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油茶对干旱胁迫的生理生化和分子响应及其适应机制研究进展

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摘要：近年来，干旱成为油茶 *Camellia oleifera* 减产的主要逆境胁迫之一。研究油茶抗旱机制，选育耐旱高产良种，是应对季节性干旱、保障油茶产业健康发展的重要途径。综述了油茶受到干旱胁迫时脱落酸 (ABA) 信号通路 (PYR/PYL-PP2C-SnRK2)、钙信号通路 (CDPK/CBL-CIPK) 等完成干旱胁迫的信号转导，诱导关键转录因子 (NAC、MYB、WRKY 家族等) 进一步调控 LEA 蛋白基因 (*CoLEA*)、渗透调节关键基因 (*CoP5S5*、*CoSUS2*、*CoBADH*)、抗氧化酶基因 (*CoPOD*、*CoCAT*、*CoSOD*) 等关键基因表达，驱动油茶通过积累渗透调节物质、诱导抗氧化酶合成、调控内源激素水平、调整光合适应性等生理生化机制变化来增强抗逆性的调控应答网络。现有研究已初步建立了“信号感知—基因调控—生理响应”的框架，但相关研究深度不足，关键基因挖掘和本体验证滞后，高温干旱等复合胁迫研究缺乏。关键调控网络解析、复合胁迫机制等是未来油茶干旱胁迫研究的重要方向。表 2 参 165

关键词：油茶；干旱胁迫；生理生化适应；分子调控；综述

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Research progress on physiological, biochemical and molecular response and adaptation mechanisms of *Camellia oleifera* to drought stress

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Abstract: In recent years, drought has become a major abiotic stress leading to yield decline in *Camellia oleifera*. Investigating the drought resistance mechanisms of *C. oleifera* and breeding drought-tolerant, high-yielding varieties are crucial approaches to addressing seasonal drought and ensuring the sustainable development of the *C. oleifera* industry. This article provides an overview of the signal transduction pathways involved in drought stress in *C. oleifera,* including the abscisic acid (ABA) signaling pathway (PYR/PYL-PP2C-SnRK2) and the calcium signaling pathway (CDPK/CBL-CIPK). These pathways induce the expression of key transcription factors (NAC, MYB, WRKY families, etc.), which further regulate the expression of critical genes, including LEA protein genes (*CoLEA*), osmotic regulation key genes *(CoP5S5, CoSUS2, CoBADH)*, and

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antioxidant enzyme genes (*CoPOD*, *CoCAT*, *CoSOD*), thereby driving the regulatory response network of *C. oleifera* to enhance drought resistance through physiological and biochemical mechanisms, including the accumulation of osmotic adjustment substances, induction of antioxidant enzyme synthesis, regulation of endogenous hormone levels, and adjustment of photosynthetic adaptability. A “ signal perception-gene regulation-physiological response” framework for drought resistance has been preliminarily established, but the depth of related research is insufficient. The key gene mining and ontology verification are lagging behind, and there is a lack of research on compound stresses such as high temperature and drought. Key regulatory network analysis and compound stress mechanisms are important directions for future research on drought stress in *C. oleifera*. [Ch, 2 tab. 165 ref.]

Key words: *Camellia oleifera*; drought stress; physiological and biochemical adaptation; molecular regulation; review

油茶 *Camellia oleifera* 是山茶科 Theacease 山茶属 *Camellia* 的常绿小乔木或灌木，广泛分布于中国湖南、江西、浙江、广西、福建等 18 个省 (自治区)，在东南亚地区也有少量分布[1−3]。油茶籽油营养丰富，除富含多种不饱和脂肪酸外，还含有甾醇、生育酚、角鲨烯等多种营养成分，在降低血脂、胆固醇，预防心血管疾病等方面有显著效果[4−5]。随着经济发展和人民生活水平的提高，中国对食用油，特别是高品质食用油的需求持续增加，已经成为世界上第一大食用油消费国和第二大产油国[6]。发展油茶产业在保障国家油料安全和共同富裕中具有重要意义[7]。

近年来，随着温室效应加剧，极端干旱事件频发[8−9]。7—10 月的季节性干旱作为中国南方分布最广、危害最严重的干旱类型，是造成油茶减产的重要因素[10−11]。据统计，2013 年湖南省 100 多个县 (区) 遭遇 10 a 内最严重的高温干旱，导致油茶籽减产近三分之一；2021 年 8—10 月湖南又逢降雨异常偏少，油茶产量再次骤减，造成了严重的经济损失[12−13]。解析油茶对干旱胁迫的应对机制，选育抗 (耐) 旱高产油茶良种，是应对季节性干旱，保障油茶产量的重要途径之一。

植物应对干旱胁迫是个复杂的过程。研究发现：植物在感知到水分胁迫时，以脱落酸 (ABA)[14]、钙离子 (Ca^{2+})[15]、三磷酸肌醇 (IP3)[16]、环腺苷二磷酸核糖 (cADPR)[17]、一氧化氮 (NO)[18] 等为信号物质，一方面通过激活下游信号通路快速调控植物生理变化适应干旱胁迫环境，另一方面可诱导与干旱适应性相关的基因表达[19]。诱导表达的功能基因产物如脯氨酸 (Pro)[20]、甘氨酸甜菜碱 (GB)[21]、可溶性糖 (SS)[22]、胚胎发育晚期丰富蛋白 (LEA)[23] 和水通道蛋白 (AQP)[24] 等参与植物代谢途径可直接引起植物适应干旱胁迫的生理形态改变；诱导表达的调控基因产物，如钙依赖性蛋白激酶 (CDPKs)[25]、丝裂原活化蛋白激酶 (MAPKs)[26]、bZIP 转录因子 (bZIP)[27]、乙烯响应因子 (AP2/ERF)[28]、NAC 转录因子 (NAC)[29]、MYB 转录因子 (MYB)[30] 和 WRKY 转录因子 (WRKY)[31] 等，通过调控信号转导途径或作为转录因子调控下游基因的表达，引起植物形态和生理变化适应干旱环境[32−33]。

7—9 月是油茶果实膨大与油脂合成的关键期，油茶产区的季节性干旱也多发在这个时期，故农谚有“7 月干果 8 月干油”之说[13]。近年来，干旱对油茶产量的影响已引起广泛关注，也有大量研究聚焦于油茶在受到干旱胁迫时的生理生化和分子响应机制，为耐旱油茶良种选育、油茶抗旱栽培技术构建等奠定了理论基础。本文从生长、生理变化、分子调控机制、抗逆技术研发与应用转化等 4 个层面详细论述油茶对干旱胁迫的应答机制及其应用，旨在为木本油料作物的抗逆研究提供新视角。

1 干旱对油茶生长发育的影响

1.1 干旱对油茶生长的影响

油茶通常被视为一种耐旱树种，但严重干旱仍对其生长发育构成严重威胁，造成苗木成活率和生长量显著下降，抑制毛细根对氮素的吸收，改变氮素在根系中的分配，抑制花芽正常发育造成大幅减产。何小三等[34] 研究发现：重度干旱 82 d，各油茶品种扦插苗株高生长量仅为对照的 33.66%~63.07%，干物质积累量是对照的 13.57%~58.50%。研究表明：失水造成油茶苗的栽植成活率显著下降，当失水达到

30% 时，成活率由对照的 97.8% 降至 6.7%[35−36]。受到干旱胁迫时，多种植物的根系对氮素的吸收与利用被抑制，根系的生物量和氮素积累显著降低[37]。干旱胁迫抑制油茶毛细根对氮素吸收，同时促进氮素从毛细根向主根转运，使主根氮素含量增加了 93.10%[36]。GUO 等[37] 研究发现：自然干旱胁迫 45 d 后，油茶花芽的平均纵径比对照小 4.9 mm (减小 24.0%)，横径比对照小 1.4 mm (减小 15.0%)；雌、雄蕊长度比比对照小 8.0%~12.0%，单个花药中的花粉量减少至对照的 58.0%；花粉体外萌发率随干旱胁迫时间延长逐渐降低，干旱 45 d 时花粉萌发率比对照下降 61.1%；次年单株花芽数减少 62.0%，坐果率降至 1.0% 以下，实际减产超过 55.0%。综上所述，干旱胁迫对油茶营养与生殖生长均造成显著影响。

1.2　干旱对油茶果实性状与油脂品质的影响

大量研究发现：重度干旱会显著降低油茶果实产量、单果质量及含油率，降低油脂品质，但适度干旱有助于提高油茶果实产量与油脂品质。贺义昌等[38] 发现：2019 年重度干旱胁迫使‘赣无’*C. oleifera*‘Ganwu’系列油茶单果质量、干籽质量均显著降低，种仁含油率下降，油酸、亚油酸等不饱和脂肪酸含量降低，棕榈酸、硬脂酸等饱和脂肪酸含量升高，油脂品质下降。曾清苹等[39] 进一步证实，极端高温干旱使‘长林’*C. oleifera*‘Changlin’系列油茶单株产果量减少 2.11%~37.29%，单果质量减少 14.15%~56.19%，果皮厚度增加 0.35%~7.01%，产量显著降低，其生理机制可能与干旱诱导果实内源细胞分裂素和赤霉素水平下降有关[40]。钟飞霞等[41] 研究发现，轻度干旱下，油茶单果质量、出籽率、鲜果含油率均高于对照，适度干旱有利于促进油茶果实中干物质及油脂的合成，提高油茶产油量，同时使油茶果实成熟期提前。

2　干旱胁迫对油茶生理生化性状的影响

2.1　干旱胁迫对油茶渗透调节的影响

受到干旱胁迫时，植物通过积累渗透调节物质，包括可溶性糖、可溶性蛋白、脯氨酸、甜菜碱、无机离子等调节细胞渗透平衡。渗透调节物质在梭梭 *Haloxylon ammodendron*[42]、沙枣 *Elaeagnus angustifolia*[43]、刺槐 *Robinia pseudoacacia*[44]、‘新林 1 号’杨树 *Populus cathayana*×*canadensis*‘Xinlin 1’[45] 等大量木本植物的抗旱过程中均发挥重要作用。研究发现：与对照组相比，轻度、中度和重度干旱处理的油茶叶片可溶性糖含量分别增加了 3.91%、12.14% 和 26.96%，可溶性蛋白含量分别提高了 1.12%、16.76% 和 31.10%[46]。霍佩佩等[47] 研究发现：在自然干旱 32 d 过程中，不同油茶无性系的叶片渗透调节物质含量表现出相似的变化趋势，可溶性糖含量先升高后降低，游离脯氨酸含量先降低后升高，可溶性蛋白含量出现双峰。不同油茶品种抗旱性存在显著差异，‘长林 4 号’油茶 *C. oleifera*‘Changlin No.4’对胁迫敏感，而‘长林 40 号’油茶 *C. oleifera*‘Changlin No.40’抗旱性能更佳。黄钰等[48]、叶甜甜等[49]、董斌等[50] 在对油茶叶片渗透物质含量的研究中得出相似的结论。可见，渗透调节物质的积累与动态转化是油茶应对干旱胁迫的重要应答策略。

2.2　干旱胁迫对油茶保护酶系统的影响

植物保护酶系统通过提高超氧化物歧化酶 (SOD)、过氧化物酶 (POD)、过氧化氢酶 (CAT) 等活性，及时清除干旱胁迫下过量积累的活性氧，维持氧化还原平衡，保护膜结构完整，从而延缓细胞损伤并增强植株耐旱能力[51]。轻度至中度干旱下，随胁迫时间增长，油茶叶片的超氧化物歧化酶和过氧化物酶活性呈现先升后降的趋势[49]。刁兆龙[52] 发现，在胁迫初期，油茶苗超氧化物歧化酶活性、过氧化物酶活性呈上升趋势，此时复水油茶苗各保护酶活性均很快恢复正常水平；胁迫中期油茶苗超氧化物歧化酶活性、过氧化物酶活性呈先上升后下降的趋势，胁迫中期复水 30 d 后各保护酶活性基本可以恢复至正常水平或接近正常值；胁迫晚期油茶苗超氧化物歧化酶活性、过氧化物酶活性逐渐降至最小值，在此阶段复水，各指标无法恢复至正常水平。申帅帅等[53] 对海南油茶进行 12 d 的 PEG-6000 模拟干旱，发现海南油茶苗超氧化物歧化酶活性呈现先升后降的趋势，过氧化氢酶活性持续升高。此外，张涛[54] 发现：叶面喷施外源钙可以显著上调油茶超氧化物歧化酶、过氧化物酶、过氧化氢酶等保护酶活性，减轻膜脂过氧化，强化油茶的抗逆性。综上所述，随着胁迫程度加深和时间延长，油茶保护酶活性因遭受不可逆损伤而丧失修复能力，对干旱胁迫的响应呈典型的先激活后损伤的动态模式。

2.3 干旱胁迫对油茶激素的影响

内源激素在植物响应干旱胁迫中起重要调控作用，主要包括生长素 (IAA)、脱落酸 (ABA)、赤霉素 (GA)、茉莉酸 (JA)、玉米素核苷 (ZR)、油菜素甾醇 (BL) 和水杨酸 (SA) 等[55−60]。油茶通过内源激素含量的变化应对干旱胁迫。丁少净等[61] 和陈博雯等[62] 研究发现：干旱胁迫使油茶叶片生长素含量下降，脱落酸含量上升，赤霉素含量先上升后下降，玉米素核苷含量下降并维持在较低水平，玉米素核苷/生长素比值下降。郭璞瑞[13] 分析发现，随着干旱胁迫时间的增加，油茶花芽茉莉酸含量降低，水杨酸含量逐渐增加。近年来，除了内源激素在植物抗旱调控中的作用，外源激素在提高植物抗旱能力方面的应用与机制也受到关注。YANG 等[63] 通过叶面喷施不同质量浓度的脱落酸发现，适当质量浓度 (50 $\mu g \cdot L^{-1}$) 的脱落酸处理可以通过光合作用、氧化应激反应和渗透平衡等途径调节油茶幼苗的生理状态，从而帮助重构抗旱策略，且脱落酸处理增强了油茶对脱落酸信号通路的响应，提高了膜脂稳定性，并通过调节相关基因的表达增强了油茶的抗逆性。外源喷施 1.0 $mg \cdot L^{-1}$ 的油菜素甾醇能够降低受干旱胁迫的油茶叶片脱落酸水平，恢复生长素含量至健康叶片水平，有效维持叶片相对含水量，提升光合性能，并增强植株的整体抗旱能力[64]。干旱胁迫下，油茶通过下调生长促进类激素 (生长素、赤霉素、玉米素核苷) 并上调生长抑制类激素 (脱落酸、茉莉酸)，实现生长与抗逆权衡。

2.4 干旱胁迫对油茶光合作用的影响

受到干旱胁迫时，植物光合参数和光合色素含量发生显著变化。干旱胁迫下，油茶净光合速率 (Pn) 随胁迫程度加重和胁迫时间的延长而显著降低，轻度干旱时气孔关闭是净光合速率降低的主因，重度干旱时叶肉细胞活性降低等非气孔因素是主要因素[65−66]。黄拯等[67] 研究发现：随着干旱程度的增加，油茶叶片的蒸腾速率 (Tr)、气孔导度 (Gs)、水分利用效率 (WUE) 呈下降趋势，胞间二氧化碳 (CO_2) 浓度 (Ci) 总体呈现上升趋势。在重度干旱处理下，油茶叶片中叶绿素 a、b 含量均下降，叶绿素总量减少，光系统Ⅱ(PSⅡ) 的活性降低，光反应效率下降[68]。在重度干旱胁迫下，油茶叶片中丙二醛 (MDA) 质量摩尔浓度由 37.55 $nmol \cdot g^{-1}$ 显著升至 46.54 $nmol \cdot g^{-1}$，超氧阴离子 (O_2^-) 和过氧化氢 (H_2O_2) 含量亦大幅增加。大量积累的活性氧直接氧化叶绿素分子，破坏叶绿体膜结构，导致叶绿素降解加速，是叶片叶绿素含量显著降低的重要原因[69−70]。

干旱胁迫还会破坏叶片的叶绿体超微结构，引起植物叶片结构变化，具体表现为叶绿体类囊体肿胀、基粒片层断裂或解体，淀粉粒消失，外膜破裂等[71−72]。曹林青等[73] 研究发现：重度干旱诱导油茶叶片栅栏组织厚度显著降低，气孔开度减小，气孔密度上升，从而通过减少蒸腾面积和优化气体交换效率来增强保水能力，这种形态适应性调整实现了水分利用效率的优化，为油茶在干旱环境中的生存提供了结构基础。张诚诚等[74]、张规富等[75] 在对干旱胁迫下油茶叶片结构变化的研究中也得出相似的结论。

3 油茶应答干旱胁迫的分子调控网络的层级解析

3.1 干旱胁迫的分子信号转导机制

干旱胁迫下，植物通过分子信号转导机制构建起应对水分缺失的多层级调控网络。该过程始于细胞膜上渗透感应器 (OSCA 家族蛋白) 对胁迫信号的感知，信号感知后钙离子通过特定通道内流，在胞质中形成钙信号。同时，细胞质中不断累积的脱落酸也是一种信号物质，两者共同调控 Ca^{2+}-CDPK/SnRK2 通路和 Ca^{2+}-CaM-MAPK 通路，向细胞核传递干旱胁迫信号，调控下游基因表达，快速响应外界渗透压变化[76]。

脱落酸是植物响应干旱胁迫的重要激素，其信号传递通过 PYR/PYLs-PP2C-SnRK2 模块完成，具体可概括为脱落酸与 PYR/PYLs 受体结合后抑制 PP2C 磷酸酶活性，解除对 SnRK2 激酶的抑制，激活下游基因表达[77−78]。PYR/PYLs-PP2C-SnRK2 模块在拟南芥 *Arabidopsis thaliana*[79]、水稻 *Oryza sativa*[80]、玉米 *Zea mays*[81] 等植物中均有广泛的报道。除了经典的 PYR/PYLs-PP2C-SnRK2 通路外，ABA-PYR/PYLs 信号还可通过旁支模块调控特定生理响应。SHI 等[82] 发现：脱落酸信号可以通过 PYR-PP2C-CKL2 模块调节保护细胞中的肌动蛋白重组，有助于干旱胁迫下的气孔闭合。LI 等[83] 发现：PYL-PP2A-PID-PIN 磷酸化分支可以影响根尖生长素极性运输，使根在干旱胁迫下避开缺水区。在油茶脱落酸信号通路方面的研究也取得一定进展。在抗旱性评价研究中发现，以‘湘林 27’油茶 *C. oleifera*‘Xianglin

No.27’为砧木嫁接‘湘林 210’油茶 *C. oleifera*‘Xianglin No.210’后，干旱胁迫显著上调接穗中脱落酸受体基因 *CoPYL6*、磷酸酶基因 *CoPP2C75/51/24/26*、激酶基因 *CoSnRK2.8* 及下游响应因子 CoABI5 的表达，从转录层面表明 PYR/PYLs-PP2C-SnRK2 通路参与油茶干旱应答[84]。此外，在油茶近缘物种茶树 *C. sinensis* 中亦证实，干旱胁迫下 CsPYL-CsPP2C-CsSnRK2 模块广泛参与渗透调节[85−86]，为山茶属植物中该通路的保守性功能提供了旁证。

Ca^{2+}是细胞内重要的第二信使。当植物受干旱胁迫时，胞外 Ca^{2+} 通过开放的 OSCA 通道进入胞内，细胞内 Ca^{2+}浓度迅速升高，激活下游的信号通路[87−89]。在部分植物中钙依赖性蛋白激酶 (CPKs) 感知升高的 Ca^{2+} 浓度，磷酸化激活 SnRK2[90]。Ca^{2+}与 CaM 形成 Ca^{2+}/CaM 复合物，直接启动丝裂原活化蛋白激酶 (MAPK) 级联[91]。钙信号在油茶抗逆胁迫与生殖发育中起到重要作用已被多次验证。CHEN 等[92] 在油茶冷驯化样本中发现 Na^{+}/Ca^{2+}交换体、小电导钙激活钾通道 (SKOR) 等钙信号相关转运蛋白显著上调。钙信号也与油茶自交不亲和相关，研究发现，*CML41*(calmodulin-like 41) 是正向调控后期自交不亲和的枢纽基因，钙信号通路与丝裂原活化蛋白激酶、植物-病原互作等通路共同参与花粉管程序性死亡过程[93]。有研究表明，外源喷施钙可显著提高油茶对干旱胁迫的生理响应敏感性，但对于其中的机制研究较少，有待于深入探索[94]。

丝裂原活化蛋白激酶通路是高度保守的三级激酶级联系统，通过逐级磷酸化 (MAPKKK-MAPKK-MAPK) 传递信号[95]。该通路始于 MAPKKK 被受体激酶 (RAF-like 激酶等) 或活性氧 (ROS) 修饰激活，激活的 MAPKKK 磷酸化 MAPKK 的保守 Ser/Thr 残基，MAPKK 再双位点磷酸化 MAPK 的 TEY(Thr-Glu-Tyr) 基序[96−97]。油茶的 MAPK 通路在冷胁迫响应和自交不亲和性中起重要作用，XING 等[98] 首次系统描绘油茶 MAPK 级联基因家族全貌，发现 CoMAPKKK5/43/49-CoMAPKK4-CoMAPK8 为油茶冷胁迫的重要响应模块。杨进[99] 发现：CoMAPKs 负调控油茶后期自交不亲和，其表达水平与花粉管能否伸长至子房呈正相关，提升该级联活性可削弱自交障碍，为选育自交亲和型油茶提供可操作的分子靶点。MAPK 通路在油茶干旱胁迫应答中的作用还需要进一步研究。

3.2　参与油茶抗旱应答的功能基因

在干旱胁迫下，植物通过合成渗透保护蛋白与渗透调节物质、抗氧化酶，积累次生代谢产物，维持细胞水分平衡与膨压，减轻干旱对蛋白质、膜系统等关键生物大分子的损伤，增强植物的抗旱能力[100−104]。LEA 是油茶受到干旱胁迫时调节渗透压的保护蛋白。LIU 等[105] 在油茶中鉴定出 47 个 *LEA* 基因，其中许多被归类为 *LEA2* 亚家族。这些基因在基因组中广泛分布，表现出高度的保守性。在模拟干旱和梯度遮光条件下，油茶的 *LEA2* 基因表现出显著的表达响应。董斌[106] 从油茶干旱胁迫叶片转录组数据中系统挖掘出渗透调节、抗氧化酶合成和次生代谢物合成相关的功能基因。脯氨酸合成关键基因 *PYCR2* 与 *P5CS* 家族成员显著上调，促进了脯氨酸的快速积累；甜菜碱合成基因 *BADH* 高效表达，增强了细胞的保水能力；蔗糖合成酶基因 *SUS2* 高表达使可溶性糖含量持续积累，维持细胞的能量与渗透平衡。*POD* 家族的 25 个成员 *POD1*、*POD12* 以及 *CAT* 家族成员 *CAT3*、*CAT* 在干旱胁迫期间持续高表达，协同清除活性氧，保护细胞膜结构的完整性。类黄酮合成途径中的 60 个 Unigenes 显著上调，促进了槲皮素等黄酮醇的积累，从而增强抗氧化能力；倍半萜烯与三萜通路中的 28 个基因 (包括混合香树脂醇合酶和鲨烯合酶) 表达下调。申帅帅[107] 通过转录组比对耐旱型‘海大 1 号’越南油茶 *C. vietnamensis*‘Haida No.1’ 与敏感型‘万海 1 号’越南油茶 *C. vietnamensis*‘Wanhai No.1’发现，在干旱胁迫下，耐旱型品种中木质素合成通路中的 45 个 *POD* 基因、苯丙烷途径中的 10 个 *PAL* 和 *CAD* 基因、类黄酮通路中的 *LAR*、*CHS* 和 *F3H* 基因以及生长素信号通路基因 *ARF*、乙烯信号基因 *ERF*、茉莉酸信号基因 *MYC2* 和水杨酸信号基因 *PR1* 均显著上调表达。HE 等[108] 联合 mRNA 与 miRNA 测序，揭示‘湘林 1 号’油茶 *C. oleifera*‘Xianglin No.1’和‘衡东 2 号’油茶 *C. oleifera*‘Hengdong No.2’ 在干旱胁迫下的调控网络差异，发现 miR398和 miR408-3p 等关键 miRNA 通过靶向调控 *DMR6*、*EDR2* 等基因参与耐旱反应，为油茶耐旱育种提供新线索。

3.3　参与干旱胁迫应答的转录因子

转录因子是植物体内一类能够特异性识别并结合 DNA 序列的小分子蛋白，通过与下游靶基因的启动子区结合，调控基因表达。根据结合的顺式作用元件的 DNA 序列特点可将转录因子分为大约 60 个家

族，其中响应干旱胁迫的转录因子家族主要有 WRKY、HSF、AP2-EREBP、bZIP、MYB、C2H2、NAC、bHLH、BBX 等[109−110](表 1)。

表 1 转录因子与顺式作用元件在干旱胁迫应答中的作用

Table 1 Mechanism of interaction between transcription factors and cis-acting elements

转录因子	识别的顺式作用元件	在干旱胁迫中的作用	参考文献
WRKY	W-box (TTGAC/T)	激活脱落酸信号和活性氧清除网络，降低失水率并提高脯氨酸含量	[111]
HSF*	HSE $(nGAAn)_3$	上调*HSP70/90*、抗氧化酶和渗透保护基因，维持蛋白稳态与活性氧平衡	[112]
AP2-EREBP*	DRE/CRT (A/GCCGAC)	快速上调*RD29A*、*KIN1*、*COR15A*、*ERD10*等脱水保护基因	[113]
bZIP*	ABRE((Py)TACGTG)	启动*Rd29B*、*Rab18*、*SOD* 等渗透保护与抗氧化基因，减少膜损伤	[114−115]
MYB	MBS (CAACTG)	上调蜡质合成酶、抗氧化酶与LEA 蛋白基因，实现“保水-减活性氧-稳渗透”	[116−118]
C2H2*	(A/T)GATA(A/G)	上调*APX1*、*CAT2*、*FSD1*、*P5CS*等基因，降低活性氧并维持渗透势	[119]
NAC	NACRS (CATGTG)	上调*RD29A*、*LEA14*、*P5CS1*等脱水、抗氧化和渗透保护基因，增强抗旱性	[120]
bHLH	E-box(CANNTG)	结合*NCED*、*POD*、*P5CS*基因启动子，促进脱落酸、脯氨酸合成和活性氧清除	[121−122]
BBX	G-box(CACGTG)	调控光形态建成和ABA信号	[123]

说明：*表示该转录因子家族目前在油茶干旱胁迫中尚无直接研究报道，表中功能描述主要基于模式植物或近缘物种研究。

NAC 转录因子最早于 1996 年由 SOUER 等[124] 在矮牵牛 *Petunia hybrida* 中克隆获得。此后，大量的 NAC 家族成员在各种植物中被鉴定，其丰富的功能逐渐被挖掘，在干旱胁迫应答中有着重要作用[125−136](表 2)。研究表明，干旱胁迫触发脱落酸与活性氧信号，经 SnRK2、CDPK、MAPK 激酶磷酸化激活 NAC 蛋白，活化的 NAC 结合启动子中的 NACRS 等顺式元件，开启抗旱基因表达[137−140]。油茶全基因组共鉴定出 166 个 *NAC* 基因，分属 22 个亚族，启动子区富集 ABRE 和 DRE 等干旱响应元件，干旱胁迫后 36 个成员在根和叶显著上调表达。受到干旱胁迫后，*CoNAC5* 和 *CoNAC79* 在根和种仁中高表达且定位于细胞核，*CoNAC5/79* 等 7 个枢纽基因通过激活 LEA 与抗氧化酶基因表达提升油茶耐旱性[125−126]。LU 等[64] 从油茶中鉴定出 12 个 *NAC* 家族枢纽基因，外源施用油菜素内酯能够下调这些基因的表达，从而抑制过度抗旱响应，避免能量消耗与生长抑制。

表 2 NAC 家族成员参与植物干旱胁迫应答概况

Table 2 NAC transcription factor family and its physiological effects under drought stress in different species

物种	转录因子	干旱胁迫应答	参考文献
油茶	CoNAC28/51/52/56/60	干旱条件下基因表达上调，复水后下调	[125]
	CoNAC5/79	在根中高表达，可作为抗旱改良的候选因子	[126]
毛果杨	PtrNAC029	miR6445-NAC029-GSTU23模块通过调节活性氧稳态增强抗旱性	[127]
	PtrNAC006	促进根系发育，提高超氧化物歧化酶/过氧化物酶活性，降低过氧化氢积累	[128−129]
拟南芥	ANAC019/055	识别并结合ERD1启动子中的63 bp干旱响应顺式元件，正向调控基因表达	[120]
	ANAC096	与ABF2/4形成协同转录模块，持续激活下游抗旱基因表达	[130]
	ANAC016	通过 NAC016-AREB1-NAP 三岔前馈回路负调控 AREB1 表达，解除对抗旱基因的抑制	[131]
玉米	ZmNAC33	显著上调脱落酸信号、脯氨酸合成及活性氧清除相关基因	[132]
水稻	OsNAC10	根特异启动子 RCc3 驱动 OsNAC10，在田间干旱条件下显著提高水稻根系生物量、水分利用效率及籽粒产量	[133]
	OsNAC3/5/6	调控脱落酸信号、活性氧清除、根系发育和次级代谢等通路	[134]
	OsNAC52	受脱落酸快速诱导，过表达显著增强水稻及拟南芥的抗氧化与渗透调节能力	[135]
	OsNAC41	OsNAC41–RoLe1–OsAGAP模块促进根毛和侧根伸长	[136]

说明：毛果杨 *Populus trichocarpa*。

MYB 转录因子在调控植物生长发育、次生代谢过程以及响应生物与非生物胁迫中发挥作用[141−142]。MYB 转录因子在干旱胁迫中的功能已在海岛棉 *Gossypium barbadense*[143]、拟南芥[144−146]、水稻[147−148]、茶树[149] 等物种中广泛研究。油茶的 MYB 转录因子在油脂合成中起重要作用，油茶基因组鉴定出 186 个

CoMYB，其中 7 个 R2R3 型成员在油脂快速积累期高水平表达，激活脂肪酸碳链延长酶、*WRI1* 等关键酶基因，是油脂生物合成的核心调控因子[150]。油茶 CoMYB 转录因子在干旱胁迫应答过程中也发挥重要作用。在经干旱处理的油茶叶片转录组中共检测到 46 条 MYB 转录本，在干旱处理 6 和 24 h 后，分别有 27 和 32 条 MYB 转录本表达量提高了 2 倍以上。这些 *MYB* 基因的启动子区域显著富集 ABRE 和 DRE 等逆境响应顺式作用元件，并与脂肪酸延伸酶、*LEA* 等耐旱相关基因具有共表达关系[151]。

WRKY 转录因子已在拟南芥中被证实是 MAPK 级联通路的下游靶标[152]。近年来，对油茶 WRKY 转录因子家族的研究逐渐深入，该家族成员在调控角鲨烯合成[153]、炭疽病抗性[154]、叶片衰老[155]等生物过程中发挥重要作用。苏文娟等[156]鉴定了油茶 89 个 *CoWRKY* 基因，并确定 *CoWRKY20/29/56* 为干旱响应基因，其在干旱处理 12 h 后表达量显著上调，分别达到对照组的 24.2、32.3 和 34.8 倍。

在干旱胁迫中，bHLH 家族成员通过整合脱落酸信号通路和活性氧稳态调控发挥关键作用，拟南芥 *AtbHLH112* 通过激活 *RD29A*、*RD22* 等胁迫响应基因表达，显著增强植株抗旱性[157–158]。此外，*AtbHLH68* 通过调控脱落酸合成与降解基因的表达平衡维持脱落酸含量水平，增强拟南芥的抗旱性[159]。谢荟清等[160]在油茶中鉴定出 127 个 *CobHLHs* 基因，其中有 106 个参与油茶干旱胁迫响应过程，*CobHLH071* 在受到干旱胁迫时下调表达，干旱胁迫 12、48 h 时表达量分别为对照的 0.07 和 0.24 倍；*CobHLH006*、*CobHLH082* 在干旱胁迫时高表达，*CobHLH006* 的表达量在胁迫 12、48 h 时为对照的 8.2、54.1 倍，*CobHLH082* 的表达量在 48 h 才出现显著上调。

BBX 家族主要通过光信号途径参与植物生长发育。近年研究发现，BBX 家族在干旱响应中亦发挥重要作用[161]。拟南芥 *BBX21* 通过抑制 *HY5* 基因表达负调控脱落酸信号 (BBX21-COP1-HY 模块)，进而影响气孔关闭和水分流失，影响抗旱性[162]。花生 *Arachis hypogaea* B-box 转录因子 AhBBX6 通过强化抗氧化系统并激活下游靶基因，正向调控花生对盐胁迫和干旱胁迫的耐受性[163]。刘亚男等[164]研究发现：油茶 CoBBX22 作为转录抑制子，抑制活性氧清除基因与脱落酸信号通路关键基因的表达，显著削弱转基因拟南芥的耐旱性。该团队还发现油茶 CoBBX24 作为转录激活子，上调脱落酸信号与活性氧清除基因表达，延迟叶片衰老，显著增强植株耐旱性[165]。

4　总结

本文全面梳理了油茶在干旱胁迫环境下的生理适应机制以及分子调控网络。油茶在感知干旱胁迫时激活 PYR/PYLs-PP2C-SnRK2 模块信号通路[84]，信号传导至油茶 *NAC*、*MYB*、*WRKY* 等调控基因和功能基因，调控 *LEA* 保护蛋白基因、*P5CS*/*BADH* 渗透调节基因、*POD*/*CAT* 抗氧化酶基因及苯丙烷-类黄酮次级代谢通路基因表达，在生理层面实现光合稳定、激素调节、渗透势和过氧化防御及营养与生殖生长平衡等多层次适应性改变。

油茶抗干旱的机制研究起步较晚，基础薄弱。当前研究仍面临从“基因挖掘”到“功能验证”再到“育种应用”的多重断层。与模式作物相比，油茶作为多倍体木本植物，存在基因组复杂、童期长 (5~6 a)、遗传转化体系不成熟等瓶颈，其抗旱基因的功能验证及精准育种难以实现。现有研究多聚焦于基因表达模式分析，缺乏关键基因的直接功能证据；基因编辑技术在油茶中的成熟应用还是空白，稳定转化体系未建立，严重制约了从实验室到田间的技术转化。未来研究可从以下方向开展深入全面的探索。①在干旱信号感知与转导层面，多倍体基因组的同源冗余是首要障碍。油茶中大量同源基因并存，导致单一组学难以精确定位上游感知元件 (如 OSCA 离子通道、受体激酶)。可基于已有油茶六倍体参考基因组，通过亚基因组注释与同源基因表达分析筛选油茶特异的信号节点；在功能验证环节，鉴于稳定转化周期长，可建立原生质体瞬时转化与钙离子成像联用体系，结合异源表达系统验证离子通道活性，逐层解析上游信号如何触发下游生理适应。②在关键抗旱基因功能验证层面，油茶存在稳定遗传转化体系不成熟、童期长等核心瓶颈。目前仅可获得少量转化愈伤，难以批量培育完整阳性转基因植株，大幅制约基因功能的整株表型鉴定。未来研究可分梯度搭建验证平台：初期可以尝试构建 TRV-VIGS 瞬时沉默体系与发根农杆菌 *Agrobacterium rhizogenes* 介导毛状根转化平台，完成候选基因根系、叶片水平的功能初筛；针对必须在完整植株水平鉴定抗旱表型的基因，可利用不同基因型砧木-接穗嫁接组合，结合接穗中目标基因的 VIGS 瞬时沉默或过表达，快速建立基因表达量与抗旱表型的关联，绕开稳定转化与漫长

童期。远期需持续优化以胚状体、胚性愈伤为受体的稳定转化再生流程，并考虑六倍体油茶多同源拷贝冗余的基因组特征，设计靶向多个同源拷贝的协同 sgRNA 组合，探索单倍体诱导材料，简化遗传背景。③在复合胁迫研究层面，田间干旱常与高温、强光叠加，而木本植物表型鉴定周期长、背景变异大。 未来可构建标准化人工气候室复合胁迫平台，结合叶绿素荧光成像与高光谱遥感等无损表型组技术，实现高通量动态监测；同时，充分发挥油茶嫁接繁殖的产业优势，利用不同抗旱性砧木构建组合，系统解析地下部 (砧木) 对地上部 (接穗) 在复合胁迫下的信号重编程与资源分配机制，揭示植株在生长维持与防御激活之间的权衡关系。

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