWA和ZmNUWA)和MORF蛋白的辅助下招募非典型PPR-DYW蛋白(DYW2和ZmDYW2A/2B)，完成特定位点的RNA编辑(图1B)。在叶绿体中可能还需要ORRM1以及OZ1的辅助(Wang et al., 2024)。(3) PPR-E蛋白结合到编辑位点上游的RNA，在P型PPR蛋白(bCCP1、ZmGRP23和GRP23)和MORF蛋白的辅助下招募非典型PPR-DYW蛋白(PCW1或MEF8/8S)，完成特定位点的RNA编辑(图1C)。

6 PPR编辑因子在植物生长发育中的功能

PPR编辑因子突变严重抑制植物的生长发育，使植

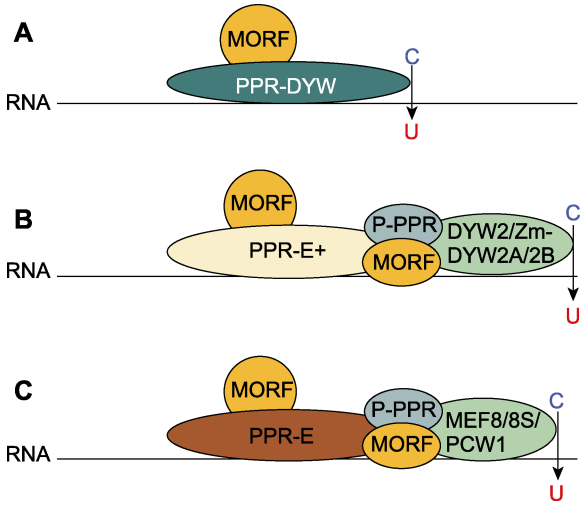

图1 PPR蛋白参与RNA C→U编辑的工作模型
(A) PPR-DYW; **(B)** PPR-E+; **(C)** PPR-E

Figure 1 Models of PPR proteins involved in RNA C→U editing
(A) PPR-DYW; **(B)** PPR-E+; **(C)** PPR-E

物呈现矮小、白化或黄化等表型；抑制胚发生和胚乳发育，导致小籽粒、籽粒发育缺陷、空果皮和胚缺失等；抑制花粉发育，造成雄性不育；导致逆境响应改变(附表1)。定位于线粒体的PPR编辑因子功能缺失抑制线粒体中氧化磷酸化呼吸途径中复合物的组装和活性或蛋白质翻译，破坏线粒体的结构和功能，抑制植物生长发育和种子发育，导致育性降低或不育(附表1)。定位于叶绿体的PPR编辑因子功能缺失常破坏叶绿体光合作用复合物的组装和活性及抑制蛋白质翻译等，导致植物生长发育迟缓、胚致死，呈现白化或黄化等表型(附表1)。玉米中叶绿体定位的PPR-DYW蛋白qKW9功能缺失，导致叶绿体*ndhB*-246位点的编辑缺失，引起光合效率降低，突变体呈现玉米穗变小，产量降低(Huang et al., 2020)。然而，多项研究显示，拟南芥PPR编辑因子功能缺失突变体在正常条件下与野生型一致，未表现出任何生长发育缺陷(附表1)。其中一些可能在正常条件下不具有生长发育表型的突变体，在胁迫条件下表现出对某种胁迫敏感或抗性增强的表型。例如, AHG11功能缺失在正常条件下与野生型一致，但是*ahg11*突变体表现出对盐、脱落酸以及茉莉酸等胁迫敏感的表型(Murayama et al., 2012)。*slg1*突变体生长发育较野生型略迟缓，但表现出抗旱性显著增强(Yuan and Liu, 2012)。因此，这些正常条件下对植物生长发育无影响或影响较小的突变体为筛选抗性植物提供了可能的候选材料。

7 人工合成PPR编辑因子的潜在应用价值

PPR蛋白具有特异识别和结合RNA及催化RNA编辑的特性。人工合成PPR蛋白可在不改变基因DNA序列的情况下，改变RNA的遗传信息(McDowell et al., 2022)。因此，人工合成PPR可作为工具对RNA中特定位点进行编辑，进而定向改造编码的蛋白。目前，科学家已进行了一些尝试并取得了较好的效果。Royan等(2021)人工合成PPR蛋白可在体外、大肠杆菌以及拟南芥叶绿体中对其识别的位点进行有效编辑；Bernath-Levin等(2022)人工合成S型PPR蛋白，在大肠杆菌中表达后可对特定位点进行RNA C→U编辑；Lesch等(2022)在人类细胞系中表达小立碗藓PPR-DYW蛋白PpPPR56和PpPPR65，发现PPR蛋白可有效地对RNA进行C→U编辑，当特异地改变PPR基序中2个关键碱基识别氨基酸时，可以改变PPR蛋白识别和编辑的位点，这说明PPR-DYW蛋白同样可在异源细胞核和细胞质中进行RNA编辑(Lesch et al., 2022)。因此，通过定向改造自然的PPR或人工合成PPR可在不改变DNA序列的情况下，对突变的基因进行修正或对一些RNA位点进行准确编辑。人工合成PPR可用于对胞质雄性不育基因进行修正，并利用诱导性启动子对该PPR的表达进行调控，进而准确地对胞质雄性不育进行人为控制。人类多种疾病由线粒体基因突变导致，可利用人工合成PPR对突变基因进行修正，进而治疗疾病。然而，PPR基序识别RNA特异性不高，过量表达容易脱靶，因此提高人工合成PPR蛋白的RNA识别和结合特异性是目前亟待解决的关键问题。

8 研究展望

目前，虽然对PPR蛋白参与RNA编辑进行了较多研究，但是仍有一些问题需要进一步回答。(1) 高等植物细胞器中RNA编辑由编辑复合体完成，除PPR蛋白外，还需要多种因子参与，如MORF、ORRM、OZ1和ISE2 (Sun et al., 2016; Sandoval et al., 2019)。这

些编辑因子如何协同参与RNA编辑尚不清楚。(2) 研究表明，PPR-E蛋白识别编辑位点后招募非典型PPR-DYW蛋白PCW1和MEF8/8S；PPR-E+蛋白招募非典型PPR-DYW蛋白AtDYW2和ZmDYW2A\2B进行RNA编辑(Andrés-Colás et al., 2017; Guillaumot et al., 2017; Yang et al., 2022b; Wang et al., 2023, 2024)。然而PPR-E/E+蛋白负责编辑的一些位点(如PCW1、MEF8/8S、AtDYW2和ZmDYW2A\2B)都不负责编辑或者只负责其中一部分(Andrés-Colás et al., 2017; Guillaumot et al., 2017; Yang et al., 2022a; Wang et al., 2023, 2024)。这暗示PPR-E/E+蛋白除招募非典型PPR-DYW蛋白作为脱氨酶以外，还可能招募其它脱氨酶。典型的PPR-DYW蛋白是可能的候选脱氨酶，但还需要进一步验证。

作者贡献声明

于晓琳，李西雅：查阅文献和撰写文章主要内容；夏冰玉洁：查阅文献和撰写PPR编辑因子突变体表型部分；李昊：参与PPR结构和展望部分的撰写；谭保才：文章框架设计和规划；王勇：文章整体框架设计和规划、文章修改以及质量控制。

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Research Advance of PPR Proteins Involved in the Mechanism of Organelle RNA C→U Editing

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Abstract Mitochondria and chloroplasts are semi-autonomous organelles harboring their own genomes. RNA editing is essential for the correct expression of organelle genes. The mostly identified RNA editing is cytidine (C)-to-uridine (U). Multiple editing factors have been reported to be involved in RNA C→U editing. The PPR-motifs array in PPR proteins specifically target editing sites, and the DYW domains in PPR-DYW proteins catalyze the deaminase in the C→U editing. This paper aims to review the recent advance of PPR proteins involved in RNA C→U editing, and to discuss the potential application value of synthetic PPR editing factors.

Key words PPR proteins, RNA C→U editing, mitochondria, chloroplasts

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附表 1 高等植物中参与 RNA C→U 编辑的 PPR 基因突变体表型
Appendix table 1 The mutant phenotype of PPR genes involved in the RNA C→U editing in higher plants

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通讯作者/团队简介

王勇，博士，副研究员，硕士生导师。其研究团队主要从事玉米种子发育关键基因克隆、功能解析和RNA加工机制研究，系统解析了多个基因的功能，并明确了这些基因参与细胞器RNA加工以及玉米种子发育的分子机制。相关成果以第一作者身份发表在*Plant Cell*、*Plant Commun*、*PLoS Genet*、*Plant J*和*Front Plant Sci*等学术期刊；以合作者身份在*Nat Commun*、*Proc Natl Acad Sci USA*、*New Phytol*、*Plant Physiol*、*J Integr Plant Biol*和*J Exp Bot*等国际主流学术期刊发表论文10余篇。主持国家自然科学基金等项目多项。

附表 1 高等植物中参与 RNA C→U 编辑的 PPR 基因突变体表型
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基因名	亚类	物种	影响的编辑位点数量	编辑位点	亚细胞定位	表型	参考文献
Emp21	DYW	玉米	81		线粒体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Wang et al., 2019
DEK36	E+	玉米	3	*atp4*-59, *nad7*-383, *ccmF*$_N$-302	线粒体	胚发生和胚乳发育严重抑制，呈现籽粒发育缺陷表型	Wang et al., 2017
EMP9	E+	玉米	2	*rps4*-335, *ccmB*-43	线粒体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Yang et al., 2017
DEK39	PLS	玉米	2	*nad3*-247, 275	线粒体和叶绿体	胚发生和胚乳发育严重抑制，呈现籽粒发育缺陷表型	Li et al., 2018
DEK10	E	玉米	3	*nad3*-61, 62, *cox2*-550	线粒体	胚发生和胚乳发育严重抑制，呈现籽粒发育缺陷表型	Qi et al., 2017
Emp7	E	玉米	1	*ccmF*$_N$-1553	线粒体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Sun et al., 2015
Smk1	E+	玉米	1	*nad7*-836	线粒体	胚发生和胚乳发育严重抑制，呈现小籽粒表型，部分植株可活，但植株矮小	Li et al., 2014
PPR226 3	DYW	玉米	2	*nad5*-1550, *cob*-908	线粒体和叶绿体	胚发生和胚乳发育严重抑制，呈现小籽粒表型，部分植株可活，但植株矮小	Sosso et al., 2012
Emp5	DYW	玉米	10	*rpl16*-458, *nad9*-190, *nad9*-356, *cox3*-245, *cox3*-257, *rps12*-71, *rps12*-221, *rps12*-269, *rps12*-284	线粒体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Liu et al., 2013
Emp18	DYW	玉米	2	*atp6*-635, *cox2*-449	线粒体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Li et al., 2019
PCW1	DYW atypical	玉米	102		线粒体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Wang et al., 2023

ZmDYW2A/ ZmDYW2B	DYW atypical	玉米	100		线粒体和叶绿体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Wang et al., 2024
bCCP1	P	玉米	66		线粒体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Wang et al., 2023
ZmNUWA	P	玉米	99		线粒体和叶绿体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Wang et al., 2024
Smk4	E	玉米	1	*cox1*-1489	线粒体	胚发生和胚乳发育严重抑制，呈现小籽粒表型，植株可活，但植株矮小	Wang et al., 2020
Smk6	E+	玉米	5	*nad1*-740, *nad4L*-110, *nad7*-739, *mttB*-138,139	线粒体	胚发生和胚乳发育严重抑制，呈现小籽粒表型	Ding et al., 2019
Emp80	E+	玉米	2	*nad7*-769, *atp4*-118	线粒体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Zhao et al., 2022
Emp17	DYW	玉米	4	*ccmF*$_C$-799, 906, 966, *nad2*-677	线粒体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Wang et al., 2021
ZmPPR26	DYW	玉米	8	*atpA*-1148, *ndhF*-62, *rpl20*-308, *rpl2*-2, *rpoC2*-2274, *petB*-668, *rps8*-182, *ndhA*-50	叶绿体	白化苗表型	Liu et al., 2021
PPR27	DYW	玉米	8	*ccmF*$_N$-1357, *rps3*-707, decreases the editing at 6 other sites	线粒体	胚发生和胚乳发育严重抑制，呈现空果皮表型	Liu et al., 2020
Dek48	DYW	玉米	15	*nad3*-185, -215, *nad4*-376, -977 decreases the editing at 11 other sites	线粒体	胚发生和胚乳发育严重抑制，呈现籽粒发育缺陷表型	Yang et al., 2022
Dek46	DYW	玉米	2	*nad7-i3*-878, *nad7-i4*-1581	线粒体	胚发生和胚乳发育严重抑制，呈现籽粒发育缺陷表型	Xu et al., 2020
qKW9	DYW	玉米	1	*ndhB*-737	叶绿体	胚发生和胚乳发育抑制，呈现小籽粒表型，植株发育正常，果穗偏小	Huang et al., 2020

Dek504	E+	玉米	2	*nad3*-44, 317	线粒体	胚发生和胚乳发育严重抑制，呈现籽粒发育缺陷表型	Wang et al., 2022
Dek55	E	玉米	24	*atp1*-1490, *ccmFN*-287, *matR*-1877, *rps13*-56, decreases the editing at 20 other sites	线粒体	胚发生和胚乳发育严重抑制，呈现籽粒发育缺陷表型	Ren et al., 2020
Dek605	DYW	玉米	1	*nad1*-608	线粒体	胚发生和胚乳发育严重抑制，呈现籽粒发育缺陷表型	Fan et al., 2020
ATP4	P	玉米和水稻	1	*rps8*-182	叶绿体	白化苗表型	Zhang et al., 2020
OGR1	DYW	水稻	7	*nad4*-401,416,433, *nad2*-1457, *ccmC*-458, *cox2*-167, *cox3*-572	线粒体	种子不透明，生长迟缓和植株分蘖少	Kim et al., 2009
PPS1	DYW	水稻	5	*nad3*-155, 172, 173, 190,191	线粒体	生长缓慢，营养期矮化和发育迟缓，花药小而短，花粉不育	Xiao et al., 2018
OsPGL1	DYW	水稻	2	*ccmFC*-543, *ndhD*-878	线粒体和叶绿体	黄化苗和植株矮小	Xiao et al., 2018a
PPR756	E	水稻	3	*atp6*-368, *ccmC*-236, *nad7*-83	线粒体和叶绿体	在早期营养阶段生长迟缓，叶片更绿，花粉不育，结实率低	Zhang et al., 2020b
OsPGL3A	DYW	水稻	2	*rps8*-182, *rpoC2*-4106	叶绿体	白化苗表型	Xu et al., 2024
GmPGL2	E+	大豆	9	*ndhB*-139627, 141281,141424,141650, ndhD-120618, *ndhE*-119873, *ndhF*-124681, *rps16*-56313, *rps18*-66641	叶绿体	黄化、植株矮小和光合效率降低等	Feng et al., 2021
NUWA	P	拟南芥	223	223	线粒体和叶绿体	胚致死	Guillaumot et al., 2017
DYW2	DYW atypical	拟南芥	392	392	线粒体和叶绿体	胚致死	Guillaumot et al., 2017
MEF8/8S	DYW atypical	拟南芥	38	151	线粒体	胚致死	Verbitskiy et al., 2012a, Yang et al., 2022b
PPME	P	拟南芥	2	*nad1*-898, 937	线粒体	植株严重矮小、种子	Leu et al., 2016

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CLB19	E+	拟南芥	2	*clpP*-69942, *rpoA*-78691	叶绿体	灰白和黄化苗表型	Chateigner-Boutin et al., 2008
AEF1=MPR25	E+	拟南芥	1	*atpF*-12707	叶绿体	黄化苗表型	Yap et al., 2015
OTP80	E+	拟南芥	1	*rpl23*-86055	叶绿体	正常生长条件下没有表型	Hammani et al., 2009
CRR21	E+	拟南芥	1	*ndhD*-116785	叶绿体	NDH 活性抑制	Okuda et al., 2007
MEF13	E+	拟南芥	8	*nad5*-1916, 1665, *ccmFc*-50,415, *nad2*-59, *nad7*-213, *nad4*-158, *cox3*-314	线粒体	生长发育迟缓	Glass et al., 2015
SLO2	E+	拟南芥	7	*mttb*-66,144,145, *nad1*-40, *nad4L*-110, *nad7*-739, *nad1-2*	线粒体	植株矮小、生长发育迟缓	Zhu et al., 2012
GRS1	E+	拟南芥	4	*nad6*-103, *rps4*-377, *nad4L*-55, *nad1*-265	线粒体	生长发育迟缓和不育	Xie et al., 2016
CWM1	E+	拟南芥	3	*nad5-59*8, *ccmC*-463, *ccmB*-428	线粒体	纤维素不足	Hu et al., 2016
COD1	E+	拟南芥	3	*cox2*-698,253, *nad4*-1129	线粒体	胚致死	Dahan et al., 2014
AHG11	E+	拟南芥	1	*nad4*-376	线粒体	ABA 和盐胁迫等敏感	Murayama et al., 2012
MEF25	E+	拟南芥	1	*nad3*-308	线粒体	正常生长条件下没有表型	Arenas et al., 2013
SLG1	E+	拟南芥	1	*nad3*-250	线粒体	生长发育迟缓、ABA 敏感和抗旱性增加	Yuan and Liu, 2012
CRR4	E	拟南芥	1	*ndhD*-1	叶绿体	正常生长条件下没有表型	Kotera et al., 2005
OTP87	E	拟南芥	2	*atp1*-1178, *nad7*-24	线粒体	植株矮小、生长发育迟缓	Hammani et al., 2011
SLO1	E	拟南芥	2	*nad4*-449, *nad9*-328	线粒体	植株矮小、生长发育迟缓	Sung et al., 2010
MEF3	E	拟南芥	1	*atp4*-89	线粒体	正常生长条件下没有表型	Verbitskiy et al., 2012
MEF9	E	拟南芥	1	*nad7*-200	线粒体	正常生长条件下没有表型	Takenaka, 2010
MEF12	E	拟南芥	1	*nad5*-374	线粒体	正常生长条件下没有表型	Hartel et al., 2013
MEF18	E	拟南芥	1	*nad4*-1355	线粒体	正常生长条件下没有表型	Takenaka et al., 2010

MEF19	E	拟南芥	1	*ccmB*-566	线粒体	正常生长条件下没有表型	Takenaka et al., 2010
MEF20	E	拟南芥	1	*rps4*-226	线粒体	正常生长条件下没有表型	Takenaka et al., 2010
OTP71	E	拟南芥	1	*ccmFN2*-176	线粒体	正常生长条件下没有表型	Chateigner-Boutin et al., 2013
SLO4	E	拟南芥	1	*nad4*-1033	线粒体	根系生长抑制、晚花和生长发育迟缓	Weissenberger et al., 2017
DYW1	DYWatypical	拟南芥	1	*ndhD*-1	叶绿体	正常生长条件下没有表型	Boussardon et al., 2012
QED1	DYW	拟南芥	5	*matK*-2931, *rpoB*-23898, *accD*-58642, *rps12*-69553, *ndhB*-95608	叶绿体	Landsberg 生态型呈现生长迟缓和黄叶表型	Wagoner et al., 2015
OTP82	DYW	拟南芥	2	*ndhB*-95644, *ndhG*-118858	叶绿体	正常生长条件下没有表型	Okuda et al., 2010
DOT4	DYW	拟南芥	1	*rpoC1*-21806	叶绿体	锯齿状白色到淡绿色的镜像对称的针状叶片	Hayes et al., 2013
YS1	DYW	拟南芥	1	*rpoB*-25992	叶绿体	黄化苗表型	Zhou et al., 2009
OTP86	DYW	拟南芥	1	*rps14*-37161	叶绿体	正常生长条件下没有表型	Hammani et al., 2009
RARE1	DYW	拟南芥	1	*accD*-57868	叶绿体	高温生长缺陷，表现为黄化和生长迟缓表型	Huang et al., 2023
LPA66	DYW	拟南芥	1	*psbF*-63985	叶绿体	植株生长迟缓，叶片呈现淡绿色	Cai et al., 2009
ELI1	DYW	拟南芥	1	*ndhB*-95650	叶绿体	正常生长条件下没有表型	Hayes et al., 2013
OTP85	DYW	拟南芥	1	*ndhD*-116494	叶绿体	正常生长条件下没有表型	Hammani et al., 2009
AtECB2	DYW	拟南芥	1	*accD*-265	叶绿体	子叶白化，没有真叶	Yu et al., 2009
Emb2261/ECD1	DYW	拟南芥	2	*rps14*-2, 149	叶绿体	胚胎致死	Sun et al., 2018
OTP84	DYW	拟南芥	3	*psbZ*-35800, *ndhB*-94999, *ndhF*-112349	叶绿体	正常生长条件下没有表型	Hammani et al., 2009
MEF11	DYW	拟南芥	3	*cox3*-422, *nad4*-124, *ccmFN2*-344	线粒体	生长稍慢，对化合物洛伐他汀的耐受性增强	Verbitskiy et al., 2010
MEF7	DYW	拟南芥	4	*ccb206*-28, *cob*-325, *nad2*-1433,	线粒体	正常生长条件下没有表型	Zehrmann et al., 2012

				nad4L-41			
MEF1	DYW	拟南芥	3	*rps4*-956, *nad7*-963, *nad2*-1160	线粒体	正常生长条件下没有表型	Zehrmann et al., 2010
MEF35	DYW	拟南芥	3	*rpl16*-209, *cob*-286, *nad4*-1373	线粒体	幼苗发育略迟缓，开花期与野生型一致	Brehme et al., 2015
MEF26	DYW	拟南芥	2	*nad4*-166, *cox3*-311	线粒体	正常生长条件下没有表型	Arenas et al., 2014
REME1	DYW	拟南芥	2	*nad2*-558, *orfX*-552	线粒体	正常生长条件下没有表型	Bentolila et al., 2010
MEF10	DYW	拟南芥	1	*nad2*-842	线粒体	生长发育迟缓	Hartel et al., 2013b
MEF14	DYW	拟南芥	1	*matR*-1895	线粒体	正常生长条件下没有表型	Verbitskiy et al., 2011
MEF21	E+	拟南芥	1	*cox3*-257	线粒体	正常生长条件下没有表型	Takenaka et al., 2010
MEF22	DYW	拟南芥	1	*nad3*-149	线粒体	正常生长条件下没有表型	Takenaka et al., 2010
MEF100	DYW	拟南芥	4	*nad1*-493, *nad4*-403, *nad7*-698, *ccmFN2*-356	线粒体	生长发育迟缓，叶片呈深色卷曲，植株矮小	Gutmann et al., 2021
MEF46	E+	拟南芥	1	*nad5*-1958	线粒体	正常生长条件下没有表型	Brehme et al., 2020
MEF47	E	拟南芥	2	*nad3*-64, *ccmC*-614	线粒体	轻微的发育迟缓	Brehme et al., 2020
DG409	PLS	拟南芥	5	*clpP*-559, *rpoA*-200, *accD*-1568, *rps3*-1344, *nad7*-1505	线粒体和叶绿体	幼苗叶片灰绿色，成苗逐渐转绿，植株矮小，籽粒干瘪	Wang et al., 2023a
MREF1	E+	拟南芥	1	*nad5*-242	线粒体	正常生长条件下没有表型	Kobayashi et al., 2020
MREF2	DYW	拟南芥	1	*atp1*-1292	线粒体	正常生长条件下没有表型	Kobayashi et al., 2020
OTP970	DYW	拟南芥	1	*ndhB*-149	叶绿体	正常生长条件下没有表型	Fu et al., 2022
MEF28	DYW	拟南芥	1	*nad4*-1417	线粒体	正常生长条件下没有表型	Bayer-Császar et al., 2024
MEF34	DYW	拟南芥	2	*nad2*-89, 90	线粒体	正常生长条件下没有表型	Bayer-Császar et al., 2024

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