·综 述·

DGAT 和 *PDAT* 基因在调控植物油脂合成中的作用

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摘 要：我国植物油料产需缺口大，严重依赖进口。二酰甘油酰基转移酶(diacylglycerol acyltransferase, DGAT)与磷脂:二酰甘油酰基转移酶(phospholipid: diacylglycerol acyltransferase, PDAT)是负责三酰甘油合成并影响植物油脂产量和品质的两个关键酶。本文综述了 *DGAT* 与 *PDAT* 基因的国内外研究进展，重点总结了二者在油料植物油脂合成中的生物学功能，在逆境胁迫下影响植物脂质代谢与生长发育的分子机制，以及合成生物学背景下 *DGAT* 和 *PDAT* 基因在驱动油脂合成中的重要作用，同时对深入开展 *DGAT* 和 *PDAT* 基因的机理研究与应用进行了展望，为深入了解植物油脂合成的分子机制，利用 *DGAT* 和 *PDAT* 基因改良油料作物品质、提高油料产能提供了依据。

关键词：油料作物；油脂合成；非生物胁迫；分子育种

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Regulatory roles of *DGAT* and *PDAT* genes in plant oil synthesis

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Abstract: There is a large gap between production and demand of plant oil in China, which leads to the heavy reliance on imports. Diacylglycerol acyltransferase (DGAT) and phospholipid: diacylglycerol acyltransferase (PDAT) are two key enzymes responsible for the synthesis of triacylglycerol, thereby affecting the yield and quality of plant oil. This paper comprehensively reviews the research progress in *DGAT* and *PDAT* in terms of their biological functions in plant oil synthesis, the molecular mechanisms of regulating plant lipid metabolism, growth, and development under stress, and their roles in driving oil synthesis under the background of synthetic biology. Furthermore, future research and application of *DGAT* and *PDAT* are prospected. This review aims to provide a basis for deeply understanding the molecular mechanism of plant oil synthesis and improving the quality and productivity of oil crops by the utilization of *DGAT* and *PDAT* genes.

Keywords: oil crops; oil synthesis; abiotic stress; molecular breeding

我国植物油自给率只有 35%左右，是油料进口大国[1]。随着人民生活水平的日益提高，面对逐渐复杂严峻的国际形势，油料供给被“卡脖子”的风险不断加大。加快提升国内油料产能，保障“油瓶子”基本安全，显得愈加紧迫和必要。

植物油脂主要以三酰甘油(triacylglycerol, TAG)的形式大量储存在种子中，叶片和其他组织器官中也有少量存在，在能量代谢、种子萌发、植株衰老、信号转导、维持细胞膜稳态和抵御各种非生物逆境胁迫中发挥重要作用。TAG 合成有 2 条途径(图 1)：一是依赖酰基 CoA 的 Kennedy 途径，即甘油-3-磷酸依次在甘油-3-磷酸酰基转移酶、溶血磷脂酸酰基转移酶、磷脂酸磷酸酶的催化下生成二酰甘油(diacylglycerol, DAG)，最终 DAG 由二酰甘油酰基转移酶(diacylglycerol acyltransferase, DGAT)催化生成 TAG；二是不依赖于酰基 CoA 的途径，由磷脂作为酰基供体，利用磷脂:二酰甘油酰基转移酶(phospholipid: diacylglycerol acyltransferase, PDAT)催化 DAG 生成 TAG。*DGAT* 和 *PDAT* 作为负责 TAG 组装最后一步酰化反应关键酶的编码基因，始终是国内外研究人员关注的重点。然而不同油料植物中 DGAT 和 PDAT 对酰基底物的亲和性有很大差异，*DGAT* 和 *PDAT* 基因对油脂产量和脂肪酸组成的调控作用及其相对重要性也并不一致。本文全面总结了 *DGAT* 和 *PDAT* 基因调控不同油料植物油脂合成的研究进展，以期为深入理解其在脂质代谢中的生物学功能，促进油料作物遗传改良与产能提升提供依据。

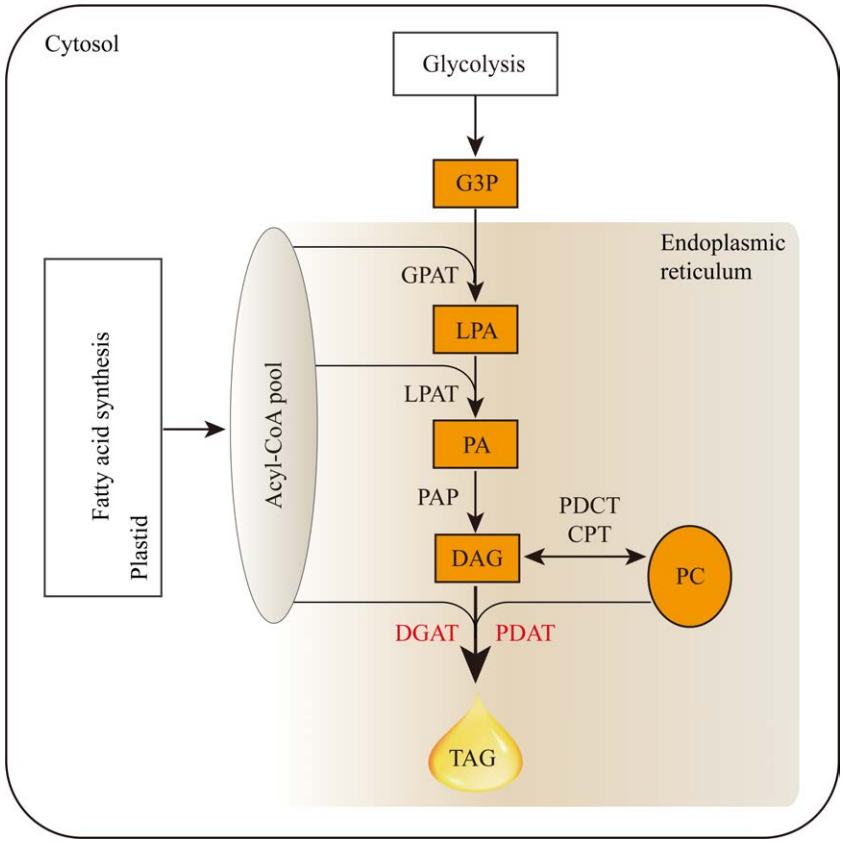

图 1　植物 TAG 的生物合成途径　G3P：甘油-3-磷酸；LPA：溶血磷脂酸；PA：磷脂酸；DAG：二酰甘油；PC：磷脂酰胆碱；TAG：三酰甘油；GPAT：甘油-3-磷酸酰基转移酶；LPAT：溶血磷脂酸酰基转移酶；PAP：磷脂酸磷酸酶；PDCT：磷脂酰胆碱甘油二酯胆碱磷酸转移酶；CPT：CDP-胆碱:1,2-二酰基甘油胆碱磷酸转移酶；DGAT：二酰甘油酰基转移酶；PDAT：磷脂:二酰甘油酰基转移酶。

Figure 1　Pathways of TAG biosynthesis in plants. G3P: Glycerol-3-phosphate; LPA: Lysophosphatidic acid; PA: Phosphatidic acid; DAG: Diacylglycerol; PC: Phosphatidylcholine; TAG: Triacylglycerol; GPAT: Glycerol-3-phosphate acyltransferase; LPAT: Lysophosphatidic acid acyltransferase; PAP: Phosphatidic acid phosphatase; PDCT: Phosphatidylcholine diester choline phosphotransferase; CPT: CDP-choline: 1,2-diacylglycerol choline phosphotransferase; DGAT: Diacylglycerol acyltransferase; PDAT: Phospholipid: diacylglycerol acyltransferase.

1　*DGAT* 和 *PDAT* 基因在调控植物油脂合成中的作用

1.1　*DGAT* 基因在调控植物油脂合成中的作用

根据蛋白结构和亚细胞定位的不同，真核生物 DGAT 可分为 4 个亚类，分别是 DGAT1、DGAT2、DGAT3 和 WSD/DGAT。DGAT1 和 DGAT2 都是定位于内质网的膜结合蛋白酶。DGAT1 是 O-酰基转移酶(membrane-bound O-acyltransferase, MBOAT)超家族成员，该家族的所有成员都被预测具有 8–10 个跨膜结构域(transmembrane domain, TMD)。DGAT2 属于溶血磷脂酰基转移酶(lysophospholipid acyltransferase, LPLAT)超家族，所含 TMD 较少[2]。DGAT3 属于类硫氧还原蛋白(thioredoxin-like, TRX-like)

家族，在细胞质中发挥作用，因此又被称为胞质 DGAT。WS/DGAT 是一种双功能酶，不仅具有 TAG 合成功能，在蜡酯合成途径中也发挥重要作用，但相比 DGAT1、DGAT2 和 DGAT3，其研究还相对较少。

1.1.1 *DGAT1* 基因在调控植物油脂合成中的作用

研究人员先后对拟南芥[3]、油菜[4]、亚麻荠[5]、麻疯树[6]、陆地棉[7]和大豆[8-9]中的 *DGAT1* 进行功能研究，证明了 *DGAT1* 能有效促进种子中 TAG 的累积，含油量最大增幅可达 20%以上。*DGAT1* 能够调控碳源流向油脂合成[10-14]，种子含油量的增加伴随着蛋白质、可溶性糖和淀粉含量的降低[6,15-16]。但也有部分研究指出，*DGAT1* 过表达能够打破种子含油量与蛋白质含量的负连锁，即在提高含油量的同时，不降低甚至还可以提高蛋白质含量[10]。在烟草[17]、亚麻荠[18]和大豆[19]中沉默 *DGAT1* 基因可导致种子含油量明显降低，降幅最大可达 49%。拟南芥 *AtDGAT1* 能够调控花粉中 TAG 及亚麻酸(C18:3)的积累，从而影响成熟花粉粒结构和种子发育[20]。此外，*DGAT1* 在植物营养组织的油脂合成中也发挥重要作用[21-23]，过表达 *AtDGAT1* 可使烟草叶片 TAG 累积量增加 20 倍[24]。

油脂合成是由多个基因协同调控的。越来越多的研究开始关注 *DGAT1* 与其他油脂合成相关基因的协同作用。在文冠果[25]和牡丹[26]种子发育过程中，*DGAT1* 和甘油-3-磷酸脱氢酶 1 基因 *GPD1* 具有相同的表达模式，推测二者协同促进了油脂的快速合成。亚麻 *LuDGAT1* 与溶血磷脂酰胆碱酰基转移酶基因 *LuLPCAT* 共同过表达[27]，蓖距花属植物 *CpuDGAT1* 与 *CvLPAT2*、脂肪酰基载体蛋白硫酯酶 B1 基因 *CvFatB1*[28] 共同过表达可有效促进含有不饱和脂肪酸或中链脂肪酸的 TAG 合成。WRINKLED 1 (WRI1) 转录因子在调控碳流向油脂合成的过程中起重要作用。与拟南芥 *AtDGAT1* 单独过表达的烟草叶片相比，*AtDGAT1* 与 *AtWRI1* 协同过表达的烟草叶片中 TAG 含量提高了 5 倍以上[29]。油菜 *BnDGAT1* 与 *BnWRI1* 及 *BnGPAT9* 共同在拟南芥中过表达，种子含油量相当于 3 个基因单独过表达的总和[12]。在大豆中共表达 *AtDGAT1* 和 *AtWRI1* 后，蔗糖代谢和糖酵解代谢增强，但种子油脂含量并没有明显提高[30]。

不同植物 DGAT1 对酰基底物有不同偏好，对脂肪酸组成的影响也不尽相同。如拟南芥 DGAT1 偏好利用油酸(C18:1)和棕榈酸(C16:0)[31-32]，大豆 DGAT1 偏好利用 C18:3 合成 TAG[33]。而油菜和亚麻荠 DGAT1 的亲和底物则较为广泛，C16:0、C18:1 和 C18:2 都是良好的酰基供体[34-35]。拟南芥[36]和亚麻荠[18]中 *DGAT1* 的缺失或沉默均能导致种子中 C18:3 水平大幅增加。此外，研究人员通过对比分析 DGAT1 氨基酸序列发现，油菜[34]、大豆[11]等植物 DGAT1 功能区域中单个氨基酸位点的改变可以有效提高 DGAT1 酶活性，增加种子或叶片中的 TAG 含量，改变脂肪酸组成。这种氨基酸位点特异性突变的方法也被认为是遗传改良油脂品质和培育高含油量品种的一条重要途径。

1.1.2 *DGAT2* 基因在调控植物油脂合成中的作用

早期研究认为，拟南芥 *AtDGAT1* 对种子油脂累积的贡献占主导地位，而 *AtDGAT2* 在营养组织的油脂合成中起主要作用[3,37]。过表达 *AtDGAT2* 能使烟草叶片的 TAG 含量提高约 22 倍，是过表达 *AtDGAT1* 叶片的 2 倍[32]。近年来的研究结果表明，*AtDGAT2* 与 *AtDGAT1* 在功能上具有冗余性，*AtDGAT2* 过表达能够恢复拟南芥 *dgat1* 突变体种子的低含油量表型；*AtDGAT2* 过表达拟南芥植株的叶片和种子 TAG 含量分别提高了

27%–31%和 26%–32%[36,38]。大豆 *GmDGAT2* 在叶片、花丝和种子等不同组织中均有表达，能有效提高种子中的脂肪酸含量[16,23,33,36,39]。Abdelghany[40]通过关联分析不同国家 633 份大豆种质基因和油分表型还发现，*GmDGAT2* 是区分高低油分含量大豆品种的重要选择标记。在烟草腺苷二磷酸葡萄糖焦磷酸化酶小亚基基因 *NtSSU* 缺失突变体中过表达油莎豆 *CeDGAT2*，可有效降低淀粉合成对碳同化产物的竞争，促进 TAG 合成[41]。在油莎豆、文冠果、牡丹等植物的种子与非种子器官中，*DGAT2* 协同 *DGAT1* 及 *GPD1* 的高水平表达可促进油脂快速积累[21-22,25-26,42]。

DGAT2 在富集不寻常脂肪酸和多不饱和脂肪酸的油料植物中扮演重要角色。斑鸠菊中 *VgDGAT2* 对斑鸠菊酸积累的影响要明显大于 *VgDGAT1*。*VgDGAT2* 和 *VgDGAT1* 分别与琉璃菊环氧合酶基因 *SlEPX* 在大豆中共表达后，种子中斑鸠菊酸含量分别提高了 26%和 15%[43]。在拟南芥中过表达桐树 *VfDGAT2* 与脂肪酸去饱和酶基因 *VfFAD* 能有效提高叶片中的桐油酸含量，TAG 含量增加 1 倍以上[44]。亚麻 *LuDGAT2* 与长链脂酰 CoA 合成酶 8 (*LuLACS8*)基因协同过表达，可有效提高种子中 C18:3 含量[45-46]。类似地，亚麻荠[35]、紫苏[42,47]和牡丹[22]的 DGAT2 在叶片和种子中也表现出对 C18:3 的强烈偏好性。麻疯树 DGAT2 偏爱 C18:2 酰基底物[6]，蒜头果 DGAT2 则更偏好利用含有超长链脂肪酸(very-long chain fatty acid, VLCFA)的 DAG 进行 TAG 组装[48]。

1.1.3 *DGAT3* 基团在调控植物油脂合成中的作用

DGAT3 的发现极大地丰富和扩展了植物脂质代谢的研究。最初在花生中鉴定到的 *AhDGAT3* 只在发育早期的种子和花中表达[49]。随后，*AhDGAT3* 被证明在根、叶和种子发育中后期也有较高水平的表达量[50-51]，能够促进种子中 C18:1 脂肪酸的累积[52]。拟南芥 *AtDGAT3* 在萌发的种子中高度表达[53]，油茶 *CoDGAT3* 在茎中的表达量最高[54]，大豆 *GmDGAT3* 在花中表达量最高[55]，它们均能有效提高烟草不饱和脂肪酸含量。在大豆中过表达 *AhDGAT3*，可导致脂肪酶基因 *lipase* 上调表达，C18:1 和总脂肪酸含量提高，并且株高、有效分支数、单株荚数和粒重等农艺性状也有不同程度的改善[8]。棉籽[56]和油莎豆块茎[57]中的 *DGAT3* 表达量明显高于 *DGAT1* 和 *DGAT2*，推测其可能是影响 TAG 合成的关键基因。

1.2 *PDAT* 基因在调控植物油脂合成中的作用

2000 年，研究人员在酿酒酵母、向日葵、蓖麻和还阳参属植物中发现，磷脂酰胆碱(phosphatidylcholine, PC)和 DAG 可以分别作为酰基的直接供体和受体合成 TAG，而催化这一途径的酶则被命名为 PDAT[58]。植物中的 PDAT 与动物中的卵磷脂胆固醇酰基转移酶(lecithin cholesterol acyltransferase, LACT)高度同源，它们都属于 α/β 水解酶(α/β hydrolase, ABH)超家族。植物 PDAT 主要可分为 PDAT1 和 PDAT2 这 2 个亚类。以拟南芥为例，其 PDAT1 和 PDAT2 的氨基酸序列相似度为 57%，均定位在内质网[59]。目前国内外 *PDAT* 基因在调控植物油脂合成的研究均集中于 *PDAT1*，而 *PDAT2* 少有报道。

拟南芥 *AtPDAT1* 和 *AtDGAT1* 在功能上存在冗余，*AtDGAT1* 可以完全补偿 *AtPDAT1* 的缺失，*pdat1* 突变体种子油脂含量和脂肪酸组成较野生型没有发生明显变化；通过 RNAi 干扰 *dgat1* 突变体中 *AtPDAT1* 的表达，花粉和种子发育将严重受阻，油脂含量会降低 70%–80%[3,36,60]。*AtPDAT1* 过表达可使拟南芥叶片 TAG 含量提高 28 倍，在促进营养组织油脂合成中的作用远远

大于 *AtDGAT1*[61]，并且有利于提高拟南芥幼苗的生长速度[62]。Woodfield 等[63]通过分析不同脂质组分比例，推测油菜种子中的 DGAT 对 TAG 合成的贡献可能大于 PDAT，但高油品系油菜籽中 *BnPDAT1* 的基因表达量明显高于低油品系[64-65]。在油菜中过表达 *AtPDAT1* 会导致种子总含油量有小幅度下降，同时 TAG 与磷脂的不饱和度降低[66]。大豆 *GmPDAT1* 在根、茎、花、叶、豆荚和发育种子中均有表达[55,67]，*GmPDAT1* 在烟草中的瞬时表达使叶片油脂含量提高了 4.2 倍[55]。

PC 是脂肪酸脱饱和与酰基编辑的内质网定位位点。PDAT 以 PC 作为酰基供体，可能参与到比 DGAT 更加复杂的脂质代谢过程中。前人研究结果表明，*PDAT1* 在斑鸠菊、蓖麻、牡丹等植物种子中高水平表达，推测其在促进不寻常脂肪酸或多不饱和脂肪酸的累积中比 *DGAT2* 发挥更加重要的作用[22,68-70]。乌桕 *SsPDAT1* 在油菜中过表达，种子总含油量提高了 8.1%–10.8%，C18:2 水平提高了 19.6%–28.9%，而 C18:3 水平降低了 27.3%–37.1%[71]。Yuan 等[72]研究发现，亚麻荠 *CsPDAT1* 在花、叶组织中具有较高表达量，*CsPDAT1* 在烟草中的瞬时表达使叶片 C18:3 含量提高了 45%。Marmon 等[18]和 Lager 等[35]的研究结果则表明，*CsPDAT1* 更偏爱 C18:2 底物，其过表达能显著提高种子中 C18:2 含量。

1.3 逆境胁迫下 *DGAT* 和 *PDAT* 基因对植物油脂合成的影响

DGAT 和 *PDAT* 介导的 TAG 合成在衰老、能量储备及胁迫应答等生物过程中扮演着关键角色，并有利于促进逆境胁迫下油料植物油脂产量的提高(表 1)。早期研究发现，拟南芥幼苗中 *AtDGAT1* 表达水平受脱落酸、葡萄糖、盐、冷和渗透胁迫诱导[80]。脱落酸不敏感蛋白 ABI4 和 ABI5 在低氮、脱落酸、茉莉酸、水杨酸、盐和渗透胁迫条件下能够激活 *AtDGAT1* 的表达，促进 TAG 合成[81-82]。DGAT1 可与二酰基甘油激酶(diacylglycerol kinase, DGK)协同平衡磷脂酸(phosphatidic acid, PA)、DAG 和 TAG 含量比例，在调控拟南芥细胞膜的稳定性和流动性和植株耐冷性方面发挥重要作用；*dgat1* 突变体植株在低温环境中将累积更高的 PA 和 DAG，从而刺激呼吸爆发氧化酶同源蛋白 D (respiratory burst oxidase homologue D, RBOHD)产生活性氧，破坏细胞膜的稳定性[83-84]，且这一表型与水杨酸信号通路密切相关[73]。Wang 等[74]研究结果还表明，低温条件下 N6-甲基腺苷(N6-methyladenosine, m6A)转录修饰水平的增加对拟南芥 *AtDGAT1* 基因翻译效率的提高具有重要意义，有利于增强植株的耐冷性。烟草 *NtDGAT3* 表达受冷胁迫强烈诱导，协同磷脂酶 D 基因(*NtPLD*)参与调控低温环境下叶片的膜脂代谢[76]。大豆中 DGAT1 酶活性及其编码基因的转录表达在高 CO_2 浓度和高温逆境中显著升高[85]，南美油藤中 *PvDGAT1* 和 *PvDGAT2* 的转录表达也受到高温逆境的强烈诱导[86]，有利于增强逆境下植物的脂肪代谢和油脂累积。大豆、紫苏、向日葵等多种植物 *PDAT* 的基因表达广泛地响应低温、干旱、盐、脱落酸、乙烯和茉莉酸甲酯等环境变化[68,87-89]。在拟南芥幼苗中，*AtPDAT1* 介导的 TAG 合成能有效减轻游离脂肪酸对细胞的毒害作用，并为淀粉合成缺陷突变体植株提供油脂作为替代能量，维持其正常生长[61,79]。与 *AtDGAT1* 类似，*AtPDAT1* 介导的 TAG 合成能够延缓拟南芥植株衰老，提高抗寒性，*AtPDAT1* 过表达可使长期低温环境下的种子油脂产量提高 280%[77-78]。

Lee 等[90]研究发现，拟南芥 MYB96 转录因子通过调控 *AtDGAT1* 和 *AtPDAT1* 的转录来影响 TAG 合成，以增强幼苗对干旱胁迫的适应能

表 1 植物中 *DGAT* 和 *PDAT* 基因的功能

Table 1 Functions of *DGAT* and *PDAT* genes in plants

Gene source	Genetic experiment material	Functions	References
DGAT1			
Jatropha curcas	*Jatropha curcas*	Increase oil content, reduce protein and soluble sugar content, change fatty acid composition in seeds and leaves	[6]
Glycine max	*Glycine max*	Enhance TAG synthesis, affect the accumulation of C18:1 fatty acid, sugar and protein in seeds, regulate seed weight and plant aging	[8-9,19]
Vernonia galamensis	*Glycine max*	Increase oil content, affect the accumulation of unsaturated fatty acids in seeds	[10]
Vernonia galamensis, *Glycine max*, *Ricinus communis*, *Xanthoceras sorbifolia*, *Hippophae rhamnoides*	*Arabidopsis thaliana*	Increase oil content in seeds	[11,14,16]
Arabidopsis thaliana	*Arabidopsis thaliana*	Increase TAG content and affect seed fatty acid composition in seeds, regulate pollen development	[11,20,36]
Brassica napus	*Arabidopsis thaliana*	Increase seed oil content, especially co-overexpressed with *BnWRI1* and *BnGPAT9*	[12]
Sesamum indicum	*Glycine max*	Increase oil content, decrease protein and soluble sugar content, affect fatty acid composition in seeds, regulate seed size	[13,15]
Paeonia suffruticosa, *Cyperus esculentus*, *Perilla frutescens*, *Glycine max*	*Nicotiana tabacum*	Increase oil content in leaves, affect the accumulation of unsaturated fatty acids	[21-23,47]
Arabidopsis thaliana	*Glycine max*	Enhance sucrose metabolism and glycolysis, when co-overexpressed with *AtWRI1*	[30]
Arabidopsis thaliana	*Arabidopsis thaliana*	Enhance plant cold tolerance by increasing TAG content	[73-75]
DGAT2			
Jatropha curcas	*Jatropha curcas*	Increase TAG content, affect fatty acid composition in seeds and leaves	[6]
Hippophae rhamnoides	*Arabidopsis thaliana*	Increase oil content in seeds	[14]
Paeonia suffruticosa, *Cyperus esculentus*	*Nicotiana tabacum*	Increase TAG content, affect fatty acid composition in seeds and leaves	[21-22,41]
Glycine max	*Nicotiana tabacum*	Increase oil content in leaves	[23]
Arabidopsis thaliana, *Glycine max*, *Ricinus communis*	*Arabidopsis thaliana*	Increase TAG content, affect fatty acid composition in seeds and leaves	[36,38]
Glycine max	*Glycine max*	Increase oil content and C18:2 fatty acid content in seeds	[39]
Perilla frutescens	*Nicotiana tabacum*, *Arabidopsis thaliana*	Increase TAG content, affect fatty acid composition in seeds and leaves	[42,47]
Moringa oleifera	*Arabidopsis thaliana*	Increase the content of very-long chain fatty acid in seeds	[48]

(待续)

(续表 1)

Gene source	Genetic experiment material	Functions	References
DGAT3			
Arachis hypogaea	*Glycine max*	Increase oil content and C18:1 fatty acid content in seeds	[8]
Glycine max	*Nicotiana tabacum*	Increase oil content and C18:1 fatty acid content in leaves	[55]
Nicotiana tabacum	*Nicotiana tabacum*	Enhance plant cold tolerance	[76]
PDAT1			
Paeonia suffruticosa	*Paeonia suffruticosa*, *Nicotiana tabacum*	Increase C18:3 fatty acid content in leaves	[22]
Glycine max	*Nicotiana tabacum*	Increase oil content in leaves by 4.2 times	[55]
Arabidopsis thaliana	*Brassica napus*	Decrease oil content slightly, change fatty acid composition in seeds	[66]
Sapium sebiferum	*Brassica napus*	Increase oil content and C18:2 fatty acid content, reduce C18:3 fatty acid content in seeds	[71]
Arabidopsis thaliana	*Arabidopsis thaliana*	Increase TAG content in seeds and leaves, delay plant senescence and enhance cold tolerance	[75,77-78]
Arabidopsis thaliana	*Arabidopsis thaliana*	Increase the turnover rate of fatty acids, maintain membrane lipid homeostasis, mediate TAG synthesis as energy reserve in leaves	[79]

力。本课题组通过对油茶叶片和果实进行转录组分析发现，弱光逆境下 *CoDGAT1* 和 *CoPDAT1* 表达量显著下调，TAG 分解代谢增强，是导致含油量降低的一个重要因素[91]。在高温和低温胁迫过程中，拟南芥 *DGAT1-3* 和 *PDAT1-2* 基因家族中任何一个成员的缺失都会限制 TAG 的累积，导致叶片损伤[75]。这些研究结果进一步揭示了逆境胁迫下 TAG 合成是一个复杂的生物学过程，是由 DGAT 和 PDAT 共同介导的。

2 *DGAT* 和 *PDAT* 基因在驱动植物油脂合成中的作用

合成生物学是指采用工程学的理念，有目标地设计和控制基因表达，改造或重新构建一个具有新功能的生命体[92]。随着合成生物学技术的不断发展，*DGAT* 和 *PDAT* 基因在驱动植物油脂合成与工业化生产方面也将发挥重要作用[93]。如由于可可豆产量有限，全球正面临着可可脂供应短缺的危机。可可果实中的 *TcDGAT1* 与 *TcGPAT*、*TcLPAT* 在酿酒酵母中协同表达，野生型菌株中的可可脂含量可提高 8 倍以上，这为以酿酒酵母为细胞工厂高效生产可可脂提供了一条有效的技术途径[94]。Liu 等[95]在水稻胚乳中特异表达拟南芥 *AtDGAT1*，同时利用 CRISPR/Cas9 技术敲除了 ADP-葡萄糖焦磷酸化酶大亚基 2 基因(*OsAGPL2*)和线粒体单链 DNA 结合蛋白 1 基因(*OsMTSSB1*)，将碳源引流至油脂合成通路，水稻种子含油量从 2.3%提升至 11.7%，为高产的水稻、玉米等淀粉类作物改造为油料作物提供了新思路。蓖麻种子中富含的羟基脂肪酸(hydroxy fatty acid, HFA)是重要的工业原料，但蓖麻籽中的蓖麻毒蛋白和高致敏性蛋白，导致其难以大规模种植。在拟南芥中表达蓖麻脂肪酸羟化酶基因 *RcFAH* 可使种子中 HFA 含量提高至 17%，但总含油量也大幅下降；而将 *RcPDAT1* 与 *RcFAH* 共表达，不仅能进一步提高 HFA 含量，还可使含

油量恢复到接近野生型的水平[69,96]。然而，未来想要通过合成生物学技术实现 HFA 的商业化生产，还需进一步筛选和鉴定更加高产的表达宿主植物/微生物以及更加完善的脂质代谢途径。

3 展望

DGAT 和 *PDAT* 基因参与的植物油脂合成是一个复杂的生物学过程，涉及众多代谢通路，并受植物种类、组织部位和环境条件的影响。目前 *DGAT* 和 *PDAT* 的分子机理研究多是基于模式植物拟南芥和烟草开展的。对大部分油料作物的 *DGAT* 和 *PDAT* 研究还集中于基因克隆、表达模式与基因序列特征分析。因此，未来有必要利用现代分子生物学手段深入探究不同油料作物 *DGAT* 和 *PDAT* 基因在种子和非种子器官油脂累积中的生物学功能，解析其与油脂合成相关转录因子的上下游关系，构建更加完整的脂质代谢网络。*DGAT* 和 *PDAT* 能够调控碳流向油脂合成方向，但是这一过程中二者如何影响糖、氨基酸以及次级代谢产物的累积与分配尚不明确，不利于提升研究人员对油料作物产量和品质形成的认识。

DGAT 和 *PDAT* 所编码的氨基酸在物种间具有丰富的多样性，不同植物中 *DGAT* 和 *PDAT* 酶活性和酰基底物选择性也具有很大差异。进一步明确 *DGAT* 与 *PDAT* 在调控植物种子油脂合成中的相对贡献，特别是深入解析特色草本和木本油料作物中 *DGAT2*、*DGAT3* 和 *PDAT* 的生物学功能，探明其调控多不饱和脂肪酸、不寻常脂肪酸合成的分子基础，挖掘优异等位变异并运用于新品种选育，对于提高植物油脂产品附加值具有重要意义。此外，*DGAT* 和 *PDAT* 在影响脂质代谢应答干旱、盐、温度等胁迫中扮演重要角色。如何调控 *DGAT* 和 *PDAT* 基因表达，促进油料作物在非生物逆境中的生长发育和油脂累积是一个值得探究的课题。

随着遗传转化、基因测序、CRISPR 基因编辑、DNA 合成与组装、蛋白合成与组装等合成生物学技术的蓬勃发展，让利用 *DGAT* 和 *PDAT* 对不同生物脂质代谢途径进行设计和改造，并与其他脂质代谢关键基因进行模块化组装，定向插入到宿主基因组中变得更加高效，从而助力作物遗传改良，油脂大规模商业化生产和新脂质分子的构建与应用。目前在油脂合成工程中，催化 *DGAT* 和 *PDAT* 在工业产油微藻中表达是提高含油量的常用策略。但如何利用高等油料植物中的 *DGAT* 和 *PDAT* 基因对微藻油脂合成途径进行优化，提高产油率，并最终获得理想的细胞工厂还需进一步探索与研究。

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