东北农业科学　2025,50(2):93-99
Journal of Northeast Agricultural Sciences　DOI: 10.16423/j.cnki.1003-8701.2025.02.013

玉米淀粉合成关键酶的研究进展

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摘　要:玉米(*Zea Mays* L.)淀粉是在一系列酶的催化下合成的,是一个极其复杂的过程。本文综合了近几年玉米淀粉合成关键酶已有的文献成果,系统总结了四种关键酶在淀粉合成中的作用,分析了淀粉合成关键酶的调节因素,重点阐述了ADP-葡萄糖焦磷酸化酶(AGPase)、淀粉合酶(SS)、淀粉分支酶(SBE)、淀粉去分支酶(DBE)四种关键酶的特性及调控机理。研究表明:多种关键酶协同参与玉米淀粉合成过程,且其作用受多种基因表达调控。淀粉依次在淀粉合酶、ADP-葡萄糖焦磷酸化酶、淀粉分支酶及淀粉去分支酶的作用下合成;同时,四种关键酶的作用也受到各种基因的表达调控。通过总结、归纳国内外玉米淀粉合成关键酶的研究成果,为玉米淀粉合成及品质改良提供新的思路和方法。

关键词:玉米淀粉;ADP-葡萄糖焦磷酸化酶;淀粉合酶;淀粉分支酶;淀粉去分支酶
中图分类号:Q946.5　　**文献标识码**:A　　**文章编号**:2096-5877(2025)02-0093-07

Research Progress on Key Enzymes in Maize Starch Biosynthesis

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Abstract: Maize (*Zea mays* L.) starch biosynthesis is a highly complex process catalyzed by a series of enzymes. This article summarizes the existing literature on key enzymes in maize starch synthesis in recent years, systematically summarizes the roles of four key enzymes in starch synthesis, analyzes the regulatory factors of key enzymes in starch synthesis, and focuses on the characteristics and regulatory mechanisms of four key enzymes: ADP glucose pyrophosphorylase (AGPase), starch synthase (SS), starch branching enzyme (SBE), and starch debranching enzyme (DBE). Research indicates that multiple key enzymes cooperatively participate in maize starch synthesis, with their activities regulated by the expression of various genes. starch synthesis proceeds sequentially under the action of starch synthase, ADP-glucose pyrophosphorylase, starch branching enzyme, and starch debranching enzyme. Meanwhile, the functions of the four key enzymes are also regulated by the expression of various genes. By summarizing both domestic and international research on the key enzymes involved in maize starch synthesis, this review provides new insights and methodologies for improving starch synthesis and quality in maize.

Key words: Maize starch; ADP glucose pyrophosphorylase; Starch synthase; Starch branching enzyme; Starch debranching enzyme

玉米由其野生祖先大刍草驯化而来[1-3],经过长期的驯化和改良,其野生特性已发生显著改变[4],高产始终是玉米育种的主要目标。从其热带起源开始,玉米就适应了各种环境,成为全球生产力最高的农作物[5]。此外,世界不同地区的消费者偏好和饮食习惯导致对淀粉类食品的不同需求,并需要具有不同理化性质的谷物淀粉,现在有许多针对特定目的而开发的新型玉米,例如青贮玉米[6]、蜡质玉米、优质蛋白玉米[7]、爆裂玉米以及甜玉米等[8-9]。玉米作为我国第一大粮食作物,种植面积自2009年以来一直居于我国各作物首位[10]。玉米需求的日益多样化使得玉米已成为最重要的农作物之一,提供食物、饲料和生物燃料等资源[11]。

由于人口增长和环境恶化对粮食生产的需求增加,人们对改进农作物育种策略的兴趣日益浓

收稿日期:2024-04-14
项目基金:陇南市科技计划项目(2023-S·QKJ-30、2023-S·QKJ-33);甘肃省青年科技基金项目(21JR7RK915)
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厚[12]。而淀粉占人类日常食物摄入量的55%~75%,并且是家畜饲料的主要来源[13],因此,谷物淀粉生产的进步尤为重要。在玉米籽粒中,淀粉含量占成熟种子的75%左右,因此淀粉是玉米产量的主要贡献者[14]。在玉米中通过研究淀粉合成的关键酶,分析调控淀粉含量和淀粉品质等性状的生理作用,是实现农业和工业未来发展的重要举措。

1 淀粉的生物合成

玉米是我国重要的粮食和饲料作物,其种植面积和总产量位居首位,也是最适合作为工业原料且加工深度最高的粮食作物。籽粒中淀粉含量直接决定了玉米的产量与品质。玉米淀粉是在一系列酶的催化下合成的,是一个极其复杂的过程。如图1所示,首先在玉米叶片中通过光合作用产生蔗糖,蔗糖在*shrunken1*(*Sh1*)基因编码的蔗糖合酶催化下转化为UDP-葡萄糖和果糖[15]。UDP-葡萄糖在UDPG焦磷酸化酶作用下形成G-1-P,下一步骤中由*shrunken 2*(*Sh2*)和*brittle endosperm2*(*Bt2*)基因编码的AGPase是玉米淀粉合成的限速酶[16-18],AGPase将ATP和G-1-P转化为ADP-Glc和焦磷酸盐(PPi)[19]。BT1是负责ADPG转移进入玉米胚乳造粉体中的腺苷酸转运蛋白[20-21],ADPG通过BT1转运蛋白从细胞质转运到造粉体中,并被用作淀粉合成的底物[22]。淀粉合酶(SS)将G-1-P分子顺序添加到正在生长的淀粉链非还原末端上,延长葡聚糖链合成淀粉。玉米中由*waxy1* (*WX1*)基因编码的颗粒结合型淀粉合酶(GBSS)负责直链淀粉合成[23-24],直链淀粉延伸因子1(*Ae1*)基因编码SBEIIb亚型,该亚型水解支链淀粉中的环状α-1,4糖苷键,并将其与支链淀粉中的环状α-1,6糖苷键分支点重新连接形成支链淀粉。*sugary1* (*Su1*)基因编码的异淀粉酶类型的去分支酶,在淀粉分支酶(SBE)和淀粉去分支酶(DBE)的共同作用下形成支链淀粉[25]。

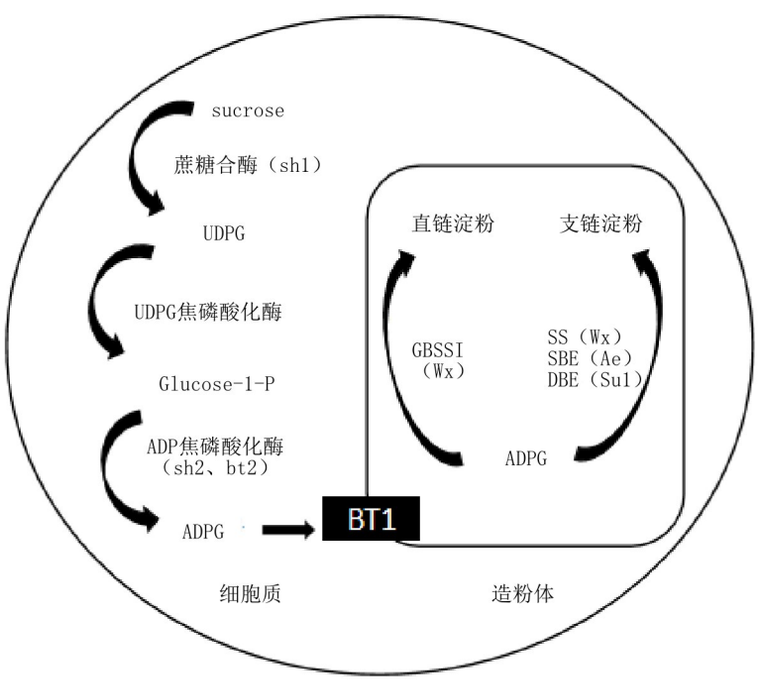

图1 淀粉的生物合成途径

Fig.1 The biosynthetic pathway of starch

2 玉米淀粉合成的关键酶

玉米胚乳中,淀粉由支链淀粉和直链淀粉组成,AGPase负责合成ADP葡萄糖(ADPG),ADP葡萄糖是淀粉合成的底物。支链淀粉至少由淀粉合酶(SS)、淀粉分支酶(SBE)和淀粉去分支酶(DBE)共同参与,支链淀粉中α-1,4糖苷键的延伸主要由淀粉合酶完成;它在淀粉合成相关酶(SSRE)中具有最多的亚型和最复杂的功能[26]。淀粉分支酶(SBE)是唯一作用于葡聚糖产生由α-1,6糖苷键连接的分支的酶,它包括三种类型:SBEI(SBE1),SBEII和SBEIII[27]。淀粉去分支酶(DBE)可水解α-1,6糖苷键,纠正淀粉合成中的错误分支,保证支链淀粉的有序合成[28]。在玉米胚乳中,参与支链淀粉合成的酶通常以多酶复合物的形式起作用[29]。直链淀粉由颗粒结合的淀粉合酶I(GBSSI)合成,该

酶由蜡质(*Wx*)基因编码,GBSSI控制直链淀粉在淀粉颗粒表面磷酸化后以低聚物的形式合成[30]。

2.1 ADP葡萄糖焦磷酸化酶(AGPase)

AGPase催化G-1-P和ATP转化为ADP-Glc和焦磷酸,AGPase是一种变构酶,是淀粉生物合成过程中的关键酶,也是淀粉合成的限速酶,其活性受小效应分子的调节。在植物中,AGPase被3-磷酸甘油醛(3-PGA)激活,并被无机磷酸盐(Pi)灭活[31]。在叶绿体中磷酸三糖的含量升高也会导致3-PGA含量升高,从而激活AGPase。磷酸三糖含量降低同样会导致3-PGA降低和Pi升高而抑制AGPase的活性[32]。AGPase在糖中也会被NADP-硫氧还原酶C和硫氧还蛋白Trx*f*1还原而被糖激活,这会导致两个小亚基之间失去二硫键[33],氧化还原激活提高了AGPase对3-PGA和Pi的变构调节的敏感性[34]。

AGPase是由两个大亚基和两个小亚基组成的异源四聚体,*Bt2*和*Sh2*分别编码AGP酶的小亚基(SSU)和大亚基(LSU),从葡萄糖1-磷酸和ATP生成ADP-葡萄糖(ADPG)和焦磷酸盐。淀粉生物合成中的经典突变体包括玉米的*sh2*和*bt2*,它们都缺乏胚乳中的AGPase活性。编码AGPase大小亚基的基因通过复制产生,并且这两个亚基都是AGPase活性所必需的。植物AGPases具有组织特异性,尽管每个亚基都具有显著的序列同源性,但小亚基通常比大亚基更保守[35]。通过对编码大亚基基因的序列分析将AGPase分为四类:茎/块茎、叶、果实/根以及胚乳AGPase。AGPase之间的差异在酶活性调节性质上也是可以分辨的,叶片、马铃薯块茎和番茄果实对3-PGA和Pi敏感,而胚乳AGPase(除水稻外)对3-PGA和Pi较不敏感。对AGPase调节特性的修饰提高了马铃薯块茎、玉米、小麦以及水稻的淀粉产量[36]。

2.2 淀粉合酶(SS)

淀粉合酶通过α-1,4糖苷键在线性葡聚糖链的非还原端添加葡萄糖基单元,通过葡聚糖链的不断延伸合成淀粉。淀粉合酶可以分为颗粒结合型淀粉合酶(Granule bound starch synthase, GBSS)与可溶性淀粉合酶(Soluble starch synthase, SSs)两大类[37]。大多数植物中含有多种同工型的淀粉合酶,根据氨基酸序列的不同,它们可以分为六类:SSI, SSII, SSIII, SSIV, SSV和GBSS[38]。GBSS更多参与直链淀粉多糖链的延伸,而SSs更多参与支链淀粉多糖链的合成延伸[39]。目前研究表明,GBSS存在GBSSI和GBSSII两种同工型酶,其中GBSSI编码蜡质基因,负责存储组织中的直链淀粉合成。GBSSII负责编码果皮、叶、茎以及根等组织中直链淀粉的合成[40]。研究发现,除SSV尚无相关研究报道外,SSI, SSII和SSIII对于建立正确的支链淀粉结构有重要作用。SSI先将分支延长至大约8~10 Glc单位的长度,SSII进一步将这些链延长至大约13~18 Glc单位[41]。SSIII则合成长的且跨簇的支链淀粉链。SSIV似乎在淀粉颗粒形成的起始阶段中起着至关重要的作用[42],对支链淀粉的结构或直链淀粉的合成没有重大影响[43]。

谷物胚乳中GBSS的突变影响了直链淀粉的合成。玉米中GBSSI由*Waxy*(*Wx*)基因编码,*wx*突变体的籽粒总淀粉含量没有变化,但直链淀粉的合成受到影响,含量大幅度降低,因此认为GBSSI催化直链淀粉合成。玉米中SSIIa是由*Sugary2*(*Su2*)基因编码的,*Su2*突变使直链淀粉含量增加,支链淀粉中短葡聚糖链的丰度增加和中间长度链减少,糊化温度降低。SSIII是由*Dul*基因编码的,在胚乳中高水平表达。*Du1*突变后玉米胚乳光泽变暗,直链淀粉的含量增加,支链淀粉的含量降低,链长分布改变,链长分析揭示该酶负责合成DP 25-36的葡聚糖链[44]。

2.3 淀粉分支酶(SBE)

淀粉分支酶(SBE)是一种葡萄糖基转移酶,是支链淀粉中α-1,6糖苷键保持高度规则的型态所必需的[45]。暂存淀粉和储藏淀粉均由直链淀粉和支链淀粉聚合物组成,其中支链淀粉是淀粉的主要成分,约占玉米贮藏淀粉的70%[46]。SBE通过将α-1,6糖苷键分支点引入线性α-1,4糖苷键连接的葡聚糖链来催化支链淀粉的形成。引入支链不仅改变了淀粉的许多化学和物理性质,而且通过增加非还原末端的数量促进了淀粉的合成。因此,SBE对植物中合成淀粉的数量和质量至关重要[47]。

根据SBE的结构相关性将它们分为两个不同的家族,并根据玉米的原型家族成员进行命名。SBEI家族由玉米SBEI、水稻SBEI以及豌豆SBEII组成。SBEII家族包括玉米SBEIIa和SBEIIb、水稻SBEIII以及豌豆SBEI[48]。在玉米中鉴定出三种SBE亚型:SBEIa、SBEIIa以及SBEIIb,但它们的表达方式差异很大。其中编码SBEIa、SBEIIa以及SBEIIb的基因存在组织特异性并且在籽粒发育过程中受到差异调节。虽然SBEIa的体外特性不同于SBEIIa和SBEIIb,但*sbeIa*或*sbeIIa*的突变体研究显示,籽粒中的淀粉结构并没有因为缺乏

SBEIa或SBEIIa而受到影响[49]。相反，缺乏*sbeIIb*的突变体导致胚乳支链淀粉结构发生重大变化[50]。研究发现SBE亚型之间在酶学性质上具有显著的差异性，属于SBEI家族的SBE对直链淀粉的亲和力比较高，并且更优先使用较短的葡聚糖链来进一步形成淀粉分支。并且SBEI和SBEII家族在种子发育过程中受到不同的调控，SBEII家族基因比SBEI家族基因更早在发育的种子中表达[51]。

SBEI和SBEII编码基因呈现时间和组织特异表达。SBEI在胚发育早期表达量相对较高，而SBEII在较晚时期表达。玉米中SBEIIb专一表达于胚和胚乳中，而SBEIIa则表达于胚、叶和其他营养组织中。SBEI在SBEII之后表达，且以直链淀粉为底物催化长链α-1,6糖苷键的分支链，SBEII以支链淀粉为底物，催化短链α-1,6糖苷键[52-53]。

2.4 淀粉去分支酶(DBE)

淀粉生物合成所必需的第三种酶是能水解α-1,6糖苷键的淀粉去分支酶(DBE)。在植物中存在两种DBE类型，为支链淀粉酶型淀粉去分支酶(PUL)和异淀粉酶型淀粉去分支酶(ISA)[53-54]。DBE蛋白由三个ISA蛋白和一个PUL蛋白构成，通过比较DBE编码基因的碱基序列，并推测ISA和PUL在植物进化过程中同时形成，并且编码的基因严格保守，在多糖链的合成过程中起不同的作用，功能并不重叠。

ISA突变通常会导致淀粉含量下降，支链淀粉结构异常、颗粒形态改变以及异常高度分支的多糖积累[55-57]。ISA3蛋白通常参与葡聚糖的分解代谢，其在淀粉积累中起主要作用，在生物合成中也与ISA1/ISA2的功能有部分重叠[58]，但是，ISA1和ISA2对于淀粉分解代谢不是必需的。遗传分析表明，ISA1和ISA2在半结晶支链淀粉的生成中很重要[59]。在马铃薯块茎中，ISA1或ISA2的反义下调会引起相同的淀粉表型异常。研究发现，在块茎和叶中，ISA1和ISA2蛋白通过形成复合物而共同发挥作用[60]。ISA2可能具有调节性，缺少ISA1的突变体中淀粉颗粒的大小、形状以及数量均表现出异常，并且支链淀粉的结构也发生改变。这些表型在包括玉米、水稻以及大麦在内的作物和组织之间具有显著的一致性[61]。支链淀粉酶型淀粉去分支酶(PUL)容易水解支链淀粉的α-1,6糖苷键，但对糖原的水解活性很小[62]。PUL突变的纯合籽粒中淀粉降解功能受损，因此，PUL的水解活性有助于淀粉的分解代谢[63]。

3 玉米淀粉关键酶基因的表达调控

淀粉的代谢是能量代谢的枢纽，广泛参与植物生长发育的各个进程。在转录水平上，淀粉合成关键酶的表达受一系列转录因子(TF)的调节。碱性亮氨酸拉链(bZIP)家族、MYB家族、NAC家族等转录因子在籽粒胚乳发育中起重要作用[64-65]。DNA甲基化也与淀粉生物合成有关，淀粉合成关键酶基因通常由于甲基化而表现出表达降低，研究表明DNA甲基化参与直链淀粉合成的调控[66]。翻译后磷酸化对淀粉合成调控有着重要作用，淀粉合成关键酶形成的多酶复合物的形成取决于蛋白质磷酸化。例如，玉米SBE亚型中通过磷酸化改变SBEIIa和SBEIIb的活性，进而影响淀粉合成[67]。激素在玉米胚乳淀粉的合成中起着至关重要的作用，赤霉素(GA)通过TF *GAMyb*在淀粉降解中起作用，ABA调节发育中的种子中的淀粉的合成[68]。环境是胚乳中淀粉合成的决定因素，高温(HT)对淀粉合成的负面影响尤为明显。HT显著下调淀粉合成相关酶(SSRE)的表达并诱导编码α淀粉酶的基因表达，导致垩白颗粒和籽粒空瘪；高温还显著破坏AGP酶异源四聚体的稳定性，显著降低ADPG合成，影响玉米胚乳中的淀粉积累[69]。

4 展 望

淀粉作为植物碳水化合物的主要储存形式，不仅是所有生物体最重要的能量来源，还是重要的工业原料和添加剂[70-71]，更是人类作为食品和工业原料的重要可再生资源。淀粉由葡萄糖聚合物(支链淀粉和直链淀粉)组成[72]，在ADP-葡萄糖焦磷酸化酶(AGPase)和淀粉合酶(SS)、淀粉分支酶(SBE)和淀粉去分支酶(DBE)参与合成淀粉并将其组装成半结晶淀粉颗粒，并以半结晶颗粒的形式存在于质体内[73]。

籽粒胚乳中的每种淀粉合成相关酶(SSRE)都存在于多种同工酶中，这些同工酶可以与其他同工酶或同源多聚体在体内形成异源多酶复合物以发挥其功能。参与玉米淀粉合成的关键酶ADP-葡萄糖焦磷酸化酶(AGPase)、淀粉合酶(SS)、淀粉分支酶(SBE)和淀粉去分支酶(DBE)的表达受到不同因素的调节，任何一种关键酶的表达受阻都会影响淀粉的结构和含量。淀粉合成改变通常伴随着对产量和质量方面的负面影响，籽粒胚乳中淀

粉合成的减少可导致多种初级和次级代谢物(如糖、脂肪酸、氨基酸和植物甾醇)的积累普遍增加[1]。在未来玉米育种中,进一步优化淀粉合成是提高籽粒品质的重要方向。

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