

· 专题论坛 ·

miR172-AP2模块调控植物生长发育及逆境响应的研究进展

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摘要 MicroRNA (miRNA)是一类具有调控能力的非编码小分子RNA, 通过与靶基因mRNA特异或非特异性结合, 诱导靶基因mRNA降解或抑制其翻译, 从而调控植物的生长发育。其中, miR172的靶基因AP2所编码的转录因子为植物所特有, miR172在转录后或翻译水平对AP2进行表达调控, 进而调控植物的花发育、时序转换、小穗形态、块茎和果实发育、结瘤(豆科)以及逆境响应等过程。该文综述了近年来miR172-AP2模块在植物生长发育调控方面的最新研究进展。

关键词 miR172, AP2转录因子, 表达调控, 植物生长发育

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MicroRNA (miRNA)是广泛存在于真核生物中、由20–24个核苷酸组成的非编码RNA, 在转录后水平调控靶基因表达(Carrington and Ambros, 2003; Bartel, 2004)。miRNA在调控植物种子休眠、粒形和株型等生长发育过程及逆境响应中发挥重要作用(王幼宁等, 2016; Saminathan et al., 2019; Miao et al., 2019, 2020)。植物中miRNA生成过程与编码蛋白基因类似, 起初由RNA聚合酶II转录形成一段称作初级转录物的pri-miRNA的核苷酸序列, 长度几百到几千个碱基不等, 且在5'和3'端分别带有甲基鸟苷帽子和polyA尾巴(Rogers and Chen, 2013)。pri-miRNA根据其自身序列的互补性可形成1至数个发夹茎环结构, 进而在细胞核内被Dicer-like DCL1酶、双链结合蛋白辅因子HYL1以及锌指蛋白SE切割成具有茎环结构的前体miRNA (pre-miRNA)。pre-miRNA很不稳定, 很快又被DCL1、HYL1和SE进一步剪切成约22 nt的miRNA-miRNA*二聚体(Kurihara and Watanabe, 2004; Jones-Rhoades et al., 2006; 陈丽等, 2018), 该二聚体首先被HEN1 (HUAENHAN-CER1)

甲基化来增强其稳定性, 随后在转运蛋白HST (HASTY)的作用下进入沉默复合体(RISC)状态, 且其中一条成熟单链miRNA保留在复合体中, 与互补的靶标mRNA特异性结合来调控其表达水平(Li et al., 2005; Park et al., 2005; Brodersen et al., 2008; 张俊红等, 2014)。

miRNA家族中, miR172是较早被发现同时也是被研究最透彻的成员之一(Park et al., 2002), 其靶基因主要编码AP2/ERF (APETALA2/ethylene responsive factor)类转录因子。AP2/ERF转录因子为植物所特有, 且几乎参与植物生长发育调控的各个环节。miRNA172通过特异或非特异性结合AP2/ERF的mRNA, 以mRNA剪切和翻译抑制2种方式调控AP2/ERF靶基因的表达, 从而调控植物众多生长发育过程(Jung et al., 2007; Zhu et al., 2009; 刘炜嫻等, 2018)。近期, 研究者在miRNA172-AP2模块调控植物花器官发育、时序转换、块茎及果实发育、根瘤形成和胁迫响应等方面取得一系列研究进展(王幼宁等, 2016; 赵晓晖等, 2017; Luan et al., 2018;

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Saminathan et al., 2019)。本文以miRNA172-AP2模块为中心,在简要介绍miR172和AP2的结构、功能及互作模式基础上,重点论述miRNA172-AP2模块参与的植物生长发育及胁迫响应调控,深入解析其生物学效应和分子机制,并初步建立由miR172-AP2模块介导的植物生长发育分子调控网络。

1 miR172的结构及表达特点

miR172在植物的生殖转换、花器官形成及胁迫响应等方面具有重要调控作用(Wu et al., 2009; 王幼宁等, 2016; 赵晓晖等, 2017; Luan et al., 2018; Saminathan et al., 2019)。miR172在高等植物中高度保守,虽然不同物种中miR172成员的数目和长度可能不同,但在亲缘关系较近的物种间序列高度保守,暗示其不同物种中可能具有相似的调控方式和生物学功能。

虽然miR172家族成员成熟miRNA的序列高度保守,但功能上并非简单重复。研究表明,miR172各成员启动子序列及其包含的顺式作用元件并不相同,从而决定了它们表达的时空特异性(Zhu and Helliwell, 2011; 刘炜嫻等, 2018)。双子叶模式植物拟南芥(*Arabidopsis thaliana*)中存在5个miR172成员,即miR172a-1、miR172a-2、miR172b-1、miR172b-2和miR172c (Chen, 2004)。虽然拟南芥miR172各成员的表达模式不尽相同,但根据其表达量和表达模式总体可分为2类:一类包括miR172b-2和miR172c,它们在拟南芥生长发育过程中表达量一直很低;另一类包括miR172a-1、miR172a-2和miR172b-1,它们的表达量随着拟南芥的生长发育逐渐升高,到生殖生长阶段达到峰值(Jung et al., 2007)。在表达的组织特异性方面,除了在植物根中未检测到miR172的表达,在其它包括花、叶片、茎和角果等组织中均检测到其表达(赵晓晖等, 2017)。单子叶模式植物水稻(*Oryza sativa*)中存在4个miR172成员(miR172a-miR172d),它们在苗期表达均较强,但同样各成员表达也具有一定的组织特异性。例如,miR172c在水稻籽粒中不表达(Zhu et al., 2009)。综上,miR172在植物中的表达具有明显的时空特异性(Zhu and Helliwell, 2011; 赵晓晖等, 2017)。

2 AP2转录因子的结构和功能

转录因子的最重要特征是通过与靶基因启动子区

的特定顺式作用元件结合来激活或抑制靶基因转录,从而参与植物的生长发育及其与环境的互作调控。AP2/ERF转录因子很早便被发现与拟南芥的花发育有关(Jofuku et al., 1994)。随着研究的不断深入,其在许多植物生长发育过程中的重要性开始显现。

AP2/ERF类转录因子均含有1个由60–70个氨基酸残基组成的高度保守的AP2/ERF结构域(Riechmann and Meyerowitz, 1998)。该结构域包含3个反向平行的 β 折叠和1个几乎与 β 折叠平行的 α 螺旋。 β 折叠在识别目标基因的顺式作用元件上具有重要作用, α 螺旋可能介导与其它转录因子的互作(Nakano et al., 2006)。根据保守结构域差异,可将AP2/ERF转录因子进一步分为4个亚家族,即AP2、ERF、DREB (dehydration-responsive element binding protein)和RAV (related to ABI3/VP1) (Xie et al., 2019)。AP2亚家族含有2个AP2/ERF结构域,主要参与调控植物花器官发育;另外,最新研究表明,该亚家族还参与调控植物根系发育和孤雌生殖(Khanday et al., 2019; Li et al., 2019a)。RAV亚家族含有1个AP2/ERF及1个B3结构域(Swaminathan et al., 2008),该亚家族成员参与植物激素及胁迫响应(Hu et al., 2004; Sohn et al., 2006; Zhang et al., 2019; Zhao et al., 2019)。ERF和DREB亚家族均仅包含1个AP2/ERF结构域,两者的区别在于AP2/ERF结构域的第14和19位氨基酸不同,DREB亚家族这2个位置分别是缬氨酸(Val)和谷氨酸(Glu),而ERF亚家族分别为丙氨酸(Ala)和天冬氨酸(Asp),功能上两亚家族均参与植物响应生物和非生物胁迫(Dubouzet et al., 2003; Bäumler et al., 2019; He et al., 2019; Wang et al., 2019a)。

3 AP2转录因子的表达调控模式及其与miR172的作用方式

各AP2/ERF亚家族转录因子所识别的顺式作用元件具有一定的特异性。例如,AP2亚家族可与启动子中gCAC(A/G)N(A/T)TcCC(a/g)ANG(c/t)顺式作用元件结合来调节靶基因的表达,进而调控植物的花器官发育、开花时间及时序转换等(Boutillier et al., 2002; Lei et al., 2019; Wang et al., 2019b)。RVA亚家族由于含有AP2/ERF和B3结构域,因此可识别CAACA和CACCTG基序。ERF亚家族主要识别启动子区域的

GCC-box, DREB亚家族则可与干旱胁迫响应和冷诱导响应元件(A/GCCGAC)结合,从而调节植物的非生物胁迫响应(Dubouzet et al., 2003; Agarwal et al., 2010; Mizoi et al., 2012; Bäuml et al., 2019; Wang et al., 2019a)。

目前,常用的miRNA靶基因鉴定方法包括生物信息学预测、AGO蛋白免疫共沉淀、双荧光素酶和降解组测序等(董淼等, 2013)。miRNA主要通过剪切靶基因mRNA和抑制靶基因翻译2种途径调控靶基因,但具体方式取决于miRNA与其靶基因mRNA的互补程度及作用位置(Hutvagner and Zamore, 2002; Llave et al., 2002; Schwab et al., 2005; Jung et al., 2007; Zhu et al., 2009)。miRNA172与AP2家族基因的互补区域通常位于靠近3'UTR的CDS区,主要调控方式为抑制AP2靶基因翻译,但也存在部分与靶基因mRNA完全互补从而对其进行剪切调控的情况(Aukerman and Sakai, 2003; Schmid et al., 2003; Chen, 2004; Mathieu et al., 2009)。当miRNA通过抑制翻译对靶基因进行调控时,两者将表现出协同表达模式(Zhu et al., 2009)。例如,水稻中miRNA172及其靶基因*OsIDS1*和*RSR1*在包括胚和胚乳在内的大多数组织中表达模式一致;同样,过量表达miR172也会导致各发育阶段穗子中的*OsIDS1* (*OsINDETERMINATE SPIKELET1*)和*RSR1* (*Rice Starch Regulator1*)表达呈现出升高或降低的动态变化模式,表明miR172对靶基因的调控具有时空特异性。在玉米(*Zea mays*)中,miR172通过剪切靶基因*GL15*的mRNA来调控玉米从营养生长向生殖生长的过渡(Lauter et al., 2005)。此外,在大豆(*Glycine max*)、马铃薯(*Solanum tuberosum*)和拟南芥中也有类似报道,即miR172通过切割其靶基因的mRNA来调控植物的生长发育(Wang et al., 2014)。

4 miR172-AP2模块对植物生长发育的调控

4.1 调控植物的花器官形成

AP2在模式植物拟南芥中被发现时便认为与植物花器官特征调控相关(Kunst et al., 1989)。拟南芥的花包括花萼、花瓣、雄蕊和心皮4轮器官,其特征由A、B和C三类基因控制(Bowman et al., 2012)。AP2属于

A类基因,不仅参与第1轮花萼特征的调控,还与B类基因AP3和PI (*PISTILLATA*)共同控制第2轮花瓣的形成;并可通过拮抗C类基因AG (*AGAMOUS*)的作用抑制雄蕊和心皮的发育(Shannon and Meeks-Wagner, 1993; Elliott et al., 1996)。miR172在拟南芥花器官中具有优势表达,且miR172过表达植株花器官发育异常,与ap2突变体类似(Park et al., 2002),主要原因在于miR172从翻译水平抑制了AP2的表达(Aukerman and Sakai, 2003; Chen, 2004)。时空表达分析结果表明,AP2表达产物主要积累于花器官外周,与miR172信号在第2或第3轮花器官处有瞬时重叠(Wollmann et al., 2010)。尽管miR172和AP2共表达时间非常短暂,但两者共同调控花分生细胞的时序进程,在花器官发育中发挥决定性作用(Ji et al., 2011)。

miR172-AP2模块除了在拟南芥中参与花器官发育调控,在烟草(*Nicotiana tabacum*)中也有类似作用。将拟南芥miR172在烟草中过表达同样会导致烟草花结构发育异常,与ap2突变体类似(Mlotshwa et al., 2006),表明miR172-AP2模块在花器官发育调控方面具保守性。最新研究表明,miR172-AP2模块在油菜(*Brassica campestris*)、大岩桐(*Sinningia speciosa*)和玫瑰(*Rosa rugosa*)等双子叶植物中也参与花器官发育的调控(François et al., 2018; Li et al., 2019b; Wang et al., 2019b)。此外,该调控模式也存在于单子叶植物中。例如,水稻AP2家族成员*OsSNB*和*OsIDS1*在小穗向小花转变及花器官形态建成过程中发挥关键作用。*OsSNB*突变会导致花发育异常。例如,小穗向小花转变显著延迟,产生额外颖苞,花中浆片异常膨大进而发育成内外稃等;在*OsSNB*单突变基础上同时突变*OsIDS1*则会进一步增强相关表型。水稻中过表达miR172也会导致花器官发育异常,形成类似*Ossnb*突变体的表型(Lee and An, 2012; Wang et al., 2015a),暗示miR172可能通过调控AP2基因*OsSNB*和*OsIDS1*的表达来影响水稻花器官的发育。另一禾本科单子叶植物玉米,其花为单性花,含有雄穗和雌穗两种花序。玉米的ts (*tassel/seed*)突变体由于雄穗中的雌蕊不退化从而形成两性花,导致雄穗雌化并进而开花结实(Chuck et al., 2007; Acosta et al., 2009)。利用具有雄穗雌化现象的玉米突变体ts4和ts6开展目标基因克隆,结果显示这2种

突变体分别是由于miR172及其靶基因*IDS1*突变所致,表明miR172-AP2模块在玉米性别决定中同样具有关键作用(Chuck et al., 2007)。而*IDS1*的异位表达会推迟小穗向花转变,从而使单个小穗产生多个小花(大于2朵)。*IDS1*同源基因*SID1 (SISTER OF INDETERMINATE SPIKELET 1)*突变会进一步增强*ids1*突变体的表型,表明这2个基因在玉米花器官发育过程中的功能具有累加作用(Chuck et al., 2008)。禾本科植物的浆片在开花过程中具有重要作用,即在特定时期吸水膨胀,从而撑开颖壳,完成开花过程。已知大麦(*Hordeum vulgare*)的闭花受精特性由AP2家族的*Cly1 (Cleistogamy 1)*基因控制,该基因表达也受到miR172调控;当*Cly1*序列中与miR172结合的位点发生突变时,会干扰其mRNA与miR172结合,从而减弱miR172的翻译抑制作用,进而产生非常小的浆片而无法开颖,最终发生闭花受精(Nair et al., 2009; Anwar et al., 2018)。可见,miR172-AP2模块在不同植物中的功能非常保守,且对植物花器官发育调控极为重要,miR172通过抑制AP2家族成员的表达,进而影响AP2基因与B类和C类基因间的互作,最终调控花器官发育、雌雄分化和开花等过程。

4.2 调节植物的时序转换

miR172-AP2模块还广泛控制植物由营养生长向生殖生长的过渡,而开花是生殖生长转换的标志。已知拟南芥中miR172靶基因有6个,分别为AP2、*TOE1*、*TOE2*、*TOE3*、*SMZ*和*SNZ*。在拟南芥中过表达miR172会引起极端早花表型,虽然抑制或敲除miR172单个靶基因也会导致早花,但其表型显著弱于miR172过表达材料。只有同时敲除6个靶基因才出现与miR172过表达一致的极端早花表型,表明miR172-AP2模块是控制拟南芥开花时间的主效调控因子(Aukerman and Sakai, 2003)。

水稻中,miR172通过抑制AP2基因*OsIDS1*和*SNB*的表达来解除它们对靶基因*Ehd1 (Early heading date1)*的抑制,从而诱导开花(Lee et al., 2014)。最近,大岩桐中也有类似报道,即过表达miR172抑制*SsAP2*表达从而诱导早花(Li et al., 2019b)。此外,在大豆、牵牛花(*Pharbitis nil*)和麻风树(*Jatropha curcas*)中也有miR172-AP2模块参与开花时间调控的报道(Glazińska et al., 2009; Zhao et al., 2015;

Tang et al., 2018)。因此,我们推测植物主要通过miR172-AP2分子模块调节开花时间来实现其营养生长向生殖生长的过渡。

此外,miR172-AP2模块在植物营养生长期不同阶段转变过程中也发挥重要作用(Wu et al., 2009)。例如,*GL15 (Glossy 15)*是1个控制玉米幼苗向成熟期转变时间的AP2基因,其表达同样受到miR172调控(Moose and Sisco, 1994, 1996; Lauter et al., 2005)。可见,miR172-AP2模块在植物时序转换调控中也发挥关键作用。AP2家族成员众多,在功能上兼具共性和特异性,解析其分子机制可为生产实践中利用特定的miR172-AP2互作模块开展分子设计育种提供可能,从而实现真正精准育种。

4.3 影响植物果实发育和豆科植物根瘤形成

miR172-AP2模块对果实发育的调控至关重要。拟南芥中,miR172-AP2模块可通过调节果荚发育来影响其果实发育。同时,蛋白FUL与ARF (Auxin Response Factor)可直接互作并结合到miR172前体编码基因的启动子区来激活miR172表达,进而抑制其下游靶基因AP2及*TOE3*的表达,最终促进果实发育(José Ripoll et al., 2015)。水稻AP2基因*RSR1*突变导致其籽粒变大、千粒重及稻米直链淀粉含量增加(Fu and Xue, 2010)。进一步研究表明,*RSR1*正是受miR172调控的靶基因(Wang et al., 2015a),但*RSR1*调控下游靶基因导致水稻籽粒变化的分子路径尚无报道。已知*RSR1*在水稻籽粒中不表达,暗示miR172-*RSR1*模块对稻米粒形和品质的影响可能为间接作用,即通过调控其它组织的生长发育来影响果实发育。综上,miR172-AP2模块对单子叶和双子叶植物果实发育均具有调控作用。

根瘤菌不仅能感染豆科植物根系形成根瘤,还可与其共生固氮。在苜蓿(*Medicago sativa*)中首先证实miR166和miR169参与根瘤发育的调控(Comber et al., 2006; Boualem et al., 2008)。百脉根(*Lotus corniculatus*)中的研究也表明,miR171、miR397和miR156与根瘤的发育、病毒感染和固氮能力密切相关(De Luis et al., 2012; Wang et al., 2015b)。在大豆中过表达miR482、miR1512、miR1515、miR156及miR167均可以显著改变大豆根瘤的数量(Li et al., 2010; Wang et al., 2015c)。因此,miRNA在豆科植物

结瘤和共生固氮过程中发挥重要作用。

之前的研究表明,根瘤菌处理3小时的大豆根中miR172表达显著上调(Subramanian et al., 2008),且在成熟的根瘤中miR172c高度表达(Wang et al., 2009)。而在大豆中过表达miR172c可促进根瘤菌的感染和根瘤的形态发生,从而增加根瘤数量(Yan et al., 2013)。此外,miR172还可调控结瘤因子(NF)的表达(Martin et al., 2009)。例如,miR172的靶基因*GmNINC1*编码1个AP2家族转录抑制子,可直接结合关键早期结瘤因子基因*ENOD40*的启动子并调节其表达,从而调控结瘤数目(Wang et al., 2014)。此外,考虑到miR172自身表达受到1个AON (autoregulation of nodulation)结瘤自调控信号的抑制,表明miR172-AP2模块可能是整合NF和AON信号通路的关键节点。后续研究表明,miR172在菜豆(*Phaseolus vulgaris*)和百脉根等豆科植物根瘤形成过程中同样发挥重要作用(Holt et al., 2015; Nova-Franco et al., 2015),表明miR172-AP2模块在调控豆科植物结瘤及共生固氮方面的功能相对保守。进一步探讨miR172-AP2模块调控豆科植物结瘤固氮的机理,将会促进豆科植物结瘤和固氮过程遗传机制的解析与调控网络的完善,并有助于将其更好地应用于作物育种实践。

4.4 调控禾本科植物的穗型

禾本科植物的单株产量主要取决于单株分蘖数、每穗粒数和粒重3个要素,而每穗粒数主要受穗发育的影响。在水稻中过表达miR172导致一次枝梗数显著减少,颖花数目无变化,但二次枝梗颖花数目显著减少。反之,miR172干扰材料的一、二次枝梗数及其颖花数目均显著增加。进一步研究表明,AP2家族基因*SNB*和*OsTOE1*过表达及干扰材料的表型与miR172正好相反,暗示*SNB*与*OsTOE1*可能是miR172的靶基因(Wang et al., 2015a)。

利用全基因组关联分析结合遗传定位克隆到1个控制大麦穗粒密度的基因*Zeo* (*ZEOCRITON*),即大麦AP2的直系同源基因*HvAP2*。大麦密穗表型的产生是由于*HvAP2*基因的miR172识别位点发生突变,从而减弱miR172对其表达的调控,造成穗轴延伸受阻,最终影响小穗在花序上的分布所致(Houston et al., 2013)。小麦的*Q*基因是1个典型的驯化基因,控制小麦脱粒性、粒形、穗长和株高等多个驯化相关性状。

基因克隆结果表明,*Q*基因属于AP2家族,且其表达在mRNA水平受miR172的剪切调控(Simons et al., 2005; Liu et al., 2018)。miR172-AP2模块在禾本科植物中参与穗型的调控,表明其功能的保守性。深入研究该模块控制作物穗部形态的分子机理,并结合目前已获解析的多个粒形调控基因信息,可为今后通过分子设计育种优化穗部和粒形性状,培育高产优质作物新品种奠定基础。

5 miR172-AP2模块参与植物逆境胁迫响应

植物不像动物可以躲避逆境,因此其进化出特有的复杂且精细的分子调控机制来应对各种环境胁迫。许多研究表明,miRNA在植物响应各种生物和非生物胁迫过程中具有重要作用。miR172作为miRNA家族中非常保守的一员,其自身表达受低温、盐碱和干旱等多种胁迫诱导,同时它也可通过调控AP2类转录因子参与植物响应各种环境胁迫(Zhou et al., 2008; Frazier et al., 2011; Yang et al., 2013; Candar-Cakir et al., 2016)。当然,miR172-AP2的具体调控模式还与植物种类及其响应的逆境因子密切相关。拟南芥中,ABA及渗透胁迫可诱导miR172与其靶基因*SNZ*共表达。miR172b过表达或*snz*突变体对ABA及渗透胁迫的敏感性增强,证明miR172通过控制其靶基因*SNZ*来介导拟南芥对渗透胁迫的响应(Zou et al., 2013)。干旱胁迫可诱导miR172e的表达,同时过表达miR172e又可显著增强拟南芥对干旱的抗性。进一步研究表明,干旱通过诱导*GI* (*GIGANTEA*)表达促进miR172e的积累以抑制下游靶基因*TOE1*的表达,进而影响*TOE1*蛋白与*WRKY44*的互作,最终实现对植物抗旱能力的调控(Han et al., 2013)。在大豆中过表达miR172c或敲除*GmNINC1*均可增强大豆的耐盐性;反之,干扰miR172的表达或过表达*GmNINC1*均增强了大豆的盐敏感性(Sahito et al., 2017)。此外,在拟南芥中过表达大豆miR172c也可显著增强拟南芥对干旱及盐胁迫的耐受性(Zou et al., 2013)。尽管目前人们对拟南芥和大豆中miR172介导的植物响应逆境胁迫机制有了较清晰的认识,但在其它植物特别是水稻和小麦等重要作物中的相关研究仍停留在全基因组表达分析层面,还未涉及具体分子机制的解析

与调控网络的构建。例如,香蕉(*Musa nana*)遇到冷胁迫后miR172的表达会显著上调,初步推测miR172可能在冷应激反应中起中心协调作用(刘炜娜等, 2018)。此外,在番茄(*Lycopersicon esculentum*)中过表达miR172a和miR172b显著增强了其对致病疫霉的抗性,潜在分子机理也与以miR172-AP2模块为核心的表达调控路径相关(Luan et al., 2018)。

综上, miR172-AP2模块在植物响应各种生物和非生物胁迫过程中的功能相对保守,但目前关于其分子机制的研究还不够深入。植物如何感知逆境信号并将其传递给miR172-AP2调控模块,以进一步实现对下游逆境响应因子的表达调控还知之甚少,尤其在重要作物中的相关功能和机理研究更为欠缺。

6 研究展望

近年来, miR172-AP2调控模块在植物生长发育中的关键作用已有大量报道。模式植物拟南芥miR172-AP2模块参与调控植物花器官发育、时序转换、果实发育及逆境响应等多个方面(图1)。此外,人们对其上游miR156-SPL模块调控的分子机制也有了清晰的认识(Wu et al., 2009; Aguilar-Jaramillo et al., 2019)。尽管如此,围绕miR172-AP2模块目前仍有许多科学问题亟待阐明。例如, miR172-AP2模块在其它植物特别是农作物中的研究才刚刚起步,尚停留在简单的转录分析层面,且对其上下游分子调控机制的探究仍很欠缺,基本是简单套用拟南芥中已发现的调控模式,

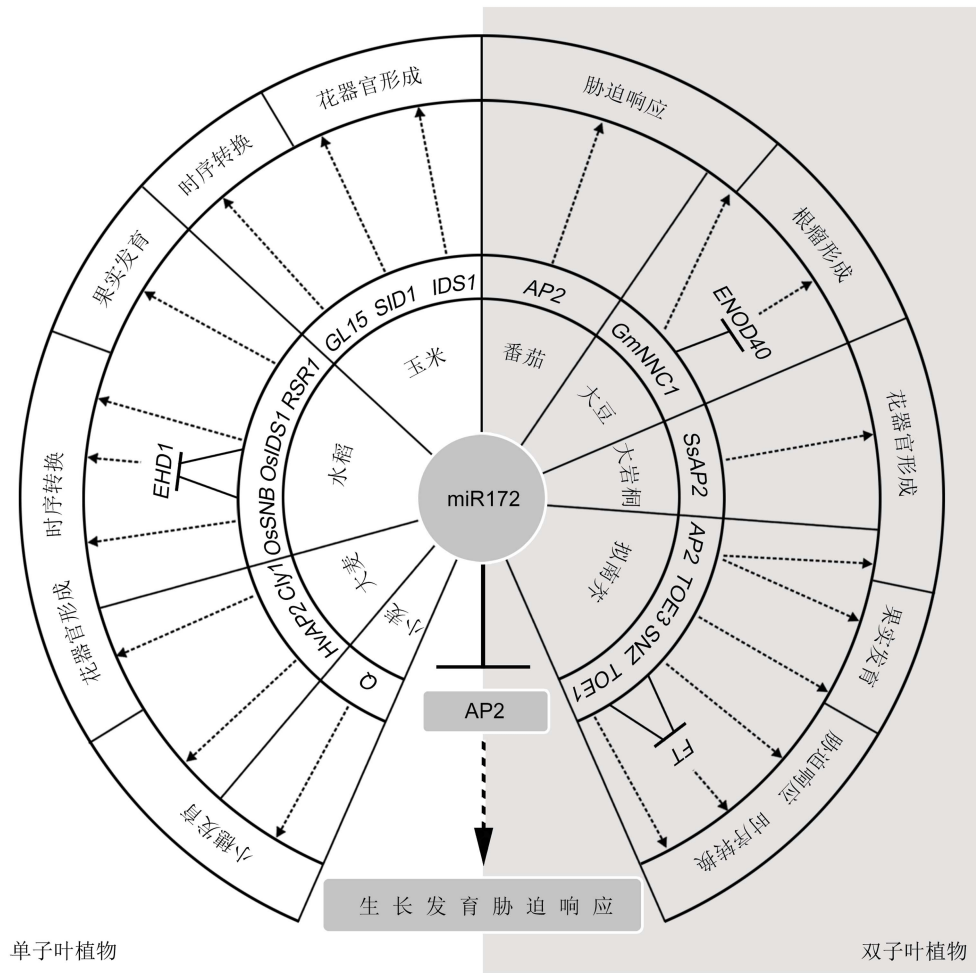


图1 miR172-AP2模块参与调控植物的生长发育和逆境响应

Figure 1 The processes of plant growth and development, and stress response regulated by miR172-AP2 module

缺乏对该模块参与的新分子调控路径和遗传网络的探索。考虑到miR172-AP2模块参与调控的生物学过程大部分与花器官和果实发育有关,因此作物中miR-172-AP2模块分子机理的系统解析将有助于利用其进行高产优质育种。此外,miR172序列在不同物种中总体上比较保守,但在非核心核苷酸序列上存在显著差异,这可能是决定其靶基因特异性及其与靶基因作用方式差异的主要原因,但有关miR172序列与其靶基因特异性之间的联系还不清楚。目前,对miR172-AP2模块的研究尚处于探索阶段,仅初步明确了该模块所调控的生长发育事件,对其作用的时空特异性仍认识不足。例如,在植物发育的特定时期,该模块在不同组织或细胞类型中的精确调控模式仍然未知。

随着各种现代生物学实验技术、仪器设备和分析方法的不断改进,可用于研究miRNA的手段更加多样。例如,可借助CRISPR/Cas9定点突变技术并综合多组学分析等研究方法,反向探索miR172更多新的靶基因,解码AP2家族成员的新功能及miR172-AP2模块可能参与的新的植物生长发育过程,并揭示其生物学效应,进而系统解析并完善以miR172-AP2模块为中心的分子调控网络,为更多重要生物学问题的阐明及今后生产实践中的作物改良奠定基础。

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Advances in the Regulation of Plant Growth and Development and Stress Response by miR172-AP2 Module

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Abstract MicroRNA (miRNA), a kind of regulatory non-coding small RNA, induces degradation of target mRNA or inhibits its translation by specific or non-specific binding, thereby regulating plant growth and development. AP2, the target of miR172, encodes transcription factors that are unique to plants. miR172 regulates the expression of AP2 at the post-transcriptional or translational levels, thus regulating plant floral development, phase transition, spikelet morphology, tuber and fruit development, nodulation in legumes and stress response. Here we summarize the recent advances in the regulation of plant growth and development by miR172-AP2 regulatory module.

Key words miR172, AP2 transcription factor, expression regulation, plant growth and development

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