科学通报 2025 年 第 70 卷 第 25 期: 4297 ~ 4314
中国农业大学生物学院建院40周年专辑 评 述
《中国科学》杂志社 SCIENCE CHINA PRESS

植物抗旱性研究进展

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2025-05-08 收稿, 2025-07-03 修回, 2025-08-08 接受, 2025-08-08 网络版发表
国家重点研发计划(2022YFF1001602, 2023YFF1001302)和国家自然科学基金(32171940)资助

摘要 干旱是限制植物生长和农作物产量的主要非生物胁迫. 深入了解干旱对植物生长发育的影响、植物应答干旱胁迫的分子调控网络、挖掘抗旱相关基因资源, 有利于建立和扩展植物逆境生物学理论体系, 将为作物分子设计育种提供理论支撑和基因资源. 本文综述了拟南芥和主要农作物抗旱性研究的主要进展, 重点从干旱胁迫信号的感受与传递的分子机制, 以及干旱对植物生长发育的影响两个方面展开讨论, 具体包括叶片表皮蜡质合成、气孔的发育与运动、根系生长调控以及植株生殖发育的改变. 最后梳理了40年以来(1984~2024)中国农业大学生物学院在抗旱研究的代表性成果. 这些研究成果为农作物抗旱节水的新品种分子设计育种等提供了理论依据和基因资源.

关键词 干旱胁迫, 信号应答, 生长发育, 基因克隆

近年来, 全球气候变化对农业生产的影响日益凸显. 由气候变化引起的降水模式改变和温度升高, 直接影响作物的水分利用效率和生长发育[1]. 干旱、洪涝等极端天气事件的频发, 对作物的生长和产量构成了严峻威胁[2]. 其中, 干旱发生频率高、持续周期长、波及范围广, 已经成为主要的气象灾害. 干旱不仅常见于干旱与半干旱地区, 即使在年总降水量较高的区域, 若生长季内降水分配不均, 仍可引发植物的干旱胁迫. 植物如何感知和响应干旱胁迫是一个重要的生物学问题. 由于植物对干旱胁迫的响应需与生长发育相协同, 因此理解干旱胁迫信号、激素与生长发育途径间的互作尤为重要. 本文首先阐述逆境激素脱落酸(abscisic acid, ABA)的信号转导途径和应答干旱胁迫的转录调控分子机制. 另外, 以叶片表皮蜡质合成、气孔发育与运动、根系生长及生殖发育等关键抗旱性状为切入点, 综述了拟南芥(*Arabidopsis thaliana*)、水稻(*Oryza sativa*)、小麦(*Triticum aestivum*)和玉米(*Zea mays*)在干旱胁迫影响植物生长发育方面的主要研究进展. 这些研究成果对于理解植物如何适应干旱环境、提升作物的抗旱能力具有重要的科学价值, 也将有助于推动农业的可持续发展, 确保全球粮食安全.

1 干旱胁迫信号的感受与传递

在干旱条件下, 土壤中的水分蒸发加快, 而降雨补充不足, 会影响到植物根际环境的水势. 当植物根际环境的水势降低到一定程度时, 就会引发渗透胁迫, 造成植物无法从土壤吸收到水分. 植物对渗透胁迫的应答包括: (1) 信号感知与上游信号传导; (2) 钙离子信号、(3) 脱落酸介导的信号; (4) 下游基因应答[3]. 深入探究植物响应干旱胁迫信号的感受与传递分子机制, 寻找作物抗旱遗传改良可行的策略和可操作的分子靶点, 在拓展科学认知边界与推动实际生产发展方面, 均有

引用格式: 刘升学, 马爱芳, 秦峰, 等. 植物抗旱性研究进展. 科学通报, 2025, 70: 4297–4314
Liu S, Ma A, Qin F, et al. Research advances in plant drought resistance (in Chinese). Chin Sci Bull, 2025, 70: 4297–4314, doi: 10.1360/CSB-2025-0645

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重要意义.

1.1 以PYR-PP2C-SnRK2 为核心的ABA信号传递途径

当植物遭受干旱胁迫时, ABA大量积累, ABA受体pyrabactin resistance(PYR)/PYR1-LIKE(PYL)/regulatory components of ABA receptor(RCAR)与ABA结合, 并与A类蛋白磷酸酶(PP2Cs, protein phosphatase 2Cs)相互作用, 从而激活Ⅲ类SNF1相关蛋白激酶2(SnRK2s, sucrose non-fermenting 1-related protein kinase 2s)[4~7]. SnRK2s作为一类丝氨酸/苏氨酸蛋白激酶, 广泛存在于植物中, 在拟南芥抗旱方面, SnRK2.6(OST1, open stomata 1)受到深入研究, 其参与调控众多干旱相关基因的表达、离子通道活性以及代谢途径[8~10], 是植物抗旱反应的枢纽, 其激活状态直接影响植物对干旱胁迫的应对能力(图1). ABA激活的SnRK2s通过对质膜离子通道蛋白的磷酸化修饰, 精确调节细胞内外的离子浓度. 在干旱胁迫下, 离子通道的调控有助于维持细胞的膨压, 控制气孔的开闭, 减少水分的损失, 优化水分的利用效率[11~13].

除了对离子通道的调控外, OST1还在转录调控方面发挥着重要作用, 被ABA激活的OST1直接磷酸化ABF(ABA-responsive element binding factors)、AREB(ABA-responsive element binding proteins)等转录因子, 促进一系列抗旱相关基因的转录, 这些受调控的基因参与维持细胞渗透平衡、清除活性氧、修复受损细胞膜等生理过程, 全方位提升植物在干旱环境下的生存能力[14~16]. 活性氧(reactive oxygen species, ROS)在植物的抗旱信号传导中发挥着双重作用: 一方面, 过量的ROS会导致细胞损伤和氧化应激, 从而影响植物的生长与发育; 另一方面, 适量的ROS作为信号分子参与调节植物的生理过程. 例如, ROS能够诱导气孔关闭, 增强植物对干旱的抗受性[17]. 研究发现, ROS与ABA信号通路之间存在密切的相互作用, ROS的产生能够增强ABA的信号传导, 促进植物的抗逆反应[10,18,19]. 位于细胞膜上的NADPH(nicotinamide adenine dinucleotide phosphate)氧化酶RBOHD(respiratory burst oxidase homolog protein D)和RBOHF在ABA诱导的ROS生成和气孔关闭中具有正向作用[20], 而ABA激活的OST1则通过磷酸化作用进一步激活RBOHF[21].

ZmOST1受干旱和ABA处理诱导, ZmOST1可以回补拟南芥*ost1-1*突变体对ABA处理后气孔敏感性的表型[22]. ZmPP2C-A10(clade A PP2C phosphatases 10)ABA信号传递途径的成员, 删除该基因启动子ERSE(endoplasmic reticulum stress response element)元件, 降低*ZmPP2C-A10*的表达量, 提高玉米苗期的抗旱性[23]. 王等研究表明, 在干旱或ABA处理条件下, ZmPP2Cs解除对ZmSnRK2.2的抑制, ZmSnRK2.2磷酸化转录因子ZmAL14(Alfin-like 14), 减弱其与*ZmROP8*(*Rho-like guanosine triphosphatase*(*GTPase*))启动子的结合, 从而解除对*ZmROP8*表达的抑制. 而高水平的*ZmROP8*减少ROS的积累, 增强玉米抗旱能力[24]. 郭等通过筛选转基因过表达玉米库, 鉴定到ZmPP84(clade F PP2C 84)是干旱胁迫响应的负调控因子, 可以使ZmMEK1(mitogen-activated protein kinase kinase 1)去磷酸化抑制气孔关闭, 从而抑制ZmMEK1-ZmSIMK1(stress-induced MAP kinase 1)信号通路[25]. 阴离子通道ZmSLAC1(slow anion channel 1)在保卫细胞中特异表达, 其突变体*zmslac1*表现出干旱敏感表型. 蛋白激酶ZmCPK35(calcium-dependent protein kinase 35)和ZmCPK37(calcium-dependent protein kinase 37)也能在保卫细胞中表达, 并与ZmSLAC1互作, 调控其通道活性. 在*zmcpk37*突变体中, ABA激活的S型阴离子通道电流受到抑制, 而过表达*ZmCPK35*和*ZmCPK37*则能增强该电流. 田间实验显示, 过表达*ZmCPK35*和*ZmCPK37*的植株在干旱条件下具有增产优势, 表明它们在玉米抗旱性遗传改良中具有潜在应用价值[26]. Hu等人[27]发现在正常条件下, 干旱负调控因子ZmCPK2磷酸化并激活转录因子ZmYAB15(YABBY transcription factor 15), 促进其DNA结合活性, 激活下游基因如*ZmSTRK1*(*stress-responsive receptor-like kinase 1*)的表达. 在干旱或ABA诱导的钙离子振荡条件下, 干旱正调控因子ZmCPK17被激活, 磷酸化并抑制ZmCPK2, 从而减弱ZmYAB15的活性, 激活抗干旱反应. Liu等人[28]发现另外一个CPK家族蛋白激酶ZmCRK1(CPK related protein kinase 1)也负调控玉米抗旱性, 其磷酸化质膜上的H^+-ATP酶ZmMHA2并抑制其质子泵活性, 导致ABA诱导的H^+外排受损.

RAF(rapidly accelerated fibrosarcoma)类激酶通过激活SnRK2s的活性, 在ABA/干旱和渗透胁迫信号途径中发挥关键作用. 在轻度干旱胁迫下, B2亚族的RAF激酶被激活, 通过对SnRK2s进行磷酸化修饰, 启动其激活进程. 而在更为严重干旱条件下, 脱水应激激活的B3亚族RAFs可进一步增强SnRK2s的活性, 表明B2和B3亚

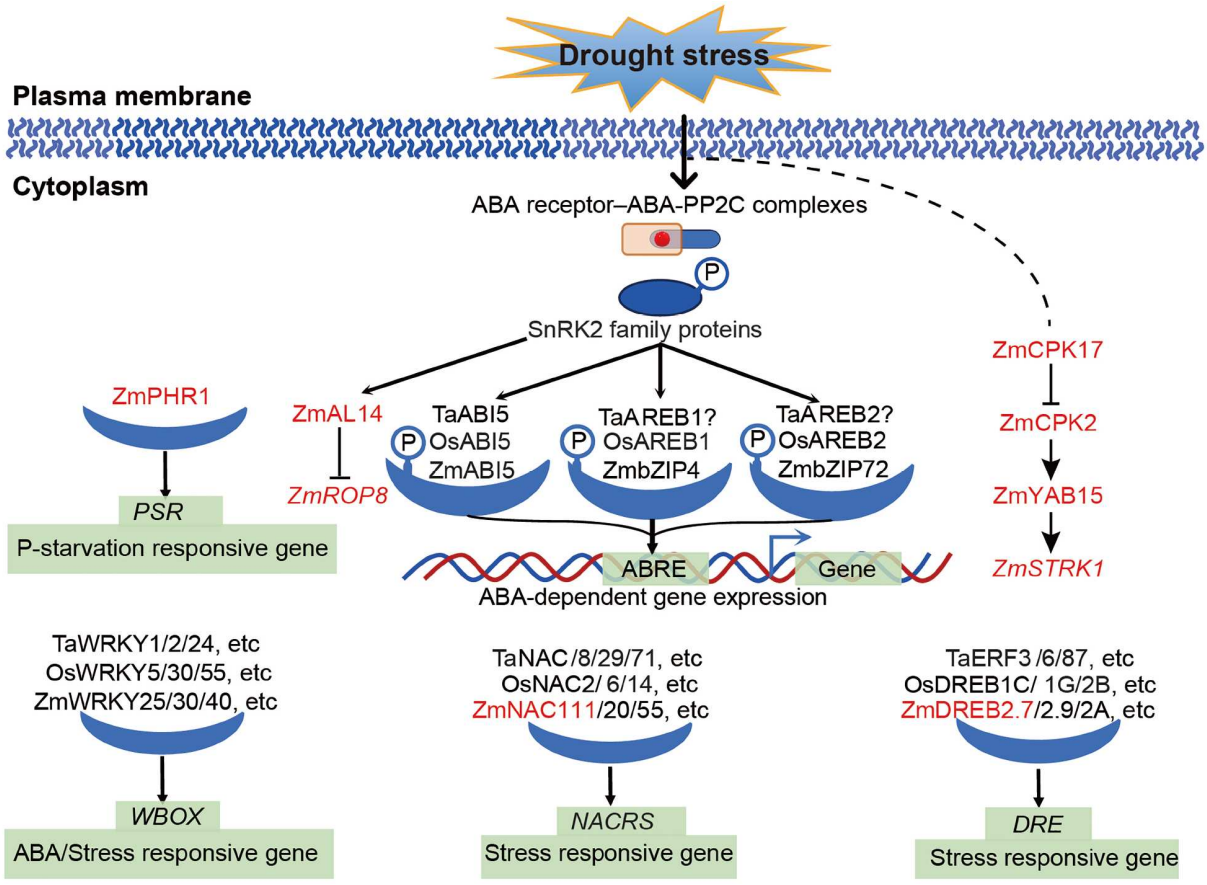


图 1 干旱应答过程中的转录调控网络. 在干旱条件下, ABA复合物(PYR-ABA-PP2C)激活SnRK2蛋白激酶家族蛋白, 进而磷酸化并激活下游的转录因子(ABI5和AREBs). 这些转录因子结合到ABA依赖性基因启动子区域的ABA应答基序上(ABA-responsive elements, ABRE), 诱导这些基因的表达, 从而增强植物的抗旱能力. 此外, 转录因子ZmPHR1通过调控磷酸盐应激响应基因的表达, 调节磷营养稳态, 增强玉米抗旱. 图中红色圆代表ABA分子, 红色字体标注的部分为中国农业大学生物学院研究成果. 图中问号代表已公布的基因组预测存在, 但尚无文献报道的基因

Figure 1 Transcriptional regulatory network in the drought response process. Under drought conditions, the ABA complex (PYR-ABA-PP2C) activates the SnRK2 protein kinase family proteins, and then phosphorylates and activates downstream transcription factors (ABI5 and AREBs). These transcription factors bind to the ABA-responsive motifs (ABA-responsive elements, ABRE) in the promoter regions of ABA-dependent genes, inducing the expression of these genes, thereby enhancing the drought resistance of plants. In addition, the transcription factor ZmPHR1 regulates phosphorus nutrition homeostasis by regulating the expression of the phosphate starvation responsive gene expressions and enhances drought resistance in maize. The red circles in the figure represent ABA molecules, and the parts labeled in red are the research results reported by the colleagues in College of Biological Sciences at China Agricultural University. "?" indicates genes predicted in published genomes but not reported in literature

组的RAF蛋白激酶激活依赖ABA的SnRK2.2/2.3/2.6 (ABA依赖的SnRK2s), 而B4亚组的RAF激酶RAF16/18/20/24/35/40/42则以不依赖ABA的方式激活I类SnRK2s (非ABA依赖的SnRK2s), I类SnRK2s与mRNA去帽复合物的支架蛋白(varicose, VCS)互作并对其进行磷酸化修饰, I类SnRK2s-VCS信号模块在调控干旱响应基因的表达以及根系结构和发育方面起重要作用. 此外, SnRK2B/SnRK2.10通过磷酸化脱水素蛋白ERD10/ERD14(early response to dehydration proteins)提高拟南芥抗旱性[29]. 具体而言, RAF激酶在感知渗透胁迫信号后, 通过磷酸化SnRK2s, 促进其活性的增强. 此过程不仅可以在缺乏ABA的条件下独立进行, 同时也能与ABA信号通路协同作用, 共同调控植物的抗旱反应[30~40]. 这种双重调控机制使植物能够更灵活地应对不同强度和持续时间的干旱胁迫, 从而提高其生存能力和适应性.

此外, 研究表明, 有些RAF激酶在植物响应干旱中起负调控因子的作用, 在高渗透压条件下, AGC激酶IREH1(IRE1-like protein)与蛋白磷酸酶2A(PP2A, protein phosphatase 2A)形成复合体, 通过抑制B1亚族

RAF13的活性, 进而正调控拟南芥的胁迫响应, 该研究提出了一种独立于SnRK2调控RAF蛋白活性的调控方式, 揭示了植物在干旱条件下优化生长与应激反应的分子机制[41]. C5亚组的RAF激酶RAG19/HT1(regulator of ABI1-GTPase 19/high leaf temperature 1)通过抑制OST1以及GHR1(guard cell hydrogen peroxide-resistant 1)对SLAC1的激活, 进一步抑制CO_2诱导的气孔关闭, 从而负调控拟南芥的抗旱性[42]. C5亚族RAF36和RAF22也负调控拟南芥干旱响应, SnRK2通过直接磷酸化进而诱导其降解[43]. 巩志忠课题组发现RAF22通过磷酸化ABI1增强其磷酸酶活性, 而ABI1也能通过去磷酸化反过来增强RAF22的激酶活性, 形成一个正反馈回路. 而在干旱应激条件下, ABA激活的OST1则通过磷酸化抑制RAF22的活性, 从而调节植物在干旱条件下的生长与应激反应之间的平衡[44]. 这项研究揭示了RAF22、ABI1和OST1之间的动态调控机制, 为理解植物在干旱应激下优化生长和环境适应的分子机制提供了新的见解.

综上所述, 非ABA依赖的抗旱响应机制在植物应对干旱胁迫中具有重要意义. 通过RAF的激活和SnRK2s的磷酸化修饰, 植物能够独立或协同ABA信号通路, 灵活应对不同强度和持续时间的干旱胁迫, 从而提高其适应性和生存能力.

1.2 应答干旱胁迫的转录调控

干旱胁迫下, 拟南芥中多种转录因子(transcription factors, TFs)被激活或抑制, 从而调控下游基因的表达. 这些转录因子主要包括AREB/ABFs、DREBs、NACs、MYBs和WRKYs等家族成员. AREB/ABFs是ABA信号通路的关键转录因子, 能够结合到ABA响应元件(ABA-responsive elements, ABRE), 激活下游基因的表达. 研究表明, AREB1、AREB2和ABF3在干旱应激下被磷酸化并激活, 从而调控多种干旱响应基因的表达[16]. DREBs(dehydration-responsive element-binding proteins)是CBF(C-repeat binding factor)家族的成员, 能够结合到干旱响应元件(drought responsive element, DRE). DREB通过调控蜡质的合成进而提高拟南芥的抗旱性[45,46]. 转录因子DREB2A的表达并不受ABA诱导, 但它能够正向调控渗透胁迫和热胁迫[47,48], 然而, DREB2A上游的调控组分尚不明晰. MYB转录因子[49~51]和WRKY转录因子[52,53]也参与了干旱应激反应. 例如, MYB60负调控拟南芥对干旱的响应[52], 而MYB30是ABA信号的正调控因子[54]; WRKY46/54/70正调控BR信号, 而负调控干旱响应[55]. 其他植物的一些*WRKY*基因转入拟南芥后增强了抗旱性[56~58].

许多研究揭示了AP2/ERF、DREB、NAC、bZIP、bHLH、WRKY、ABF等在作物干旱信号转导中的作用[59]. 在干旱胁迫下, OsERF71调节*OsABI5*、*OsPP2C68*、*OsP5CS1*和*OsP5CS2*基因的表达, 过表达*OsERF71*显著提高了对干旱胁迫和盐胁迫的耐受性, 较野生型显著降低了离体叶片失水速率[60]. ERF家族转录因子OsLG3通过清除活性氧正调控水稻抗旱性, 增强*OsLG3*表达可以调高地上部鲜重和苗期存活率[61]. OsNAC2直接结合了胁迫响应基因*OsLEA3*(late embryogenesis abundant 3)和*OsSAPK1*(stress-activated protein kinase 1)启动子[62]. OsSPL10(squamosa promoter binding protein-like 10)可以调控靶基因*OsNAC2*的表达水平, 调节ROS的积累, 参与控制气孔开关, 正调控水稻抗旱性[63]. OsNAC17正调控木质素合成基因, 促进木质素在叶和根中的积累, 过表达(*OsNAC17OX*)转基因植株, 表现出抗旱性, 而敲除(*OsNAC17-KO*)转基因植株表现出干旱敏感表型[64]. 在干旱条件下, OsNAC52上调胁迫响应基因*RD29B*和*KIN1*, 增强*OsNAC52*表达可以降低转基因植株的叶片脱水速率, 正调控水稻苗期抗旱性[65]. OsbZIP23是ABA信号通路的成员, 与组蛋白修饰(histone H3K4 trimethylation, H3K4me3)协同调控干旱响应基因的表达, 从而正调控水稻的抗旱性[66]. *OsWRKY55*在根、茎、叶、叶鞘、花序等均有表达, 并与4个丝裂原活化蛋白激酶(mitogen-activated protein kinases, MAPKs), 即OsMPK7、OsMPK9、OsMPK20-1和OsMPK20-4互作. 过表达*OsWRKY55*导致苗期抗旱性和株高的降低[67]. OsABF1可以上调靶基因*COR413-TM1*(*cold-inducible thylakoid membrane protein 1*)的表达进而提高水稻的抗旱性, 并在ABA信号通路中形成反馈调节[68]. *OsMYB1R1*是穗部特异表达基因, 负调控水稻苗期抗旱性, 其RNAi株系苗期存活率显著高于野生型, 过表达株系显著低于野生型[69].

*TaERF-6-3A*负调控小麦抗旱性, 过表达植株中的胁迫响应基因*RD29A*和*P5CS1*表达下调, 对干旱和盐胁迫的敏感性, 苗期存活率显著低于野生型[70]. 过表达*TaMYBsm3-D*拟南芥比野生型提高了脯氨酸含量和降低了MDA含量, 干旱胁迫响应基因(*P5CS1*、*DREB2A*和*RD29A*等)表达量也显著高于野生型[71]. *TaWRKY1-2*正调控小麦抗旱性, 基因沉默材料的MDA含量升高、

脯氨酸和叶绿素含量降低、苗期存活率降低、胁迫相关基因(*TaPOD*、*TaSOD*和*TaP5CS*)的表达水平受到抑制[58]. 过表达*TaWRKY2*转基因小麦幼苗降低了叶片失水速率, 提升了叶片中脯氨酸和可溶性糖含量, 提高了苗期存活率, 增加了穗长和穗粒数, 增强了小麦抗旱性[72]. *TaWRKY24*受干旱、盐、ABA、茉莉酸甲酯和乙烯利的诱导表达, 过表达*TaWRKY24*增加了转基因植株的脯氨酸含量、降低了活性氧和丙二醛的含量, 最终正调控小麦的抗旱性[73].

在玉米中, *ZmDREB2.7*基因的遗传变异与368份玉米自交系的苗期存活率显著相关, *ZmDREB2.7*启动子的多个插入、缺失显著相关, 而且以一种单体型存在, 在F2群体中, *ZmDREB2.7*优异单体型材料的苗期存活率显著高于对照[74]. Mao等人[75]通过GWAS方法, 发现*ZmNAC111*基因的遗传变异与苗期存活率显著相关, 而且该基因启动子存在82-bp的MITE(miniature inverted-repeat transposable element)转座子插入, 可以作为模板合成小RNA分子, 调节启动子的DNA和组蛋白的甲基化状态, 进而调控*ZmNAC111*基因的表达. 在玉米中, 增强*ZmNAC111*表达水平有助于提升叶片气孔在干旱压力下的关闭效率, 提高苗期存活率. Liu等人[76]利用224份玉米自交系, 在正常条件和两个干旱梯度的处理下, 获得了627份转录组数据, 以每种处理下的基因表达量为表型, 通过GWAS分析鉴定到73573个eQTLs (quantitative trait loci), 60%的eQTLs定位到1个候选基因. 通过孟德尔随机化分析, 鉴定到97个基因的表达量与玉米抗旱性直接相关的候选基因, 并确认了导致它们表达量差异的遗传变异位点. 其中, 脱落酸8′-羟化酶基因(abscisic acid 8′-hydroxylase gene)启动子变异影响了基因表达, 负调控玉米苗期抗旱性, 敲除突变体的苗期存活率显著高于野生型.

2 干旱对植物生长发育的影响

植物固着生长, 经常遭受多种非生物和生物胁迫威胁, 这些胁迫通常以协同的方式相互作用, 严重影响植物的生长和生产力. 当干旱发生后, 植物体内会发生一系列形态、生理、生化变化, 以维持其营养生长和生殖生长或提高干旱胁迫下生存概率, 这种能力统称为抗旱性[77,78]. 其具体又可分为三种表现方式: (1) 逃旱(drought escape)指在干旱条件下, 缩短营养生长到生殖生长阶段的过渡时间, 以确保成功完成生命周期或促进进入休眠状态, 直到环境胁迫消失; (2) 避旱(drought avoidance)指在干旱条件下, 通过形态生理调节维持较高的组织水势, 避开干旱对机体的影响, 例如, 根系构型优化、叶片卷曲、气孔开闭、叶表皮蜡质沉积等; (3) 耐旱(drought tolerance)指在干旱条件下, 通过主动积累渗透保护剂(如脯氨酸、甜菜碱)、激活抗氧化酶系统(superoxide dismutase, SOD; peroxidase, POD; catalase, CAT)及产生胁迫响应激素(ABA; jasmonic acid, JA), 从而保障细胞结构完整和代谢功能稳定的适应机制[78,79]. 目前对于植物抗旱性的评价和鉴定主要有以下几个方面: (1) 严重干旱胁迫下植株的存活率; (2) 持续中度干旱胁迫下植株生长发育的改变, 如根系大小、开花时间、植株高度等; (3) 生理生化指标: 气孔开闭、叶片表皮蜡质、渗透调节物质含量、抗氧化酶活性等; (4) 产量指标: 单株籽粒产量、生物量等[80,81]. 通过对叶片表皮蜡质、气孔调控、根系构型及生殖发育等关键抗旱性状的研究(图2), 可以加深我们对植物适应干旱环境的理解, 为系统解析植物抗旱性的遗传基础提供宝贵的信息.

2.1 干旱促进叶表皮细胞蜡质合成与沉积

植物表皮角质层存在于所有陆生植物与空气相接触的部位, 扮演着疏水性屏障的重要角色, 能够调控水分在表皮细胞的细胞壁与大气之间的流动[82]. 角质层由表皮细胞产生的角质和表皮蜡质所组成. 在植物角质层所含的蜡质中, 依据其分布位置的差异, 可进一步细分为表皮蜡质和内部蜡质. 诸多研究证实, 表皮蜡质的含量以及其自身结构在植物的整个生长发育进程以及抗逆性方面, 均起着至关重要的作用[83]. 研究表明, 表皮蜡的成分受遗传和环境因素的影响, 尤其是在干旱条件下, 植物通过增加蜡质的积累以增强抗旱能力[84,85]. 在干旱胁迫下, 表皮蜡的合成受到严格的基因调控, 例如拟南芥转录因子DREB26(dehydration-responseive element-binding protein 26)能够直接结合并激活*KCS2*(*3-ketoacyl-CoA synthetases 2*)和*CER1*(*eceriferum 1*)的启动子, 从而调控蜡的合成, 增加表皮蜡的含量, 提高抗旱能力[45]. 另一个AP2/DREB型转录因子RAP2.4(related to apetala 2.4)在干旱胁迫下也能够直接结合并激活*KCS2*和*CER1*(*eceriferum1*)的启动子, 调控蜡的合成以提高抗旱能力[45]. 此外, *MYB96*基因在干旱胁迫下被诱导表达, MYB96蛋白能够直接结合及激活*KCS1*、*KCS2*、*KCS6*等蜡质合成基因的启动子, 从而增加表皮蜡的含量, 进一步提高抗旱能力[46].

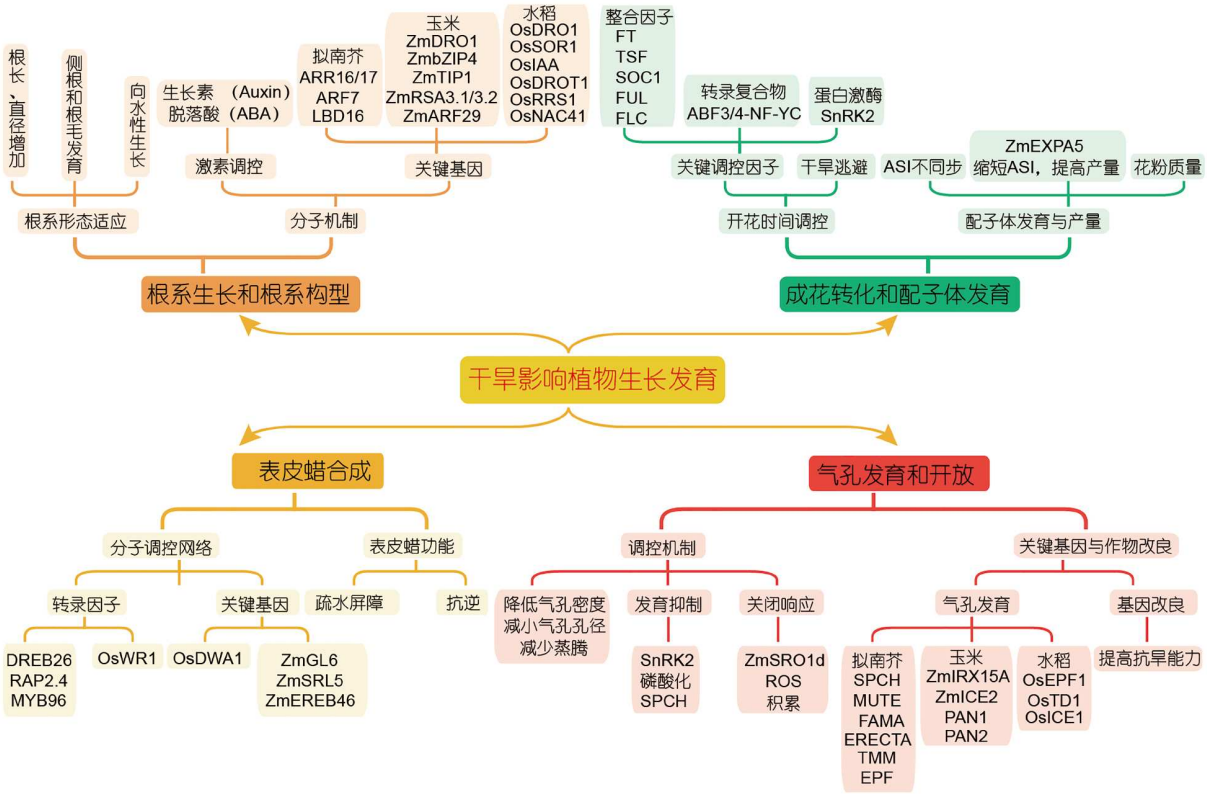


图 2 干旱胁迫影响植物生长和发育的复杂性. 干旱影响植物的表皮蜡形成、气孔发育、根系发育及成花转化. 这些过程涉及蛋白质的修饰和基因表达调控等复杂的生理生化过程

Figure 2 The complexity of drought stress on plant growth and development. Drought affects the epidermal wax formation, stomatal development, root system development, and floral organ transition. These processes are governed by intricate physiological and biochemical mechanisms, including protein modification and the regulation of gene expression

乙烯响应因子OsWR1(wax synthesis regulatory gene 1), 可以结合蜡质合成基因*OsLACS2*(long-chain acyl-CoA synthetase)和*OsFAE1*(fatty acid elongase 1)启动子的DRE和GCC元件, 正调控水稻蜡质合成. 过表达*OsWR1*能提高水稻苗期抗旱性, 而RNAi植株降低苗期抗旱性[86]. 水稻基因*DWA1*(drought-induced wax accumulation 1)正调控表皮角质层蜡质的累积, 在干旱胁迫下, *dwa1*突变体表皮蜡质累积减少, 降低了水稻苗期抗旱性[87]. 玉米GL6(glossy6)蛋白参与角质层蜡质的细胞内运输, 功能缺失突变体的表皮蜡质数量降低, 增加了叶表皮角质层通透性, 加快了失水速率, 导致幼苗抗旱性降低, 这个研究为解析角质层蜡质从生物合成位点运输到质膜的过程打开了大门[88]. *ZmSRL5*(*semi-rolled leaf 5*)通过调控玉米表皮蜡质结构, 来影响叶片表皮的通透性和抗旱性. *srl5*突变体的叶表皮蜡质结构缺陷、分布不均, 破坏了叶表皮的角质层屏障, 加快了叶片失水速率, 导致玉米抗旱性降低[89]. *ZmEREB46*(*ethylene-responsive element-binding protein 46*)调控叶表皮长链蜡质合成的相关基因的表达, *zmereb46*突变体叶片的角质层通透性增加, 表皮蜡质数量减少, 苗期存活率显著低于野生型[90]. 可见, 通过基因工程技术提升作物的表皮蜡积累, 可能成为增强作物抗旱能力的有效策略.

2.2 干旱抑制气孔的发育和开放

气孔是由保卫细胞组成的表皮结构, 是植物调节气体交换和水分蒸腾的场所. 气孔是通过保卫细胞膨胀的变化来调节开放和关闭, 达到平衡光合作用对CO_2的吸收和蒸腾作用[91]. 气孔的密度、尺寸和孔径会随环境的变化而发生适应性调整, 以保持植物生长和生存之间的最佳平衡[92]. 气孔发育是一个复杂的过程, 涉及一系列细胞分裂和细胞命运决定步骤. 在双子叶植

物拟南芥中，气孔发育从未分化的表皮细胞(原生表皮细胞)开始，这些细胞进入气孔系统，形成具有不对称分裂能力的细胞，例如，分生母细胞和保卫母细胞[93]. 这一过程由一系列关键的转录因子和信号通路调控，例如，SPCH(speechless)、MUTE(a master regulator of stomatal differentiation)、FAMA(final proliferation/differentiation switch during stomatal development)转录因子和MAPK(mitogen-activated protein kinase)信号通路. 上游涉及多种信号分子和受体. 例如，EPF(epidermal patterning factor 1)家族的肽类激素(如EPF1和EPF2)和其受体，如ERECTA和TMM(too many mouths)，这些信号分子通过MAPK信号通路调控气孔的分布和密度，确保气孔在叶片表面的正确排列[94,95]. 干旱是影响气孔发育的重要环境因素之一. 干旱条件下，植物通过调节气孔密度和大小来提高水使用效率. 研究表明，干旱激活的SnRK2会直接磷酸化气孔发育的关键转录因子SPCH，导致SPCH蛋白降解，从而抑制气孔发育[96]. 这一机制有助于植物在水资源有限的情况下减少水分散失，提高抗旱能力.

拟南芥气孔功能及发育的调控得到了充分的研究，近些年在主要农作物气孔发育的研究上，也取得一系列重要进展. 过表达*OsEPF1*(*epidermal patterning factor 1*)可以降低水稻叶片气孔密度，提高水分利用效率[97]. 过表达*OsDT11*(*drought tolerance 11*)增强水稻苗期抗旱性，降低苗期水分散失速率和气孔密度，提高叶片中ABA的浓度[98]. *OsERA1*(*enhanced response to ABA1*)是水稻干旱胁迫反应的负调节因子，其CRISPR/Cas9(clustered regularly interspaced short palindromic repeats(CRISPR)/CRISPR-associated protein 9)敲除突变体能快速关闭气孔，促进主根发育，显著提高苗期抗旱性[99]. 过表达*HvEPF1*(*hordeum vulgare epidermal patterning factor 1*)减少了气孔密度，提高了水分利用效率和苗期抗旱性[100]. 过表达*TaHXK3-2A*(*hexokinase 3-2A*)降低了叶表皮铺板细胞大小、增加了气孔密度，导致蒸腾速率变大而产生干旱敏感表型[101]. Zhang等人[102]首次通过玉米自然群体GWAS分析克隆到调控叶片气孔密度的基因*ZmIRX15A*(*irregular xylem 15A*)，位于第二个外显子3 bp变异(InDel1089)会改变mRNA的二级结构，进而影响*ZmIRX15A*的翻译效率，通过调节气孔密度和导度，从而调控光合速率和蒸腾速率. Zhou等人[103]通过反向遗传学手段分离到*zmice2-1*(*inducer of cbf expression2-1*)突变体，研究发现，*ZmICE2*通过影响细胞的分裂和分化进程，从而调控气孔发育以及参与玉米表皮的形态建成，这与水稻种不同，*OsICE2*仅参与调控气孔发育，而*OsICE1*起主要作用[104]. 玉米假受体激酶PAN1(pangloss1)和PAN2(pangloss2)在玉米气孔发育中共同发挥作用，促进副卫母细胞的极化分裂[105,106]. 其与SCAR/WAVE复合体协同促进气孔的不对称分裂[107]. PAN2在气孔关闭中起关键作用，即使在副卫细胞正常分裂的情况下，*PAN2*的缺失也会导致气孔关闭缺陷. 相比之下，*PAN1*的缺失仅在副卫细胞异常的情况下影响气孔关闭[108]. *ZmSRO1d*(similar to RCD-one 1d)基因是玉米苗期抗旱GWAS的候选基因[109]，Gao等人[110]研究发现，*ZmSRO1d*编码区的3个显著的SNP可以划分两种单体型：*ZmSRO1d-S*(干旱敏感)和*ZmSRO1d-R*(抗旱). *ZmSRO1d-R*中SNP131(第44位突变: 丙氨酸到甘氨酸)和SNP134(第45位突变: 缬氨酸到丙氨酸)，促进ZmSRO1d-R与Zm14-3-3.1互作，导致定位从细胞核拓展到细胞膜. 此外，ZmSRO1d-R中的SNP488(第161位突变：甘氨酸到丙氨酸)，增强了ZmSRO1d-R和ZmRBOHC互作，提高保卫细胞中的ROS含量，促进气孔关闭. 理解气孔发育的分子机制为农业改良提供了新的策略. 通过基因工程技术调控气孔发育相关基因，可以培育出具有优化气孔特性的作物，提高其抗旱能力和水分利用效率.

2.3 干旱调控根生长和重塑根系构型

研究表明，干旱条件下，植物的根长和直径均有所增加，根系深入土壤，以获取更多的水分和营养[111~113]. 这种根系适应机制不仅提升了植物在干旱环境中的生存能力，也加快了其对水分变化的响应，这种根系可塑性构成了植物应对干旱压力的重要生理适应策略，有效增强了其抗旱能力. 此外，干旱条件下，植物的向水源生长能力也得到了增强，植物根系能够感知土壤水分梯度，并向水分丰富的区域生长. 这一过程通过根系中的水分感知信号通路实现，涉及生长素和脱落酸等多种激素的调节. 通过强化向水能力，植物在干旱环境下能够有效获取水分，从而提高其生存能力和生长效率[114~116]. 在水分不足的情况下，植物通过调节生长素的分布，增强根系向水源的响应. 其中，生长素的不均匀分布导致根系向水源弯曲生长，从而提高水分吸收效率[117]. 同时，根系的结构和形态也会因水分分布的变化而发生适应性变化，如侧根数量的增加和根毛的发育，以增强水分捕获能力[118]. 植物的根尖能够感知

土壤中水分梯度, 并朝向高水势的方向生长, 这是根的向水性, 也是应对水分稀缺的环境的重要策略. Chang等人[119]鉴定到*ARR16*/*17*(*type-A response regulator*)会在低水势的根尖一侧上调表达, 促进分生组织区的细胞快速分裂, 导致根尖往高水势一侧弯曲生长. 植物根系通过调整可塑的生长结构来适应土壤条件, 其中, 转录因子ARF7(auxin response factor 7)诱导*LBD16*(*lateral organ boundaries-domain 16*)在侧根细胞中不对称表达, 引导根系向水生长. SUMO化修饰负调控ARF7的DNA结合活性. 干燥的条件促进ARF7的SUMO化修饰, 而潮湿的条件则抑制ARF7的SUMO化修饰, 启动转录调控, 促进侧根形成[120].

水稻基因*DRO1*(*deep rooting 1*)受生长素负向调控, 参与根尖细胞伸长, 促进根响应重力向下弯曲. 高量表达*DRO1*使根的生长方向深入土壤, 将*DRO1*导入浅根水稻, 改良了根系结构, 也保持了相对于受体品种的高产性能[121]. *qSOR1*(*quantitative trait locus for soil surface rooting 1*)是*DRO1*同源基因, 也受生长素信号途径直接负调控, 具有类似*DRO1*的根系生长角度调控功能[122]. 然而, 玉米*ZmDRO1*基因, 不同于水稻*DRO1*受生长素负向调控抑制, 而是受ABA诱导. ABA诱导启动子驱动*ZmDRO1*的转基因玉米可以提高干旱胁迫下的产量, 而且正常条件下不减产[123]. 水稻E3泛素连接酶SOR1(soil-surface rooting 1)可以泛素化降解OsIAA26(indole acetic acid 26), 位于AFB2-auxin-OsIAA9信号模块下游. 在乙烯或者生长素处理下, TIR1/AFB2与OsIAA9互作、并降解OsIAA9, 释放出SOR1去调控降解OsIAA26蛋白, 从而抑制根伸长生长. 反之, 在缺乏乙烯和生长素的情况下, OsIAA9抑制SOR1的E3连接酶活性, 从而稳定了OsIAA26, 促进了正常的根伸长[124]. 水稻*DROT1*(*drought 1*)在苗期根、茎和叶的维管束中特异性表达, 调控维管组织细胞壁中纤维素的含量和晶体结构, 增强*DROT1*表达可以提高苗期存活率和产量; *DROT1*启动子区域的关键SNP变异赋予*DROT1*更高表达量, 进而增强抗旱性[125]. 水稻*RRS1*(*robust root system 1*)编码一个R2R3型MYB家族转录因子, 可以激活生长素信号通路的*OsIAA3*基因的表达, 从而调控根系发育, 负调控水稻苗期存活率和产量. 以旱稻IRAT109为供体亲本、水稻Yuefu为轮回亲本, 得到*RRS1*的渗入系IL20, IL20的根长显著大于Yuefu[126]. *RoLe1*(*root length 1*)正向调控水稻根系发育与抗旱性, 在干旱条件下, *RoLe1*过表达株系的根系干生物量和产量均显著高于野生型. OsNAC41可以调控*RoLe1*(*root length 1*)表达, 参与*OsNAC41-RoLe1-OsAGAP*模块调节旱稻根系发育与抗旱性. 以干旱敏感型水稻Yuefu为受体, 导入旱稻IRAT109的*RoLe1*抗旱基因型, 构建的近等基因系(NIL-*proRoLe1*$^{-526T}$)表现出显著增强的抗旱性[127]. ZmbZIP4正向调控胁迫响应基因*ZmLEA2*、*ZmRD20*、*ZmRD21*和*ZmRab18*以及ABA合成相关基因*NCED*、*ABA1*、*AAO3*和*LOS5*的表达. 玉米中增强*ZmbZIP4*表达量, 促进ABA合成和根系发育, 提高玉米的抗旱性[128]. *ZmTIP1*(*tip growth defective 1*)是玉米苗期抗旱GWAS的候选基因[110], 过表达*ZmTIP1*的玉米根毛显著长于野生型, 提高了干旱下的苗期存活率, 这源于ZmTIP1促进了底物蛋白ZmCPK9的质膜定位, 可能促进根毛生长, 并增强玉米对干旱的抗受能力[129]. Ren等人[130]通过GWAS和根系转录组联合分析, 鉴定到81个玉米根系构型相关的基因, 实验数据表明, ZmRSA3.1(root system architecture 3.1)和ZmRSA3.2, 通过与ZmARF4(auxin response factor 4)、ZmARF29和ZmIAA38互作, 参与生长素通路调控玉米根系构型发育.

2.4 干旱影响成花转化和配子体育性

被子植物生活史是从种子到种子的过程, 包括, 种子萌发、营养生长、生殖生长、开花和传粉受精、种子的形成, 其中生殖生长又可分为: 花的发育、配子体的形成与发育. 花的发育包括3个阶段: 成花决定、花的发端和花器官形成. 成花决定是茎顶端分生组织(shoot apical meristem, SAM)向花分生组织(floral meristem, FM)的转变的过程, 在拟南芥中主要存在6条诱导途径: 光周期途径(photoperiod)、自主途径(autonomous)、春化途径(vernalization)、赤霉素(gibberellin, GA)途径、温度途径(ambient temperature)以及年龄途径(plant age)[131,132]. 这些信号途径既各自独立运行, 又相互紧密交织, 最终将成花信号传递到关键整合因子: FT(flowering locus T)、TSF(twin sister of FT)、SOC1(suppressor of overexpression of constans 1)等[133~135], 激活花分生组织特异基因的表达: *FUL*(*fruitfull*)、*CAL*(*cauliflower*)、*LFY*(*the transcription factor leafy*)和*AP1*(*apetala1*)等[136], 进而促进花器官形成. 花器官的形成是配子体发育的前提和基础, 花器官中的造孢细胞(sporogenous cell)发育成配子母细胞, 经过减数分裂产生四分体(tetrad). 在雄性配子体的产生过程中, 所有四

个小孢子都发育成有活力的花粉粒. 然而, 在雌性四个大孢子中, 仅一个会继续发育单细胞胚囊, 而其余的三个大孢子以一种程序性细胞死亡的形式退化, 单细胞胚囊再经过三次有丝分裂, 最终形成“七胞八核”的雌配子体(即为胚囊)[137]. 配子体发育是植物生殖周期中的一个敏感阶段, 而干旱作为一种常见的非生物胁迫, 对配子体的发育具有显著影响. 干旱条件对植物的开花时间和模式也产生了显著影响, 通常在干旱环境下, 植物会选择提前开花, 以确保在水分减少之前完成其繁殖过程, 这种现象被称为“干旱逃避”. 通过调节开花时间, 拟南芥能在最佳水分条件下生长和繁殖, 从而提高存活率[138~140]. 此外, 干旱胁迫可能影响花粉的质量和授粉的成功率, 进而对植物的产量造成影响. 干旱胁迫下, 转录因子ABF3(ABA-responsive element(ABRE)-binding factors 3)和ABF4(ABA-responsive element (ABRE)-binding factors 4)通过与NF-YC(nuclear factor Y subunit C)形成复合体来调节*SOC1*(*suppressor of overexpression of Constans1*)基因的表达, 从而促进拟南芥的抗旱性和开花时间[138]. 同时, SnRK2(SNF1-related protein kinase 2)通过磷酸化底物SNS1(SNF1-related protein kinase 2(SnRK2)substrate 1), 促进开花基因*FT*(*flowering locus T*)的表达, 从而影响干旱条件下的开花时间[140,141].

玉米是雌雄同株异花作物, 雌花序和雄花序着生在不同的位置发育, 散粉和吐丝之间的同步对于保证授粉和粮食生产至关重要. 在开花期遭遇干旱胁迫, 雌花会延迟吐丝, 但对散粉影响较小[142]. Lu等人[143]构建了一个522份材料的玉米作图群体(305玉米自交系和217份重组自交系), 联合连锁分析与关联分析, 提高了数量性状作图的准确性, 筛选到*GRMZM2G164400*等ASI相关的基因. Liu等人[144]比较了干旱对玉米雌雄穗发育的影响, 发现干旱延缓了雌穗的发育, 降低了花丝的生长速率, 推迟了吐丝时间, 导致ASI(anthesis and silking interval)的增加[144]. Liu等通过候选基因关联分析鉴定到*ZmEXPA4*(*α-expansin4*)与干旱下的ASI显著相关, 利用雌穗中受干旱胁迫诱导表达的启动子驱动*ZmEXPA4*的表达, 可以显著缩短干旱下的ASI, 而且不影响其他农艺性状. Tao等人[145]通过扩张蛋白基因家族的候选基因关联分析鉴定到*ZmEXPA5*与干旱下的ASI显著相关, 玉米中过表达*ZmEXPA5*可缩短干旱下的ASI, 并在正常浇水和干旱条件下均显著提高籽粒产量.

3 建院40年以来中国农业大学生物学院在抗旱方面取得的进展

生物学院在拟南芥抗旱领域取得了显著的进展(图3), 巩志忠教授团队在拟南芥抗旱研究方面也取得了丰富成果. 通过EMS诱变和正向筛选, 该团队鉴定到一个位于细胞膜上的类受体激酶GHR1, 其通过与阴离子通道SLAC1互作并磷酸化激活SLAC1, 从而促进气孔关闭. 研究结果表明, 蛋白磷酸酶ABI2(ABA-insensitive 2)能够抑制GHR1的活性[146]. 采用相同的正向筛选方法, 该团队还鉴定到一个新蛋白EAR1(enhancer of ABA co-receptor 1), 该蛋白通过与ABA信号通路中的PP2C磷酸酶相互作用来增强其活性, 从而负调控ABA信号传导. EAR1与PP2C的N端结合, 释放其自抑制作用, 增强PP2C的磷酸酶活性, 并间接抑制SnRK2激酶的活性和ABA信号传导[147]. 巩志忠团队进一步研究了E3泛素连接酶调控拟南芥抗旱性中的调控作用, 发现拟南芥中的U-box E3连接酶PUB12(plant U-box E3 ligases 12)和PUB13能与ABA信号通路中的ABI1蛋白相互作用, 并在ABI1与ABA受体相互作用时对ABI1进行泛素化修饰, 从而促进ABI1的降解. 这一机制在ABA信号传导中起到了关键作用[148]. 另外两个U-box E3连接酶PUB10和PUB11通过泛素化降解干旱正调控因子LRR1(leucine rich repeat protein 1)和KIN7(kinase 7), 从而负向调控植物的抗旱能力[149]. 类受体蛋白激酶BAK1(BRI1-associated receptor kinase 1)通过磷酸化激活位于质膜上的氢离子ATP酶AHA2, 从而增强了AHA2的活性, 正调控ABA诱导的气孔关闭[150]. 综上所述, 巩志忠团队在鉴定到多个与参与干旱响应的调控因子, 它们在调控气孔关闭和ABA信号转导过程中具有重要作用, 为理解植物抗旱机制提供了新的见解.

秦峰教授团队利用GWAS在玉米抗旱性研究方面也取得了突出的成果, 按研究性状可以分为3个方面. (1) 在极端干旱条件下玉米苗期抗旱性研究. 通过评估经历严重缺水后幼苗存活率(seedling survival rate, SR), 来衡量玉米早期生长阶段对干旱环境的适应能力. 以玉米苗期存活率为性状, 采用GWAS识别影响其幼苗干旱耐受性的遗传位点, 先后鉴定到*ZmDREB2.7*[74]、*ZmNAC111*[75]、*ZmVPP1*[109]、*ZmTIP1*[129]、和*ZmSRO1d*[110]. (2) 干旱条件下的ASI. 玉米是雌雄同株异花作物, 雌花序和雄花序分别长在植株的中部和顶端. 干旱对雌花序和雄花序的发育均有影响, 但对雌花

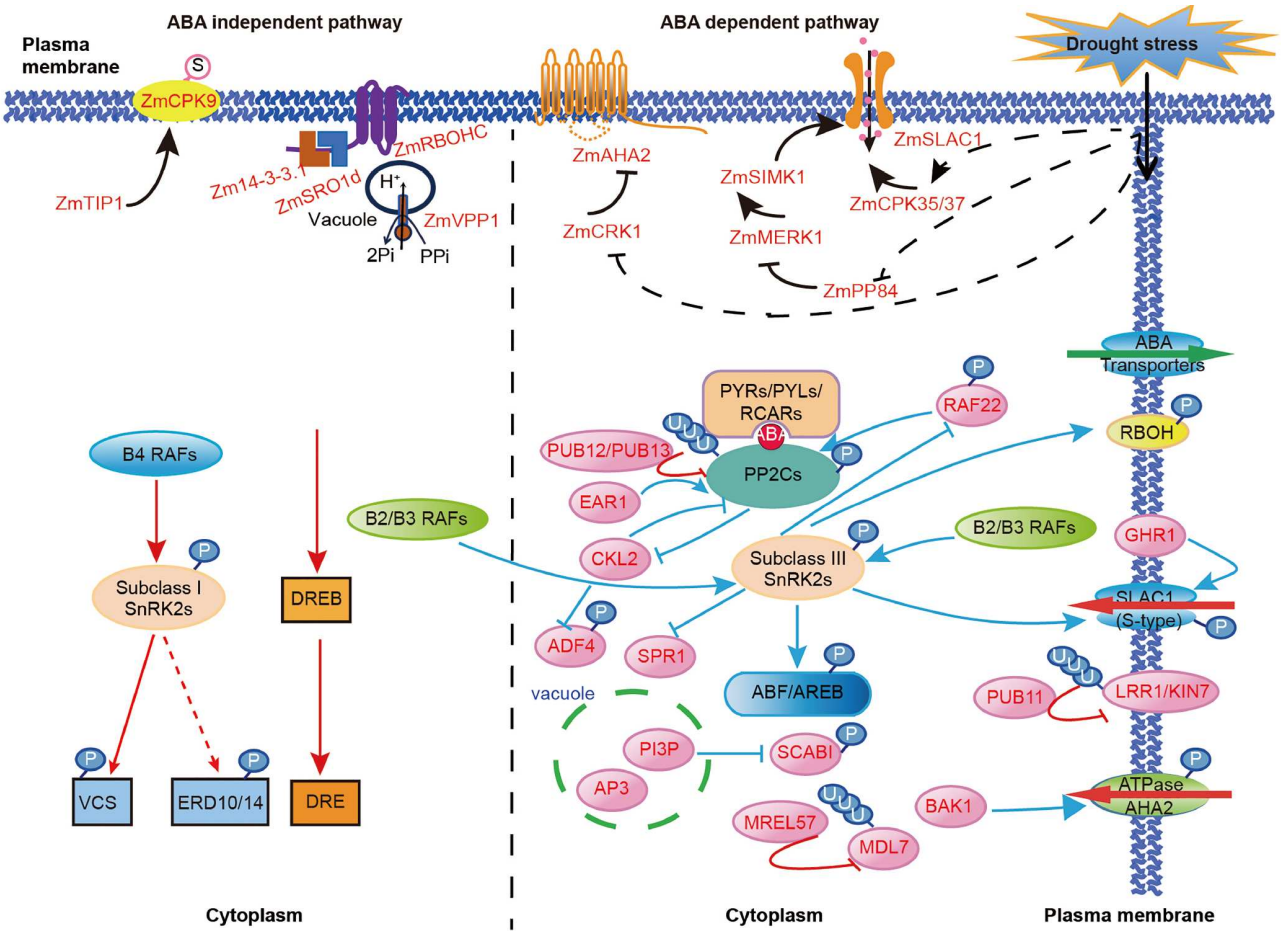


图 3 干旱信号的感受与传递. 植物在干旱胁迫下形成复杂的信号传导网络, 包括ABA依赖性和非ABA依赖途径. 这些途径通过一系列的蛋白相互作用和磷酸化事件, 最终调控离子通道活性、活性氧稳态以及相关基因的表达, 最终提高植物的抗旱性. 图中红色部分是中国农业大学生物学院报道的研究成果

Figure 3 Perception and signal transduction of drought stress. Plants develop intricate signaling networks in response to drought stress, comprising both ABA-dependent and ABA-independent pathways. These pathways orchestrate a series of transcriptional and post-translational regulations, which ultimately modulate ion channel activity, Reactive Oxygen Species (ROS) homeostasis, and the expression of drought-related genes, thereby enhancing plant drought tolerance. The parts labeled in red are the research results reported by the colleagues in the College of Biological Sciences at China Agricultural University

序的影响更为显著. 干旱会推迟雌花序的吐丝时间, 导致雌雄花序开花时间间隔增大, 降低雌花授粉的效率, 从而影响结实率和产量. 利用在开花期干旱诱导型启动子驱动*ZmEXPA4*的表达, 可显著降低干旱导致的ASI[144]. (3) 根部相关性状. 根系是作物感知和吸收水分的器官, 根毛是根尖部位的一种细胞结构, 可以增大根系的表面积, 也是吸收水分的主要部位. ZmTIP1可以介导硫酰基化修饰促进底物蛋白ZmCPK9定位在质膜. 在玉米中, 过表达*ZmTIP1*能增加根毛长度和抗旱性. 另外, 秦峰团队筛选了224份抗旱性不同的玉米自交系, 在正常灌溉和两种干旱处理条件下, 取叶片进行二代测序, 共得到627份转录组数据, 进行了eQTL分析. 进一步采用孟德尔随机化分析, 鉴定到97个基因, 其表达量变化与抗旱性直接相关, 并定位到影响表达量变化的遗传变异位点[76]. 为了深入解析玉米抗旱的遗传基础, 组装了热带抗旱玉米自交系CIMBL55基因组, 其包含了65个抗旱候选基因的优异等位基因型, 将为深入研究玉米抗旱性的提供了基因组信息, 对分子设计和智慧育种提供可选择的靶点[151].

郭岩教授团队成功鉴定到一种新型的肌动蛋白结合蛋白SCAB1(stomatal closure-related actin binding protein 1), 该蛋白与肌动蛋白丝特异性结合并稳定其

结构, 从而有效调节气孔运动. 研究结果表明, SCAB1在体外和体内均能结合并维持肌动蛋白丝的稳定性其缺失导致气孔对脱落酸的敏感性降低, 并延缓了肌动蛋白丝的重组过程. 这些发现揭示了SCAB1在调控气孔闭合过程中对肌动蛋白丝动态的重要作用[152]. 此外, 该团队发现磷脂酰肌醇3-磷酸(PI3P, phosphatidylinositol-3-phosphate)能够特异性结合SCAB1并抑制其寡聚化, 从而调控F-actin的稳定性, 进一步调控气孔闭合和液泡重塑, 突出了PI3P在ABA诱导的气孔闭合过程中的重要调控作用[153]. 另一项研究表明, SCAB1作为一个关键的分子开关, 通过其磷酸化状态的动态变化, 整合早期的Ca^{2+}信号和后期的ABA信号, 从而调控F-actin的重组和气孔闭合. 这一机制确保了植物在高渗透环境下高效调控气孔的张开与关闭, 从而减少水分散失[154]. 酪蛋白激酶样蛋白2(CKL2, casein kinase-like protein-2)通过与肌动蛋白解聚因子ADF4(actin-fepolymerizing factor-4)相互作用并对其进行磷酸化修饰, 进而抑制其肌动蛋白解聚活性, 促进肌动蛋白丝在干旱及ABA诱导的气孔闭合过程中的重组[155]. 进一步研究表明, CKL2的激酶活性在干旱胁迫下通过ABA-PYL-PP2C模块被激活, 促进气孔闭合. 此外, CKL2还磷酸化PYL1、ABI1和ABI2来调控其稳定性, 进而微调ABA信号通路[156]. 该团队还发现AP3M复合体(AP3 complex)在拟南芥中具有结合和切割肌动蛋白丝的活性, 它通过将蔗糖转运蛋白SUC4等分选至液泡膜, 影响液泡形态和气孔运动, 强调了肌动蛋白丝的动态性和适配蛋白复合物功能在植物细胞活动中的关键作用[157]. 综上所述, 郭岩团队的研究表明: 肌动蛋白在拟南芥中受到SCAB1、PI3P、CKL2、AP3M等多种因子的精细调控, 这些调控过程与孔运动和液泡形态等细胞活动密切相关, 形成一个复杂而有序的调控网络, 对植物在干旱胁迫下减少水分散失以及增强抗旱性起着至关重要. 另外, 毛同林教授团队揭示了E3泛素连接酶MREL57(microtubule-related E3 ligase 57)通过泛素-26S蛋白酶体系统(UPS)调控微管稳定性, 从而在植物响应干旱胁迫和脱落酸(ABA)诱导的气孔关闭中起关键作用. 研究发现, MREL57与微管稳定蛋白WDL7(wave-dampened2-like7)相互作用并泛素化降解WDL7, 促进微管解聚和气孔关闭, 揭示了ABA信号通路中微管动态调控的新机制[158]. 王向锋副教授团队研究发现, 拟南芥ABA信号通路的核心组分OST1磷酸化微管相关蛋白SPR1(MAP spiral 1), 导致其从微管上解离, 进而促进微管解聚和气孔关闭, 揭示了ABA信号与微管动态调控之间的直接联系[159].

武维华院士团队发现转录因子ZmPHR1(phosphate starvation response1)是大量元素磷吸收的重要调控因子, 敲除突变体*zmphr1*的体内磷含量降低, 植株生物量减少, 出现低磷胁迫敏感表型. 在正常灌溉、干旱处理、高温条件下, *ZmPHR1*过量表达株系的产量显著高于野生型, 进一步的实验证实, *ZmPHR1*通过调控磷稳态来提高玉米抗旱性[160]. CPK32可以磷酸化FCA蛋白的WW结构域, 影响蛋白FCA与FY的互作, 进而调控开花抑制因子FLC的表达, 实现花期调节[161]. 玉米钙依赖型蛋白激酶ZmCPK35和ZmCPK37通过调节玉米保卫细胞S型阴离子通道ZmSLAC1的通道活性从而调控玉米的抗旱性并影响干旱下的产量性状[26]. 这些成果完善了作物抗逆高效的理论体系, 为创制抗逆高效作物新种质提供了基因资源和选择靶点.

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Summary for “植物抗旱性研究进展”

Research advances in plant drought resistance

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In recent years, global climate change has intensified the effects of critical environmental stressors, such as drought, flooding, and extreme temperatures, on plant growth and crop yield. Drought stands out as a major meteorological hazard due to its high frequency, prolonged duration, and widespread impact. Drought is not only prevalent in arid and semi-arid regions, but may also trigger stress in areas with higher annual precipitation where uneven distribution occurs during the growing season. As a significant abiotic stress, drought constrains plant growth and diminishes crop yields. A deeper understanding of drought's effects on plant growth and development, the molecular regulatory networks underlying plant responses to drought stress, and the exploration of drought-resistant gene resources will advance the establishment and expansion of the theoretical framework in plant stress biology. These efforts will further provide theoretical foundations and genetic resources for molecular design breeding of drought-resistant crops.

This review summarizes major advances in drought resistance research in *Arabidopsis thaliana* and major crops. The first section elucidates the signal transduction pathway of abscisic acid (ABA) and the molecular mechanisms of transcriptional regulation in response to drought stress. Under drought conditions, formation of the ABA complex (PYR/PYL/RCAR-ABA-PP2C) releases SnRK2 protein kinases, which subsequently phosphorylate and activate downstream transcription factors (ABI5 and AREBs). These transcription factors bind to ABA-responsive elements (ABREs) in the promoters of ABA-dependent genes. Meanwhile, DREB transcription factor, also known as CBFs, regulates the stress-inducible expression of genes via ABA-independent pathways. The promoters of these drought-responsive genes frequently harbor the dehydration-responsive cis-element (DRE).

Drought detrimentally affects plants by reducing germination, suppressing leaf expansion and tillering, diminishing dry matter accumulation, and decreasing grain yield. Plants have evolved physiological and molecular mechanisms to mitigate these damaging effects. The second section details the molecular mechanisms of drought stress signal perception and transduction, as well as the impact of drought on plant growth and development. Specific aspects include leaf epicuticular wax deposition, stomatal development and movement, root growth, and reproductive development. Here, we summarize recent progress in cloning and functionally characterizing drought resistance genes, alongside technological advances developed to alleviate drought's threat to crop production. Our results further suggest that the integration of multi-omics data, more reference genome information, and robust statistical analyses is likely to facilitate the identification of other causal genes associated with drought resistance. Elucidating how plants perceive and respond to drought stress at the molecular level is fundamental to developing molecular approaches for enhancing crop tolerance. Molecular breeding approaches, such as marker-assisted selection, gene pyramiding, and genome editing, can fully utilize the growing repository of favorable alleles to precisely improve drought-resistant traits.

Finally, this article summarizes representative achievements in drought resistance research over the past four decades (1984–2024) from the College of Biological Sciences at China Agricultural University. These findings provide both theoretical foundations and genetic resources for molecular design breeding of drought-tolerant and water-saving crop varieties.

drought stress, signal response, growth and development, gene cloning

doi: 10.1360/CSB-2025-0645