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玉米花序分枝和穗粒数发育的分子调控

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摘要：玉米是我国第一大粮食饲料作物，对保障我国粮食安全具有重要战略意义。玉米是雌雄同株异花植物，雄穗为圆锥花序，雌穗为肉穗花序。玉米花序和小花的分化与发育是穗粒数形成和小花育性决定的发育生物学基础，与籽粒产量密切相关，因而这一研究领域受到广泛关注，并取得了丰硕的成果。近年来，为了提高玉米粮食产量和更加深入地解析产量形成分子网络，研究学者在玉米花序分枝发育和穗粒数形成的遗传控制和分子调控机制等研究方向取得了一系列新的研究进展。本研究主要聚焦花序特异性转录因子基因、非编码序列及其调控基因、活性氧清除和糖代谢相关酶基因、乙烯等激素生物合成和信号途径关键基因以及膜系统与信号传导相关基因等，对这些基因在玉米花序分枝、小穗和小花发育进程中的生物学功能与作用途径进行了综述，并对生物技术发展推动全基因组序列分析、激素与代谢物交互网络分析以及精准育种等进行了展望，以期为玉米花序发育、穗粒数和籽粒产量的分子遗传调控网络构建和玉米高产育种提供参考。

关键词：玉米（*Zea mays* L.）；花序；分枝发育；穗粒数；调控网络

Molecular Regulation on the Development of Reproductive Branches and Kernel Number in Maize Inflorescences

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Abstract：Maize（*Zea mays* L.）is the most important food and feed crop which plays an important strategic role in food security in China. Maize is the monoecious plant species，tassel is panicle and ear is spadix. The differentiation and development of inflorescences and florets are the basis for the number and fertility of florets in maize ultimately resulting in a formation of grain yield. Therefore，this research field is of significant interest and fruitful achievements have been made. In the past few years，in order to improve maize grain yield and further analysis the molecular network of yield formation，the latest progresses in the field of genetic modulation and regulatory mechanism on inflorescence branching and kernel number have been reported. In this paper，we briefly summarize our understanding of the genes and their acting pathways in the development of inflorescence branches，spikelets and florets. This review focuses on the inflorescence-specific transcription factors，non-coding sequences and their regulators，enzymes involved in the reactive oxygen species（ROS）scavenging and carbohydrate metabolism，key factors in ethylene biosynthesis and signal pathway，and major players in membrane system and signal transduction. And we make prospects for the development of biotechnology to promote whole genome sequence analysis，interaction network analysis of hormones and metabolites，and precision breeding. We aim to

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provide an insight in understanding of the crucial genetic factors and pathways controlling inflorescence development, which has implications for future research on the genetic regulatory network of inflorescences and florets, as well as on the high-yield breeding in maize.

Key words: maize (*Zea mays* L.); inflorescence; branch development; kernel number; regulatory network

玉米花序起源于具有无限分化能力的干细胞团：茎尖分生组织（SAM，shoot apical meristem）。玉米茎尖分生组织的形态常为半球状，可持续分化产生数目不等的叶原基。经生殖转换，半球状的茎尖分生组织伸长生长，形态变长，功能转换为花序分生组织（IM，inflorescence meristem）。玉米具有两个独立发育的花序：即由主茎顶端分生组织转换和分化而产生的雄花序（male inflorescence meristem/tassel）、由腋生侧枝顶端分生组织（AM，axillary meristem）转换和分化而产生的雌花序（female inflorescence meristem/ear）。雌花序分生组织先后经历小穗成对分生组织（SPM，spikelet pair meristem）、小穗分生组织（SM，spikelet meristem）、小花分生组织（FM，floral meristem）的分化，形成上位花（UF，upper floret）和下位花（LF，lower floret），随后下位花退化，上位花授粉后发育形成籽粒；雄花序的分化进程与雌花序相似，只是雄花序分生组织基部可分化产生分枝分生组织（BM，branch meristem），每个分枝分生组织也可经历小穗成对分生组织、小穗分生组织、小花分生组织，上位花和下位花的分化进程，雄性小穗上的上位花和下位花均可正常发育[1]。由此可见，玉米雌花序的分化和发育直接决定花序上的小花数，而小花的分化和发育则决定小花的育性和授粉潜力，因而，花序和小花的分化与发育是穗粒数形成的生物学基础，而雄花序的分化与发育则是雄穗分枝数、小花数和小花育性的生物学基础。由于花序的分化与发育是一个非常耗能的过程，适度抑制雄花序的分化和发育，减少雄穗分枝数和小穗数，有助于营养和能量供给雌穗和籽粒发育，进而提高玉米籽粒产量。鉴于花序分化与发育对玉米籽粒产量的重要性，长期以来，玉米花序分化和发育的调控研究备受关注。近年来，这一热点研究领域成果丰硕，许多新的功能基因及其所参与的调控途径被相继发现。本研究将对玉米花序分枝和穗粒数发育的遗传调控和分子机制的相关研究进展进行简要综述（图 1）。

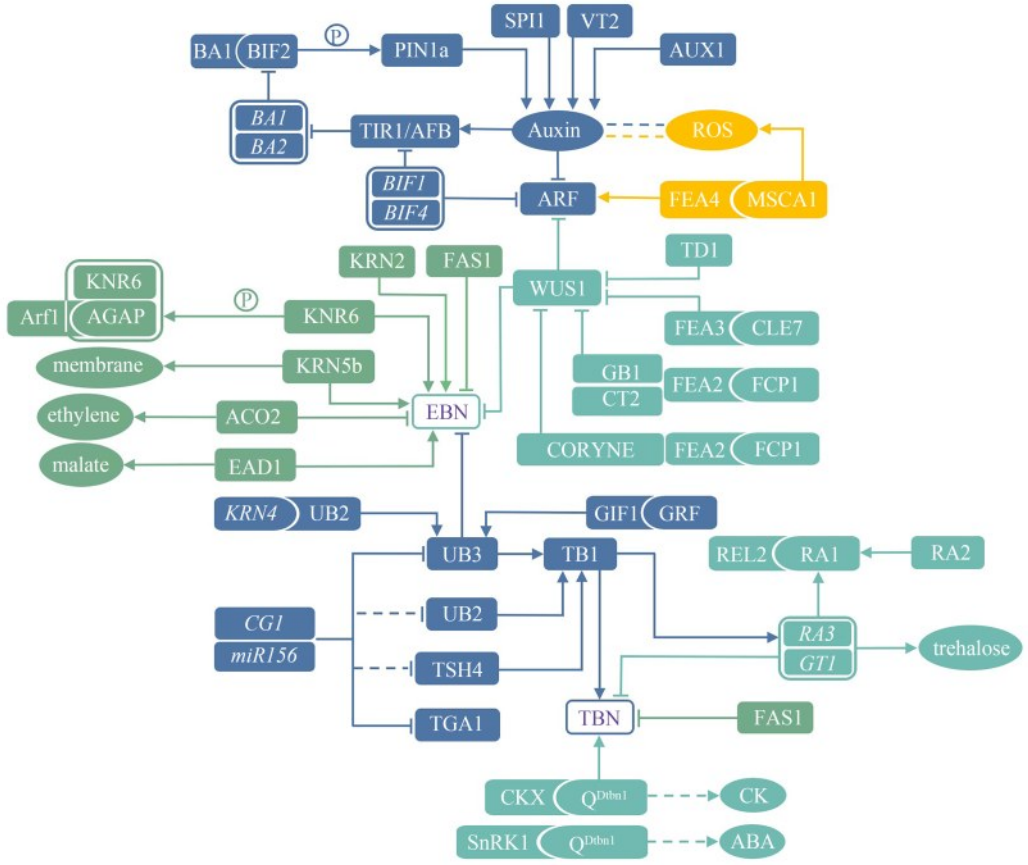
1　转录因子调控途径

转录因子作为反式作用因子与下游基因 5'端上游特定序列结合，调控下游基因的时空表达。玉米中的 *DROOPING LEAF11*（*DRL*）和 *DRL2* 是拟南芥 *CRABS CLAW*（*CRC*）的同源基因[2]，编码 YABBY 转录因子家族蛋白。*drl1* 突变体雌穗败育，心皮不融合且无法包被珠心，雄穗有额外的小花和花药；*drl2* 突变体增强 *drl1* 的表型，并且小花分化减少[3-4]。*DRL1* 与 MADS-box 家族转录因子编码基因 *ZEA AGAMOUS1*（*ZAG1*）互为靶基因，调控下游基因在小花中的表达[3-4]。Du 等[5]发现 *fas1* 显性突变体花序主轴缺失，雌雄花序分枝增多，这一表型是由于一段 160 kb 基因组区间内 *ZmMADS8* 和 *DRL2* 拷贝数增加导致产生新的启动子，使得 *ZmMADS8* 和 *DRL2* 在花序分生组织原基异位表达所致。

生长调控因子（*GRF*，*GROWTH REGULATION FACTOR*）是一类参与调控茎叶发育的植物特异转录因子，能正向调控细胞的增殖。GRF 与生长调控因子互作因子（GIF，GRF-INTERACTING FACTOR）相互作用形成特异性转录复合物行使功能。拟南芥中，GIF1 与 GRF3、GRF5 相互作用[6-7]。*gif1* 突变体叶片变窄，叶片细胞数量减少；过表达 *GIF1* 可促进叶片原基细胞增殖，叶片增大[8]。玉米的 GIF 家族有 3 个成员，GIF1、GIF2 和 GIF3。玉米中功能缺失突变体 *gif1* 茎尖分生组织不能正常增殖、植株发育迟缓、叶片狭窄、雌穗和雄穗多分枝、雌穗心皮不融合；在雄花序中，GIF1 与多个 GRF 相互作用，并且 GIF1 可与其靶基因 *UNBRANCHED3*（*UB3*）启动子特异结合，调控 *RAMOSA2*（*RA2*）、*TERMINAL EAR1*（*TE1*）、*VANISHING TASSEL2*（*VT2*）、*TASSELSHEATH4*（*TSH4*）、*ZEA FLORICAULA/LEAFY1*（*ZFL1/2*）等花序形态建成相关基因的表达[9]。在雌花序中，GIF1 与 RAMOSA1 增强子 2（REL2，RAMOSA1 enhancer locus2）互作，负调控 CLAVATA-WUSCHEL（CLV-WUS）途径、RAMOSA 途径以及油菜素类脂（BR，brassinosteroid）相关途径，正调控茉莉酸（JA，jasmonate）相关途径[10]。

KERNEL ROW NUMBER2（*KRN2*）是 WD40 domain-containing proteins（WD40）转录因子家族基因，WD40 蛋白分子均含有 6~16 拷贝的 Trp-Asp（WD）保守结构域。*krn2* 突变体花序分生组织变大，穗行数增加；*KRN2* 在水稻里的同源基因 *OsKRN2* 的突变体 *oskrn2* 二级枝梗数与穗粒数增多；*KRN2* 在玉米

和水稻驯化和改良中受到选择，对*KRN2*和*OsKRN2*基因编辑可提升10%玉米籽粒产量和8%水稻籽粒产量[11]。这一研究揭示了玉米和水稻中控制重要性状的关键基因的趋同选择规律，这一规律也可为作物遗传改良以及新作物的从头驯化提供理论指导。



方框：遗传互作关系；实线：已被验证的关系；虚线：尚未被验证的关系；三角形箭头：促进关系；T形箭头：抑制关系；双虚线：二者之间存在交互作用；Ⓟ：磷酸化作用；EBN：雌穗分枝数；TBN：雄穗分枝数

Blocks: Genetic interaction; The solid line: The relationship that has been confirmed; The dashed line: The relationship that has not been confirmed; Triangle arrows: Promoting relationships; T-shaped arrows: Inhibition relationships; The double dashed line: An interaction between each other; Ⓟ: Phosphorylation; EBN indicates Ear branch number; TBN indicates tassel branch number

图1 玉米花序分枝和穗粒数发育基因调控网络

Fig.1 Regulatory network of inflorescence branch and kernel number development genes

2 非编码序列参与的调控途径

非编码RNA基因调控其靶基因在植物发育与环境适应中起重要作用。非编码序列包括内含子、UTR（Untranslated region）区、顺式调控元件、染色质环锚点（Chromatin loop anchor）、非编码RNA基因以及一些转座子家族。在玉米亚基因组中，非编码序列与基因表达以及功能多样性相关[12]。玉米中非编码序列也参与调控花序分枝发育。*UNBRANCHED2*（*UB2*）和*UB3*为SQUAMOSA PROMOTER BINDING PROTEIN-LIKE（SPL）转录因子家族基因；*ub2*；*ub3*双突变体表现为雌穗扁化，产生更多的穗行数和更少的雄穗分枝[13]。*KRN4*是穗行数的主效QTL，位于*UB3*下游60 kb的基因间区，携带有1.2 kb转座子插入的*KRN4*等位基因家系中，*UB3*表达量降低，花序分生组织增大，穗行数增多[14-15]。*KRN4*表现出开放染色质状态，对*UB3*启动子具有较高的增强活性；*KRN4*可招募以UB2为中心的转录复合体并结合于*UB3*启动子区域，进而调节*UB3*的表达；*KRN4*的序列变异能增强*ub2*和*ub3*突变体的扁穗表型[16]，表明*KRN4*通过染色质互作远程精确调控*UB3*的表达水平，进而影响花序分生组织发育。

CORNGRASS1（*CG1*）是1个miR156基因，*CG1*能靶向SPL家族转录因子编码基因*TEOSINTE GLUME ARCHITECTURE1*（*TGA1*）的转录本[17]。*cg1*突变体表现为较小的雌穗和不分枝的雄穗，包裹着苞

叶，并且小花排列不规则[18]。SPL转录因子家族基因*TSH4*、*UB2*和*UB3*都具备miR156的靶位点。*tsh4*突变体雄穗分枝减少，穗行数减少且籽粒排列紊乱，推测*miR156*可能作用于*TSH4*、*UB2*和*UB3*，通过调控它们的表达并影响花序分生组织的活力。

3　代谢物参与的调控途径

3.1　活性氧

植物干细胞内氧化还原平衡受活性氧（ROS，reactive oxygen species）调控，氧化还原状态的改变能影响植物干细胞的功能[19]。ROS包括超氧阴离子（O_2^-）、过氧化氢（H_2O_2）和羟基自由基（•OH）。O_2^-/H_2O_2平衡能调控茎尖分生组织分化。拟南芥中，O_2^-在SAM的中心区域积累，激活*WUSCHEL*（*WUS*）表达以维持SAM的功能；H_2O_2在外围积累，促进分化[20]。谷氧还蛋白（GRX，GLUTAREDOXINS）可通过氧化还原和谷胱甘肽化修饰调控靶蛋白参与植物器官发育[21]。水稻中的*MICROSPORELESS1*（*MIL1*）编码CC-型谷氧还蛋白，其突变体*mil1*影响花药发育[22]。玉米中编码谷氧还蛋白的基因*MALE STERILE CONVERTED ANTHER1*（*MSCA1*）及其同源基因*ZmGRX2*、*ZmGRX5*存在较强的功能冗余，*msca1;zmgrx2;zmgrx5*突变体植株花序分生组织活性降低，小穗分枝发育受阻，单穗籽粒数显著下降[23]。这3个GRX蛋白能负调控花序发育关键转录因子*FASCIATED EAR4*（*FEA4*），而*FEA4*可通过调节生长素响应因子（*ARF*，*AUXIN RESPONSE FACTOR*）参与生长素信号途径，进而调控雌花序小穗成对分生组织的确定性[24]；另外，MSCA1可以作为电子供体直接还原FEA4，破坏其分子间二硫键，改变其单体/二聚体的平衡状态，即GRX蛋白对FEA4的修饰直接改变了FEA4的氧化还原状态并影响FEA4的转录激活活性，表明*MSCA1*、*ZmGRX2*和*ZmGRX5*作为重要的氧化还原调节因子，通过调控FEA4蛋白活性参与ROS信号传导，调控雌穗花序分生组织的发育。

3.2　海藻糖

糖是细胞能量和碳骨架的供体，也是调控生长发育的重要信号分子。植物中的海藻糖-6-磷酸（T6P，trehalose-6-phosphate）含量与糖含量显著正相关，被称作糖水平的指示剂[25]。另外，T6P具有类似胰岛素的功能[26]。水稻中，调控T6P积累的糖诱导表达转录因子OsNAC23影响植株光合速率、碳源的源-库转运、花序和种子等库器官发育，进而调控水稻籽粒产量[27]。海藻糖-6-磷酸磷酸酶（TPP，trehalose-6-phosphate phosphatase）能催化海藻糖代谢，在玉米中异源表达水稻*OsTPP1*可提升玉米9%~49%的产量[28]。

在玉米中，经典的RAMOSA途径突变体*ra1*、*ra2*和*ra3*在雌花序和雄花序中都表现出高度分枝的花序表型[29-31]。*RA3*编码TPP蛋白，可能直接通过海藻糖相关糖信号参与花序发育[31]。*GRASSY TILLER1*（*GT1*）是同源异型盒-亮氨酸拉链蛋白（HD-ZIP，homeodomain-leucine zipper）I类转录因子。*GT1*表达水平受*TEOSINTE BRANCHED1*（*TB1*）的正向调控，影响植株分蘖[32-33]。*ra3*突变体部分心皮减少，而*gt1;ra3*双突变体的心皮完全被抑制，雌、雄花序的分枝相对*ra3*减少[34]，表明*GT1*与*RA3*遗传互作共同调节腋生侧枝顶端分生组织确定性和雌花中心皮的抑制，说明海藻糖既能通过RAMOSA途径参与花序分枝的发育，也受转录因子TB1和GT1的调控。

3.3　苹果酸

苹果酸是三羧酸循环、乙醛酸循环、C4和景天酸代谢途径的中间代谢物，作为碳、氮、硫的间接氢载体提供NADH，调节ROS的产生和清除[35-37]。玉米*EAR APICAL DEGENERATION1*（*EAD1*）编码铝激活的苹果酸转运体蛋白（ALMT，ALUMINUM ACTIVATED MALATE TRANSPORTER），该蛋白定位于细胞质膜。*EAD1*在玉米幼穗木质部导管组织中特异表达，具有外排苹果酸盐活性；*ead1*功能缺陷突变体幼穗顶端退化、穗长变短、幼穗顶端苹果酸盐含量降低，在幼穗发育早期补充苹果酸盐可使突变体的雌穗表型向野生型部分回复，过表达*EAD1*能增加穗长和行粒数[38]，表明苹果酸盐能通过EAD1介导的幼穗维管组织运输，参与调控玉米雌穗发育过程。水稻中，*EAD1*的同源基因为*OsALMT7/PANICLE APICAL ABORTION1-1*（*PAAB1-1*），其突变体*paab1-1*花序发育后期的顶端小穗退化[39]，说明该基因功能在玉米和水稻中是保守的，且苹果酸盐是直接影响雌穗发育的重要代谢产物。

4　植物激素参与的调控途径

4.1　乙烯

乙烯（Ethylene）是一种化学结构非常简单的气体激素，参与种子萌发、开花、叶片衰老、果实成熟以及非生物胁迫响应等生理过程[40-41]。1-氨基环丙烷羧酸氧化酶（ACO，1-aminocyclopropanecarboxylic acid oxidase）参与乙烯合成的最后一步[42]。在玉米中，抑制乙烯生物合成或响应可提高干旱和低氮条件下的籽粒产量[43]。乙烯与玉米花序分枝发育和小

花育性有关。Ning等[44]发现一个与穗长、小花数目以及育性相关的数量性状位点*qEL7*。*qEL7*的候选基因*ZmACO2*编码参与乙烯合成的ACO酶。*ZmACO2*在小穗成对分生组织的近轴区域、小穗分生组织的半圆区域、小花分生组织和颖片的连接部分表达；敲除*ZmACO2*的家系的果穗长度更长、行粒数更多、穗重更高；相反，相较于野生型家系，过表达家系的果穗长度更短、行粒数更少、穗重更低，表明*ZmACO2*是一个负调控玉米穗长、行粒数和穗重的功能基因；而*ZmACO2*有利自然变异和新创制的启动子编辑的等位基因均能提高杂交种籽粒产量。综上表明，可以通过精细调节乙烯生物合成和信号传导来调控花序和小花发育，进而改良玉米籽粒产量。

4.2 生长素

生长素生物合成分为色氨酸依赖合成途径和非色氨酸依赖合成途径。类黄素单加氧酶（YUC，YUCCA）和色氨酸转氨酶（TAA，tryptophan transaminas）是色氨酸依赖合成途径重要的酶。早期研究证实，玉米中*SPARSE INFLORESCENCE1*（*SPI1*）编码YUC，*VT2*编码TAA，这两个基因中的任何一个突变均严重影响生长素生物合成，并导致花序分枝、小穗和小花发育受到明显抑制，雌穗结实急剧减少[45-46]。AUXIN/LIKE-AUX（AUX/LAX）和PIN-FORMED1（PIN1）分别为生长素输入和输出载体，参与生长素的极性运输。玉米生长素输入载体ZmAUX1突变后雌穗秃尖，雄穗分枝和小花数目减少[47]。*BARREN INFLORESCENCE2*（*BIF2*）编码Ser/Thr蛋白激酶，与调节拟南芥生长素运输的基因*PINOID*（*PID*）同源，*bif2*突变体表现为雄穗光秃，雌穗分枝减少[48]。拟南芥中PID能磷酸化AtPIN1，并调控AtPIN1的亚细胞定位，控制生长素的运输[49]。玉米中BIF2能磷酸化ZmPIN1a，从而影响ZmPIN1a的定位，调控腋生分生组织的发育，并且ZmPIN1a能与bHLH转录因子BARREN STALK1（BA1）互作[50-51]。*BA1*与*BA2*遗传互作并共定位于细胞核。*ba1*与*ba2*表型类似，雌穗缺失，雄穗分枝和小花数目减少，且*ba1*在*ba2*突变体中表现出剂量效应，表明*BA1*和*BA2*共同调控AM发育[52-53]。生长素在细胞中与核受体复合蛋白结合。TRANSPORT INHIBITOR RESISTANT1/AUXIN SIGNALING F-BOX（TIR1/AFB）是SKP/CULLIN1/F-Box（SCF）E3泛素连接酶底物识别亚单元。生长素与TIR1/AFB结合，促进TIR1/AFB与AUX/IAA互作并泛素化AUX/IAA。泛素化修饰的AUX/IAA随后被酶解，激活生长素响应基因*ZmARF*表达[54]。*BARREN INFLORESCENCE1*（*BIF1*）和*BIF4*编码的AUX/IAA蛋白作用于腋生分生组织的生长素信号传递[55]。*bif1*和*bif4*的突变体均会出现小花败育的表型，并且下游与腋生分生组织起始相关的生长素信号响应基因*BA1*和*BA2*表达量下降[52,55]。总之，生长素生物合成、转运及信号途径的各个环节对花序分枝和穗粒数发育都至关重要。

4.3 其他激素

细胞分裂素和脱落酸信号通路可能参与了玉米雄穗分枝数的调控。Qin等[56]利用关联群体鉴定到与玉米雄穗分枝数相关的位点Q^{Dtbn1}。Q^{Dtbn1}属于S8类的F-box蛋白家族，与水稻中的*LARGER PANICLE*（*LP*）高度同源[57-58]。Q^{Dtbn1}可能通过SCF复合体和编码细胞分裂素氧化酶/脱氢酶（CKX，CYTOKININ OXIDASE/DEHYDROGENASE）的*OsCKX*基因通过细胞分裂素途径调控雄穗分枝数。蔗糖非发酵型蛋白激酶（SnRK，SUCROSE NON-FERMENTING-1-RELATED PROTEIN KINASE）SnRK1和SnRK2与脱落酸（ABA，abscisic acid）信号途径相关[59-60]。Q^{Dtbn1}与SnRK1蛋白相互作用，同时SnRK2的底物在Q^{Dtbn1}超表达植株中下调，说明ABA信号途径可能参与了玉米雄穗分枝数的调控。

5 膜系统与信号传导

生物膜系统包括细胞膜、细胞核膜以及内质网、高尔基体、线粒体等有膜围绕而成的细胞器膜。*KERNEL NUMBER PER ROW6*（*KNR6*）是一个影响玉米雌穗小花数目、穗长和行粒数并调控玉米产量的QTL，其功能基因编码丝氨酸/苏氨酸蛋白激酶KNR6，KNR6与ADP核糖基化因子GTP酶激活蛋白（AGAP，ARF-GTPase ACTIVATES PROTEIN）互作并磷酸化AGAP[61]。*agap*敲除突变体花序和根发育缺陷、全株矮化、叶片变短；高尔基体结构异常，内吞作用和囊泡聚集受到影响[62]。拟南芥中，AGAP家族基因*VASCULAR NETWORK DEFECTIVE3*（*VAN3*）参与生长素信号在反式高尔基体网络中的运输，功能丧失的*van3*突变体叶片维管系统发生紊乱[63]。水稻中*OsAGAP*与生长素载体的囊泡运输有关，超表达*OsAGAP*抑制水稻初生根和次生根的发育[64]。AGAP可能与Arf1互作形成KNR6-AGAP-Arf1复合体通过囊泡运输途径调控花序发育，影响穗长和行粒数[62]。磷脂是细胞膜的骨架成分，也是质膜上的受体和信号物质，能响应外界信号刺激。磷脂酰肌醇（PI，phosphatidyl inositol）是指磷脂酰甘油的磷脂

基团上连接了一个肌醇环结构形成的化合物。磷脂酰肌醇的肌醇环上的碳原子可以被磷酸化，形成磷脂酰肌醇磷酸（PIP，phosphatidyl inositol phosphate）。磷脂酰肌醇磷酸主要分为PI(3)P、PI(4)P、PI(5)P、PI(3,4)P_2、PI(3,5)P_2、PI(4,5)P_2和PI(3,4,5)P_3等7类化合物[64]。穗行数QTL *qKRN5b*的候选基因编码属于核酸内切酶/核酸外切酶/磷酸酶（EEP，exonuclease endonuclease phosphatase）家族的磷脂酰肌醇磷酸5-磷酸酶（5Ptase），参与磷酸肌醇代谢途径。PI(4,5)P_2和PI(3,4,5)P_3是KRN5b的特异性底物[65]。拟南芥中，5Ptase蛋白COTYLEDON VASCULAR PATTERN2（CVP2）及其同源蛋白CLAVATA1（CLV1）定位于内质网膜系统[66]水解膜上的PI(4,5)P_2，而CVP2则通过水解PI(3,4,5)P_3，调节叶片对ABA的敏感性和叶片维管组织的发育模式[67]。*KRN5b*在幼穗的维管组织表达，*krn5b*突变体造成了维管形成层发育障碍，最终小穗成对分生组织发育异常。*KRN5b*对花序发育的调控可能与内源磷酸肌醇的含量平衡和维管组织的形成密切相关[68]。

6　展望

转录因子和非编码序列分别参与花序分枝和穗粒数发育的分子调控。通过全基因组分析，基因近远端包含潜在顺式调控元件的开放染色质区域（OCR，open chromation region）也参与调控花序分枝早期发育[69-70]。同时，转录因子和非编码元件之间的动态互作精细调控花序分枝和穗粒数发育[71]。例如，长链非编码RNA（lncRNA，long non-coding RNA）可能作为远端调控因子调控转录因子表达[72]。随着测序技术的发展，可以通过三代测序技术鉴定参与花序分枝和穗粒数发育调控的非编码区，探究非编码区的遗传效应、作用机理、有利等位变异的演化规律及育种利用途径。

植物激素之间以及代谢物与激素之间交互作用，共同调控花序分枝和穗粒数发育。乙烯和其他激素的交互作用调控花序分枝和穗粒数发育。乙烯能刺激生长素合成但抑制JA合成，同时也能影响BR、CK和赤霉素（GA，gibberellins）的含量[44, 73]。ROS与Auxin可能通过交互作用调控花序分枝和穗粒数发育。在*grx*三基因突变体中，Auxin相关基因差异表达，GRX-FEA4可能通过ROS与Auxin交互作用调控花序分枝和穗粒数发育。因此，解析激素与激素之间，激素与代谢物之间的关系，能帮助我们进一步了解花序分枝和穗粒数发育的调控网络。

花序分枝和穗粒数发育调控途径的人工定向优化与优异等位基因创制，有利于高效利用玉米产量关键基因，实现精准改良。大部分与花序分枝和穗粒数发育相关突变体具有剧烈的表型变异，通过启动子编辑获得弱突变基因能有效提高产量。Liu等[74]针对*ZmCLE7*和*ZmFCP1*启动子区域，利用染色质转座酶可及性测序（ATAC-seq，assay for transposase-accessible chromatin with high-throughput sequencing）和微球菌核酸酶测序技术（MNase-seq，micrococcal nuclease sequencing）等数据进行染色质开放区域的分析，结合进化分析，预测启动子区域可能的保守调控位点，设计sgRNA靶向其启动子区域，获得*ZmCLE7*和*ZmFCP1*的弱突变体，有效提高雌穗产量。本研究也概述了糖信号、苹果酸信号以及磷脂酰肌醇参与花序分枝及穗粒数发育的调控途径，这可能是研究花序各类分生组织起始和维持分子机理的新方向。同时本研究建立了花序分枝和穗粒数发育基因调控网络（图1），有利于拓展对玉米花序分枝和穗粒数发育的调控认知。随着单细胞测序技术和3D基因组技术的发展，下一步可以从细胞水平阐述花序分枝和穗粒数发育并确定分枝发育相关边界基因[70, 75]，为今后发现并完善复杂的花序分枝和穗粒数发育分子调控网络提供新的思路。

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