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水稻抗非生物逆境功能基因的发掘

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摘　要：水稻遭受的非生物逆境包括干旱、淹涝、盐害、低温、高温等。非生物逆境抗性有着复杂的遗传和分子基础，解析水稻非生物逆境抗性的机制将有助于抗逆新品种的培育。抗逆性受到很多小效应遗传位点的控制，成百上千个与形态和生理响应以及发育相关的基因和抗逆性相关。尽管在水稻中已鉴定了很多抗逆相关基因，但直接利用抗逆基因进行水稻抗逆遗传改良的成功例子还非常少。最近的抗逆基因功能研究发现，很多基因在形态和生理水平响应或调控不同的逆境，这为理解水稻复杂的抗逆机制提供了新的线索。现简要概述了近年来水稻主要非生物逆境抗性相关基因分离和功能鉴定方面的研究进展。

关键词：水稻；功能基因；数量性状位点；干旱胁迫；淹涝胁迫；盐胁迫；冷胁迫；高温胁迫
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The exploitation of rice functional genes for abiotic stress

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Abstract: The major abiotic stresses for rice include drought, submergence, salinity, low temperature, heat, etc. Abiotic stress resistance has complex genetic and molecular bases. Elucidation of the mechanisms underlying stress resistance of rice will accelerate the development of new varieties with enhanced resistance to the abiotic stresses.

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Stress resistance is controlled by numerous small-effect loci. Hundreds of genes controlling various morphological and physiological responses and developmental processes are involved in stress resistance, and these genes are collectively called stress-related genes. Although numerous genes have been characterized for their diverse roles in stress resistance, very few of them have been successfully applied in breeding, suggesting the complexity of stress resistance. Recent functional studies uncovered many genes that control various morphological and physiological responses to different stresses, which may provide new insight into understanding the complex mechanisms of stress resistance in rice. The progress in genetic, genomic, and molecular studies of stress resistance in rice in recent years is briefly reviewed in this article.

Key words: *Oryza sativa*; functional genes; quantitative trait locus (QTL); drought stress; submergence stress; salinity stress; low temperature stress; heat stress

水稻 (*Oryza sativa*) 是世界范围内最重要的粮食作物之一，非生物逆境 (干旱、淹涝、高盐、低温、高温等) 是降低水稻产量的主要因素。提高水稻的非生物逆境抗性将增加农业产量并扩大耕种面积，缓解人口压力，因而，培育具有非生物逆境抗性的水稻品种十分重要 [1]。植物的抗逆性具有复杂的遗传基础，对不同逆境的抗性存在不同的并且可能会重叠的分子和生理基础。人们对植物响应和适应不同逆境的分子基础的理解主要来自于模式植物拟南芥 (*Arabidopsis thaliana*)。水稻在相对良好的环境条件下得到驯化，因而对大部分非生物逆境敏感，然而，在水稻资源里也存在丰富的非生物逆境抗性遗传变异。过去 10 多年中，人们对水稻抗逆性进行了多方面的研究，包括种质资源的挖掘和育种以及抗逆性的遗传、基因组和基因功能鉴定等。本文重点对近年来水稻中重要抗逆功能基因的发掘鉴定做简要回顾。

1 抗旱性相关功能基因的发掘

干旱一直是造成全世界作物减产的重要因素，并将日益严重地威胁粮食生产安全。水稻对干旱非常敏感，并且对水分需求量大而利用率低。鉴于全球，特别是中国淡水资源日趋紧张的现状，培育节水抗旱水稻不仅是绿色超级稻培育的重要目标之一，而且对农业可持续发展具有十分重要的意义 [2]。

植物在形态、生理、生化、细胞、分子水平上进化出了很多机制来应对缺水或干旱胁迫环境。植物的抗旱性 (drought resistance) 包括逃旱性 (drought escape)、避旱性 (drought avoidance)、耐旱性 (drought tolerance)、复水抗旱性 (drought recovery) 等 4 类。其中，避旱性和耐旱性是水稻中两种主要的抗旱机制，而逃旱性和复水抗旱性研究较少 [3]。

尽管与抗旱相关性状 (例如根性状、叶片性状等) 的遗传定位研究非常多 [4]，但图位克隆基因的成功案例还非常有限。其中一个突出的进展是 Uga 等 [5] 克隆和鉴定到的通过改变根系结构提高避旱性的 QTL 基因 *DEEPER ROOTING 1* (*DRO1*)。*DRO1* 能够控制根的生长角度，受到生长素的负调控并参与根尖的细胞延长和根的向地弯曲。通过回交将 *DRO1* 导入浅根水稻品种，表现出根深增加，干旱条件下的产量较野生型高。但目前报道的绝大部分水稻抗旱相关基因是通过功能基因组手段或候选基因途径鉴定获得的。

1.1 干旱胁迫表达谱研究

在全基因组水平发掘抗逆功能基因的主要方法包括基因组关联分析 (genome wide association study, GWAS)、正向突变体筛选和各种“组学”方法，如转录组、蛋白质组、代谢组等。由于水稻抗旱性遗传基础的复杂性，目前利用 GWAS 和正向突变体筛选方法克隆鉴定抗旱基因的报道非常少，而干旱胁迫后转录组水平变化的研究不少。Zhang 等 [6] 通过对苗期干旱敏感品种珍汕 97 和旱稻品种 IRAT109 在干旱条件下的比较转录组分析，发现了 436 个差异表达的基因，其中包括与光合作用相关的基因。Cheah 等 [7] 通过对抗旱品种 Vandana 和 Aday Sel 与旱敏感品种 IR64 在温室进行旱处理，然后在营养生长期取叶片进行高通量测序分析 microRNA 的差异表达谱，鉴定到 4 类重要的 microRNA，它们可能分别参与淀粉代谢、抗氧化防御、呼吸作用和光合作用的调控。

在基因家族水平进行干旱响应基因表达谱的研究为深入的功能分析提供了有用的信息。在水稻中报道的响应干旱胁迫的基因家族很多，包括一些调控基因家族，如 AP2/EREBP[8]、NAC (NAM、ATAF 和 CUC)[9]、WRKY[10]、HD-ZIP[11]、TIFY [12]、CIPK[13]、类受体激酶 [14]、含 XHS 结构域家族 [15]、

核糖体失活蛋白[16]；还有一些功能蛋白或者编码酶的基因家族，如乙醛脱氢酶家族[17]和含BURP结构域的家族[18]。

1.2 抗旱相关基因的鉴定

表达谱分析表明成千上万的基因响应干旱胁迫，但目前这些基因中只有一小部分得到功能验证。研究者从表达谱数据中挑选候选基因用于功能分析往往会根据一定条件进行筛选，如候选基因的表达要响应干旱胁迫，或者和已知的胁迫相关基因的序列相似，或者有相应突变体，这可能是目前功能被验证的抗旱相关基因数量较少的重要原因(水稻中鉴定的部分重要抗旱相关基因如表1所示)。

水稻中鉴定的抗旱相关基因中很多编码转录因子，特别是多个bZIP家族的转录因子基因参与抗旱性调控。在水稻中超表达拟南芥来源的bZIP转录因子ABF3，苗期水稻表现出叶片卷曲延迟和干旱胁迫后的枯萎[19]，超表达水稻内源的bZIP转录因子基因*OsbZIP16*[20]、*OsbZIP23*[21]、*OsbZIP46*[22]、*OsbZIP71*[23]和*OsbZIP72*[24]均能提高水稻的抗旱性。

NAC是一类有高度保守的DNA结合结构域的植物特异性转录因子。*SNAC1* (*STRESS-RESPONSIVE NAC 1*) 属于NAC家族，在保卫细胞中特异性地受干旱胁迫诱导表达。*SNAC1*超表达水稻在严重的大田干旱条件下，抗旱性明显提高，并且没有表现出明显的表型变化和产量降低。进一步分析发现，*SNAC1*超表达水稻气孔开度明显降低，表明保卫细

表1 水稻中鉴定的部分重要抗逆基因

基因名	主要检测的性状或鉴定方法	抗逆机制
抗旱基因		
SNAC1[25]	存活率、结实率、株高等	上调许多与胁迫相关的基因的表达
OsNAC6[26]	存活率、相对株高等	调控非生物和生物胁迫应答基因的表达
OsbZIP23[21]	相对产量、发芽率、根长等	诱导与ABA响应相关基因的表达
OsNAC10[27]	叶绿素荧光、根直径、产量	增大中柱、根皮层和表皮层
OsSIK1[41]	存活率、叶绿素和丙二醛含量	激活抗氧化系统
OsbZIP46[22]	存活率、相对产量、发芽率等	正调控ABA信号，激活抗旱相关基因
OsSIK2[39]	存活率、根长、株高等	调节下游相关基因的表达
DWA1[50]	存活率、水分散失率、蜡质积累量	调控干旱诱导的角质层蜡质沉积
DRO1[5]	深根比、根弯曲角度、单株产量等	参与根尖细胞的伸长并引起根的向地性弯曲
耐淹基因		
Sub1A[63]	乙烯、淀粉和叶绿素含量、株高等	抑制乙烯和赤霉素介导的代谢途径
SNORKEL1; *SNORKEL2*[60]	延长节间数目、节间延伸长度、乙烯和赤霉素含量	通过赤霉素促进节间延长，从而与大气进行气体交换
耐盐基因		
OsHKT1; *OsHKT2*[98]	转基因爪蟾卵母细胞电流振幅，不同盐浓度下酵母生长状态	维持Na^+/K^+稳态
SKC1[72]	Na^+、K^+含量，转基因爪蟾卵母细胞中的电流和电压强度	选择性转运Na^+，维持Na^+/K^+稳态
OsKAT1[100]	Na^+、K^+含量，K^+/Na^+浓度比	作为K^+通道维持Na^+/K^+稳态
OsHAK21[101]	Na^+、K^+含量	转运K^+离子
耐低温基因		
Osmyb4[116]	相对电导率、光合系统II稳定性	影响参与低温诱导途径基因的表达
qLTG3-1[104]	发芽率	
OsRAN2[132]	存活率、平均根细胞有丝分裂指数等	促进细胞核内微管蛋白输出，维持细胞分裂
LTG1[130]	株高、地上部分长度、穗长、千粒重等	通过依赖生长素的途径影响低温条件下的生长
OsCOLD1[109]	存活率、每穗粒数、单株穗数、千粒重等	调控G蛋白信号途径，增强低温耐受
耐高温基因		
OsHSP101; *OsHSA32*[157]	发芽率	正反馈调控，在转录后水平延长苗期水稻热适应时间
OgTT1[152]	蛋白酶体活性、千粒重、单株产量、主穗结实率等	高效去除细胞毒性变性蛋白和维持热响应途径

胞的水分利用率和脱落酸 (abscisic aid, ABA) 敏感性可能得到提高，促进了超表达材料的抗旱性增强 [25]。其他 NAC 家族成员，如 *OsNAC6*[26]、*OsNAC10*[27]、*OsNAC9*[28] 和 *OsNAC5*[29] 也被报道参与水稻抗旱性调控。

一些 DREB/CBF 类转录因子参与不依赖于脱落酸的干旱响应途径，这有助于提高水稻的抗旱性。超表达 *OsDREB1A* 和 *OsDREB1B* 的水稻出现生长缺陷 [30]，而超表达 *OsDREB1F* 和 *OsDREB1G* 并没有表现出明显的生长迟缓 [31-32]。此外，DREB2 类转录因子也能提高转基因水稻的抗旱性 [32-33]。

水稻中锌指蛋白基因家族的一些成员在抗旱过程中也发挥了作用。锌指蛋白基因在抗逆过程中一般会发挥正调控作用，但 *DST* 基因却负调控水稻的抗旱性。该基因编码的锌指蛋白通过调控 H_2O_2 的产生以减少气孔关闭 [34]。Xu 等 [35] 发现超表达 *OsZFP252* 植株的抗旱性增加，脯氨酸、可溶性糖的含量上升且存活率升高。

多种类型的蛋白激酶也在水稻的抗旱过程中发挥了重要作用，如促分裂原活化蛋白激酶 (mitogen-activated protein kinase, MAPK) 级联途径信号 [36-37]、类钙调磷酸酶 B 互作蛋白激酶 (calcineurin B-like calcium sensor interacting protein kinase, CIPK)[13]、钙依赖蛋白激酶 (calcium-dependent protein kinase, CDPK 或 CPK)[38] 和类受体激酶 [39-41]。OsMAPK5 是水稻中鉴定的首个 MAPK 级联信号，*OsMAPK5* 基因能正调控非生物逆境 (包括干旱) 抗性，但负调控生物逆境抗性 [36]。

一些作为转录调控因子的核蛋白 (如 OsSKIPa[42] 和 OsRIP18 [43]) 同样参与水稻抗旱性调控。OsSKIPa 是人类 SKIP (Ski-interacting protein) 蛋白在水稻中的同源物，超表达 *OsSKIPa* 水稻在生殖生长期的抗旱性显著提高，部分原因可能是由活性氧 (reactive oxygen species, ROS) 清除能力增加和很多逆境相关基因被激活 [42]。E3 泛素连接酶、含 RING 结构域的蛋白和 F-box 蛋白参与蛋白质的降解，编码这些蛋白质的基因在水稻抗旱性方面有的发挥了正调控作用 (如 *OsSDIR1*[44]、*OsRDCP1*[45] 和 *OsSQS1*[46])，有的发挥了负调控作用 (如 *OsDIS1*[47]、*OsDSG1*[48] 和 *MAIF1*[49])。

另外，Zhu 和 Xiong[50] 发现了一个之前从未报道的编码巨型蛋白 (2 391 个氨基酸) 的基因 *Drought-Induced Wax Accumulation 1*(*DWA1*)，通过调控逆境诱导的蜡质积累增加水稻的抗旱性。

2　水稻耐淹涝相关基因的发掘

淹水 (submergence) 或洪涝 (flooding) 会影响植物对氧气、二氧化碳、光和营养物质的摄取，从而抑制光合作用，加速能量消耗，使植株生长萎缩，甚至死亡 [51]。水稻在形态结构方面对淹涝的适应包括维持叶片表面气膜 [52]、产生通气组织促进水上和水下器官的气体交换 [53]、产生乙烯刺激皮层细胞和表皮细胞的程序性死亡 [54-56]，以及乙烯和 ROS 介导的不定根生长产生的机械力调控表皮细胞死亡 [57] 等。不同于水稻抗旱性的遗传基础的复杂性和多基因控制的特点，水稻对淹涝的抗性是由少数主要调控因子控制。水稻对淹涝胁迫的适应包括逃淹性 (submergence escape) 和耐淹性 (submergence tolerance)，它们分别由 *SNORKEL* (*SK*) 和 *SUBMERGENCE-1* (*Sub1*) 控制 (基因的基本信息如表 1 所示)，两者都属于 *ETHYLENE RESPONSIVE FACTOR* (*ERF*) 类转录因子基因 [51]。

2.1　逃淹性相关基因的鉴定

深水稻 (deep water rice) 通过快速延长叶片和节间，保持顶端叶片在水层以上，以维持气体交换和光合作用来适应淹水环境 [58]。深水稻的叶片快速生长响应淹涝胁迫，涉及到一种特有的生物学和环境方面的适应过程。Zheng 等 [59] 利用水稻品种 IR64 和旱稻品种 Azucena 构建双单倍体群体，在干旱和浸水两种条件下鉴定到了几个控制种子根长、不定根数和总根干重的 QTL。Hattori 等 [60] 克隆到响应淹涝的关键基因 *SNORKEL1* 和 *SNORKEL2*，两者通过编码参与乙烯信号的响应因子来应对淹涝胁迫。在深水条件下，水稻中乙烯积累并诱导这两个基因的表达。*SNORKEL1* 和 *SNORKEL2* 基因编码产物通过赤霉素显著促进节间的伸长。

2.2　耐淹性相关基因的鉴定

和深水稻的逃淹性机制不同，耐淹水稻表现出生长萎缩，这有利于减少能量消耗，保证水稻在遭受淹涝胁迫时存活数周并在淹涝退去后有足够的能量恢复生长 [61]。Xu 等 [62] 在耐淹性籼稻品种 FR13A 的 9 号染色体上定位到了一个主要的耐淹 QTL (*Sub1*)，该位点能解释约 70% 的表型变异。耐淹品种的 *Sub1* 区域含有成簇的 3 个相似的编码 ERF 类转录因子的基因 *Sub1A*、*Sub1B* 和 *Sub1C*，其中 *Sub1A* 研究得最深入。Fukao 等 [63] 报道 Sub1A 在水稻遭受淹涝时，通过负调控编码降解淀粉和蔗糖的酶的基因表达来降低能量消耗，正调控编码乙醇脱氢酶 (alcohol dehydrogenase, ADH) 和丙酮酸脱羧

酶 (pyruvate decarboxylase, PDC) 基因的表达来促进对低氧环境的适应；另外，Sub1A 在淹涝胁迫下还抑制乙烯的合成和细胞壁松动扩张蛋白的表达，维持较高的叶绿素 *a* 和叶绿素 *b* 的含量。Barding 等 [64] 用磁共振的方法分析淹涝胁迫时 *Sub1A* 控制的代谢物，发现 *Sub1A* 参与碳水化合物的消耗、氨基酸的积累和地上部分的延长。另外，*Sub1A* 还通过增加 ABA 响应，激活 ROS 清除，诱导胁迫特异性转录因子和下游基因来提高水稻对氧化胁迫和干旱胁迫的抗性 [65]，抑制水稻开花 [66]。

除了 *Sub1A* 和 *SNORKEL* 赋予水稻对淹涝的抗性，其他一些基因，如 *OsETOL1*[67] 和 *GID1*[68] 同样参与对淹涝的响应。

到现在为止鉴定的所有耐涝关键基因 (*Sub1A* 和 *SNORKEL*) 都编码 ERF 类转录因子，这类转录因子参与乙烯信号转导途径。然而，水稻响应和适应洪水或淹涝的具体机制尚未完全揭示清楚。

3 水稻耐盐相关基因的发掘

土地盐渍化严重影响了作物的种植范围和产量潜力。植物对土壤中盐的响应分为两个阶段：渗透胁迫阶段和离子胁迫阶段。渗透胁迫能导致细胞脱水，降低细胞膨压和根生长速率，抑制光合作用和地上部分生长速率；离子胁迫使植物细胞中积累过多的 Na^+ 和 Cl^-，降低生长速率和产量。植物三种主要的耐盐机制为：(1) 渗透胁迫耐受，有助于维持生长和水的摄取；(2)Na^+ 排出，把有毒的离子从地上部分排出；(3) 组织耐受，让有毒离子进入液泡或特定的组织，使盐分区域化 [69]。因为盐胁迫响应的复杂性和盐耐受机制的差异性，作物的耐盐机制大部分仍然不清楚。研究人员在水稻中主要进行了耐盐 QTL 的定位、表达谱分析和盐耐受相关基因的功能鉴定。

3.1 耐盐QTL的鉴定

Koyama 等 [70] 用 RIL 群体在 4 号染色体上鉴定了 10 个和耐盐相关的 QTL。Lin 等 [71] 利用 Nona Bokra (耐盐的籼稻品种) 和 Koshihikari (对盐敏感的粳稻品种) 杂交得到的 F_2 和 F_3 群体检测到了 3 个在高盐条件下控制幼苗存活天数的 QTL，8 个控制地上部分和根中 Na^+ 与 K^+ 浓度的 QTL。随后，Ren 等 [72] 在水稻 1 号染色体上克隆到了一个耐盐基因 *SKC1*，该基因在维持离子稳态方面发挥了重要作用，超表达 *SKC1* 基因能显著提高水稻的耐盐性。Lee 等 [73] 通过鉴定水稻 RIL 群体在苗期的盐耐性，检测到两个和盐耐受相关的 QTL(*qST1* 和 *qST3*)。 Pandit 等 [74] 用不同组织的盐离子浓度和盐胁迫敏感指数 (小穗育性，粒重和籽粒产量) 作为标准，检测到了 8 个控制盐离子浓度的 QTL 和一个与敏感指数相关的 QTL。

3.2 耐盐相关基因的鉴定

基因芯片技术已被广泛用来分析水稻响应盐胁迫的表达谱 [75-77]。表达谱数据表明，盐胁迫下差异表达基因主要是编码细胞色素氧化酶 P450(使水杨酸失活) 和 ABA 信号途径相关的基因 [78-79]。而蛋白质组学研究 [80-84] 显示，盐胁迫会导致参与糖酵解和碳水化合物代谢的酶积累，对能量的需求增加，ROS 清除酶表达量上升以及促进参与核苷酸和脂肪代谢的蛋白质的表达。

在水稻中已鉴定出很多参与耐盐的基因 (部分重要基因的信息如表 1 所示)。一些基因通过产生渗透调节物质，如糖 [85]、脯氨酸 [86] 和甜菜碱 [87]，有效提高了转基因水稻的耐盐性。很多调节蛋白，包括蛋白激酶、磷酸化酶、钙调蛋白、转录因子和信号因子也被证实参与水稻耐盐性调控。超表达依赖于 Ca^{2+} 的蛋白激酶 OsCDPK7[38]、OsCPK21[88] 能提高水稻耐盐性。Ma 等 [89] 报道了钙调蛋白能够提高水稻的耐盐性，部分原因可能是限制了根中 Na^+ 的积累。同样，一些转录因子也参与激活多种胁迫相关基因的表达并提高水稻的耐盐性，如 bZIP[21]、DREB[90]、NAC[25-26,91-92] 和锌指蛋白 [34,93-94]。

此外，很多参与离子平衡的转运蛋白基因也与耐盐性有关。OsNHX1 是水稻中第一个鉴定出来的 Na^+/H^+ 反向转运子，位于液泡膜上，在区室化细胞质中的 Na^+ 与 K^+ 进入液泡提高水稻的耐盐性方面发挥了重要作用 [95-96]。水稻中另外 4 个 NHX 类反向转运子基因 (从 *OsNHX2* 到 *OsNHX5*) 同样在区室化细胞质中的 Na^+ 与 K^+ 进入液泡过程中发挥了重要作用 [97]。OsHKT1(Na^+ 转运子)、OsHKT2(Na^+/K^+ 偶联转运子) 和 OsVHA 可能是通过维持胞质中低 Na^+ 水平和合适的 Na^+/K^+ 比来赋予水稻耐盐性 [98-99]。OsKAT1 与其他 K^+ 通道蛋白合作，在水稻遭受盐胁迫时通过维持胞质中离子稳态提高植株耐盐性 [100]。2015 年，Shen 等 [101] 报道的定位于质膜的在木质部薄壁组织和单个内胚层细胞中表达的钾转运子 OsHAK21，在介导盐胁迫下质膜对 K^+ 的吸收并维持 Na^+/K^+ 平衡方面可能非常重要。另一种 K^+ 转运子 OsHAK1 在维持 K^+ 介导的生长和对不同 K^+ 浓度范围的盐耐受方面也发挥了重要作用 [102]。

4　水稻耐低温相关基因的发掘

4.1　耐低温的遗传定位和基因克隆

低温胁迫包括冷害和冻害，一般把低于 0 ℃定义为冻害。水稻在苗期和生殖生长期都会经常遭受低温胁迫。为揭示水稻响应低温胁迫的遗传机制，通过不同的作图群体鉴定出了很多和低温胁迫耐受相关的 QTL[103-108]。2015 年，Ma 等 [109] 报道的 *OsCOLD1* 是在水稻中通过图位克隆获得的一个重要耐低温基因。*OsCOLD1* 编码一个 G 蛋白信号途径的调节因子，它通过与 G 蛋白的互作来激活 Ca^{2+} 通道，从而使机体做出相应的抵抗低温的生理变化。*OsCOLD1* 基因中的一个单核甘酸多态性位点 SNP2 对 G 蛋白的 GTP 酶活性起到关键作用，包含 SNP2 的等位基因可能是粳稻驯化过程中适应低温的选择结果。Lv 等 [110] 对 529 份水稻种质资源进行自然条件下苗期自然低温胁迫和快速冷害 (cold shock) 胁迫，通过 GWAS 鉴定到 132 个相关位点，其中 12 位点同时与两种胁迫的耐受性相关。

4.2　水稻耐低温相关基因的鉴定

很多编码转录因子的基因在响应低温胁迫时发挥了重要作用 (部分重要基因的信息如表 1 所示)。转基因超表达 *OsDREB1A*[111]、*OsDREB1B*[112] 和 *OsDREB1F*[32] 使水稻的耐冷性增加。编码 MYB 类转录因子的基因 (如 *OsMYB3R-2*[113-114]、*Osmyb4*[115-116]、*MYBS3*[115-116]、*OsMYB2*[117])，编码锌指蛋白的基因 (如 *OsISAP1*[118]、*OsCOIN*[119]、*OsISAP8*[120]、*OsZFP177*[121]、*OsZFP245*[122]、*OsZFP182*[123]) 和其他编码转录因子的基因 (如 *OsbHLH1*[124]、*SNAC2*[91]、*OsNAP*[125]、*ROS-bZIP1*[126]、*OsbZIP52/RISBZ5*[127]) 都参与水稻冷胁迫响应或调控低温耐受性。值得注意的是，这些转录因子中很多还参与对其他逆境胁迫的调控，如超表达 *OsDREB1F* 还能提高水稻的抗旱和耐盐能力。

多种蛋白激酶也同样参与水稻低温调控，如 MAPK、CIPK、CDPK 家族中的一些成员调控水稻对冷胁迫的响应。超表达 *OsMEK1*[128] 和 *OsMAPK5*[36] 能够提高苗期水稻对冷害的耐受。逆境响应的 CIPK 基因 *OsCIPK03*[13] 和 CDPK 基因 *OsCDPK7*[38] 与 *OsCDPK13*[129] 在水稻遭受冷胁迫时能起正调控作用。另外，近几年发现的 *OsLTG1* 编码一种酪蛋白激酶 I，该酶通过依赖于生长素的途径影响水稻在低温环境下的生长适应 [130]。

参与代谢途径、物质合成和转运的多种蛋白质也参与水稻对冷胁迫的耐受。例如，超表达很多编码解毒物质或渗透调节物质的基因均能增加水稻对冷胁迫的耐受性，包括编码抗坏血酸过氧化物酶的基因 *OsAPXa*[131]，编码 Ran GTP 酶的基因 *OsRAN2* [132] 和 *OsRAN1*[133]，以及 *CMO*[134] (编码胆碱单加氧酶，用于合成甜菜碱)、*WFT1* 和 *WFT2* [135](合成果聚糖)、*OsTPS1*[136]、*OsGSK1*[40]、*OsTPP1*[137] 等。超表达编码水通道蛋白的基因 *OsPIP1;3* 和 *OsPIP2;7* 的转基因水稻低温耐受性显著提高，这很可能归因于细胞中水转运的增加和水平衡的维持 [138-141]。*OsHOS1* 编码一个水稻泛素连接酶，能够调控冷胁迫信号途径 [142]。*OsSRFP1* 编码的 E3 泛素连接酶通过负调控抗氧化酶介导的 ROS 清除，来调节水稻对非生物逆境的响应 [143]。水稻中其他参与冷适应的功能蛋白还包括 OsSPX1(含 SPX 结构域的蛋白)[144]、OsSFR6[145]、OsPRP3 (花特异性的富含脯氨酸的蛋白)[146]、富含甘氨酸的 RNA 结合蛋白 [147]、OsLti6a/b (脱水蛋白)[148] 和 OsCYP19-4 (免疫亲和蛋白)[149]。

5　水稻耐高温相关基因的发掘

高温对植物的影响主要包括：(1) 增加生物膜流动性，从而影响生物膜及膜上蛋白的功能；(2) 蛋白质折叠和蛋白质复合体的组装；(3) 影响酶活性从而影响细胞代谢等 [150-151]。对水稻耐高温功能基因的研究不仅有利于解析高温响应的机理，还有利于培育抗高温品种，提高水稻产量。

5.1　水稻耐高温的遗传定位和基因克隆

通过正向遗传学图位克隆耐高温基因的研究较少。Li 等 [152] 通过构建染色体片段替换系，定位到至少 5 个与水稻耐热性相关的 QTL，并对第 3 染色体上的位点精细定位，克隆到 *OsTT1* 基因。*OsTT1* 编码一个 26S 蛋白酶体的 α2 亚单位，分析发现第 99 位氨基酸的差异决定了不同品种间的耐热性。超表达 *OsTT1* 可以增强水稻的耐热性，说明 *OsTT1* 确实在水稻高温响应中发挥重要作用。Ye 等 [153] 在 IR64/N22 的高世代群体中精细定位到了一个在高温胁迫下能增加小穗育性的位点 *Qhtsf4.1*，并进行了功能验证。Hirabayashi 等 [154] 在药用野生稻中鉴定到的一个新的数量性状位点 *qEMF3* 能促进提前开花，逃避高温胁迫。

5.2　水稻耐高温相关基因的鉴定

水稻响应高温胁迫是一个复杂的过程，受到不同代谢途径中的很多蛋白质的调控。高温胁迫通常会诱导水稻叶片中热激蛋白 (heat shock proteins,

HSPs) 的合成[155-158]。一个预测的水稻花药冷激蛋白同时也受到高温的诱导[159]。此外，Gammulla 等[160]通过蛋白质组学的方法发现，用于蛋白质合成的 5 个延长因子和 3 个起始因子在高温胁迫下会受到抑制，未折叠和错误折叠蛋白的水解以及泛素介导的蛋白酶体系统参与高温响应的调控。

最近十几年以来，在水稻中通过转基因的方法鉴定了很多在高温胁迫耐受过程中发挥作用的基因 (部分重要基因的信息如表 1 所示)。超表达 *OsHSP17.7*[161] (对紫外线 B 也有抗性)、*OsHSP18.6*[162]、*OsHsp101*[162]、*OsHsfA2e*[163]、*OsHSF7*[164]、*OsDREB2B*[165]、*OsWRKY11*[166]、*ZFP177*[121]、*OsAKR1*[167]、*OsLEA5*[168] 和敲除 *OsGSK1*[40] 能提高水稻的高温抗性。另外，2016 年，Liu 等[169] 鉴定了一个苗期耐热基因 *OsHTAS*，该基因编码一个定位于细胞核和胞质的 E3 泛素连接酶，OsHTAS 通过促进 H_2O_2 诱导的气孔关闭提高水稻的耐热性。与耐高温相关基因编码多种蛋白质，包括热休克蛋白、转录因子、类糖原合酶激酶 -3 和醛 - 酮还原酶，表明水稻响应高温胁迫是一个复杂的过程。

6 其他非生物逆境

除了干旱、淹涝、低温或高温胁迫外，水稻还可能受到很多其他非生物逆境胁迫，如紫外线、臭氧、有毒矿物质等。

6.1 臭氧

臭氧是一种对植物有毒害作用的空气污染物，通过气孔进入植物并快速和周围叶肉细胞的质外体作用，产生 ROS 并激发一系列的信号级联和植物防御反应，最终产生叶片损伤、光合能力降低和衰老加快，进而影响产量[170]。Frei 等[171] 通过基因表达谱和生化分析，鉴定到两个影响叶片黄褐化的 QTL：*OzT3* 和 *OzT9*。Chen 等[172] 发现含 *OzT8* 片段的日本晴在臭氧胁迫时能保持叶片的碳同化速率和光合能力。Ueda 等[173] 报道了水稻中一个新的基因 *OsORAP1* 在臭氧胁迫时能特异性诱导细胞死亡。

6.2 紫外线

平流层臭氧的消耗导致 UV-B (280~320 nm) 辐射并到达地球表面，UV-B 辐射增加会降低作物的生长速率和产量[174]。Sato 等[175] 在水稻中鉴定了 3 个和紫外线 -B 抗性相关的 QTL，其中 *qUVR-10* 的效应最大，能解释约 40% 的变异。后续的研究发现，*qUVR-10* 编码一个环丁烷嘧啶二聚体 (cyclo-butane pyrimidine dimer, CPD) 光裂合酶，日本晴和栽培稻 Kasalath 中的 CPD 光裂合酶发生单个氨基酸的替换会表现出不同的 UV-B 抗性[176]。另外，超表达 *OsWRKY89* 能够提高水稻对 UV-B 的抗性[177]。

6.3 有毒矿物质

全世界大约 50% 的耕地为酸性土壤，其中铝毒是酸性土中最重要的限制水稻生长的要素[178]。水稻的耐铝性是一个复杂的数量性状，目前在不同的作图群体中一共鉴定出了 33 个耐铝毒的 QTL[179-185]。这些 QTL 分布在水稻所有 12 条染色体上，其中有 4 个 QTL (分布于 1 号、2 号、3 号、9 号染色体) 虽然是在独立的研究中鉴定到的，但到目前为止还没有克隆出相关基因。另一方面，在水稻中通过筛选铝敏感突变鉴定了 5 个耐铝基因 (*STAR1* 和 *STAR2*[186]、*ART1*[187]、*Nrat1*[188]、*OsALS1*[189])。Famoso 等[190] 通过双亲 QTL 分析和 GWAS 分析研究了水稻耐铝的遗传结构，共鉴定出 48 个和铝耐受相关的 QTL，其中 3 个 QTL 和 3 个铝敏感突变体 (*art1*、*star2*、*nrat1*) 对应的基因位置一致。此外，上调表达一个镁转运基因 *OsMGT1* 能提高水稻耐铝毒能力[191]。

硅能够提高植物的抗逆性，但人们对硅在重金属污染下保护植物的机制了解不多。Kim 等[192] 发现硅通过调控 P 型重金属 ATP 酶、硅响应基因的表达和内源性植物激素的含量来缓和重金属胁迫。

7 展望

尽管成百上千的非生物逆境抗性相关的 QTL 或功能基因已经被鉴定出来，但水稻对单一逆境抗性的遗传和分子机制仍有待深入揭示。更多研究方法的综合应用可望促进对水稻抗逆性的遗传和分子基础的解析。这些方法包括整合传统的 QTL 定位和关联分析进行遗传鉴定、高通量突变体筛选 (尤其是针对逆境相关基因)，抗逆品种和逆境敏感品种之间的比较转录组、蛋白质组和代谢组分析，以及对不同方法获得的数据进行生物信息学分析或基于先验知识的系统分析。

抗逆性是一个复杂的系统“性状”，只能通过一些构成性状或形态生理指标部分地反映出来。因而，选择合适的抗逆相关表型和准确而有效的表型鉴定技术对于揭示水稻抗逆的遗传和分子机制是非常重要的。大多数的基因功能研究是在温室或盆栽条件下进行的表型鉴定，因而有必要使水稻在实验条件下的生长环境尽可能接近大田生产条件下的自然胁迫环境，从而发掘真正有潜力用于抗逆性遗传改良的功能基因，这对于抗逆功能基因组研究成果向抗逆育种应用研究的转化尤为重要。

致谢：由于章节篇幅限制，作者对相关主题文献可能的漏引或未完全引用表示歉意。同样的原因，养分胁迫功能基因的鉴定由本专刊另文综述。

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