·综述·

水稻耐盐碱的分子机制和遗传改良研究进展

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摘　要：水稻(*Oryza sativa* L.)是我国最重要的粮食作物之一，水稻的产量关系到国家粮食安全。盐碱复合胁迫对水稻生长发育具有显著负面影响，导致水稻有效穗粒数、千粒重、精米率等产量指标下降。伴随盐碱地比例的上升以及可用耕地的持续减少，水稻种植与生产正面临严峻挑战。我国是全球第 3 大盐碱土分布国，提升水稻耐盐碱性并改良盐碱地，对于保障国家粮食安全具有重大意义。近年来，水稻耐盐碱性的研究取得了显著进展，本文从渗透调节、激素调节、活性氧清除以及光合作用和气孔调节等方面综述了水稻耐盐碱相关的分子机制，同时论述了耐盐碱水稻的遗传改良方法及其未来面临的问题和发展方向，为耐盐碱水稻的研究和应用提供了理论支持。

关键词：水稻；盐碱胁迫；分子机制；遗传改良；数量性状位点定位

Advances in molecular mechanisms and genetic improvement of saline-alkali tolerance in rice

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Abstract: Rice (*Oryza sativa* L.) is among the most vital cereal crops in China, and its yield has a

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direct bearing on national food security. Saline-alkali combined stress significantly negatively impacts the growth and development of rice, leading to reductions in key yield components such as the number of effective panicles, 1 000-grain weight, and milled rice rate. With the increasing proportion of saline-alkaline land and continual reduction of arable land, rice cultivation and production face severe challenges. As China ranks third globally in saline-alkali soil distribution, enhancing the saline-alkali tolerance of rice and ameliorating saline-alkaline land hold significant importance for ensuring national food security. Significant advances have been achieved in the research on saline-alkali tolerance of rice in recent years, this review synthesizes molecular mechanisms underlying the saline-alkali tolerance of rice, encompassing osmoregulation, plant hormonal regulation, reactive oxygen species scavenging, photosynthesis, and stomatal regulation. Concurrently, we examine genetic enhancement approaches for saline-alkali tolerance in rice and discuss persistent challenges and future research trajectories. This work aims to advance both fundamental research and practical applications of saline-alkali tolerant rice.

Keywords: rice; saline-alkali stress; molecular mechanism; genetic improvement; quantitative trait locus (QTL) mapping

水稻是全球最重要的粮食作物之一，关系到全球数十亿人口的生存发展。如今，随着气候变暖、海平面上升、灌溉不当与次生盐渍化加剧，全球盐碱土面积持续扩大，约 10 亿 hm^2 的土地受到影响[1]。我国盐碱地总面积达 9 913 万 hm^2，约占国土面积的 10.3%，在我国沿海滩涂、东北与黄淮海平原及内陆干旱半干旱区分布广泛[2]。土壤盐碱化引起的盐碱胁迫会导致水稻体内离子失衡、水分吸收困难、光合作用受阻等，具体表现为叶片干枯、产量下降甚至死亡[3]。因此，土地盐碱化已成为严重影响我国水稻生产的非生物因素[4]，对国家粮食安全产生威胁。在此背景下，挖掘耐盐碱水稻种质资源并推动其应用已成为保障我国农业可持续发展的重中之重[5]。未来亟需从 3 个方面深化研究：(1) 生理机制解析。探明渗透调节、活性氧清除及激素调控等生理响应途径。(2) 分子网络阐明。揭示耐盐碱相关基因调控网络与信号传导机制。(3)技术结合应用。融合传统育种、分子标记辅助育种与基因编辑等技术创制耐盐碱新品种并运用于农业实践。研究体系围绕提升粮食产能的核心目标，聚焦农业科技发展，对保障粮食安全具有重大现实意义，可提供关键科技支撑。

1 盐碱胁迫造成的生理影响

盐碱胁迫是指土壤中可溶性盐分和碱性物质积累，导致土壤溶液的 pH 和盐浓度上升、土壤透水性变差，进而影响植物的正常生长和发育。盐碱胁迫分为盐胁迫(以 NaCl 等中性盐为主)和碱胁迫(以 Na_2CO_3 和 $NaHCO_3$ 等碱性盐为主)。在自然条件下植物会同时受到盐分和碱性物质积累带来的影响，因此盐胁迫常伴随碱胁迫，给植物造成双重危害。最新研究表明，盐碱稻田中有效氮作为影响水稻产量的核心土壤养分指标，与土壤 pH 值呈显著负相关；由于土壤 pH 值由 CO_3^{2-}、HCO_3^-主导调控，以碳酸盐/碳酸氢盐为主的碱胁迫对水稻产量的抑制效应显著强于以 Na^+为主的盐胁迫，降低 CO_3^{2-}、HCO_3^-浓度并提升硝酸铵含量，已成为提高盐碱稻田产量的关键措施[6]。盐碱胁迫对水稻造成的生理影响主要包括：(1) 渗透胁迫抑制水分吸收。高浓度的 Na^+、Cl^-等可溶性盐分会降低土壤溶液的渗透势。当低于水稻根细胞的水势时，根系吸水受到抑制，诱发渗透胁迫。(2) 破坏水稻体内的离子平衡。盐碱土壤中过量的 Na^+进入根系，破坏细胞结构，并且与 Ca^{2+}、K^+争夺离子

通道，导致细胞内 K^+、Ca^{2+}的浓度下降[7]，K^+/Na^+的离子平衡被打破。此外，碱胁迫引起的土壤溶液 pH 过高会直接导致 Ca 元素吸收受阻[8]，Ca^{2+}的缺失会使细胞膜通透性下降，离子渗漏加剧，离子平衡被进一步打破[9]。(3) 影响光合作用效率。盐碱胁迫往往会导致水稻叶片气孔关闭，二氧化碳的吸收降低，叶绿素合成减少，继而引发二氧化碳缺失和光捕获能力降低，导致光合速率下降；此外，盐碱胁迫还会抑制光合作用过程中核酮糖-1,5-二磷酸羧化酶(ribulose-1,5-bisphosphate carboxylase/oxygenase, Rubisco)的活性，其活性降低会直接影响光合作用的产物合成[10]。(4) 导致活性氧(reactive oxygen species, ROS)积累。盐碱胁迫会诱导水稻细胞内活性氧的产生，如超氧阴离子(superoxide anion, O_2^-)、过氧化氢(hydrogen peroxide, H_2O_2)等，这些活性氧会损伤叶绿体等细胞器，还会导致酶等大分子物质失活、细胞膜破裂，造成氧化应激。(5)影响淀粉合成和籽粒发育。对水稻而言，其产量和籽粒品质是至关重要的考量因素，盐碱胁迫会破坏水稻的正常生长节奏，导致水稻对氮、钙、磷、钾等元素的吸收受阻，造成营养缺陷，影响籽粒的品质[11]。而水稻籽粒的品质又与淀粉的合成过程紧密相连，ADP 葡萄糖焦磷酸化酶(ADP-glucose pyrophosphorylase, AGPase)和可溶性淀粉合成酶(soluble starch synthase, SSS)参与淀粉的合成，在水稻灌浆期中发挥重大作用，盐碱胁迫可明显抑制 AGPase 和 SSS 的活性，导致籽粒淀粉合成减少，千粒重降低，最终减产[12]。总之，盐碱胁迫严重危害水稻正常的生长发育，解析其耐盐碱分子调控网络对作物改良和农业生产至关重要。

2 水稻耐盐碱性的分子机制

2.1 离子平衡与渗透调节以及渗透保护物质的积累

在面临盐碱胁迫时，耐盐碱水稻会采取多重策略进行渗透调节(图 1)：(1) Na^+/H^+逆向转运蛋白(salt overly sensitive 1, SOS1)通过排出胞质Na^+并抑制 Na^+内流，减少细胞内 Na^+积累[13-14]。(2) 利用液泡膜 Na^+/H^+逆向转运蛋白(sodium hydrogen exchanger 1, NHX1)将 Na^+置于液泡中进行区隔化同时调节液泡的 pH 和离子平衡[15-16]。(3) K^+转运蛋白(high-affinity potassium transporter, HKT)会优先吸收 K^+并阻断 Na^+内流，K^+通道蛋白(*Arabidopsis* K^+ transporter, AKT)可以维持细胞内 K^+水平，保障酶活性和细胞功能，二者协作帮助水稻胞内 Na^+/K^+维持平衡[17]。此外，本课题组最新研究表明，K^+外排逆向转运蛋白能促进 Na^+或 K^+通过细胞膜交换为 H^+，在 pH 调节、离子稳态、渗透平衡中起着至关重要的作用；研究进一步发现，敲除编码该蛋白的基因 *OsKEA1* 后，其突变体表现出活性氧积累加剧以及叶绿体完整性受损的现象；这证实了 *OsKEA1* 在水稻盐胁迫响应中的关键作用，*OsKEA1* 可成为作物耐盐性遗传改良的重要靶点[18]。(4) 水稻中 Ca^{2+}依赖的蛋白激酶信号通路中的钙传感器蛋白(calcineurin b-like protein, CBL)和丝氨酸/苏氨酸蛋白激酶(CBL-interacting protein kinase, CIPK)在渗透调节中同样发挥重要作用[19]。Ca^{2+}与 CBL 的 EF-hand 结构域特异性结合，诱导 CBL 构象变化，被激活的 CBL 与 CIPK 结合，形成 CBL-CIPK 复合物，CIPK 可以磷酸化 SOS1 的 C 端自抑制域，使其转运活性提升 5 倍以上，从而促进细胞内 Na^+的排出，维持细胞内离子平衡[20-21]。(5) 当细胞大量失水时，水通道蛋白(aquaporin protein, AQP)就会以高速率和低能耗的方式运输水分子，可以将细胞外的水分转移到胞内并将细胞内多余的活性氧物质转运到细胞外[22]。此外，Na^+区室化机制研究取得了诸多新的进展。Ramakrishna 等[23]通过低温纳米级二次离子质谱离子微探针技术证实：SOS1 可能也具有将钠隔离到液泡中的功能，除了质膜外，SOS1 在晚期内体/前液泡以及液泡中强烈积聚，表明 SOS1 在液泡钠隔离中发挥作用。Liu

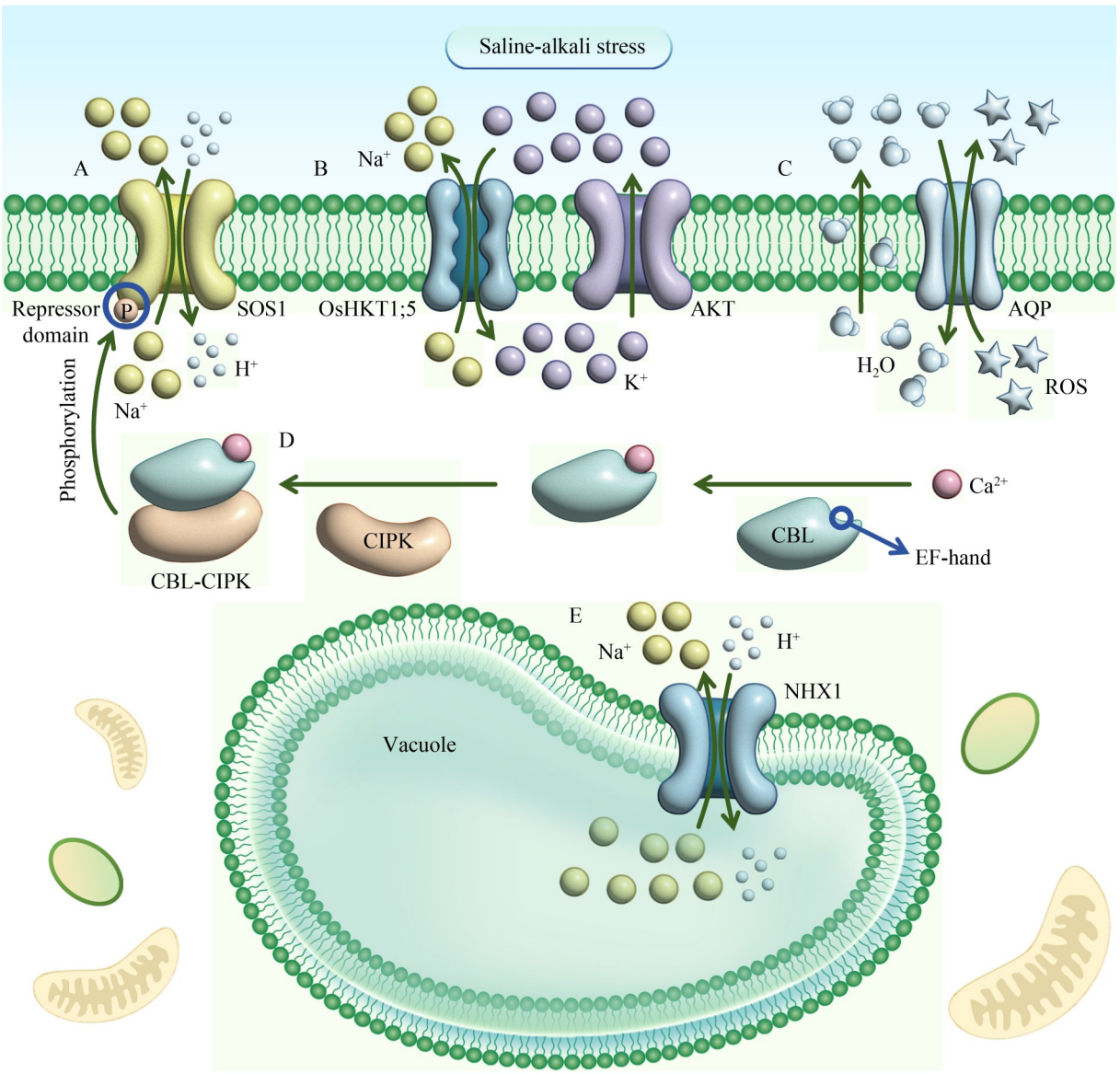

图1　水稻渗透调节机制　A：SOS1通过转运Na^+来降低Na^+在细胞内的积累。SOS1：Na^+/H^+逆向转运蛋白。B：HKT和AKT协同作用帮助维持细胞内Na^+/K^+平衡。HKT：K^+转运蛋白；AKT：K^+通道蛋白。C：AQP帮助运输水分子到细胞内并排出细胞内多余活性氧。AQP：水通道蛋白；ROS：活性氧。D：Ca^{2+}依赖的蛋白激酶信号通路介导细胞内Na^+的排出。CBL：钙传感器蛋白；CIPK：丝氨酸/苏氨酸蛋白激酶。E：NHX1将Na^+区隔在液泡中来帮助调节离子平衡。NHX1：液泡膜Na^+/H^+逆向转运蛋白。

Figure 1　Mechanism of rice osmotic regulation. A: SOS1 reduces the accumulation of Na^+ in cells by transporting Na^+. SOS1: Salt overly sensitive 1. B: The synergistic effect of HKT and AKT helps maintain intracellular Na^+/K^+ balance. HKT: High-affinity potassium transporter; AKT: Arabidopsis K^+ transporter. C: AQP helps transport water molecules into cells and eliminate excess reactive oxygen species within the cells. AQP: Aquaporin protein; ROS: Reactive oxygen species. D: The Ca^{2+} dependent protein kinase signaling pathway mediates the efflux of Na^+ from cells. CBL: Calcineurin b-like protein; CIPK: CBL-interacting protein kinase. E: NHX1 isolates Na^+ in vacuoles to help regulate ion balance. NHX1: Sodium hydrogen exchanger 1.

等[24]进一步研究发现，在盐胁迫下，SOS1 蛋白会发生部分内吞并定位于液泡膜，这对植物细胞内液泡的 Na^+区隔化具有关键作用。而这一过程依赖于丝氨酸/苏氨酸蛋白激酶(salt overly sensitive 2, SOS2)对 FREE1 蛋白(内吞体分选转运复合物 I 分选所需的 FYVE 结构域蛋白)的磷酸化；SOS2 通过磷酸化 FREE1，调控了内吞体的分选和内膜融合过程，共同促进 Na^+在液泡中的区室化，增强植物耐盐性。

为应对盐碱胁迫造成的渗透调节紊乱，水稻会迅速积累无机离子及有机分子作为渗透调节物质[25]。主要包括糖类(蔗糖、海藻糖、淀粉)、蛋白质、氨基酸(脯氨酸、精氨酸)、多元醇(山梨醇、甘露醇)和酰胺(谷氨酰胺、天冬酰胺)等[26-27]。其中脯氨酸具有参与渗透调节、保护质膜完整性的功能。甜菜碱可保护细胞中蛋白质和酶的活性，维持生化反应正常进行，减少电解质渗漏[28]。肌醇则能作为第二信使参与胁迫响应的细胞信号转导，并且其本身具有高水溶性，能帮助细胞储水，降低水稻植株在盐碱胁迫下脱水的风险[29]。这些渗透调节物质的累积和协同作用有助于维持水稻植株内的渗透调节和离子平衡稳定，有效提升水稻等作物的盐碱耐受性[30]。

2.2 氮素调控水稻耐盐碱性

氮素是植物体内蛋白质、核酸、叶绿素和激素的重要组成部分，能够增强水稻应对盐碱胁迫的能力。在土壤盐碱化挑战下，水稻叶片中氮代谢关键酶(谷氨酰胺合成酶、谷氨酸合成酶、硝酸还原酶等)活性上升，促进氮代谢进程，以提高抗逆性[31]。水稻还会通过增加根表面积和根系深度来提高氮素吸收[32]。在此过程中，耐盐碱水稻的根际效应至关重要。根际效应是植物根系活动导致根周土壤微生物活性、理化性质及养分转化过程显著改变，进而影响植物养分吸收的现象；研究表明，耐盐碱水稻根际区域富集了特定的硝化菌群，且与硝化相关的功能基因 *amoA* 的表达在根际区域显著增强，这导致了硝化速率和氮素转化效率在根际土壤中显著高于非根际土壤。这些发现揭示了根际效应帮助水稻吸收氮素的机制，为氮素吸收的研究提供了新的角度[33-34]。此外，适量施用氮肥可有效缓解水稻生长障碍及氮素匮乏，显著提高叶片净光合速率与光合产物积累量，提高水稻功能叶中超氧化物歧化酶(superoxide dismutase, SOD)和过氧化物酶(peroxidase, POD)活性，使作物在盐碱胁迫下仍能保持较好的生长状态。

2.3 抗氧化机制和活性氧清除

土壤盐碱化对水稻的另一主要危害是诱发氧化胁迫。高盐碱环境下，水稻体内活性氧水平急剧升高，引发氧化损伤。为应对此胁迫，耐盐碱水稻激活抗氧化防御系统：产生谷胱甘肽(glutathione, GSH)、抗坏血酸(ascorbic acid, AsA)、α-生育酚和类黄酮等物质，能够有效地清除 ROS；激活过氧化氢酶(catalase, CAT)以及参与 AsA-GSH 循环相关酶系的活性[35]；通过 G 蛋白介导的细胞信号转导途径调节来降低氧化损伤。

H_2O_2 是植物细胞中的重要信号分子，但过量的 H_2O_2 会导致氧化损伤，因此，维持 H_2O_2 的平衡有利于植物的正常生长和环境适应(图 2)。当土壤盐碱化造成危害时，H_2O_2 在植株体内大量积累，过氧化氢酶(catalase, CAT)被蛋白激酶磷酸化并激活，CatC 可以催化过氧化氢分解为水和氧气，维持 H_2O_2 的稳态。CAT 的活性和稳定性受磷酸化调节，过氧化氢酶磷酸酶 1 (phosphatase of catalase 1, PC1)能特异性去磷酸化 CatC 的第 9 位丝氨酸，从而抑制其四聚化及其在过氧化物酶体中的活性；因此，PC1 可以作为一种分子开关，通过去磷酸化失活 CatC，负调控水稻的耐盐碱性[36]。已有研究表明，盐耐受性受体样胞浆激酶 1 (salt tolerance receptor-like cytoplasmic kinase1, STRK1)能够磷酸化并激活 CatC 来提高水稻的盐碱耐受性，Tian 等[37]研究发现，DHHC 型锌指蛋白 DHHC09 可以在 Cys5、Cys10 和 Cys14 位点对 STRK1 进行 S-酰

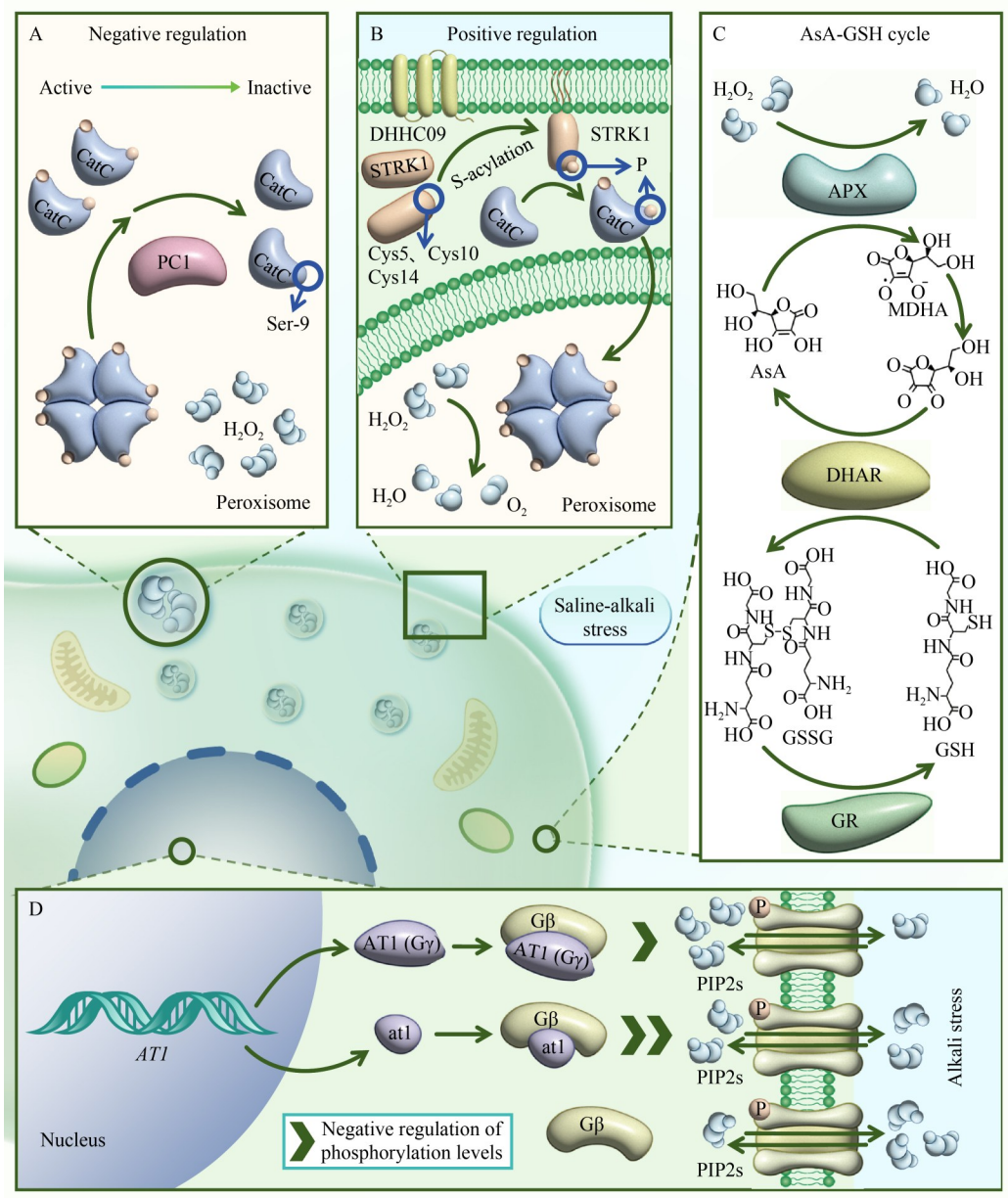

图2　盐碱胁迫下过氧化氢的清除机制　A：PC1负调控H_2O_2稳态。PC1：过氧化氢酶磷酸酶1；CatC：过氧化氢酶C；H_2O_2：过氧化氢。B：STRK1介导H_2O_2的清除。STRK1：盐耐受性受体样胞浆激酶1。C：谷胱甘肽循环清除H_2O_2。APX：抗坏血酸过氧化物酶；MDHA：单氢抗坏血酸自由基；DHAR：脱氢抗坏血酸还原酶；ASA：抗坏血酸；GSSG：氧化型谷胱甘肽；GR：谷胱甘肽还原酶；GSH：谷胱甘肽。D：PIP2s控制H_2O_2输出。PIP2s：过氧化氢输出蛋白。

Figure 2　The clearance mechanism of hydrogen peroxide under salt alkali stress. A: PC1 negatively regulates the steady state of H_2O_2. PC1: Phosphatase of catalase 1; CatC: Catalase C; H_2O_2: Hydrogen peroxide. B: STRK1 mediated clearance of H_2O_2. STRK1: Salt tolerance receptor-like cytoplasmic kinase1. C: Glutathione cycle clears H_2O_2. APX: Ascorbate peroxidase; MDHA: Monodehydroascorbate radical; DHAR: Dehydroascorbate reductase; ASA: Ascorbic acid; GSSG: Oxidized glutathione; GR: Glutathione reductase; GSH: Glutathione. D: PIP2s controls H_2O_2 output. PIP2s: Hydrogen peroxide output protein.

化并将其锚定在质膜上，STRK1 就会将 CatC 磷酸化并向 CatC 传递信号，从而清除大量积累的 H_2O_2。另外，AsA-GSH 循环也是水稻体内一个关键的 H_2O_2 清除机制，在这个循环中，抗坏血酸过氧化物酶(ascorbate peroxidase, APX)通过 ASA 将 H_2O_2 还原为 H_2O，同时产生中间产物单氢抗坏血酸自由基(monodehydroascorbate radical, MDHA)和脱氢抗坏血酸(dehydroascorbic acid, DHA)；随后，脱氢抗坏血酸还原酶(dehydroascorbate reductase, DHAR)将 MDHA 和 DHA 还原为 AsA，同时消耗还原型谷胱甘肽 GSH；谷胱甘肽还原酶(glutathione reductase, GR)最终将氧化型谷胱甘肽(oxidized glutathione, GSSG)还原为 GSH，完成循环，从而保护细胞免受氧化损伤[38]。盐碱胁迫还可能触发一系列信号转导机制，以调节水稻的生理状态。Zhang 等[39]通过基因组关联分析发现一个耐碱相关基因 *AT1*，其编码一种 G 蛋白 γ 亚基；PIP2s 是一种 H_2O_2 输出蛋白，在碱胁迫下，G 蛋白 γ 亚基 AT1 可能与 G 蛋白 β 亚基配对，负向调控 PIP2s 的磷酸化水平，从而降低 H_2O_2 输出活性，导致 H_2O_2 过度积累，使植物对碱性胁迫敏感；AT1 的截短形式 at1 能进一步抑制 H_2O_2 输出活性，导致植物对碱胁迫的超敏感性。盐碱胁迫下的抗氧化机制是一个复杂的过程，涉及多种酶和抗氧化剂以及基因表达调控。这些机制共同作用，帮助水稻减轻氧化应激，从而提高水稻对盐碱胁迫的耐受性。

2.4 激素调节降低盐碱胁迫危害

水稻对盐碱胁迫的响应受到脱落酸(abscisic acid, ABA)、生长素(indo-3-acetic acid, IAA)、乙烯(ethylene, ETH)、油菜素内酯(brassinolide, BR)、独脚金内酯(strigolactone, SL)、褪黑素(melatonin, MT)等多种激素构成的复杂调控网络的共同控制。为增强对盐碱环境的适应性，水稻通过精密调节特定激素的水平和活性，优化其生理与代谢过程(图 3)。

ABA 是植物应对逆境的核心激素，在水稻面临盐碱胁迫时可通过多层次的生理和分子机制协调水稻的适应性响应。当水稻感知到盐碱胁迫信号时，ABA 水平迅速上升，并与 ABA 受体蛋白 PYR/PYL/RCAR 结合，再与蛋白磷酸酶 2C (protein phosphatase 2C, PP2C)相互作用并抑制 PP2C 的活性，然后激活 SNF-1 相关蛋白激酶 2 (SNF1-related protein kinase 2, SnRK2)，SnRK2 通过磷酸化 ABA 响应元件(ABA responsive element, ABRE)或 ABRE 结合因子(ABA responsive element binding factor, AREB/ABF)，激活阴离子通道蛋白(slow anion channel-associated 1, SLAC1)和植物特异性阴离子通道蛋白(aluminum-activated malate transporter 12, ALMT12)，引起保卫细胞中 K^+和阴离子外流，细胞膨压下降，ROS 被清除，气孔关闭，从而帮助水稻适应盐碱逆境[40]。盐碱胁迫导致 ABA 积累，还会激活与扩张蛋白 EXPANSIN 表达有关的基因，抑制细胞增殖的同时促进根分生组织的细胞增大，最终导致原发根肿胀；根的肿胀有利于水分养分的流动和根的分枝，能够提高水稻的耐盐碱性[41]。Jiang 等[42]通过实验揭示了 OsGAPC1-OsSGL 调控模块在盐碱胁迫响应中的作用；该研究阐明了在盐胁迫条件下转录因子 OsSGL 通过直接结合 ABA 合成相关基因 *OsNCED3* 以及 ABA 应答基因 *OsRAB21* 等，抑制其转录；关键糖酵解酶 OsGAPC1 通过与 OsSGL 互作，增强了 OsSGL 对 *OsNCED3* 的转录抑制；而盐胁迫又会诱导 OsGAPC1 发生乙酰化修饰，这种修饰部分解除了对 *OsNCED3* 转录的抑制作用，使 ABA 合成有所恢复。这些发现共同揭示了一个水稻盐胁迫响应的负调控机制，阐明了 ABA 合成的动态调节过程，并凸显了植物在抗逆性与生长调控之间维持的微妙平衡。外源 ABA 的处理能降低 Na^+/K^+，提高 Mg^{2+}和 Ca^{2+}等矿质离子的含量，显著提高叶片的抗氧化能力；ABA 处理还会引起 1-氨基环丙烷-1-羧酸(1-aminocyclopropane-1-carboxylic acid, ACC)、反式玉米素(trans-zeatin, TZ)等含量的上升，表

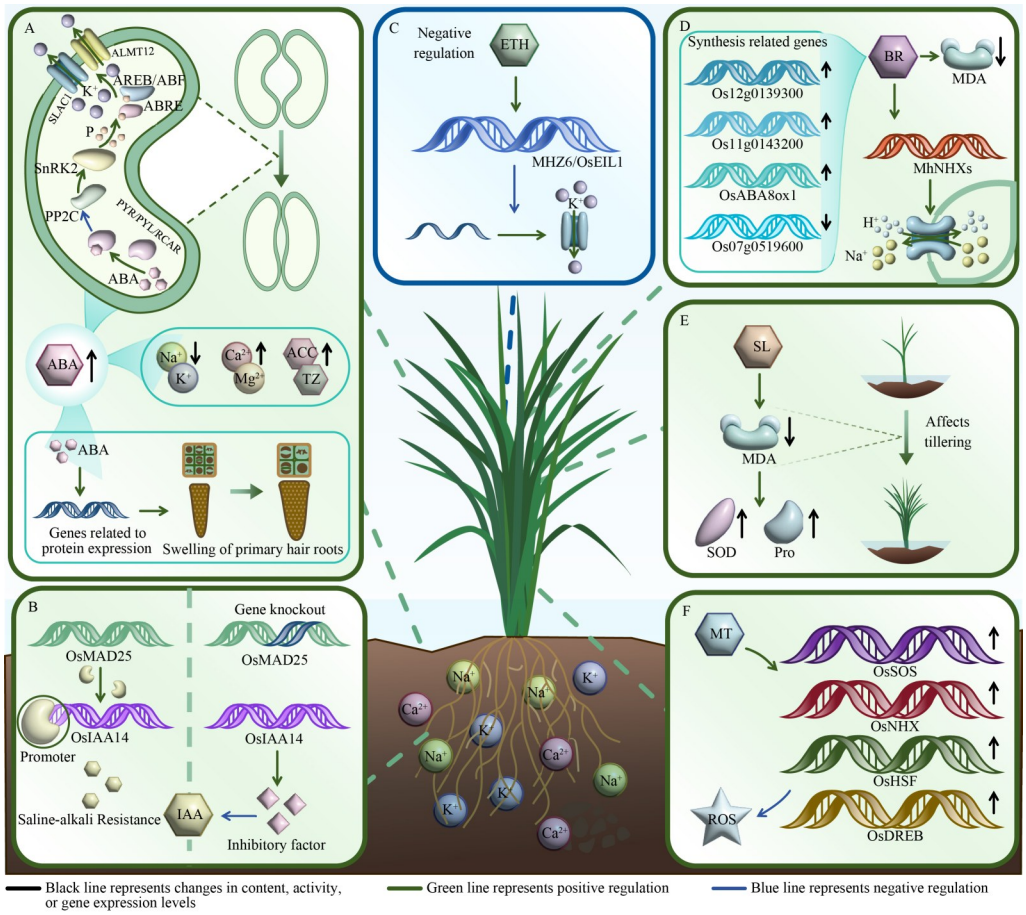

图3　激素网络协同调节应对盐碱胁迫　A：ABA通过其信号途径清除细胞内活性氧，维持离子平衡和细胞稳态。ABA：脱落酸；PYR/PYL/RCAR：ABA受体蛋白；PP2C：蛋白磷酸酶2C；SnRK2：SNF-1相关蛋白激酶2；ABRE：ABA响应元件；AREB/ABF：ABRE结合因子；SLAC1：阴离子通道蛋白；ALMT12：植物特异性阴离子通道蛋白；ACC：1-氨基环丙烷-1-羧酸；TZ：反式玉米素。B：*OsMAD25*通过调控IAA的含量来影响水稻耐盐碱性。IAA：生长素。C：ETH通过上调其响应基因的表达负调控水稻耐盐性。ETH：乙烯。D：BR通过调控Na^+/H^+反转运基因的表达来缓解离子毒害。BR：油菜素内酯；MDA：丙二醛。E：SL帮助水稻缓解氧化应激。SL：独脚金内酯；SOD：超氧化物歧化酶；Pro：脯氨酸。F：MT通过上调盐胁迫响应基因的表达来提高耐盐性。MT：褪黑素；ROS：活性氧。

Figure 3　Hormone network coordinated regulation to cope with salt alkali stress. A: ABA scavenges intracellular reactive oxygen species through its signaling pathway, maintaining ion balance and cell homeostasis. ABA: Abscisic acid; PYR/PYL/RCAR: Abscisic acid receptor protein; PP2C: Protein phosphatase 2C; SnRK2: SNF1-related protein kinase 2; ABRE: ABA responsive element; AREB/ABF: ABA responsive element binding factor; SLAC1: Slow anion channel-associated 1; ALMT12: Aluminum-activated malate transporter 12; ACC: 1-aminocyclopropane-1-carboxylic acid; TZ: Trans-zeatin. B: *OsMAD25* affects the salt and alkaline tolerance of rice by regulating the content of IAA. IAA: Indo-3-acetic acid. C: ETH negatively regulated rice salt tolerance by up regulating the expression of its response genes. ETH: Ethylene. D: BR alleviates ion toxicity by regulating the expression of Na^+/H^+ antiporter genes. BR: Brassinolide; MDA: Malondialdehyde. E: SL helps rice alleviate oxidative stress. SL: Strigolactone; SOD: Superoxide dismutase; Pro: Proline. F: MT can improve salt tolerance by up regulating the expression of salt stress response genes. MT: Melatonin; ROS: Reactive oxygen species.

明通过 ABA 处理可以平衡内源激素，维持细胞内稳态[43]。

生长素在水稻逆境胁迫中也发挥重要作用，Seo 等[44]分别构建了 *OsMAD25* 的敲除突变体、过表达突变体和 RNAi 沉默突变体；结果发现 *OsMAD25* 的过表达植株根系生长状况良好，表现出耐盐碱性，机制研究发现 *OsMAD25* 的转录因子直接结合 *OsIAA14* (编码生长素信号抑制因子)的启动子来抑制其转录，表明生长素含量的提高有助于水稻应对盐碱胁迫。乙烯是参与耐盐碱信号的另一类重要激素，对水稻耐盐性有负调控作用。乙烯含量升高，会上调乙烯信号响应基因 *MHZ6*/*OsEIL1* (编码植物凝集素受体蛋白激酶)，抑制 K^+转运蛋白表达，破坏细胞内离子平衡，从而增加水稻对盐的敏感性。

BR 是一种类固醇激素，通过提高抗氧化系统的酶活性、积累渗透调节物质来帮助水稻降低丙二醛(malondialdehyde, MDA)含量和相对电导率来减轻盐碱胁迫的危害。BR 的合成受多种基因调控，且这些调控基因在盐碱胁迫下呈现差异化表达特征：*Os12g0139300*、*Os11g0143200*、*OsABA8ox1* 表达上调，*Os07g0519600* 表达下调。这类具有胁迫响应特异性的 BR 合成相关基因，可以作为潜在的分子靶点运用到耐盐碱水稻的选育中；BR 还可以通过调控 Na^+/H^+反转运基因 *OsNHXs* 的表达水平，来调节 Na^+/K^+含量，以此缓解离子毒害[45]。独脚金内酯是一种新型植物激素，能够调控植物分枝，影响水稻的分蘖，从而影响单位面积的产量。Ling 等[46]发现对水稻幼苗施用独脚金内酯会显著降低 MDA 含量，提高脯氨酸含量和 SOD 活性，降低盐碱胁迫对水稻幼苗的伤害和生长的限制。MT 作为一种新型激素，已被证明能够增强植物的抗逆性。Khan 等[47]发现外源 MT 能提高水稻盐胁迫和干旱胁迫应答基因 *OsSOS*、*OsNHX*、*OsHSF* 和 *OsDREB* 的表达水平，证实了 MT 是通过抑制 ROS 积累、上调盐胁迫响应基因的表达等方式来提高水稻植株的耐盐碱性。通过这种激素网络的协调作用，水稻能够更好地适应盐碱环境，维持正常的生理功能和生长发育。

2.5 光合作用和气孔调节

盐碱胁迫通过多种途径影响光合作用，降低水稻的光合效率，阻碍其正常生长和发育。光合作用受阻主要体现在光反应和暗反应这 2 个阶段，对于光反应来说主要有以下影响：水稻幼苗的光系统Ⅱ (photosystem Ⅱ, PSⅡ)反应中心受损，最大光化学效率(maximum quantum efficiency of photosystem Ⅱ, Fv/Fm)显著降低；光合电子传递受阻，实际光化学效率(photosystem Ⅱ quantum yield, ΦPSⅡ)和光化学猝灭系数(photochemical quenching coefficient, qP)显著下降，阻碍光合电子传递链的正常运行；非光化学猝灭(non-photochemical quenching, NPQ)显著增加，光系统压力增大；叶绿素 a、叶绿素 b 和类胡萝卜素的含量显著减少，光捕获能力下降[48-49]。对于暗反应的影响在于：由于气孔关闭，CO_2 的供应减少，进而引起卡尔文循环速率降低[50]。

当土壤盐碱化加剧，离子平衡被打破，细胞内过量积累的 Na^+会直接置换叶绿体内囊体包膜中的 Mg^{2+}，破坏叶绿体结构。盐碱胁迫还会引起叶绿体光能复合体电子传递能力下降，光量子与氧分子大量结合，细胞中活性氧的产生和清除平衡失调，导致细胞内产生过量的活性氧[51]。总之，盐碱胁迫通过多种机制影响光合作用，包括直接损害光合机构、限制 CO_2 的吸收、干扰电子传递和光合色素的合成，以及通过离子毒害和矿质营养失衡间接影响光合作用效率。这些生理生化反应共同导致水稻的光合能力下降，进而影响其生长和产量。面对上述挑战，水稻将启动一系列的适应性机制，一方面是通过提升 POD 和 SOD 的活性，从而有效清除光合作用过程中产生的 ROS，来保护 PSII 免受活性氧的损害。Guan 等[52]研究发现，叶绿

体定位基因 *OsCu/Zn-SOD* 过表达植株在盐碱复合胁迫下，表现出相较于野生型更高的 SOD 活性、鲜重、根长及株高；表明 *OsCu/Zn-SOD* 通过增强 SOD 活性，有效缓解盐碱胁迫造成的氧化损伤进而保护光系统反应中心提高水稻植株的耐盐碱性。另一研究指出，水稻 SUV3 蛋白具有 DNA/RNA 解旋酶和 ATP 酶活性，与野生型相比，其过表达株系在盐胁迫下脂质过氧化、电解质渗漏、H_2O_2积累显著降低，而抗氧化酶活性升高，表明其过表达可通过增强抗氧化能力和改善光合作用，赋予水稻耐盐碱性[53]。另一方面就是气孔调节，水稻通过积累脯氨酸、甜菜碱等渗透调节物质以及 ABA 这类植物激素来降低细胞渗透压，从而间接影响气孔开放[54]。

3 耐盐碱基因的鉴定与功能分析

利用基因工程技术将耐盐碱基因导入水稻中，是提升其耐盐碱能力的有效途径。因此，发掘潜在的耐盐碱基因并应用于农业实践是当前育种研究工作的重中之重。本文总结了水稻中多个耐盐碱相关基因的功能，包括谷氨酰胺合成酶基因家族、钠离子转运蛋白基因家族、锌指蛋白基因家族等多个基因家族。这些基因通过不同的分子机制参与水稻对盐碱胁迫的应答反应，包括调节渗透平衡、离子转运、转录调控等过程，为培育耐盐碱水稻品种提供了重要的潜在功能基因和理论依据(表 1)。

谷氨酰胺合成酶在植物氮代谢中起着关键作用，同时也参与了植物对非生物胁迫的响应。在水稻中，谷氨酰胺合成酶基因家族中的 *OsGS2* 和 *OsGS1;1* 在调节水稻耐盐碱性方面作用显著。它们都编码细胞质谷氨酰胺合成酶，其过表达的转基因水稻表现出更强的渗透胁迫和盐胁迫耐受性，在生殖阶段光合性能提高，对光氧化应激也具有更强的耐受性，农艺性状随之得到改善，还能提高氮素利用率、影响糖代谢、改善稻米品质、影响水稻生长速率和灌浆程度；若其缺失或变异则会导致水稻生长放缓、灌浆不足，影响产量[55]。

钠离子转运蛋白在维持植物细胞内离子平衡、防止钠离子过度积累导致的毒害方面发挥着重要作用。水稻中钠离子转运蛋白基因家族的主要成员有 *OsHKT1;5*、*OsHKT2;1* 和 *OsHKT1;4* 等。*OsHKT1;5* 仅在维管束中表达，且主要集中于木质部导管周围的薄壁细胞，其表达受转录复合物调控，能够将 Na^+从木质部汁液中重新吸收，减少 Na^+向叶片的运输，从而响应盐胁迫[56]。*OsHKT2;1* 编码高亲和 Na^+转运蛋白，其表达受 OsPRR73 蛋白调控，OsPRR73 通过招募组蛋白去乙酰化酶 HDAC10 在转录水平上抑制 *OsHKT2;1* 的表达，减少钠离子在特定时间的吸收，避免钠离子过度积累，进而调控水稻耐盐性[57]。*OsHKT1;4* 在水稻生殖生长阶段遭受盐胁迫时发挥关键作用，负责木质部 Na^+卸载，并介导茎部 Na^+转运，有助于将 Na^+从叶片排出，减轻 Na^+对叶片细胞的毒害作用[58]。

锌指蛋白家族中 *OsZFP15* 通过参与 ABA 分解代谢加速种子萌发，增强水稻幼苗的耐盐性和耐旱性；过表达该基因会降低水稻对 ABA 的敏感性，下调 ABA 响应基因转录水平，提高耐盐耐旱性[59]。*ZFP252* 能够增强水稻对干旱和盐胁迫的抗性，其过表达可能通过调控胁迫相关基因表达，引起亲和性渗透调节物质积累，还能正调控 E3 泛素连接酶基因 *OsRING1* 的表达来提高水稻幼苗的抗逆性[60]。*OsNCA1a* 编码环型锌指蛋白，在水稻所有器官中表达，受低温、ABA、盐和干旱强烈诱导；过表达该基因能增加细胞内脯氨酸含量，增强水稻幼苗对冷、盐和干旱的抗性[61]。过表达 *OsC3H47* 会显著增强水稻幼苗对干旱和盐胁迫的耐受性，同时降低对 ABA 的敏感性，其通过 ABA 通路，参与干旱胁迫应答和胁迫后的恢复[62]。*OsTZF1* 对

表1 水稻耐盐碱相关性状重要基因

Table 1 Important genes related to salt-alkali tolerance traits in rice

Gene family	Gene name	Gene ID	Function	References
Glutamine synthetase gene family	*OsGS2*	*LOC_Os04g56400*	Overexpression enhances the tolerance of transgenic rice seedlings to osmotic and salt stress, showing improved photosynthetic performance and agronomic traits during the reproductive stage, as well as increased tolerance to photooxidative stress	[55]
Glutamine synthetase gene family	*OsGS1;1*	*LOC_Os02g50240*	Encodes cytosolic glutamine synthetase, affecting rice growth rate and grain filling; co-overexpression with *OsGS2* enhances seedling tolerance to osmotic and salt stress, improves photosynthetic performance and agronomic traits during the reproductive stage, increases nitrogen use efficiency, influences sugar metabolism, and improves rice quality	[55]
Sodium ion transporter gene family	*OsHKT1;5*	*LOC_Os01g20160*	Encodes a sodium ion transporter expressed exclusively in the vascular bundle, mainly in the parenchyma cells around the xylem vessels; its expression is regulated by a transcriptional complex, transporting Na^+ from the xylem to the xylem parenchyma cells, preventing excessive Na^+ accumulation in the shoots, thereby responding to salt stress	[56]
Sodium ion transporter gene family	*OsHKT2;1*	*LOC_Os06g48810*	Encodes a high-affinity Na^+ transporter, whose expression is regulated by the OsPRR73 protein, reducing Na^+ uptake at specific times to avoid excessive Na^+ accumulation, thereby regulating rice salt tolerance	[57]
Sodium ion transporter gene family	OsHKT1;4	*LOC_Os04g51830*	During the reproductive growth stage under salt stress, *OsHKT1;4* is responsible for xylem Na^+ unloading, mediating Na^+ transport in the stem, and facilitating Na^+ excretion from the leaves	[58]
Zinc finger protein gene family	*OsZFP15*	*LOC_Os03g60570*	Accelerates seed germination through abscisic acid (ABA) catabolism, enhancing salt and drought tolerance in rice seedlings; induced by ABA and various abiotic stresses, overexpression reduces sensitivity to ABA, downregulates ABA-responsive gene transcription levels, but increases *OsABA8ox2* transcription, improving salt and drought tolerance	[59]
Zinc finger protein gene family	*ZFP252*	*LOC_Os12g39400*	Enhances rice resistance to drought and salt stress; overexpression may regulate stress-related gene expression, induce the accumulation of compatible osmolytes, and positively regulate the expression of the E3 ubiquitin ligase gene *OsRING1*	[60]
Zinc finger protein gene family	*OsNCA1a*	*LOC_Os01g01420*	Encodes a ring-type zinc finger protein localized in the nucleus and plasma membrane; expressed in all rice organs, strongly induced by low temperature, ABA, salt, and drought; overexpression upregulates *OsP5CS* expression, increases intracellular proline content, and enhances transgenic rice resistance to cold, salt, and drought	[61]
Zinc finger protein gene family	*OsC3H47*	*LOC_Os07g04580*	Overexpression of *OsC3H47* significantly enhances drought and salt tolerance in rice seedlings while reducing sensitivity to ABA	[62]
Zinc finger protein gene family	*OsTZF1*	*LOC_Os05g10670*	OsTZF1-OX plants show improved resistance to high salt and drought stress, whereas OsTZF1-RNAi plants exhibit reduced resistance	[63]

(待续)

(续表1)

Gene family	Gene name	Gene ID	Function	References
Mitogen-activated protein kinase gene family	*OsMKK6*	*LOC_Os01g32660*	Overexpression enhances salt stress resistance in transgenic rice; when grown in high-salt solutions, transgenic seedlings show increased root and shoot length and weight, with less chlorophyll degradation	[64]
Mitogen-activated protein kinase gene family	*OsMKK1*	*LOC_Os06g05520*	Compared to wild-type, *OsMKK1* knockout mutants are more sensitive to salt stress; yeast two-hybrid experiments show that OsMKK1 strongly interacts with OsMPK4; OsMKK1 and OsMPK4 form a signaling pathway that regulates rice salt stress resistance	[65]
Mitogen-activated protein kinase gene family	*OsMPK4*	*LOC_Os06g38950*	Under salt stress, OsMPK4 interacts with the IPA1 protein, is activated, and phosphorylates the Thr180 site of IPA1, promoting its ubiquitination and degradation, reducing IPA1 protein levels, and ultimately improving rice salt tolerance	[66]
Mitogen-activated protein kinase gene family	*OsMAPK6*	*LOC_Os06g06090*	Under saline-alkali conditions, its expression is regulated, participating in maintaining Na^+/K^+ homeostasis and enhancing saline-alkali tolerance; overexpression of *OsMPK6* significantly improves saline-alkali tolerance, while knockout of *OsMPK6* increases sensitivity	[67]
Mitogen-activated protein kinase gene family	OsBBX17	*LOC_Os06g15330*	Under saline-alkali conditions, its expression is suppressed, interacting with OsMPK6 to affect saline-alkali tolerance; knockout mutants show better saline-alkali tolerance, while overexpression lines show the opposite	[67]
WRKY transcription factor gene family	*OsWRKY28*	*LOC_Os06g44010*	Belongs to the WRKY transcription factor IIa subfamily, directly activating OsDREB1B expression by binding to its promoter, positively regulating rice salt tolerance; induced by drought, low temperature, salt, and ABA treatment, overexpression lines show enhanced salt tolerance, while mutants are salt-sensitive	[68]
WRKY transcription factor gene family	*OsWRKY50*	*LOC_Os11g02540.1*	Acts as a transcriptional repressor, binding to the OsNCED5 promoter and inhibiting its transcription. Mediates ABA-dependent seed germination and seedling growth, as well as ABA-independent salt tolerance; overexpression lines show enhanced salt tolerance and reduced sensitivity to ABA-regulated seed germination and seedling establishment	[69]
WRKY transcription factor gene family	*OsWRKY54*	*LOC_Os05g40080*	Positively regulates rice salt tolerance; after salt treatment, loss of function leads to increased Na^+ accumulation in shoots, decreased K^+ content, altered Na^+/K^+ balance, and increased sensitivity to salt stress; regulates the expression of essential salt tolerance-related genes such as *OsNHX4* and *OsHKT1;5* by directly binding to the W-box motif in the *OsHKT1;5* promoter	[70]
bZIP transcription factor gene family	*OsbZIP72*	*LOC_Os09g28310*	Binds to the ABA-responsive element in the promoter region of the high-affinity potassium transporter gene *OsHKT1;1* and activates its expression, participating in the ABA signaling pathway-mediated salt and drought tolerance pathways	[71]
bZIP transcription factor gene family	*OsbZIP20*	*LOC_Os02g16680*	Binds to the ABA responsive element (ABRE) element in the OsNHX1 promoter and induces its transcription, thereby enhancing rice drought and salt stress resistance	[72]

(待续)

(续表1)

Gene family	Gene name	Gene ID	Function	References
MYB transcription factor gene family	*OsMYB106*	*LOC_Os08g33660*	*OsMYB106* forms a transcriptional complex with OsBAG4 and OsSUVH7 to regulate the expression of the major salt tolerance gene *OsHKT1;5*, activating *OsHKT1;5* expression by recognizing specific *cis*-elements	[73]
MYB transcription factor gene family	*OsFLP*	*LOC_Os07g43420*	Involved in rice salt stress response; mutants are more sensitive to salt stress, while overexpression lines show enhanced salt tolerance; directly binds to the *OsCDKB1;1* promoter and activates its expression; under salt stress, *OsCDKB1;1* expression is suppressed in *osflp* mutants	[74]
MYB transcription factor gene family	*OsMYBc*	*LOC_Os09g12770*	Binds to specific sequences in the *OsHKT1;1* promoter, upregulating *OsHKT1;1* expression and positively regulating rice salt tolerance; under salt stress, *OsHKT1;1* expression is upregulated in overexpression lines, improving salt tolerance, while *OsHKT1;1* expression is downregulated in osmybc mutants, reducing salt tolerance. OsMYBc can interact with the E3 ligase OsMSRFP , leading to its degradation and subsequent suppression of *OsHKT1;1* expression	[75]
Other salt-alkali tolerance genes	*OsAPX1*	*LOC_Os03g17690*	Reduces salt tolerance in rice seedlings by specifically inducing the expression of respiratory burst oxidase homologs (OsRBOHs), leading to increased reactive oxygen species (ROS) production	[76]
Other salt-alkali tolerance genes	*OsDMI3*	*LOC_Os05g41090*	Influenced by $NaHCO_3$, increases expression and activity in rice roots, reducing Na^+ and H^+ uptake and promoting root elongation under saline-alkali stress; upregulates the transcription of related genes	[77]
Other salt-alkali tolerance genes	*OsPPa6*	*LOC_Os02g52940*	Essential for enhancing rice alkali tolerance; mutants are affected in various aspects such as substance accumulation, growth, development, and photosynthesis, with decreased chlorophyll content under alkali stress	[78]
Other salt-alkali tolerance genes	*OsSAP6*	*LOC_Os03g57890*	Positively regulates rice saline-alkali stress tolerance; overexpression lines show superior germination rate, growth, and stress-related indicators compared to controls	[79]
Other salt-alkali tolerance genes	*SDG721*	*LOC_Os01g11952*	Directly binds to the sodium ion transporter gene OsHKT1;5, activating its expression and regulating saline-alkali stress response; affects plant saline-alkali tolerance, ROS, yield, and plant architecture	[80]
Other salt-alkali tolerance genes	*OsDSR3*	*LOC_Os01g74370*	Positively regulates rice alkali stress tolerance; overexpression lines show enhanced alkali tolerance, while knockout lines are more sensitive	[81]
Other salt-alkali tolerance genes	*OsSAPK9*	*LOC_Os12g39630*	Positively regulates rice salt tolerance and resistance to bacterial blight	[82]
Other salt-alkali tolerance genes	*OsARF18*	*LOC_Os06g47150*	Possesses transcriptional repression activity, directly binds to the promoter of the asparagine synthetase gene OsAS1 and inhibits its expression; loss of function leads to upregulated OsAS1 expression, increased nitrogen use efficiency, reduced Na^+/K^+ ratio, decreased NH_4^+ accumulation, and improved plant salt tolerance and yield; acts as a negative regulator of rice salt tolerance	[83]

(待续)

(续表1)

Gene family	Gene name	Gene ID	Function	References
Other salt-alkali tolerance genes	*OsRLCK311*	*LOC_Os11g06780*	*OsRLCK311* interacts with *OsPIP2;1*, regulating stomatal responses to stress and playing a role in plant growth responses under salt stress; overexpression in transgenic rice and *Arabidopsis* enhances salt tolerance and significantly inhibits ABA-mediated stomatal closure	[84]
Other salt-alkali tolerance genes	*OsDi19-5*	*LOC_Os01g73960*	Acts as a transcriptional repressor, interacting with OsClo5 to negatively affect the transcription of target genes *OsUSP* and *OsMST* in rice seedlings under salt stress, negatively regulating rice seedling salt tolerance	[85]
Other salt-alkali tolerance genes	*OsClo5*	*LOC_Os04g43200*	Acts as a transcriptional co-repressor, interacting with OsDi19-5 to negatively regulate rice seedling salt tolerance; enhances hypersensitivity to ABA during rice germination, binds calcium and phospholipids *in vitro*, and shows reduced and increased salt stress tolerance in overexpression and mutant lines, respectively, during germination and early seedling stages	[86]
Other salt-alkali tolerance genes	*OsMLP423*	*LOC_Os04g39150*	Overexpression in transgenic rice increases sensitivity to ABA and enhances tolerance to drought and salt stress	[86]
Other salt-alkali tolerance genes	*OsPIL14*	*LOC_Os07g05010*	Salt treatment promotes its protein degradation, enhancing SLR1 protein stability; together with the SLR1 transcription module, it integrates light and gibberellin signals to finely regulate rice seedling growth under salt stress; overexpression promotes mesocotyl elongation in the dark and improves seedling emergence rate under salt stress in direct-seeded rice	[87]
Other salt-alkali tolerance genes	*OsGTγ-2*	*LOC_Os11g06410*	Positively regulates rice adaptation to salt stress by regulating ion transporter expression; overexpression lines show improved seed germination rate, seedling growth, and survival under salt stress, while knockout lines exhibit salt stress hypersensitivity; directly binds to the promoters of the salt-induced transcription factor OsRAV2 and three ion transporter genes (*OsHKT2;1*, *OsNHX1*, and *OsHKT1;3*), regulating their expression and maintaining Na^+/K^+ homeostasis under salt stress	[88]
Other salt-alkali tolerance genes	*ONAC045*	*LOC_Os11g03370*	Plays an important role in rice ABA signaling and salt tolerance; loss of function reduces sensitivity to ABA, while overexpression increases it; knockout leads to increased ROS accumulation in roots and increased sensitivity to salt stress	[89]

ABA 的应答反应具有正向调节作用，全基因组表达分析表明其可能也作用于其他激素和逆境应答。*OsTZF1* 过表达植株提高了对高盐胁迫和干旱胁迫的抗性，而 RNA 干扰植株则盐胁迫抗性降低[63]。

丝裂原活化蛋白激酶在信号转导途径中起重要作用，参与植物对环境胁迫的响应和适应。*OsMKK6* 基因在水稻盐胁迫响应方面展现出独特功能，过表达 *OsMKK6* 的水稻在高盐溶液中生长时，幼苗根及地上部的长度和重量相较野生型植株增加，叶绿素降解较少，对盐胁迫的抗性增强[64]。对于 *OsMKK1* 基因来说，其敲除突变体对盐胁迫更敏感，酵母双杂实验表明 OsMKK1 与 OsMPK4 有较强的相互作用，二者组成信号通路共同调控水稻盐胁迫抗性[65]。丝裂原活化蛋白激酶参与多种细胞过程，在植物对盐碱胁迫的响应中具有重要作用。盐胁迫下，OsMPK4 被激活并磷酸化 IPA1 (水稻耐盐性负调

节因子)的 Thr180 位点，促进 IPA1 的泛素化降解，降低 IPA1 蛋白水平，最终提高水稻耐盐性[66]。盐碱条件下，*OsMAPK6* 参与维持 Na^+/K^+ 稳态，增强盐碱耐受性，其中，*OsMAPK6* 过表达株系的耐盐碱性显著提升，而其敲除株系的耐盐碱性则明显下降；高盐碱条件下，OsBBX17 可以与 OsMPK6 等发生互作进而调节水稻盐碱耐受性；*OsBBX17* 敲除突变体耐盐碱性好，过表达株则相反[67]。

WRKY 转录因子在植物对生物和非生物胁迫的响应中起着重要的调控作用，通过与特定 DNA 序列结合调节下游基因表达以应对植物在生长发育过程中受到的生物或非生物胁迫。*OsWRKY28* 属于 WRKY 转录因子 IIa 亚家族，通过结合启动子直接激活 *OsDREB1B* 表达，正调控水稻耐盐性，其过表达系耐盐性增强，突变体对盐敏感[68]。OsWRKY50 作为转录抑制因子，能与 ABA 合成酶基因 *OsNCED5* 启动子结合，抑制其转录；*OsWRKY50* 介导依赖 ABA 的种子萌发和幼苗生长，过表达株通过影响 ABA 水平增强植株耐盐性[69]。*OsWRKY54* 正调控水稻的耐盐性，调节了一些耐盐相关必需基因表达，如 *OsNHX4* 和 *OsHKT1;5*，通过直接结合 *OsHKT1;5* 启动子中的 W-box 基序调控其表达。盐处理后，*OsWRKY54* 功能丧失则会导致 Na^+在地上部积累，K^+含量降低，Na^+/K^+平衡改变，对盐胁迫更敏感[70]。

bZIP 转录因子参与植物多种生理过程，其中 OsbZIP72 能与高亲和力钾转运蛋白基因 *OsHKT1;1* 启动子区的 ABA 应答元件结合并激活其表达，进而参与脱落酸信号通路介导的耐盐耐旱途径[71]。OsbZIP20 蛋白能与 SAPK10 互作并被其磷酸化，它可与 *OsNHX1* 启动子的脱落酸响应元件 ABRE 结合并诱导其转录，从而增强水稻的干旱和盐胁迫抗性[72]。

MYB 转录因子通过调控下游基因表达参与植物对盐碱胁迫的适应。OsMYB106 与 OsBAG4、OsSUVH7 共同组成转录复合物调控耐盐主效基因 *OsHKT1;5* 的表达，通过识别特定顺式元件激活 *OsHKT1;5* 表达来提高幼苗耐盐碱性[73]。*OsFLP* 能调控水稻气孔发育过程中保卫母细胞(guard mother cell, GMC)对称分裂的方向来影响气孔调节；*OsFLP* 参与水稻盐胁迫应答，突变体对盐胁迫更敏感，积累了更多的活性氧和 Na^+，存活率下降。而过表达系植株的耐盐性增强[74]。*OsMYBc* 能够与 *OsHKT1;1* 启动子的特定序列结合，上调 *OsHKT1;1* 表达，进而正调控水稻耐盐性[75]。

除了上述主要的耐盐碱基因家族外，水稻中还有许多其他基因参与了对盐碱胁迫的响应和耐受过程。这些基因互相协作构成调控网络，共同帮助水稻应对盐碱胁迫。深入理解这些基因的功能和作用机制，将为培育耐盐碱水稻品种提供有力的理论支撑和潜在资源，更好地保障全球粮食安全。

4 水稻耐盐碱性的遗传改良

4.1 传统育种方法在耐盐碱育种中的应用

传统育种方法在作物改良中历史悠久，凭借长期实践积累的技术体系，在耐盐碱水稻品种培育中仍占据基础且关键的地位，传统育种方法主要包括系统选育、杂交育种和诱变育种等，其核心逻辑是通过表型筛选优株、遗传重组性状，定向培育适配盐碱环境的水稻品种。历经数十年实践，传统育种在耐盐碱水稻培育中成效显著。万宝兴等[90]通过构建“实验室梯度胁迫-田间动态监测-根系分泌物分析”的三阶筛选体系，筛选出‘闽宁 1 号’和‘宁粳 57’这 2 个耐盐碱品种，在 0.5% 盐度下亩产分别达到 487 kg 和 503 kg，较传统品种增产 51.7%–62.3%。江苏沿海地区农业科学院选育出耐盐粳稻新品种‘中科盐 4 号’，在国家耐盐碱联合体-黄淮粳稻组生

产试验中，‘中科盐 4 号’平均亩产 499.9 kg，比对照品种‘盐稻 12 号’增产 9.4%[91]。丁国华等[92]以黑龙江省耐盐碱较强的水稻品种‘龙稻 5 号’为母本、‘丰矮占 1 号’为父本杂交，通过系谱法选育出水稻新品种‘龙稻 124’，其农艺性状优良，具有耐盐碱、优质、稳产等特性，在 pH 值 8.5 的盐碱地种植每亩产量比‘龙稻 5 号’高 21.6 kg，适宜在黑龙江省第一积温带种植。

传统育种基于表型选择，利用自然变异与人工杂交创造遗传多样性，通过多代田间筛选，定向积累优良性状，培育适应特定生态条件的稳定品种。其优势在于贴合田间实际需求，经长期筛选后在复杂盐碱环境中稳定性强，但存在选育周期长、遗传改良精准性不足的短板[93]，需结合基因编辑、分子标记辅助育种等分子育种技术突破效率瓶颈，加速培育高产、优质、广适的耐盐碱水稻新品种。

4.2 分子标记辅助育种在耐盐碱育种中的应用

分子标记辅助育种(molecular marker-assisted selection, MAS)是利用与目标基因紧密连锁的分子标记，对目标性状进行间接选择的一种育种方法，具有快速、准确、不受环境条件干扰的优点[94]。运用 MAS 技术可以在较短的时间内获得具有目标性状的植株，缩短育种周期。在水稻耐盐碱基因筛选或数量性状位点(quantitative trait locus, QTL)定位中，通过对具有不同耐盐碱性的水稻材料进行分子标记分析，找到与耐盐碱性状相关的分子标记，进而确定耐盐碱基因或 QTL 的位置[95]。

水稻的耐盐碱性是由多基因控制的数量性状，其遗传机制较为复杂，在不同生长发育时期的耐盐碱能力差异明显。目前，国内外对水稻碱胁迫的研究尚不充分，对于耐盐碱基因的鉴定，目前中国科研人员已定位到上千个耐盐碱相关的数量性状位点，但大多数 QTLs 表型贡献率较小，精细定位和克隆难度较大，截至目前，只有 *AT1/GS3*、*SKC-1*、*RR22*、*DST*、*STRK1*、*STRK2*、*LRRK1*、*HST1* 等少数耐盐碱基因被克隆并解析[96]。因此，挖掘出能够提升水稻耐盐碱性的关键基因对于耐盐碱水稻的研究领域显得尤为关键。QTL 定位是基因克隆的基础，通过分析遗传群体中分子标记与数量性状之间的连锁关系，来确定控制此性状的基因在染色体上的位置。Yuan 等[97]利用籼稻‘9311’和非洲长雄蕊野生稻构建的回交自交系群体，定位了 27 个与苗期耐盐相关的 QTL；通过 QTL 定位和环境互作分析，共检测到 110 个加性效应 QTL，其中 *qPW11*、*qWN3-2* 和 *qPN1-1* 是控制盐碱胁迫下产量相关性状的重要 QTL 位点。Geng 等[98]利用超高密度遗传图谱的重组自交系(recombinant inbred lines, RIL)群体解析水稻耐盐遗传基础，定位到 20 个 QTL，其中包括 1 个主效稳定 QTL (qRCL3-1)；随后，整合比较转录组分析获得的盐胁迫特异性差异表达基因，筛选出位于该稳定 QTL 区间内的 8 个候选基因；最终，通过序列比对和变异分析，确证 *OsCam1-1* 是调控水稻耐盐性的关键候选基因。本课题组在水稻芽期耐盐 QTL 定位研究中也取得了一些成果，以‘华占’(‘HZ’)和‘热研 2 号’(‘Nekken2’)为亲本，通过不间断多代自交构建了包含 120 个株系的重组自交系群体，在芽期共检测到 16 个耐盐相关 QTL；基于 qRT-PCR 技术，对候选基因在不同 NaCl 浓度下的表达水平进行了分析，筛选出多个与水稻耐盐性相关的候选基因；进一步研究发现，*LOC_Os12g25200* 可能负调控水稻的耐盐性[99]。

全基因组关联分析(genome-wide association studies, GWAS)是一项强有力的鉴定性状相关位点和等位基因变异中有价值的自然变异的方法。相较于传统的 QTL 连锁分析，GWAS 标记密度高、定位精度高、适用性状复杂，能够快速锁定关键候选基因。Yu 等[100]通过对水稻各地方品种进行全基因组关联分析，确定了 10 个与耐盐性状相关的候选基因，并进一步鉴定到了 2 个耐盐相关的基因，分别是编码转录因子的

OsWRKY53 和编码丝裂原活化蛋白激酶激酶的 *OsMKK10.2*，揭示了水稻通过 *OsWRKY53-OsMKK10.2* 和 *OsWRKY53-OsHKT1;5* 模块协调防御离子胁迫的分子机制。研究人员利用 GAWS 技术鉴定出多个耐盐基因，如 *OsNHX1*、*OsSOS1* 等，它们在调节细胞内盐离子浓度和维护细胞稳定方面发挥重要作用[101]。Zhang 等[102]通过对水稻进行 GWAS 分析，鉴定出多个与耐盐碱性显著相关的单核苷酸多态性(single nucleotide polymorphism, SNP)位点；进一步功能验证确定了候选基因 *LOC_Os01g45550* 和 *LOC_Os05g24770*，它们与水稻萌发期的耐盐碱性有关，参与水稻对盐碱胁迫的响应。陆鲸冰等[103]基于 306 份水稻种质资源，以碱害级别、存活天数以及生长指数为指标，进行全基因组关联分析，共检测到 44 个与苗期耐碱性显著关联的位点，最终筛选出 2 个苗期耐碱性重要候选基因，分别命名为 *qAT2* 和 *qAT4*。Mei 等[104]在碱胁迫和对照条件下分析了 428 份不同水稻材料，鉴定出 90 个与水稻耐碱性相关的位点，进一步筛选得出 8 个耐碱性相关基因 *LOC_Os03g08960*、*LOC_Os01g12000*、*LOC_Os03g60240*、*LOC_Os04g41410*、*LOC_Os09g25060*、*LOC_Os11g35350*、*LOC_Os12g13300*、*LOC_Os12g09350*。Li 等[105]研究了粳稻在萌芽阶段的耐碱性，结合连锁图谱分析与全基因组关联分析开展位点定位及候选基因筛选，确定了 *LOC_Os11g37300*、*LOC_Os11g37320* 和 *LOC_Os11g37390* 为影响粳稻耐碱性的候选基因，这些基因有望成为耐盐碱育种的重要候选基因，为分子育种提供新的靶点，帮助提升水稻在盐碱性环境中的适应性。

分子标记辅助育种在水稻耐盐碱基因筛选中发挥了重要作用，但仍存在一些问题。通过优化遗传群体构建、改进表型鉴定方法、增加分子标记数量和类型、优化 QTL 定位方法[106]以及将分子标记辅助育种与基因编辑、杂交育种等技术相结合等步骤[107]，可以进一步提高传统分子标记辅助育种在水稻耐盐基因和 QTL 定位中的应用效果，为培育耐盐碱水稻新品种提供更有力的技术支持。

4.3 基因编辑技术在耐盐碱育种中的应用

CRISPR/Cas 基因编辑系统凭借其独特的成簇规律间隔短回文重复序列和 CRISPR 关联蛋白(CRISPR-associated protein, Cas)成为了一种精准的基因编辑工具，能够在对应 DNA 序列位置上精确地进行切割和修改，具有高效、精确和低脱靶率的特点。CRISPR/Cas 技术现已广泛应用于多个领域，包括基因功能研究、基因治疗以及农业育种等。与传统育种方法相比，CRISPR/Cas 基因编辑技术可以显著缩短育种周期，通过直接对目标基因进行编辑，研究人员可以快速获得具有特定性状的水稻品种。Gao 等[108]的研究发现，过表达 *osa-MIR396c* 的转基因水稻的耐盐碱胁迫能力明显低于野生型水稻。若将该基因敲除可能提高水稻的耐盐碱能力，为改良水稻耐盐碱性提供了潜在的分子靶点。拟南芥基因 *EDT1/HDG11* 可以提高拟南芥耐旱性和耐盐性，Yu 等[109]发现，在水稻中使用 CRISPR/Cas 技术将该基因敲除会使幼苗 MDA 含量上升，影响幼苗生长，证明该基因的表达有助于提高水稻耐盐性。总之，CRISPR/Cas 基因编辑系统为水稻育种提供了强大的工具，有助于推动水稻遗传改良的进程，从而对保障全球粮食安全和可持续发展产生深远影响。

5 总结与展望

近年来，对于水稻耐盐碱性的研究在生理学、分子机制及遗传育种等方面均取得了较为系统的进展，为盐碱地水稻生产和粮食安全提供了重要支撑。首先，通过对盐碱胁迫下水稻的渗透胁迫、活性氧积累及光合作用减弱等生理影响的深入分析，已经找到了多个关键胁迫响应途径和信号节点，为后续的功能基因挖掘及抗逆机制解析奠定了基础。其次，在耐盐碱

的分子机制层面，无论是离子转运蛋白(如 SOS、NHX、HKT、AKT 等)的调控，还是渗透保护物质及抗氧化系统的协同作用，都已逐渐形成从基因到表型的多层级研究框架。近年来尤为受关注的是，氮素调控与激素的协同作用不仅是缓解盐碱胁迫的关键通路，更因其明确的调控关系，为耐盐碱性改良提供了可直接利用的新分子靶点。基于这些机理与通路的研究，多个耐盐碱基因大家族(如钠离子转运蛋白、谷氨酰胺合成酶、锌指蛋白、WRKY 转录因子以及丝裂原活化蛋白激酶等)被陆续鉴定与功能验证，初步阐明了其在盐碱环境适应中的作用。最后，在育种技术上，从传统育种、分子标记辅助育种到基因编辑技术的综合运用，为培育高效稳定的耐盐碱水稻品种提供了多条可行路径。

然而，目前水稻耐盐碱研究仍然面临如下瓶颈：(1) 已有研究多集中于单一基因或单一通路，尚缺乏系统深入的多组学分析，而水稻耐盐碱性是一个多基因控制的性状，涉及的基因和调控网络复杂，并且耐盐性和耐碱性涉及的机制和基因也有所不同[110]；(2) 绝大多数耐盐碱性实验仍停留在温室或有限田间环境下，小尺度试验条件和多变的实际盐碱地条件之间尚存在较大差异，并且很多耐盐碱水稻材料在极端盐碱环境下虽能保持生长，但产量和品质尚不稳定，因此实验结果很难快速应用于育种；(3) 不同地区的盐碱土壤类型和盐度水平不同，育种实践中各项技术手段在不同地区环境与种质资源间的适用性与整合度仍需提高。这些瓶颈的存在导致部分研究成果难以在大面积生产中发挥实质性效用，也限制了对盐碱胁迫综合机理与新型抗逆设计策略的进一步挖掘。

为此，未来研究可以重点在以下方向继续深化并加以整合：第一，基于多组学和大数据分析(基因组、转录组、蛋白质组、代谢组、表观遗传组等)系统阐明不同耐盐碱基因及信号网络的互作关系，从而实现水稻耐盐碱分子机制的整合。第二，进一步聚焦“基因-环境-管理”三者的协同优化，在保证基因育种精准化的同时，通过不同氮肥类型、施肥方式、灌溉模式以及植物调节剂(如激素、渗透保护剂等)的联合管理，大幅度提高水稻对盐碱逆境的综合适应能力。第三，加强基因编辑与传统育种、分子标记辅助育种的协同，一方面利用 QTL 定位与 GWAS 深入挖掘耐盐碱核心位点，另一方面在 CRISPR/Cas9 等定向编辑技术的辅助下实现快速定向改造，通过功能验证与群体改良相结合，培育适应不同地域盐碱环境的水稻品种。第四，积极探索与其他抗逆性状(如耐旱、耐冷等)的联合育种策略，以期在综合抗逆提高和产量保障方面取得新的突破。

总之，水稻耐盐碱研究正从传统的单基因、单通路解析迈向更综合、系统的研究阶段，“分子机制+多组学整合+环境管理+精准育种”这一多维协同模式，将成为未来水稻耐盐碱研究和应用的发展方向。相信随着多元化研究方法与育种手段的不断完善，在未来能实现水稻在盐碱地中的广泛种植，这将有效提升盐碱地区耕地生产力，为保障粮食安全贡献关键力量。

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