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作物杂种优势与生物育种专辑 评 述

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作物抗旱关键调控因子的挖掘与利用

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摘要 干旱是制约作物生长发育及产量的主要非生物胁迫之一. 随着全球气候问题的加剧以及人口的不断增长, 干旱对农业生产的影响日益严重, 因此提高作物的抗旱能力对于保障国家粮食安全具有重要意义. 本文综述了近年来报道的作物抗旱关键调控因子的研究, 从形态、生理和分子水平解析作物抗旱响应机制. 随着测序技术的发展, 多组学研究展现出独特优势, 通过整合多维度、系统化的数据, 更加高效地挖掘作物抗旱关键调控因子. 抗旱基因的利用需要兼顾产量和抗性的平衡, 可通过表观调控、分子模块设计育种、诱导型启动子利用和顺式调控元件编辑实现稳产与抗旱协同改良. 本文还分析了抗旱基因在复合逆境胁迫下的作用, 为利用生物技术手段进行多基因、多标记聚合的抗旱遗传改良提供理论基础. 此外, 植物生长调节剂及根际微生物提高作物抗旱性的研究与应用, 为作物抗旱改良提供新的策略. 总之, 解析作物抗旱机制, 挖掘抗旱关键调控因子, 培育抗旱稳产、多抗广适的作物新品种, 同时将基础研究、育种实践和田间管理相结合, 是提高作物抗旱性的重要途径.

关键词 作物, 抗旱性, 调控机制, 遗传改良, 抗旱策略

干旱胁迫影响作物生长发育及产量. 过去10年中, 由于干旱造成的全球农作物减产损失已达到约300亿美元[1]. 在我国, 农作物旱灾成灾面积约占总成灾面积的52.53%, 严重制约粮食生产[2]. 随着全球气候问题加剧及人口增长, 干旱对农业生产的影响将越发严峻[3]. 因此, 深入解析作物抗旱机制, 挖掘并利用抗旱关键调控因子, 充分利用作物遗传育种改良、植物生长调节剂施加和根系微生物塑造等方法提高作物的抗旱能力, 对保障国家粮食安全和促进农业可持续发展具有重要意义.

1 作物抗旱机制

植物在漫长的进化过程中形成了多种机制来应对干旱, 包括逃旱机制、避旱机制、耐旱机制和胁迫后的干旱恢复[4,5]. 植物通过调节叶片形态及气孔密度、根系发育、光合作用、渗透调节能力、抗氧化防御体系等形态和生理生化特征来应对干旱胁迫, 这些特征也是评价植物抗旱性的重要指标[6,7]. 植物通过激素、离子和小分子物质浓度的变化等来感知和传递干旱胁迫信号, 转录调控、翻译后调控及表观遗传调控共同影响了干旱响应基因的表达[8](图1). 近年来, 越来越多的作物抗旱调控基因被报道, 为作物抗旱育种改良提供了理论基础.

1.1 作物对干旱胁迫的响应

1.1.1 叶片形态及气孔密度

当遭遇干旱胁迫时, 叶片细胞失水膨压降低, 导致叶片卷曲、萎蔫[9]. 干旱下卷叶的延迟发生是评价禾本科抗旱能力的重要指标. 叶片表面蜡质、角质层厚度、叶绒毛密度、气孔密度和开度等均影响作物的抗旱

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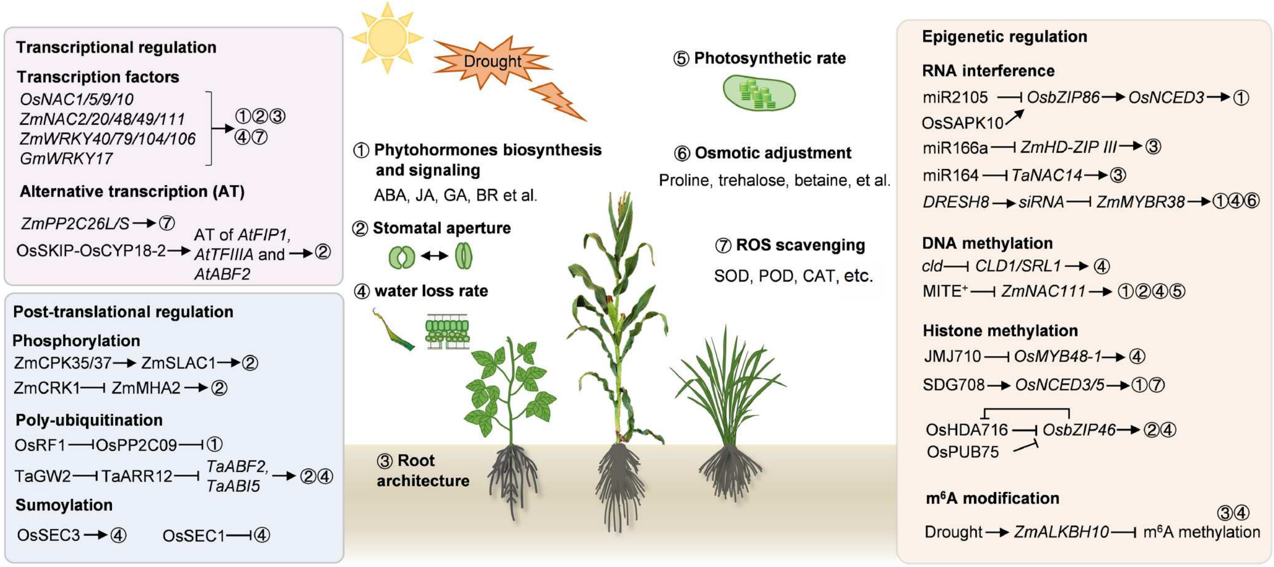

图 1 (网络版彩色)作物抗旱响应及调控机制. 作物抗旱生理响应包括激素响应、气孔导度、根系发育、叶片失水速率、光合作用、渗透及抗氧化防御的改变. 作物通过转录调控、翻译后调控及表观遗传调控, 共同影响干旱响应基因的表达

Figure 1 (Color online) Drought stress responses and regulatory mechanisms in crops. Physiological responses of crops to drought stress involve changes in phytohormone signaling, stomatal aperture, root architecture, water loss rate, photosynthetic rate, osmotic adjustment and ROS scavenging. Expression of crop drought-responsive genes is modulated via transcriptional regulation, post-translational regulation, and epigenetic regulation

性[10,11]．水稻*OsGL1-2*[12]、*DHS*[13]、*OsMYB60*[14]正调控表皮角质蜡的生物合成，提高水稻耐旱性．在玉米中，*ZmFDL1/MYB94*[15]、*ZmEREB46*[16]和*ZmSRL5*[17]均通过影响叶片表皮蜡质的积累，增加植株的抗旱性．过表达小麦*TaSHN1*[18]通过增加表皮蜡质中的烷烃含量、降低叶片的气孔密度和失水率，提高小麦抗旱性．降低气孔导度和减少气孔密度可帮助作物减少蒸腾作用导致的水分散失．水稻*OsEPF1*[19]、*OsPIL15*[20]、*OsNAC1*[21]、*HDA704*[22]负调控气孔导度提高水稻抗旱性，沉默*OsFTL4*可增加气孔关闭数量、降低气孔导度，增强水稻耐旱性[23]．玉米*ZmIRX15A*[24]调节气孔密度，*ZmCPK4*[25]、*ZmPP84*[26]、*ZmDnaJ*[27]和*ZmSLAC1*[28]介导气孔闭合，影响玉米的抗旱性．小麦*TaDREB2*和*TaDREB3*通过降低气孔密度促进抗旱[29]．TOR(target of rapamycin)信号通路中的TaTIP41通过促进脱落酸(abscisic acid，ABA)介导的气孔关闭正向调控小麦耐旱性[30]．大豆的气孔导度的控制能力较弱，这一生理特性可用于选择耐旱大豆[28]．过表达大豆*DREB1A*可以通过日光性运动的调节，改变冠层结构，减少光拦截和蒸腾损失，提高大豆的抗旱性[31]．

1.1.2 根系发育

除了地上部的形态变化，干旱同样影响作物根系发育和根系活力．根长、根系生物量、根平均直径、总根表面积、测根数目和根毛密度等根系指标均可用于评估作物抗旱能力[32,33]．根系深扎、分支夹角小、根生物量增多、侧根变多、根毛变长有利于作物吸收深层土壤水分[34,35]．水稻*DRO1*调控生长素在根尖的不对称生长，影响根系向下弯曲[36]，促进水稻抗旱，在玉米[37]和小麦[38]中的*DRO1*同源基因同样调控根系生长角度．RoLe1通过与OsAGAP互作影响根系中生长素的极性运输，调控水稻苗期和孕穗期的根系发育与抗旱性[39]．*OsABA8ox2*[40]通过ABA代谢影响根系生物量，转录因子*OsERF71*[41]、*OsNAC5*[42]、*OsNAC9*[43]和*OsNAC10*[44]影响根直径，提高水稻耐旱性．MYB转录因子*RRS1*[45]负调控根系长度和侧根密度，敲除后提高水稻耐旱性．玉米*ZmCIPK15*突变导致根生长角度变陡，促进玉米对胁迫环境的适应[46]．生长素相关基因*ZmRSA3.1*和*ZmRSA3.2*调控根长和根分支夹角小，促进形成更深的根构型[47]．*ZmCIPK3*促进种子根的长度影响玉米苗期抗旱[48]．*ZmVPP1*促进根系发育，增加侧根数目，促进玉米抗旱[49]．*ZmLRT*的敲除增加侧根数目和长度，增强玉米幼苗的耐旱性[50]．*ZmbZIP4*[51]和*ZmPTF1*[52]通过增加主根长度、侧根数目以及ABA合成，提高玉米抗旱性．敲除*ZmHB77*减少种子根形成增

加侧根密度，影响根系构型，有利于玉米幼苗抗旱[53]. *ZmTIP1*促进根毛伸长提高玉米抗旱性[54]. 小麦*LRD*负调控侧根数和侧根密度，抑制*LRD*提高小麦对水分胁迫的适应性[55]. *OPRIII*基因负调控小麦根长，*OPRIII*功能缺失的突变小麦植株具有更长的种子根[56].

1.1.3 光合作用

光合作用是作物生长发育的核心生理过程，对干旱胁迫非常敏感. 干旱胁迫早期, 气孔导度下降导致胞间CO_2浓度降低，影响暗反应CO_2的固定，光合速率降低. 随着干旱加剧, 光合电子传递和光合磷酸化受到抑制. 严重干旱时, 叶绿体膜结构被破坏, 叶绿体分解, 对光合作用产生不可逆的影响[57,58]. 在干旱胁迫下，*OsPHP1*过表达幼苗的叶绿素荧光下降，光合作用效率降低[59]. 沉默Ca^{2+}感应蛋白基因*OsSYT-5*增强了干旱处理下水稻的光合速率和水分利用率，促进水稻在正常和干旱处理下的产量[60]. *Os3BGlu6*调控ABA循环，其敲除植株光合作用速率下降，植株变矮小[61]. 过表达*ZmDnaJ*促进干旱胁迫下气孔关闭，改善玉米的光合速率和叶绿素含量, 维持维管束细胞和花环细胞排列, 降低水分流失, 促进玉米抗旱[27]. 参与叶片形态和气孔调控的基因大部分同样影响了光合作用.

1.1.4 渗透调节物质和抗氧化酶

渗透调节是细胞通过主动积累无机离子或细胞合成的有机溶质，提高细胞液浓度，降低细胞渗透势，增强细胞吸水或保水，以适应外界水分胁迫环境的机制[62]. 渗透调节物质主要有两大类: 一是细胞合成的有机溶质，如脯氨酸、甜菜碱、可溶性蛋白、可溶性糖(蔗糖、海藻糖); 二是从外界进入细胞的Na^+和K^+等无机离子. 细胞合成的有机溶质是耐旱渗透调节的关键因素. 干旱胁迫下, 植物细胞中积累大量的活性氧(reactive oxygen species, ROS). ROS可以作为信号分子或第二信使参与胁迫信号传导途径, 促进气孔关闭[63], 但是过多的ROS会造成氧化胁迫，导致膜脂、蛋白质、核酸以及其他细胞组分的严重损伤[64,65]. 植物体内清除ROS的保护机制分为酶促和非酶促两类. 酶促系统包括超氧化物歧化酶(superoxide dismutase, SOD)、过氧化物酶(peroxidase, POD)、过氧化氢酶(catalase, CAT)和抗坏血酸过氧化物酶(ascorbate peroxidase, APX)等. 非酶类抗氧化剂包括抗坏血酸、谷胱甘肽、类黄酮和花青素等. 细胞积累渗透保护剂和抗氧化酶是植物耐旱的重要机制. *OsP5CS*[66]和*OsTPS1*[67]分别编码脯氨酸和海藻糖生物合成关键酶, 在干旱胁迫下, 过表达这两个基因分别提高了水稻叶片脯氨酸含量和海藻糖含量, 提高水稻抗旱性. 过表达水稻*OsRab7*提高植株的叶绿素含量, 脯氨酸含量和抗氧化酶活性, 降低过氧化氢和丙二醛(malondialdehyde, MDA)水平, 促进转基因水稻的籽粒产量和抗旱性[68]. *OsLEA5*参与ABA诱导的过氧化氢生成, 调控抗氧化酶的表达和活性, 促进水稻对干旱和盐胁迫的抗性[69]. *OsLG3*编码ERF(ethylene responsive factor)类转录因子, 通过调控下游抗氧化酶相关基因表达，促进ROS清除，提高水稻抗旱性[70]. *ZmGLK44*调控玉米的色氨酸合成途径，在干旱胁迫下，过表达*ZmGLK44*提高玉米色氨酸含量，促进玉米抗旱性[71]. 玉米*ZmSRO1e*抑制花青素合成和ROS清除, 其过表达株系对干旱胁迫更加敏感[72]. *ZmPTPN*编码一个新型核苷酸酶，其水解核苷酸释放的磷可催化抗坏血酸限速合成酶VTC2的活性，调控抗坏血酸的合成. *ZmPTPN*的表达受到ABA信号途径下游关键转录因子HsFA6a调控，因此*ZmPTPN*可介导ABA信号途径与抗坏血酸合成途径之间的互作，促进植物抗旱性[73]. ZmSRO1d-R与Zm14-3-3.1互作并定位到质膜，通过单ADP核糖基化激活气孔保卫细胞膜上的ZmRBOHC，增强其NADPH氧化酶活性提高保卫细胞ROS含量，促进气孔关闭[74]. *ZmEREBP60*通过调控过氧化氢分解和ABA信号通路基因表达，增强玉米对干旱胁迫的耐受性[75]. 其他转录因子*ZmNF-YB16*[76]、*ZmWRKY40*[77]、*ZmWRKY79*[78]、*ZmWRKY106*[79]、*ZmMYB3R*[80]均可调控抗氧化酶表达或酶活性，促进ROS清除. *TaVQ4-D*通过渗透调节和维持ROS稳态增强了小麦的抗旱能力[81]. *TaERF87*和*TaAKS1*协同调节*TaP5CS1*/*TaP5CR1*介导的脯氨酸合成以增强小麦的抗旱性[82]. 过表达*GmNFYB17*提高大豆在干旱处理下的SOD活性和脯氨酸含量, 降低叶片损伤和MDA含量, 促进根系生长提高水分吸收，提高大豆抗旱性及干旱胁迫下的田间产量[83]. 在马铃薯中，过表达*StNAC262*增加马铃薯侧根数量和对渗透胁迫的响应[84]. 过表达*StMAPK11*提高了SOD、CAT和POD的活性，在干旱条件下促进了马铃薯的生长[85]. *BnMYBL2-1*调控ROS的清除和ABA的生物合成以提高油菜耐旱性[86].

水稻和玉米，小麦、大豆等作物的抗旱机制研究需要注意作物本身的抗旱性差异，结合生产实践中面临的抗旱胁迫进行实验设计具有重要意义. 玉米作为C4植物在干旱下可能具有较高的光合速率和水分利用率，而水稻可能气孔关闭较快，容易发生光抑制. 双子

叶植物大豆和马铃薯叶片较为宽大, 水分易散失, 因此在气孔调控抗旱机制中存在差异. 玉米和小麦的种植季节和种植区域, 往往因干旱气候频发, 导致干旱胁迫时有出现, 因此需要“深扎根”, 充分利用较深层土壤水分. 大豆根系相对较浅且多与根瘤菌共生, 然而共生关系下的抗旱机制研究较少. 此外, 马铃薯具有块茎和贮藏根, 可通过块茎和根系储水机制增强干旱适应能力.

1.2 作物干旱调控机制

1.2.1 激素响应及信号转导

植物激素在调控植物干旱胁迫响应中发挥着关键调节作用[87]. ABA信号通路是植物干旱胁迫响应中的重要途径. 正常条件下, 蛋白磷酸酶PP2CAs与SnRK2s相互作用形成复合物, 抑制SnRK2s的活性. 在干旱胁迫下, 内源性ABA水平迅速上升, ABA受体(RCARs/PYR/PYLs)通过与ABA和PP2CAs形成复合物, 抑制蛋白磷酸酶PP2CAs的活性, 释放SnRK2s. SnRK2s通过自激活或被其他激酶激活, 磷酸化ABA应答的核心转录因子AREB/ABF(abscisic acid-responsive element binding factor)、离子通道蛋白和多种转运体, 引起气孔关闭、根系生长和土壤微生物群落组装从而提高植株的抗旱性[88,89]. ABA受体*OsPYL3/5/6/7/9/10*[90,91]和*ZmPYL8/9/12*[92]正调控干旱响应. *ZmSnRK2s*和*ZmPP2Cs*参与玉米干旱应答途径[93]. *ZmPP2C-A10*是玉米PP2CA磷酸酶家族的成员, 负调控干旱响应, 其过表达导致玉米和拟南芥对干旱胁迫超敏感[94]. 小麦中的SnRK2家族基因*TaSnRK2.3/4/7/8/9*促进小麦抗旱[95]. 小麦ABA信号核心通路TaPYL9/TaPP2C6/TaSnRK2.8/TabZIP1在干旱响应中发挥重要调控作用[96]. ABA代谢相关基因*Os3BGlu6*[61]、*ZmABH4*[97]、*ZmXerico1*[98]也影响作物抗旱. 乙烯促进叶片脱落, 减少蒸腾面积和水分损失率, 因此增强乙烯的合成和信号转导促进作物抗旱. *OsETOL1*[99]和*OsARD1*[100]增强水稻的乙烯合成和抗旱性. *GmACO1*编码乙烯合成前体ACC(1-aminocyclopropane-1-carboxylate)合成酶, 过表达*GmACO1*可以显著提高大豆的抗旱性, 而RNAi转基因植株则表现为干旱敏感[101]. 乙烯响应因子ERF家族如*OsERF71/83/101*[102~104]、*ZmERF21*[105]、*GmERF135*[106]、*TaERF3*[107]均参与调控作物抗旱. 外施生长素促进干旱响应基因的表达, 促进植物抗旱[87]. 赤霉素(gibberellin, GA)活性和含量的降低可增强植物抗旱[108]. 茉莉酸(jasmonic acid, JA)信号转导途径可以与ABA途径发生交互作用, 过表达*OsJAZ1*降低水稻抗旱性[109], 而过表达*OsJAZ9*增强了植株ABA和JA水平, 促进水稻抗旱[110]. 激素调控作物生长和响应逆境胁迫的过程中存在复杂的交互作用[111], 解析激素间的互作将有助于更好地理解复杂的干旱胁迫调控网络.

1.2.2 转录调控及翻译后调控

在作物干旱响应中, 除了激素应答核心转录因子以及信号途径下游的关键转录因子外, 其他转录因子的调控同样发挥着至关重要的作用. NAC转录因子*OsNAC1/5/9/10*[21,42~44]和*ZmNAC2/20/48/49/111*[112~116]参与调控作物抗旱性. *ZmWRKY40/79/104/106*[77~79,117]和*GmWRKY17*[118]促进玉米和大豆抗旱. 其他转录因子如*MYB*、*DREB*、*CBF*等均参与作物抗旱调控[119]. 选择性剪接是指mRNA前体通过不同的剪接方式产生多样性成熟转录本的过程[120], 一些基因通过影响自身或相关基因的选择性剪接调控干旱响应. 大豆铜锌超氧化物歧化酶基因*GmCSD1a-1*可通过调节自身选择性剪接, 避免被microRNA gma-miR398c降解, 参与抗旱响应[121]. *ZmPP2C26*的非典型可变剪接产生了长短不一的两个转录本*ZmPP2C26L*和*ZmPP2C26S*, 其编码蛋白分别去磷酸化ZmMAPK3/7和ZmMAPK3, 各自过表达材料的下游磷酸化蛋白富集也存在差异. *ZmPP2C26*负调控抗旱性, 且*ZmPP2C26S*变异对干旱的敏感性高于*ZmPP2C26L*[122]. OsCYP18-2和SKIP(ski-interacting protein, 转录共调控因子和剪接体组分)互作, 拟南芥过表达*OsCYP18-2*促进*AtFIP1*、*AtTFIIIA*和*AtABF2*的表达和选择性剪接, 水稻过表达*OsCYP18-2*抗旱性增强[123].

蛋白翻译后修饰包括磷酸化、泛素化、苏木(small ubiquitin-related modifier, SUMO)化、乙酰化等, 可调节蛋白活性、稳定性、定位, 以及蛋白与其他细胞分子互作. ABA信号通路中起作用的蛋白磷酸酶PP2CA和蛋白激酶SnRK2影响植物抗旱性[124,125]. 蛋白激酶CIPKs和CDPKs通过钙离子信号通路[126]、MAPKKKs通过级联信号通路调节植物干旱响应[127]. ZmCPK35和ZmCPK37磷酸化ZmSLAC1正向调控抗旱性[28]. 干旱胁迫下, ZmCRK1蛋白水平降低, 抑制其对H^+-ATP酶的磷酸化, 导致气孔关闭促进抗旱[128]. E3泛素连接酶介导的泛素化修饰参与植物非生物胁迫的响应[129]. E3泛素连接酶OsRF1泛素化干旱负调控因子OsPP2C09, 促进水稻抗旱[130]. U-box E3连接酶OsPUB41泛素化K^+通道蛋白OsCLC6, 负调节抗旱[131]. 小麦TaARR12抑制*TaABF2*、*TaABI5*等逆境胁迫响应基

因的表达, 负调控小麦抗旱性. E3泛素连接酶TaGW2泛素化降解TaARR12, 增强小麦抗旱性[132]. SUMO化修饰对蛋白质的功能具有重要的调节作用, 在水稻中, 过表达SUMO连接酶基因*OsSCE3*增强水稻对干旱胁迫的耐受性, 而过表达*OsSCE1*使得水稻对干旱超敏感, 两个基因表现出相反的功能[133].

1.2.3 表观遗传调控

表观遗传修饰包括RNA干扰、DNA甲基化、组蛋白修饰和RNA修饰等, 广泛参与植物胁迫响应[134]. MicroRNAs(miRNAs)是一类非编码RNA, 可通过转录后基因沉默或抑制翻译起始抑制基因表达. miR2105通过抑制靶基因*OsbZIP86*表达, 负调控水稻抗旱性[135]. miR1432受干旱诱导表达, 抑制下游靶基因*OsCaML2*表达, 影响参与MAPK和激素信号转导途径的基因的表达, 正调控水稻耐旱性[136]. *ZmLRT*表达miR166a的初级转录本, miR166a转录后抑制5个发育相关的靶基因*HD-ZIP III*家族基因的表达水平, 负调控抗旱[50]. *TaNAC14*促进小麦幼苗根系生长发育增强耐旱性, miR164通过下调*TaNAC14*的表达抑制小麦幼苗根系发育, 降低耐旱性和耐盐性[137]. 干旱胁迫抑制大豆中miR166的积累, 导致靶基因*ATHB14-LIKE*表达量增加, *ATHB14-LIKE*正调控*GmPYL2*的表达响应大豆抗旱, 同时负调控*MIR166*对其进行负反馈调节[138]. 马铃薯miRNAs Stu-mi164抑制靶基因*StNAC262*的表达, 负调控马铃薯对渗透胁迫的响应[84]. DRESH8是一个由LTR类转座子构成并且包含反向重复序列的转座子, DRESH8能产生大量22-nt siRNA, 靶向调控干旱抗性基因*ZmMYBR38*的表达, 负调控干旱胁迫应答[139].

DNA甲基化在调控植物生长发育、逆境胁迫以及维持基因组稳定中具有重要作用[140]. *CLD1*/*SRL1*编码糖基磷脂酰肌醇锚定蛋白, 调控细胞壁形成、角质层发育和水分胁迫相关基因的表达. 在水稻卷叶突变体*cld1*中, SRL1第3个外显子上DNA甲基化水平增加, 显著降低*SRL1*表达[141]. *ZmNAC111*启动子区MITE的插入导致DNA甲基化水平和组蛋白修饰H3K9me2水平上升, 抑制*ZmNAC111*的表达, 降低玉米抗旱性[116].

此外, 组蛋白修饰和RNA上的N^{6}甲基腺苷(m^{6}A)修饰也参与抗旱调控. 水稻H3K36去甲基化酶JMJ70抑制*MYB48-1*表达, 负调控抗旱[142]. H3K36甲基转移酶SDG708通过促进ABA合成正调控抗旱[143]. 组蛋白去乙酰化酶OsHDA716通过赖氨酸去乙酰化抑制*OsbZIP46*的转录功能, 并通过E3连接酶OsPUB75的招募促进*OsbZIP46*的降解, 抑制下游干旱响应基因的表达. OsPUB75-OsHDA716抑制OsbZIP46的转录活性和蛋白稳定性, 而*OsbZIP46*的负反馈调节抑制*OsHDA716*的表达, 减轻OsHDA716的去乙酰化抑制作用, 促进OsbZIP46的乙酰化水平, 激活胁迫响应基因, 精细调节水稻的干旱响应过程[144]. 干旱胁迫下, ABA信号通路的关键调节因子*BnaABF3/4s*正调控*BnaA9.NF-YA7*表达, 而上调的*BnaA9.NF-YA7*可以通过抑制Bna.ASHH4s降低*BnaABF3/4s*启动子区H3K36me3水平, 抑制*BnaABF3/4s*的表达, 从而调节ABA信号的级联强度[145]. 干旱胁迫显著上调m^{6}A去甲基化酶基因*ZmALKBH10*的表达, 导致RNA整体m^{6}A甲基化水平下降. 在干旱处理前后, 这些低甲基化基因在玉米不同品种中的甲基化峰值变化存在差异, 通过影响不同通路影响玉米抗旱性[146].

2 作物抗旱改良策略

作物抗旱相关基因的挖掘和利用已经取得一定进展, 利用转基因或以成簇的规则间隔的短回文重复序列(clustered regularly interspaced short palindromic repeats, CRISPR)/Cas蛋白(CRISPR-associated system)(CRISPR/Cas)为代表的基因编辑技术将相关基因导入植株或进行基因编辑, 是作物遗传育种改良的重要途径. 此外, 外施植物生长调节剂增加作物抗旱, 以及利用根系微生物提高田间作物抗旱性也越来越多的受到关注(图2).

2.1 多组学助力抗旱关键调控因子挖掘及遗传解析

作物抗旱响应数量性状位点(quantitative trait locus, QTLs)和抗旱响应基因为作物抗旱育种改良提供了遗传资源. 全基因组关联研究(genome-wide association studies, GWAS)结合转录组、蛋白组、代谢组、表观遗传组、sRNAome、和表型组的多组学分析, 有利于构建更加精确和全面的作物抗旱基因调控网络, 从多维度解析抗旱机制. 目前, 利用群体材料定位到的抗旱相关基因见表1. Yang等人[162]通过多组学分析, 利用GWAS和eGWAS(expression-based genome-wide association study), 以及共表达网络等方法, 构建四倍体小麦响应干旱胁迫的调控网络, 鉴定了抗旱性相关候选基因*TtOTS1*, 并挖掘了关键响应模块, 丰富了小麦的抗旱遗传资源. GWAS结合代谢组学数据定位到调控色氨酸合成途径的*ZmGLK44*[71]. 高通量可视化表型鉴定

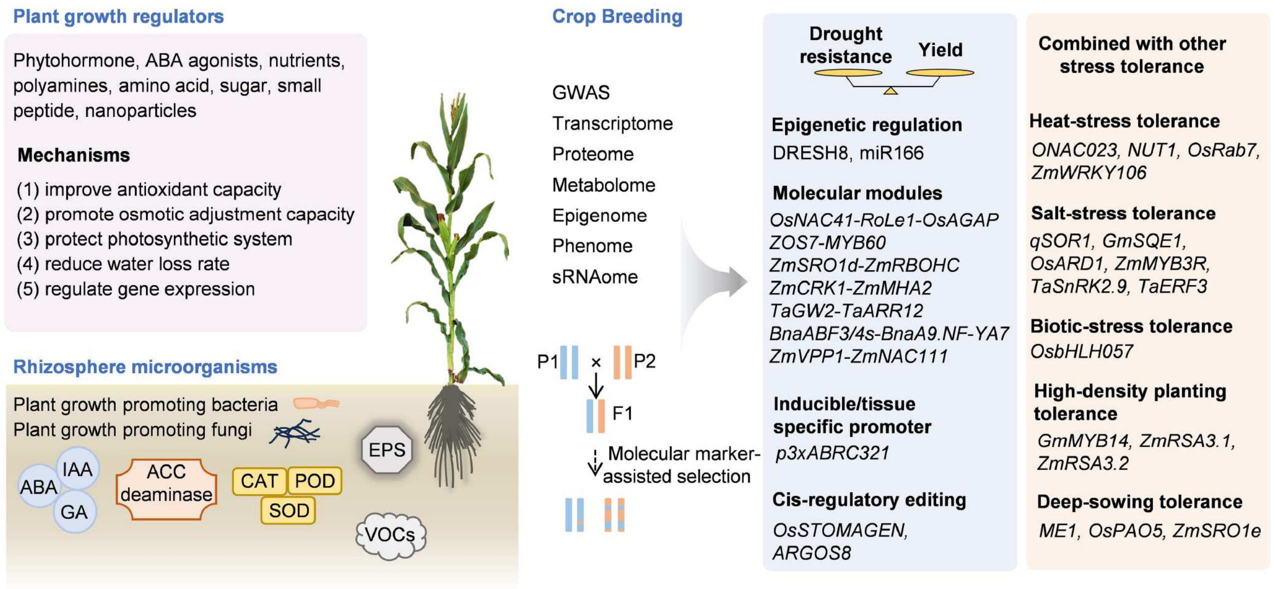

图 2 (网络版彩色)作物抗旱改良策略. 通过多组学及分子标记辅助选择挖掘并利用抗旱关键调控因子. 作物抗旱关键调控因子的利用需要综合考虑抗旱性与产量之间的平衡, 以及其对多种复合逆境胁迫的适应性. 此外, 还可以通过植物生长调节剂和根系微生物来提高作物抗旱性. 根际微生物介导植物抗旱机制包括调节植物的激素水平、合成ACC脱氨酶降低根部乙烯含量、增强植物抗氧化酶活性、产生胞外多糖(exopolysaccharides, EPS)和释放挥发性有机化合物(volatile organic compounds, VOCs)诱发植物抗旱信号转导

Figure 2 (Color online) Strategies for improving drought resistance in crops. Exploring the key regulators of crop drought resistance via high-throughput omics' GWAS and molecular marker-assisted selection. Theoretical framework for balance between drought tolerance and yield, as well as simultaneous improvement of other stress tolerance are shown. Additionally, the application of exogenous plant growth regulators and rhizosphere microorganisms also enhances crop drought resistance. Plant drought resistance mechanisms mediated by rhizosphere microorganisms including secretion of plant growth regulators, synthesis of ACC deaminase to reduce ethylene content in roots, improve plant antioxidant capacity, production of exopolysaccharides (EPS) and produce volatile organic compounds (VOCs)

为挖掘根部抗旱相关基因提供更加可行的方法, GWAS结合根部高通量图像数字化的表型组数据定位到*ZmHB77*[53]、*ZmcPGM2*和*ZmFAB1A*[163]. 现代作物栽培群体在驯化、改良过程中因遗传瓶颈效应丢失了大量的遗传多样性[164], 对来自包括野生种和地方种的、具有广泛遗传变异的群体材料进行多组学分析, 从不同水平解析作物抗旱机制, 挖掘抗旱优良等位基因并进行鉴定和功能研究, 重新利用丢失的抗旱变异位点, 将为作物抗旱育种改良提供更多选择.

2.2 抗旱关键调控因子利用与产量平衡

作物育种需要兼顾产量和抗性的平衡. 长期的驯化改良过程使作物的产量不断增加, 但也使其对环境胁迫更加敏感. 挖掘作物产量和抗性平衡机制、利用生物育种技术手段进行抗旱遗传改良, 有利于稳产高抗作物新品种的培育.

表观遗传修饰参与作物产量和抗性平衡机制. 玉米DRESH8通过产生siRNA介导抗旱基因的转录后沉默负调控干旱应答. DRESH8的缺失是抗旱有利等位变异, 但是DRESH8在玉米驯化和改良过程中受到了人工选择, 其插入显著增加了玉米产量, 因此DRESH8是平衡玉米产量和抗旱性的重要功能位点[139]. 利用短串联靶标模拟技术(short tandem target mimic, STTM)获得大豆miR166稳定遗传敲低材料GmSTTM166, miR166基因被敲除到最适水平, 在不影响产量的情况下增强了抗旱性[138].

多基因参与的分子模块在复杂性状调控中具有重要作用. 利用生物育种技术手段, 将分子模块中的多基因, 或者多个抗旱关键因子进行聚合育种, 是作物抗旱育种的重要方向之一. OsNAC41-RoLe1-OsAGAP分子模块调控水稻根系发育与抗旱性, *RoLe1*促进根长和抗旱, 其启动子*proRoLe1-526*^{T}为优良自然变异. *proRoLe1-526*^{T}基因型*RoLe1*的表达更高, 促进RoLe1对OsAGAP的降解, 减弱根系生长素内流, 促进根系生长, 有利于水稻苗期和孕穗期吸水抗旱[39]. 在干旱胁迫下, 水稻过表达锌指蛋白基因*ZOS7*可增加生物量和产量,

表 1 利用不同表型和群体材料定位到的作物抗旱相关基因

Table 1 Crop drought-resistance genes cloned according to various phenotypes and populations

物种	基因	基因功能	群体表型	群体大小	参考文献
水稻	*OsNHX1*	Na^+/H^+液泡膜反转运子	气孔指标	206	[147]
	OsLG3	ERF转录因子	存活率	392	[70]
	LAX1	bHLH转录因子	耐旱性状, 农艺性状	215	[148]
	PAPH1	PAP家族蛋白	8个抗旱性相关性状	501	[149]
	DRO1	生长素早期响应基因	根系生长角度	117	[36]
	RoLe1	编码蛋白包含NADPH依赖的FMN还原酶结构域	根长, 抗旱指数	667/243	[39]
	RRS1	MYB转录因子	根长	795	[45]
	OsSIZ2	SUMO E3连接酶	根长, 根直径	795	[150]
	OsNal1	胰蛋白酶样丝氨酸/半胱氨酸蛋白酶	21个根系性状	413	[151]
	OsJAZ1	JA信号抑制子	21个根系性状	413	[151]
	OsSROc1	水稻SRO同源基因	根部高通量图像数字化表型	120	[152]
玉米	*ZmIRX15A*	木聚糖沉积酶	气孔密度	424	[24]
	ZmKCS12	玉米角质层蜡质合成关键因子	叶绿素提取率, 失水率	389	[153]
	ZmVPP1	液泡焦磷酸酶	存活率	368	[49]
	ZmTIP1	S-酰基转移酶	存活率	368	[54]
	ZmSRO1d	SIMILAR TO RCD1 ONE 1D-RESISTANT	存活率	368	[74]
	ZmPYL8	ABA受体基因	存活率	368	[92]
	ZmPYL12	ABA受体基因	存活率	368	[92]
	ZmPP2CA10	丝氨酸/苏氨酸蛋白磷酸酶	存活率	368	[94]
	ZmNAC111	NAC转录因子	存活率	368	[116]
	ZmDREB2.7	DREB转录因子	存活率	368	[154]
	ZmEXPA4	扩张蛋白	开花-吐丝间隔	228	[155]
	ZmGLK44	Golden-like 2类转录因子	代谢谱数据	368	[71]
	ZmRSA3.1	Aux/IAA	根构型	380	[47]
	ZmRSA3.2	Aux/IAA	根构型	380	[47]
	ZmCIPK3	钙调磷酸酶B类互作蛋白激酶	根系性状	373	[48]
	ZmHB77	Homeobox-转录因子77	种子根数目, 根系结构和形态特征	>9000	[53]
	ZmcPGM2	胞质葡萄糖磷酸变位酶	根部高通量图像数字化表型	368	[163]
	ZmFAB1A	1-磷脂酰肌醇-3-磷酸5激酶	根部高通量图像数字化表型	368	[163]
小麦	*TaWD40-4B.1*	WD40蛋白	叶片萎蔫程度	198	[156]
	TaPYL1-1B	ABA受体基因	存活率	120	[157]
	TaSNAC8-6A	NAC类转录因子	存活率	700	[158]
	TaNAC071-A	NAC类转录因子	存活率	430	[159]
	TaPYL4	ABA受体基因	生长相关性状	323	[160]
	TaPP2C6	丝氨酸/苏氨酸蛋白磷酸酶	地上部高通量图像数字化表型	155	[161]
	TtOTS1	SUMO蛋白酶	生物量、根系性状及eQTL	107	[162]
大豆	*GmNFYB17*	NFYB转录因子	PEG6000处理下的萌发率	179	[83]
	GmACO1	ACC合成酶	田间抗旱表型	585	[101]

ZOS7与MYB60互作，*ZOS7-MYB60*双过表达株系表现出更强的水稻抗旱性[165]．单独突变*oshda716*或过表达*OsbZIP46*，均促进水稻抗旱和籽粒生长，在*oshda716*突变体中过表达*OsbZIP46*更加显著地提高了籽粒大小和千粒重[144]．ZmSRO1d-R-ZmRBOHC正调控玉米抗旱以及干旱胁迫下的产量，然而过表达*ZmSRO1d-R*影响正常水分条件下的产量，因此*ZmSRO1d-R*在玉米驯化和现代育种过程中被选择性淘汰．在灌溉充足的地区，可使用抗旱能力较弱、但是在正常水分条件下对产量无显著影响的*ZmSRO1d-S*等位基因；而在干旱胁迫地

区, 可选育具有*ZmSRO1d-R*等位基因的种质[74]. 在充足的水分条件下, ZmCRK1磷酸化抑制ZmMHA2活性, 气孔打开, 维持植物的正常生长. 在干旱条件下, ZmCRK1蛋白水平下降, 减弱了其对ZmMHA2的抑制作用, 导致气孔关闭响应干旱[129]. E3泛素连接酶TaGW2正调控小麦的抗旱性, 负调控籽粒大小和产量; 其底物TaARR12参与细胞分裂素信号传导, 负调控小麦抗旱性, 对籽粒大小和产量无显著影响. 在*tagw2*突变体中敲低*TaARR12*, 可同时提高小麦的抗旱性和产量[133]. BnaABF3/4s-BnaA9.NF-YA7的反馈调节可防止ABA信号过度激活, 维持油菜生长和抗旱的动态平衡[145]. 将多个抗旱基因聚合表达可以加强作物抗旱性, 抗旱基因*ZmVPP1*和*ZmNAC111*的过表达材料进行杂交获得共表达转基因材料, 与野生型相比, 共表达转基因材料苗期光合作用速率和抗氧化酶活性更高, 在干旱胁迫下, 植株产量更高[166].

组织特异表达或干旱特异诱导启动子的利用, 以及对顺式调控元件进行CRISPR/Cas9编辑等方法均可帮助我们更好的利用抗旱调控基因. *DRO1*促进作物抗旱, 然而组成型表达*DRO1*影响玉米生长发育. 利用ABA诱导型启动子(*p3xABRC321*)驱动*ZmDRO1*表达, 获得本底低表达且受ABA高诱导的转基因玉米, 可以显著提高干旱胁迫下玉米产量, 且不影响正常浇水条件下的产量[37]. 利用诱导型启动子调控基因表达可以减少能量消耗, 并维持作物在非胁迫条件下的生长和产量. 根系特异表达且受ABA诱导的基因的启动子具有更好的平衡生长和抗旱的功能[37]. 启动子区顺式调控元件编辑可以产生数量性状变异, 避免基因编码区突变可能引起的极端表型. 根据生物信息学分析设计gRNAs(guide RNAs), 利用多重CRISPR/Cas9技术对*OsSTOMAGEN*(气孔发育正调控因子)的启动子区进行编辑, 生成不同的启动子等位基因. 不同启动子等位基因的气孔密度变化范围从野生型气孔密度的70%到120%, 具有广泛的变异表型. 在干旱条件下, 不同启动子等位基因的气孔密度和气孔导度发生不同程度的变化, 表明顺式调控元件的编辑可帮助植物适应多变的环境[167]. 玉米*GOS2*基因在各个部位均有较高的表达水平, 而抗旱基因*ARGOS8*的表达却较低. 利用CRISPR/Cas9基因编辑技术将玉米*GOS2*的启动子插入*ARGOS8*基因的5′-UTR或者直接替换*ARGOS8*基因的启动子, 可以提高*ARGOS8*的表达, 提高干旱胁迫下玉米的田间产量[168].

2.3 抗旱关键调控因子利用与复合逆境胁迫机制

渗透调节、ROS信号及其清除机制、激素响应及信号转导等机制不仅调控作物抗旱, 也参与作物对其他胁迫的响应[58,127]. 干旱和耐盐及高温胁迫具有一些相同的调控机制, 因此作物抗旱基因也可能参与盐胁迫及耐高温响应. 明确抗旱关键因子在其他胁迫中的作用, 有助于发现具有多重效应的基因, 从而更有效地利用这些基因. NAC转录因子蛋白在分化为原生木质部的前体细胞核中积累, 增强根茎和鞘中的细胞壁发育并调控水分运输. ONAC023整合水稻抗旱和耐热调控. 干旱和热胁迫诱导*ONAC023*表达, OSREM1.5去磷酸化ONAC023, 促进ONAC023入核参与氧化还原、水分运输等多种胁迫响应过程, 正调控水稻抗旱和耐热性[169]. NUT1通过调控原生木质部的发育调控水分运输, 共同影响玉米对干旱和高温的抗性[170]. *DRO1*同源基因*qSOR1*控制水稻根构型变化, 提高水稻在盐碱地的产量[171]. GmNF-YC9转录因子通过调节角鲨烯单加氧酶GmSQE1活性调控甾醇合成途径. 在干旱和盐胁迫下, *GmSQE1*转基因大豆均具有较强的抗逆性[172]. 除了非生物胁迫, 抗旱基因也被报道参与生物胁迫响应. OsbHLH057通过结合AATCA顺势作用因子, 同时调控水稻纹枯病、白叶枯病, 以及抗旱性[173].

密植是提高作物产量的重要栽培策略. 然而密植条件下, 作物的根系发育和水分吸收能力受到限制, 更容易面临干旱胁迫. 密植导致作物相互遮荫, 冠层下层的叶片光照不足、光合减弱, 而干旱条件下作物气孔关闭影响CO_2输入, 进一步抑制光合效率. 因此密植对作物抗旱提出了更高的要求. 目前已有研究报道抗旱基因也可调控作物的耐密性. *GmMYB14*过表达植株内源油菜素内酯含量下降, 导致株高降低、叶面积缩小、叶柄缩短, 叶柄与主茎夹角变小, 形成紧凑的半矮秆株型, 在正常浇水和干旱处理下的产量均高于野生型, 同时在田间密植条件下产量更高[174]. 适宜的根系构型不仅有利于作物吸水应对干旱胁迫, 还可以提高密植下的产量. 生长素相关基因*ZmRSA3.1*和*ZmRSA3.2*调控玉米形成更深的根构型, 为密植玉米育种提供了新的策略和遗传资源[47]. 作物密植条件下的抗旱性表征和遗传调控机制仍需进一步研究.

适当深播是作物避旱机制之一. 旱区自然降雨量低, 土壤表层水分容易蒸发, 使得种子在萌发和出苗阶段就面临干旱胁迫, 影响出苗率并最终影响产量. 适当

深播有利于种子利用土壤深处的水分，保障玉米在旱区的萌发. 然而深播在一定程度上会抑制作物出苗，在此阶段，可将作物抗旱性状转为耐深播发育性状. 禾本科作物萌发出芽的主要决定因素是中胚轴和胚芽鞘，其中中胚轴起到的作用更大[175]. 中胚轴长度随播种深度的增加而逐渐增加，帮助植物不断向上生长. 中胚轴伸长受到激素、光照、温度等因素调控. *ME1*(即绿色革命基因*SD1*)编码GA生物合成的GA20氧化酶，正调控水稻中胚轴伸长. 土壤覆盖诱导的乙烯产生可能通过调节*ME1*的表达来促进GA的生物合成. GA浓度增加降解转录抑制因子DELLA蛋白，释放OsPIL13，OsPIL13促进*OsEXPA4*的表达，最终促进水稻中胚轴伸长和出苗[176]. 水稻PAO家族基因*OsPAO5*负调控中胚轴的伸长[177]. 玉米*ZmSRO1e*促进中胚轴伸长[178]. 充分利用耐深播基因及标记，培育耐深播品种，有利于提高旱区作物的苗期抗旱性.

2.4 植物生长调节剂及根际微生物的研究与利用

外源性植物生长调节剂，是指通过外部施用以调节植物生长发育的化合物. 它们与植物激素具有相似的效应，包括激素(植物自身合成和人工合成)、ABA激动剂、植物营养物质、多胺、氨基酸、糖类等[179]. 外源植物生长调节剂主要通过增强作物的抗氧化能力以及渗透调节，提高作物抗旱性. 外源ABA引起气孔关闭，降低蒸腾速率，增加谷胱甘肽抗坏血酸含量，促进抗旱[180]. 褪黑素通过增强根系活力和叶片角质层形成，改善光合特性，促进水通道蛋白活性，增加水分吸收和运输，提高抗氧化酶的能力，调节碳水化合物平衡，提高作物的抗旱性[181]. 多胺与植物抗旱性关系密切，通过保护叶肉细胞的结构和功能、改变内源性多胺和植物激素、提高光合作用和水分利用效率、增强渗透调节和抗氧化防御系统，缓解作物干旱胁迫[182]. 甾醇类物质和GABA促进作物抗旱. GmSQE1参与甾醇合成途径，*GmSQE1*转基因大豆抗旱性增强，且体外喷施甾醇能够显著改善大豆、小麦、谷子和玉米的抗旱性[172]. TaNHX2蛋白通过与谷氨酸脱羧酶TaGAD1互作，解除TaGAD1的抑制，促进γ-氨基丁酸(γ-aminobutyric acid, GABA)积累，从而调控气孔运动提高抗旱性[183]. 此外，小肽在干旱响应中也具有重要作用，CEL25能够将根部缺水信号传递到地上部[184]. 在水稻中，过表达小肽基因*OsDT11*提高了ABA含量，增强水稻耐旱性[185]. 纳米材料可以平衡植物的氧化剂水平，调节植物激素水平，从而在干旱胁迫下维持植物的正常生长[186]. 纳米材料能够激活和调节特定的胁迫相关基因，提高热休克蛋白和水通道蛋白的活性，帮助植物抵抗非生物胁迫[187].

干旱抑制作物根系生长和根系分泌物分泌，影响根际微生物群落的多样性及组成[188]. 根际微生物也可以通过多种间接直接或机制影响植物生长[189]. 根际促生菌(plant growth-promoting rhizobacteria, PGPR)是一类能够促进植物生长、吸收矿质养分和抵御胁迫有害微生物和非生物逆境的土壤微生物. PGPR可通过: (1) 调节植物的激素水平诱导植物产生抗逆性. 玉米接种生脂固氮螺菌*Azospirillum lipoferum*后，体内ABA、GA和吲哚-3-乙酸(3-indoleacetic acid, IAA)含量升高，抗旱性增加[190]. 固氮螺菌*Azospirillum* sp. 可合成IAA，接种后促进小麦侧根和根毛生长，根系吸水能力增强，增强小麦抗旱性[191]. (2) 合成ACC脱氨酶降低根部乙烯含量. 干旱胁迫下，根系分泌物中乙烯合成前体ACC的含量增加，乙烯浓度增加会抑制植物生长发育. PGPR可产生产ACC脱氨酶，分解ACC将其作为碳源和氮源，减少乙烯生成[192]. 接种合成ACC脱氨酶的根瘤菌后，小麦干旱处理下的侧根数、根长和根部生物量增加，根系水分和养分吸收增强[193]. 玉米接种假单胞菌*Pseudomonas fluorescens*通过降低根部乙烯含量，缓解乙烯对根系生长的抑制，增加光合色素的形成，提高光合效率，改善干旱胁迫下甜玉米的产量[194]. (3)增强植物抗氧化酶活性. 接种芽孢杆菌*Bacillus* sp.的水稻[195]和接种鞘氨醇单胞菌属*Sphingomonas* sp.的玉米[196]都具有更高的抗氧化酶活性，植株抗旱性增强. (4) 产生胞外多糖(exopolysaccharides, EPS)增强保水性. EPS是由根际细菌产生的具有高保水能力的多糖大分子，保护细菌免受脱水的损害，增强细菌在干旱胁迫下的定殖[197]，同时可优化土壤团粒结构，增加根际土壤附着，增强植物耐旱性[198]. EPS也有利于植物形成根鞘结构，促进根系吸收水分和养分[199]. (5) 释放挥发性有机化合物(volatile organic compounds, VOCs)诱发植物抗旱信号转导. PGPR可以不需要与根系直接接触，通过释放VOCs来影响植物生长和抗逆响应[200]. 假单胞菌*Pseudomonas pseudoalcaligenes*释放的VOCs如二甲基二硫化物和2,3-丁二醇，可以减少玉米幼苗的电解质渗漏和MDA积累，提高茎和根中的抗氧化酶活性[201]. 除了PGPR，根际促生真菌(plant growth promoting fungi, PGPF)和丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)也参与作物干旱胁迫响应. 耐旱型小麦品种云汉在干旱环境下招募根际真菌高山被孢霉*Mortierella alpina*, 将其施加给干旱敏感型小麦中国春, 可以激活干旱胁迫响应基因如*CIPK9*和*PP2C30*, 增强中国春的抗旱能力[202]. AMF可与大部分陆生植物根系共生形成丛枝菌根, 其庞大的地下菌丝网络可以帮助植物吸收水分和养分, 在干旱胁迫下上调植物水孔蛋白基因表达, 有利于植物耐受干旱胁迫[203].

3 展望

尽管目前已有许多作物抗旱关键调控因子的报道, 但实际被应用于育种实践的抗旱基因仍十分有限, 需要加强对作物抗旱机制的解析. 卷叶、气孔指数和存活率等地上部可见抗旱表型在抗旱机制研究中已经被大量运用, 但是对作物根部的抗旱机制解析较少, 尤其是根系抗旱表型高通量平台的建立、根系抗旱蛋白组学和代谢组学等的研究较少. 根系抗旱表型、根部抗旱多组学分析, 以及根部和地上部互作机制等仍有待进一步研究. 将作物抗旱特性转为发育性状研究也为作物抗旱机制解析提供新的方向, 如探究玉米耐深播特性、培育耐深播玉米品种, 有利于旱区玉米的苗期避旱. 此外, 在抗旱机制解析中, 还需要综合考虑作物田间实际面临的干旱胁迫和产量问题, 如干旱程度以及持续时间, 以及复合胁迫如高温、盐碱等. 除了满足作物生产的产量需求, 也要重视品质需求, 即探究高蛋白、高油分作物在干旱胁迫下的响应机制. 为了适应生产, 还应将耐密性和杂种优势考虑其中. 解析抗旱与产量、品质(高蛋白、高油分)平衡机制, 以及抗旱与其他复合逆境胁迫的调控机制, 将基础研究和育种实践相结合, 培育抗旱稳产、多抗广适的作物新品种, 是作物抗旱机制解析的最终目标.

作物抗旱关键调控因子在实际育种中的运用受到诸多限制. 目前, 抗旱基因的转基因材料创制依赖于特定的背景材料, 对育种常用的自交系只能通过传统聚合育种或分子标记辅助选择聚合育种, 将抗旱优良基因转入其中. 不依赖遗传背景的遗传转化方法仍需要进一步的探究和完善. 基于分子模块设计育种、多基因聚合育种和多基因编辑系统的方法也需要被更多的运用于作物抗旱品种培育. CRISPR/Cas编辑技术不涉及供体DNA, 将在推广应用方面更具优势. 但是利用CRISPR/Cas敲高基因的表达, 或者对基因进行表观修饰, 仍需要我们在编辑工具和靶点设计等方面不断创新, 开发出能够运用于育种实践的精准编辑系统.

植物生长调节剂及根际微生物的研究与利用为作物抗旱提供了新的策略. 外施生长调节剂需要注意在提高作物抗逆性的同时避免产生负面效应, 开发实用、高效、低毒和对作物产量及生产环境无负面影响的植物生长调节剂, 对帮助作物应对田间干旱具有重要意义. 根际微生物对作物生长和抗旱均有影响, 可开发微生物菌剂, 单独或与其他植物生长调节剂混合一同施用于根部土壤. 然而目前根际微生物调节宿主植物抗旱性的机制仍不清楚. 受限于人工培养条件, 大部分的土壤微生物无法在实验室培养, 很多研究在控制变量的实验室条件下进行, 较少有开展田间实验的研究, 导致微生物菌剂的开发受到限制. 解析根际微生物提高作物抗旱的机制, 筛选和开发适用于不同种植环境的微生物菌剂, 仍需要进一步的研究. 其他新机制、新方法的运用也在探究抗旱机制中起到重要作用, 比如基于人工智能的生物信息学分析进行蛋白结构预测和互作小分子筛选等. 干旱胁迫下的田间管理对于作物抗旱同样十分重要. 结合作物育种改良和田间管理, 能够更好地帮助作物抵御干旱胁迫.

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Summary for “作物抗旱关键调控因子的挖掘与利用”

Exploitation of key regulatory factors and breeding strategies for crop drought resistance

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Drought is one of the most severe environmental stresses affecting plant growth and productivity. Global climate change and population expansion are seriously challenging the already-stressed agricultural ecosystems. Therefore, enhancing the drought resistance of crops is of great significance for ensuring national food security. Crops respond and adapt to drought stress by modulating morphological and physiological biochemical characteristics such as leaf morphology, stomatal aperture, root architecture, photosynthesis, osmotic regulation capacity, and antioxidant defense systems. These traits are also important indicators to evaluate the drought resistance of plants. Phytohormones, ions, and small molecules participate in the perception and transduction of drought stress signals. Crop drought-responsive gene expression is modulated via transcriptional regulation, post-translational regulation, and epigenetic regulation. In recent years, diverse drought resistance genes have been identified. This review summarizes the recent research advances of GWAS and high-throughput omics approaches for developing drought stress resistance in crops, explores the roles of epigenetic regulation, molecular module-based designer breeding, tissue-specific and/or ABA/drought-inducible promoter application, and cis-regulatory element editing in balancing drought tolerance and crop yield. We also discuss the functions of drought resistance genes under combined stress conditions. It is emphasized that pyramiding genes through marker-assisted selection and other techniques to enhance drought tolerance is a promising strategy in crop breeding. In addition to crop breeding, the application of exogenous plant growth regulators and rhizosphere microorganisms has been reported to improve crop drought resistance. Exogenous plant growth regulators, such as hormones and polyamines, mainly enhance crop drought resistance by improving antioxidant capacity and promoting osmotic adjustment capacity. Rhizosphere microorganisms assist plants in withstanding drought stress by secreting plant growth regulators, synthesizing ACC deaminase to reduce ethylene content in roots, improving plant antioxidant capacity, producing exopolysaccharides, and volatile organic compounds. Finally, this review offers a perspective for future research on crop drought tolerance, emphasizing the study of multi-omics approaches in the root system, as well as the mechanisms underlying the balance between drought tolerance and crop quality. In summary, deciphering the molecular genetic basis of drought tolerance for crop breeding, combined with field management, such as the application of exogenous plant growth regulators and microbiological fertilizer, is critical for enhancing drought resistance in crops.

crops, drought resistance, regulation mechanisms, genetic improvement, drought resistance strategies

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