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水稻胚乳淀粉合成及其育种应用

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摘 要:淀粉是稻米胚乳的主要组成成分,具有重要的生物学功能和经济价值。籽粒胚乳淀粉合成和贮藏于一种异质化的质体中,即淀粉体。而籽粒形成期,胚乳中富集大量淀粉以充实淀粉体胞内空间并形成晶体状的淀粉颗粒,因此胚乳淀粉组成和结构会极大地影响稻米产量和食味品质的形成。本文综述了胚乳淀粉合成的分子途径,改良稻米产量和食味品质的分子策略,以期为优质稻米育种实践提供一定的理论依据。

关键词:淀粉;食味品质;育种改良;胚乳;水稻
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水稻(*Oryza sativa* L.)是最重要的粮食作物之一,其籽粒由胚、胚乳和种皮组成,而胚乳是籽粒发育过程中的主要贮藏器官[1]。淀粉是主要的贮藏物质,占谷物胚乳干重的85%,是人类食物中的主要能量来源,因此,淀粉合成对稻米产量形成具有重要的作用[2]。近年来由于矮杆基因[3]和杂种优势[4]的广泛利用,水稻产量得到了显著提升。然而,随着人民生活水平的提高,对稻米品质的要求也越来越高,尤其是食味品质(eating and cooking qualities,ECQs),决定了其在市场中的商品经济价值和消费者认可度,引起了消费者和研究者们的广泛关注[5]。稻米品质主要包括外观特性、食味品质和微量元素含量[6-7]。稻米品质因饮食文化的差异而表现出不同的偏好性[8],但除少数地区偏好微量元素和外观外[5],大多数国家和地区更关注食味品质[8]。

淀粉不仅是植物体内碳水化合物的主要贮藏形式,而且还具有重要的生物学功能和经济价值[9-10]。随着优质稻米市场需求量的逐渐增加,充分了解淀粉合成及其调控机制对于稻米品质的定向改良和标记辅助育种的开发具有重要的意义[11]。目前,参与淀粉代谢的酶和路径虽然均已被揭示,但关于淀粉合成的具体调控网络极其复杂,限制了对淀粉的定向改良[11-13]。本文综述了通过调控稻米淀粉合成以改良稻米产量和通过调控直链和支链淀粉合成以改良稻米食味品质的策略,以期为稻米的分子改良和育种提供一定的理论依据和实践指导。

1 水稻胚乳淀粉的合成途径

水稻淀粉合成包括临时淀粉合成和贮藏淀粉合成2种类型。临时淀粉主要发生于光合器官的质体中,受昼夜周期节律的调控表现为节律性的循环[14-15];相反,根、茎、种子胚乳等贮藏器官中长期储存的淀粉合成则依赖于从胞质中输入碳前体,即蔗糖和ATP[11,16],这一过程主要通过蔗糖转运体实现[17]。

1.1 叶片中蔗糖的合成

蔗糖的合成主要是通过叶片叶绿体中的卡尔文循环和胞质中的一系列生化反应完成[15,18]。该过程从丙糖-P到蔗糖合成共包括7个步骤,需要果糖-1,6-二磷酸醛缩酶(fructose-1,6-bisphosphate aldolase,F2BA)、果糖-1,6-二磷酸酶(fructose 1,6-bisphosphatase,F2BP)、磷酸葡萄糖异构酶

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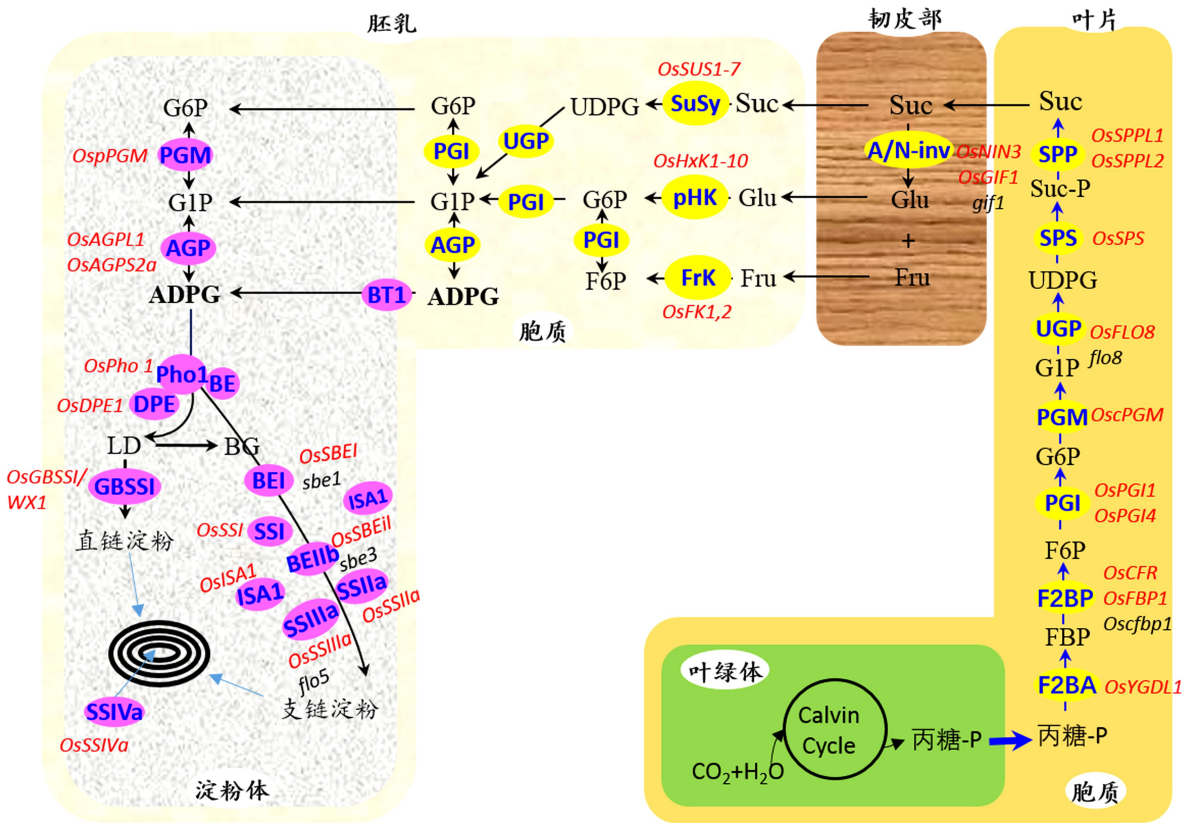
(phosphoglucoseisomerase, PGI)、磷酸葡萄糖变位酶(phosphoglucomutase, PGM)、UDPG 焦磷酸化酶(UDP-glucose pyrophosphorylase, UGP)、磷酸化合成酶(sucrose phosphate synthase, SPS)和蔗糖磷酸化酶(sucrose phosphate phosphatase, SPP)共 7 种酶参与[19-20](图 1)。



注:蓝色字体表示水稻胚乳淀粉合成途径中的酶,参与胞质和质体的酶分别用黄色和紫色背景表示,红色斜字体表示酶的编码基因,黑色小写斜体为突变体。F2BA:果糖-1,6-二磷酸醛缩酶;FBP:果糖二磷酸;F2BP:果糖-1,6-二磷酸酶;F6P:果糖-6-磷酸;PGI:磷酸异构酶;G6P:葡萄糖-6-磷酸;PGM:磷酸葡萄糖变位酶;G1P:葡萄糖-1-磷酸;UGP:尿苷二磷酸葡糖焦磷酸化酶;UDPG:尿苷二磷酸葡萄糖;SPS:蔗糖磷酸化合成酶;Suc-P:蔗糖-磷酸;SPP:蔗糖磷酸化酶;Suc:蔗糖;Glu:果糖;Fru:葡萄糖;A/N-inv:蔗糖酶;SuSy:蔗糖合成酶;FrK:果糖激酶;pHK:质体己糖激酶;BT1:腺苷酸转座子 1;AGP:ADPG 焦磷酸化酶;ADPG:ADP 葡萄糖;Pho1:质体淀粉磷酸化酶;DPE:不对称酶;BE:分支酶;LD:线性葡聚糖;BG:分支葡聚糖;GBSSI:颗粒结合淀粉合成酶Ⅰ;BEI:分支酶Ⅰ;SS:可溶性淀粉合成酶;ISA1:淀粉异构酶。

Note: The blue typefaces represent the enzymes of starch biosynthesis pathway in rice. Enzymes involved in steps for cytosol and plastids are shown in yellow and purple, respectively. Genes for starch biosynthetic enzymes are shown in red italic folds, and the rice mutants are shown in black italic. F2BA: Fructose-1, 6-bisphosphate aldolase. FBP: Fructose diphosphate. F2BP: Fructose 1, 6-bisphosphatase. F6P: Fructose-6-phosphate. PGI: Phosphoglucoseisomerase. G6P: Glucose-6-phosphate. PGM: Phosphoglucomutase. G1P: Glucose-1-phosphate. UGP: UDP-glucose pyrophosphorylase. UDPG: UDP-glucose. SPS: Sucrose-phosphate-synthase. Suc-P: Sucrose-phosphate. SPP: Sucrose phosphate phosphatase. Suc: Sucrose. Glu: Glucose. Fru: Fructose. A/N-inv: Alkaline/neutral invertase. SuSy: Sucrose synthase. FrK: Fructokinase. pHK: Plastidial hexokinase. BT1: Brittle 1 anadenylate translocator. AGP: ADP-glucose pyrophosphorylase. ADPG: ADP-glucose. Pho1: Plastidial starch phosphorylase1. DPE: Disproportionating enzyme. BE: Branching enzyme. LD: Linear dextrin. BG: Branched glucan. GBSSI: Granule bound starch synthase Ⅰ. BEI: Branching enzyme. SS: soluble starch synthase. ISA1: Isoamylase 1.

图 1　水稻胚乳淀粉合成途径

Fig.1　Starch biosynthesis pathway in rice endosperm

1.2　叶片→胚乳细胞中蔗糖的转运

叶片中合成的蔗糖通过共质体或质外体途径转运至贮藏器官中,作为淀粉体中的能量和淀粉合成的碳源,该过程因物种、器官或组织而存在差异[17,21]。水稻中主要包括 3 种方式,即细胞壁蔗糖酶将蔗糖分解为葡萄糖和果糖,然后由己糖转运体进行胞间转运[11];通过质膜结合的特异性蔗糖转运体和液泡蔗糖转运体,将蔗糖转入液泡进行临时储存[22-23];通过内吞作用吸收蔗糖,然后转入胚乳细胞的中央液泡中存储[24](图 1)。

1.3 胚乳细胞中蔗糖→淀粉的转化

转入胚乳细胞中的蔗糖在细胞质中经过一系列生化反应转化为 G6P 后,进入淀粉体进行淀粉的合成(图 1)。谷物胚乳发育过程中,淀粉通过淀粉合成酶的协同作用而合成和富集[25],包括 ADP-葡萄糖焦磷酸化酶(ADP-glucose pyrophosphorylase,AGPase),为淀粉支链延伸反应提供底物;UDPGase,用于 UGP 的合成;淀粉合成酶(starch synthase,SS),用于 α-葡聚糖链的延伸;颗粒结合淀粉合成酶(granule bound starch synthase,GBSS),用于直链淀粉的合成;分支酶(starch branching enzyme,SBE),用于支链淀粉中 α-1,6-糖苷键的形成;脱分支酶(debranching enzyme,DBE),包括淀粉异构酶(isoamylase,ISA)和支链淀粉酶(pullulanase,PUL),用于切除由 SBE 形成的错误分支链;质体淀粉磷酸化酶(plastidial starch phosphorylase1,Pho 1),用于淀粉晶体结构的形成。

1.3.1 *细胞质中蔗糖→G6P 的转化* 胚乳细胞中,转入的蔗糖在胞质中转化为 G6P 包括 3 个步骤:首先由 SuSy 降解为果糖和 UDPG[26];然后 UDPG 经 UDPase 分解为 G1P 和焦磷酸(pyrophosphoric acid,PPi);最后,G1P 由胞质葡萄糖磷酸变位酶(cytosolic phosphoglucomutse,cPGM)转化为 G6P[27]。

1.3.2 *淀粉体中 G6P→淀粉的转化* 胞质中生成的 G6P 进入淀粉体后,在 PGM、AGP、SS 等催化酶的作用下合成淀粉[28-29]。此外,由于淀粉体不具有合成 ATP 的能力,因此淀粉合成所需的 ATP 必须从胞质中转入[30]。禾谷类胚乳细胞中也会集聚胞质 ADPG,在 BT1 转运蛋白的作用下进入淀粉体用于淀粉的合成[31]。因此,目前有研究者认为,蔗糖通过胞质 SuSy 酶作用分解为 ADPG,然后 ADPG 进入淀粉体进一步合成淀粉[25, 32](图 1)。

1.4 直链淀粉和支链淀粉的合成

淀粉由线性葡聚糖和分支葡聚糖组成,葡聚糖聚合进一步形成非溶性的半晶体状淀粉颗粒,淀粉合成需要多个淀粉合成相关酶的配合,包括用于直链淀粉合成的 GBSSI;用于支链淀粉合成的可溶性淀粉合成酶 SSI、SSIIa 和 SSIIIa、分支酶 BEI 和 BEIIb、不对称酶(DPE)、质体淀粉磷酸化酶(Pho1)和淀粉异构酶(ISA)[10,14](图 1)。Pho1 分别与 DPE、BE 作用将 ADPG 转化为线性葡聚糖和分支葡聚糖,线性葡聚糖在 GBSSI/Wx 作用下转化为直链淀粉;而分支葡聚糖到支链淀粉的转化则更为复杂[33]。SSI、SSIIa 和 SSIIIa 分别用于短链(6 ≤ DP ≤ 12)、中间链(13≤DP≤24)和长链(DP >25)的合成,而 BEI 和 BEIIb 分别用于内、外分支的形成,ISA 用于切除非正确的分支链,SSIVa 则被认为位于淀粉颗粒的中央,参与淀粉结构的形成[33-34]。

2 胚乳淀粉合成途径在育种中的应用

通过常规育种方法改良稻米品质较耗时且费力,而利用基因工程、分子标记辅助选择等技术对目标基因进行调控,对水稻育种改良效果更佳且更方便。

2.1 调控淀粉含量改良稻米产量

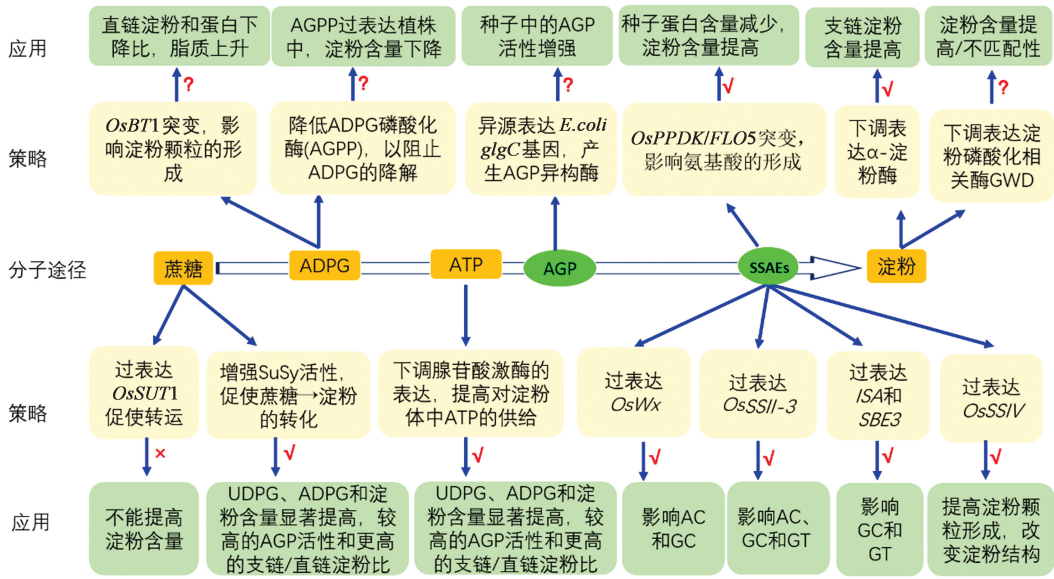
2.1.1 *促进蔗糖的降解* 由图 2 可知,通过 SuSy 活性的增强,可促使蔗糖→淀粉的转化,提高稻米的淀粉含量和产量。研究表明,SuSy-过表达株系中,UDPG、ADPG 和淀粉含量均显著高于野生型,表现为较高的 AGP 活性和支链/直链淀粉比[25-32, 35]。因此,可通过在质体中表达 SuSy 以产生更多 ADPG 从而提高淀粉含量。其机理可能是 SuSy 与酸转化酶(acid invertase)通过竞争底物蔗糖以调控淀粉的含量[35];淀粉合成速率受 SuSy-AGP-ADPG 转运体与支链淀粉共同的影响[32]。

2.1.2 *增加 ATP 的供给* 通过下调质体腺苷酸激酶(plastidial adenylate kinase,*PAK*)的表达,提高对淀粉体中 ATP 的供给(图 2)。腺苷酸激酶用于将 ATP 催化为 ADP 和 AMP,其下调表达可以提高 ADPG 和淀粉含量,这可能是由于其活性减弱而使 ATP 库增加[18]。

2.1.3 *改变 ADPG 的转运* 通过增强 BT1 蛋白的表达,以增强对胞质 ADPG 向淀粉体的转运,从而提高胚乳中淀粉含量[20, 36]。*bt*1 突变体生长异常且不育,这与胚乳淀粉体中 ADPG 转运活力下降和淀粉缺失有关[37],同时可能与线粒体中某些代谢有关[38]。*osbt*1 突变体表现为白心胚乳,直链淀粉和蛋白均下降,其中直链淀粉含量下降至 12%,但脂质含量则上升,表明 OsBT1 在淀粉合成和淀粉颗粒形成中具有重要的作用[31]。

2.1.4 *增强 AGP 活性* 通过增强 AGP 活性,以提高淀粉含量[28, 39],主要包括 2 种方式(图 2)。一是在植物体内异源表达大肠杆菌 *glgC* 基因,以产生 AGP 异构酶,可显著增强种子中的 AGP 活性[40];二是通过异源表达 AGP 大亚基的编码基因 *Sh2r6hs* 或 *SH2*[41],以及小亚基的编码基因 *BT2*,其在水稻中的异源表达可显著提高 AGP 活性和种子淀粉含量[42]。

2.1.5 *阻止淀粉的降解* 胚乳细胞中,淀粉的富集同时受淀粉合成和淀粉降解的影响,因此通过抑制淀粉



注：“√”表示该策略可行；“×”和“？”分别表示该策略不可行和尚需验证；SSAEs：淀粉合成相关酶。

Note：‘√’represents the strategy is feasible. ‘×’ and ‘?’ represent the strategy unfeasible and uncertain, respectively. SSAEs: Starch synthesis-associated enzymes.

图 2　利用胚乳淀粉合成途径改良稻米产量和食味品质的育种策略

Fig.2　Strategies for improvement on grain yields and ECQs by using mechanisms of rice endosperm starch biosynthesis

的降解以提高淀粉含量是可行的[11, 32]。α－淀粉酶[43-44]和淀粉磷酸化相关酶 GWD 在胚乳淀粉降解中具有重要的调控作用[45]。高温条件下，α－淀粉酶编码基因的下调表达会增强淀粉的含量[44]。然而，尽管 *GWD* 的下调表达也会提高淀粉的含量，但与稻米干重、分蘖数、有效穗数等性状的增加趋势并不一致[45]。

2.2　调控直链/支链淀粉改良食味品质

食味品质的形成主要受自身直链淀粉含量（amylose content，AC）、糊化温度（gelatinization temperature，GT）、香味物质、脂肪酸含量、胶稠度（gel consistency，GC）和蛋白质含量的影响[46-50]。此外，直链淀粉/支链淀粉的比例以及支链淀粉的精细结构决定了水稻籽粒的理化性质、营养品质和最终产量[51]。

水稻中，颗粒结合淀粉合成酶Ⅰ（granule bound starch synthase Ⅰ，GBSSI）过表达会提高 AC 和 GC 含量，但对 GT 含量影响较小；*SSII*-3 过表达会降低 AC、GC 和 GT 含量；*ISA* 和 *SBE*3 过表达均会降低 GC 和 GT 含量[4,52]。淀粉合成酶的过表达会明显提高淀粉含量[53]。此外，SSIIIa 和 Wx 共同参与抗性淀粉的合成，SSIIIa 对抗性淀粉的调控依赖于 *Wx* 基因的高表达，而 SSIIIa 突变则会降低 *Wx* 的表达进而导致抗性淀粉含量下降和直链淀粉-脂质复合体的减少[29]。

3　展望

水稻胚乳淀粉的合成涉及叶片中淀粉合成前体物蔗糖的合成与转运、胚乳细胞中蔗糖到 ADPG 的转化、胚乳细胞中直链淀粉和直链淀粉的合成以及淀粉颗粒的形成等生物学进程和多个不同组织的协同配合，因此根据水稻胚乳淀粉的合成机制，利用分子生物学的技术和方法，定向改良稻米的产量和品质，将极大提高水稻育种改良的效率和精确度。

淀粉合成对稻米品质的影响是水稻基础科学研究热点之一[12, 52-53]。然而，淀粉合成涉及一个复杂而有序的代谢网络和细胞学进程，需要多个淀粉合成酶的协同作用。因此，通过淀粉合成的分子机制解析稻米产量和 ECQs 的形成仍面临诸多挑战和问题，如水稻籽粒发育过程中，叶片中光合作用产物（如蔗糖）由韧皮部转运到胚乳细胞的调控机制；胚乳发育过程中，如何调控由未分化的前质体到功能性淀粉体的转化；在淀粉合成和淀粉结构形成过程中相关蛋白复合体如何实现有序调控碳的高效利用；环境-基因互作如何调控不同淀粉晶体结构的形成等均需要进一步更深入的研究。

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Starch Biosynthesis in Rice Endosperm and Its Applications in Breeding

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Abstract: As the major component of rice endosperm, starch possesses important biological functions and economic values. Amyloplast is one sort of specialized plastid for starch synthesis and storage in grain endosperm. During filling periods, grain endosperm accumulates a great amount of starch to fill the intracellular space of amyloplast for further formation of crystal starch granules. Thus, starch biosynthesis and structures in endosperm have great effects on the yields and the formation of eating and cooking qualities (ECQs). Here, we reviewed the molecular pathway of starch biosynthesis in rice endosperm, and proposed some strategies for improvement on yields and ECQs, which would provide theoretical basis for rice breeding.

Keywords: starch, eating and cooking quality, breeding improvement, endosperm, rice