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茄科植物对盐胁迫耐受性的研究进展

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摘　要

作为制约植物生长的主要非生物胁迫，盐胁迫主要通过离子毒性、渗透胁迫和次生胁迫严重威胁植物的营养吸收、光合作用及糖代谢等过程。在长期进化中，植物形成了生理、基因、代谢物等多层次的响应机制，包括维持离子稳态、合成渗透调节物质、介导植物激素信号转导以及清除活性氧等。本文综述盐胁迫对植物的危害、植物对盐胁迫的适应性调控，并着重分析茄科作物的耐盐机理及相关基因研究进展，以期为盐碱地改良和耐盐育种提供参考。

关键词

茄科，盐胁迫，抗性基因，耐盐机理

Research Progress on the Tolerance of Solanaceae Plants to Salt Stress

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Abstract

As the main abiotic stress restricting plant growth, salt stress seriously threatens the processes such as nutrient powder absorption, photosynthesis and sugar metabolism of plants mainly through ionic toxicity, osmotic stress and secondary stress. During long-term evolution, plants have developed multi-level response mechanisms such as physiology, genes, and metabolites, including maintaining ionic homeostasis, synthesizing osmotic regulatory substances, mediating plant hormone signal transduction, and eliminating reactive oxygen species, etc. This article reviews the harm of salt

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stress to plants, the adaptive regulation of plants to salt stress, and focuses on analyzing the salt tolerance mechanism of solanaceous crops and the research progress of related genes, with the aim of providing references for the improvement of saline-alkali land and salt-tolerant breeding.

Keywords

Solanaceae, Salt Stress, Resistance Gene, Salt Tolerance Mechanism

1. 引言

土壤盐渍化是对植物生长和产量影响最大的非生物胁迫，通常由过多可溶性盐累积引起，目前已经影响到三分之一以上的灌溉地区，并预计到 2050 年，全球一半以上的可耕地将面临盐渍化的危机[1]。据统计，盐碱化每年造成农业经济损失达 2730 万美元[2]。当前全球耕地面积持续缩减，开发利用盐渍土壤进行作物栽培已成为农业发展的重要方向。近年来，基因编辑技术为培育耐盐作物品种提供了有效途径。茄科植物涵盖番茄、马铃薯等 15 个世界性食物生产属，兼具营养价值和药用价值[3]。但该科作物在生殖生长期对盐胁迫敏感。开展耐盐基因挖掘及优良品种选育研究，将为盐渍土壤的高效利用提供关键技术支撑。

2. 盐胁迫对植物的影响

高盐度主要引发离子毒性、渗透胁迫和次级胁迫三种机制干扰植物的生理活动，阻碍其生长发育，进而制约农业可持续发展[4]。离子毒性打破胞内离子稳态平衡，引发细胞毒性效应，并直接损害细胞结构与生理功能。渗透胁迫则通过降低根际水势阻碍水分吸收，引发植株脱水，这些压力影响植物的所有主要过程，包括植物营养、光合作用和糖代谢。

2.1. 盐胁迫对植物营养的危害

高浓度的 Na^+和 Cl^-等可溶性盐离子引发的土壤渗透势升高和离子毒性的产生对必需营养素的获取和平衡产生负面影响，导致植物营养亏缺[5]。Na^+和 K^+之间的理化相似性会导致高浓度 Na^+竞争 K^+吸收位点[6]。K^+作为多种关键酶的辅因子，其缺失会影响光合磷酸化和蛋白质合成等基础代谢过程。植物根系的吸收主要依赖 $H_2PO_4^-/nH^+$共运子介导的跨膜运输[7]。盐胁迫下 Na^+与 $H_2PO_4^-$ 的竞争效应会降低 PO_4^{3-} 活性，引发的磷饥饿可显著改变植物能量代谢动态[8]。Cl^-的积累则干扰 NO_3^- 吸收，降低氮素利用效率[9]。值得注意的是，这些离子失衡最终造成多维度的营养系统紊乱，严重影响植物生长发育。

2.2. 盐胁迫对植物光合作用的危害

作为植物生命活动的能量来源，光合作用通过光能转化和碳同化将无机物转化为有机物，以此为后续的糖代谢提供初始碳源。但在盐渍环境下，植株通过关闭气孔限制 CO_2 供应，降低碳同化速率，光合产物输出缓慢。同时 Na^+的过量积累会竞争性抑制光合酶活性，降低叶绿素含量及光系统 II (PSII)效率[10]。ROS 爆发也会导致光系统核心复合物降解，转录组分析发现，盐处理后的白菜中参与光合作用和碳代谢相关基因显著下调，其光合效率受损[11]。

2.3. 盐胁迫对植物糖代谢的危害

糖代谢是维持植物能量稳态和代谢平衡的核心过程。海藻糖代谢和蔗糖代谢是糖代谢的重要分支，尤其是蔗糖代谢占据主导地位，其含量通常为海藻糖的 100~1000 倍[12]。盐胁迫持续抑制番茄叶片组织的蔗糖跨膜转运，导致依赖 pH 的糖摄取过程受阻[13]。蔗糖代谢平衡遭受破坏后会降低月季和大豆组织中的淀粉含量[14] [15]。尽管海藻糖在植物中的含量较低，但最近其因参与糖代谢调控而备受关注。例如盐胁迫通过降低玉米叶片 6-磷酸海藻糖水平抑制海藻糖代谢，导致光合效率下降、生殖发育受阻和籽粒败育[16]。该过程主要由能量代谢紊乱而非碳水化合物缺乏引起。

3. 植物对盐胁迫的适应性调控

3.1. 植物对盐胁迫的传感机制

为应对盐分过多对植物造成的损害，植物进化出了盐胁迫感知机制。迄今为止，植物感知 Na^+的具体途径尚不明确，Na^+传感器或受体的存在仍有待证实。然而有研究发现，NaCl 或甘露醇刺激可在几秒钟内迅速提高细胞质 Ca^{2+}水平，这一现象可能与渗透胁迫受体和 Ca^{2+}通道的偶联有关[17]。基于此，研究者鉴定到了渗透感受器(OSCA1)。该 Ca^{2+}通道介导渗透胁迫下的 Ca^{2+}信号转导，其突变会导致气孔关闭障碍和根系生长受限[18]。通过类似策略鉴定的葡萄糖醛酸基转移酶(MOCA1)基因参与糖基肌醇磷酸神经酰胺(GIPC)合成。GIPC 可直接结合 Na^+，通过阻止膜电位去极化来触发 Ca^{2+}内流[19]。越来越多的研究表明，膜联蛋白(ANNEXINs)、质体 K^+交换反向转运蛋白(KEAs)、机械敏感性离子通道 MscS-Like (MSL)和 mid1 补体活性蛋白(MCA)共同调控盐诱导的 Ca^{2+}信号和膨压变化，形成复杂的胁迫感知网络[20]-[23]。质外体中离子的过度积累会影响细胞壁成分的稳定，因此植物感知盐诱导的细胞结构变化也是识别盐胁迫的策略之一。盐胁迫下，富含亮氨酸的重复延伸素、快速碱化因子和受体样激酶模块(LRXs-RALFs-FER)负责监测细胞壁完整性[24]。此外，细胞壁相关激酶(WAKs)能识别果胶降解产物寡聚半乳糖醛酸(OGs)与 Ca^{2+}的结合，从而启动盐胁迫响应基因的表达[25] [26]。这些多样化的感知机制协同作用，共同增强植物对盐胁迫的适应性。

3.2. 植物对盐胁迫的调控机制

3.2.1. 渗透调节物质合成

渗透调节是植物为避免渗透胁迫造成的细胞缺水而进化出的主要适应性策略，植物可通过参与渗透调节的一些可溶性物质来降低细胞内的渗透压和维持细胞形态。这些渗透调节物质可分为无机离子和小分子有机物两类。无机离子一般从外界环境中摄入，如 Na^+、Cl^-、K^+和无机酸盐等，通过维持细胞内离子平衡避免毒害。小分子有机物主要包含脯氨酸(Pro)、甜菜碱、可溶性糖和多元醇等，通过降低细胞溶质渗透势来维持水分吸收。Pro 作为关键的渗透调节物质，其含量的升高促使盐分在液泡中区隔化储存，有效维持液泡与细胞质间的渗透压差。值得注意的是，耐盐番茄基因型通常表现出更高的 Pro 积累水平[27]。此外，外源施加 20 mM 甘氨酸甜菜碱可显著增强乌拉尔甘草的渗透调节能力及排盐效率，有效缓解盐害造成的影响[28]。另有实验证实，经 10 mM 可溶性糖或多元醇预处理的小麦籽粒，其抗氧化酶活性和苯类物质合成均得到显著增强[29]。

3.2.2. 活性氧清除

抗氧化防御系统中酶促反应和非酶促反应反映了植物克服氧化应激所需的一般策略，可清除一定程度的不同 ROS。酶促反应中的超氧化物歧化酶(SOD)是氧化应激防御系统的第一道防线，特异性催化 O_2^- 转化为 H_2O_2 [30]；随后产生的 H_2O_2 由过氧化物酶(POD)、过氧化氢酶(CAT)和抗坏血酸过氧化物酶(APX)

等进一步分解[31]。当酶系统不足以清除 ROS 时，抗坏血酸(AsA)、谷胱甘肽(GSH)、类胡萝卜素和类黄酮等非酶类抗氧化剂受到植物依赖。耐盐植物品系 BvM14 和 Giza9 中 AsA 和 GSH 的含量受到调控以此降低植物的氧化损伤，从而增强植物对盐胁迫的耐受性[32] [33]。这两个重要代谢产物与 APX、单脱氢抗坏血酸还原酶(MDHAR)、脱氢抗坏血酸还原酶(DHAR)和谷胱甘肽还原酶(GR)共同构成了 AsA-GSH 循环[34]，其活性和代谢水平的提升已被多项研究证实可有效缓解 ROS 毒害作用[35] [36]。

3.2.3. 植物激素调节

植物在承受不断变化的环境压力中已形成了应激反应类激素介导的抗逆机制，这些激素现已得到很好的表征，主要包括脱落酸(ABA)、茉莉酸(JA)、水杨酸(SA)和乙烯(ET)。ABA 作为参与盐胁迫响应的重要二级信号分子，被迅速积累后会增加可溶性蛋白和糖分来维持渗透稳态。乙烯则通过增强 SOS1 的表达和活性，促进 Na^+的外排和 K^+的吸收[37]。类似的，SA 在调控离子平衡和抗氧化防御发挥重要作用[38]。值得注意的是，野生番茄中 K^+和 Na^+的渗透调节能力显著高于栽培种，这可能与其 SA、ET 和细胞分裂素的差异调控有关[39]。深入研究表明，番茄耐盐机制涉及 SA 与多胺通过调控 ET 代谢途径，协同线粒体交替氧化酶(AOX)和盐过度敏感(SOS)途径形成的复杂调控网络[40]。JA 作为重要的胁迫响应激素，外源施加可上调抗氧化酶系统，显著改善小麦幼苗的耐盐性[41]。不仅如此，生长素、油菜素内酯(BR)等生长类激素也被证实在提升植物耐盐性上发挥功能。生长素不仅调控植物形态建成，其主要活性物质吲哚-3-乙酸(IAA)在长期胁迫下呈现稳定积累的趋势，尤其是在盐胁迫期间[42]。BR 主要通过构建渗透保护剂等相容的溶质、激活表面的 K^+离子转运蛋白和抗氧化剂等机制来调控耐盐性[43]。

4. 茄科植物耐盐基因研究进展

4.1. Na^+/K^+转运机制

植物通过 SOS 信号通路和液泡区隔化两大机制维持 Na^+稳态。SOS 信号通路依赖位于质膜上的 Na^+/H^+反转运体(SOS1)、丝氨酸/苏氨酸蛋白激酶(SOS2)和钙结合蛋白(SOS3)三种蛋白质的共同作用。盐胁迫触发的胞质 Ca^{2+}信号被 SOS3 感知，与 SOS2 结合后激活 SOS1 的 Na^+外排功能，这一机制已在拟南芥中得到证实[44]。番茄和马铃薯中的 SOS1 基因也被证明受到盐胁迫诱导且两者在耐盐功能上存在明显分化。具体而言，*StSOS1* 可能通过与钾转运蛋白互作以此参与胁迫响应，而 *SlSOS1* 则主要调控离子稳态及 Na^+的组织特异性分配[45] [46]。研究表明，番茄从野生种到栽培种的驯化过程导致遗传多样性的锐减和耐盐能力的大幅度降低，这与 SOS 信号通路关键基因的变异密切相关。Hong 等人发现，*SlSOS2* 基因启动子区上游存在一个与耐盐性相关的插入缺失标记变异，该变异与番茄根系 Na^+/K^+比及耐盐性显著相关。在栽培番茄中，该变异插入了一个额外的 ABI4 结合位点，使转录因子 ABI4 能更有效地抑制 *SlSOS2* 表达，导致其表达水平显著低于野生番茄[47]。此外，朱健康团队和李传友团队分别证实，*SlSOS1* 和 *SlSCaBP8* 启动子区的变异在驯化过程中同样下调了基因表达，这直接解释了栽培番茄耐盐性显著衰退的遗传基础[48] [49]。液泡区隔化则通过 NHX 家族转运体实现，以此降低细胞质中 Na^+的毒性浓度。迄今为止，NHX 家族基因已在番茄、马铃薯和辣椒等多种茄科作物中被成功鉴定，且所编码的转运蛋白活性差异直接影响品种耐盐性表现[50]-[52]。如 *LeNHX2/4* 既能外排根部 Na^+，又能调控木质部 Na^+装载和 K^+区隔化，从而赋予番茄耐盐性[53]。

高亲和性 K^+转运体(HKT)是植物体内重要的离子转运体，在系统发育上可分为 I 类(Na^+专一转运)和 II 类亚组(Na^+/K^+共转运)。通常，II 类亚组活性受外部离子组成(如 Mg^{2+}或 Ca^{2+})调控[54]。在茄科植物中，HKT 家族成员通过不同机制增强耐盐性。长叶茄 SgHKT1;1 通过调控木质部 Na^+卸载减少叶片 Na^+积累，而 SgHKT1;2 介导 Na^+循环转运，二者协同维持 Na^+稳态[55]。番茄 SlHKT1;1 维持根部低 Na^+/K^+比，

SlHKT1;2 则保护生殖器官免受 Na^+毒害，从而显著降低盐胁迫对产量的影响[56] [57]。此外，在驯化过程中，栽培番茄丧失了野生番茄特有的 SlHY5 转录因子结合位点(G/A-box)，该结合位点位于 K^+通道调节亚基 KSB1 启动子区，这一关键序列变异显著抑制了栽培品种在盐胁迫下 KSB1 的诱导表达，进而破坏根系 Na^+/K^+平衡，降低植株存活率，导致其耐盐表现明显逊于野生番茄[58]。

4.2. Cl^-转运机制

NaCl 是植物盐毒性的主要诱因。盐胁迫下，植物 Na^+积累常伴随 Cl^-增加[10] [59]。高浓度 Cl^-会抑制光合作用和生长，因此有效排除根部或茎部的 Cl^-对减轻其毒害至关重要[59]。多种转运蛋白参与 Cl^-调控，包括氯通道(CLC)、S 型阴离子通道(SLAC)和多药和有毒化合物挤出转运蛋白(DTX/MATE) [60]-[62]。CLC 充当重要的内膜 Cl^-交换器或通道，在茄科植物中发挥巨大作用[63]-[65]。譬如，烟草中的 *NtCLC2/13* 和番茄中的 *SlCLC05* 均为作物抵御盐分和调控氯稳态的新靶点[66]。SLAC 蛋白家族主要在植物阴离子摄取和气孔开闭过程中起到重要作用。SLAC1 家族编码的 S 型阴离子通道对苹果酸和 Cl^-具有高通透性。在烟草 BY-2 细胞中过表达 *AtSLAC1* 增强了 cryptogen 诱导的 Cl^-外排[62]。而沉默 *SLAC1-6* 导致番茄抗氧化酶异常增加，破坏渗透平衡[67]。其同源基因 *SLAH1* 则在盐胁迫下调控拟南芥 Cl^-积累和耐盐性，而在烟草中抑制根部 Cl^-向地上部转运[68] [69]。

DTX33/35 被证实是拟南芥中调控膨压的 Cl^-通道，其双突变体会损害质外体 Cl^-通道活性[70]。尽管 DTX/MATE 家族作为新发现的次级转运蛋白在茄科植物中的研究仍较有限，但番茄与拟南芥 *MATE* 基因的功能保守性提示其可能参与 Cl^-转运调控，然而具体作用机制尚待阐明[71]。值得注意的是，马铃薯 MATE 家族虽不参与 Cl^-转运，但其各亚科展现出明显的功能特异性，分别涉及重金属离子、SA 及类黄酮等多种物质的转运[72]。这些发现为通过优化阴离子转运蛋白选择性来提升 Cl^-外排效率提供了新思路，将有力推动耐盐作物育种的发展。

4.3. 植物激素信号传导途径

植物在盐胁迫下会通过多重信号交互以协调各种激素的合成、信号传递和代谢，从而建立起一个防御系统[73]。ABA 信号核心调节因子 SnRK2 已被证明可以直接磷酸化 ABA 反应元件结合蛋白(ABFs)，进而调控 ABA 响应基因表达[74]。辣椒中编码 SnRK2 II 亚类的 *CaDSK2-1* 特异性激活 ABA 响应基因，而 *CaDSK2-2* 虽对 ABA 不敏感但能引起 ABA 超敏反应[75]。不同茄科植物的 *SnRK2* 基因成员功能存在差异：番茄 *SlSnRK2* 通过抑制胁迫相关基因表达和降低抗氧化酶活性，负向调控植株的渗透胁迫适应能力，而 *NtSnRK2.2* 的过表达通过调节碳水化合物代谢和侧根发育来增强烟草的耐盐性[74] [76]。JA 信号通路中的 *COI1* 通过激活 ROS 清除系统提升耐盐性，如番茄 *SlCOI1* [77]。野生番茄与栽培番茄的转录组分析表明，*SABP2* 基因受野生材料的特异性诱导，这暗示了水杨酸信号通路的激活可能参与了其耐盐性调控，这也为解释栽培番茄耐盐性衰退提供了分子证据[78]。生长素可快速激活特定基因表达，其中 Aux/IAA 家族基因在耐盐调控中发挥重要作用。例如，*NtIAA26* 通过调节 K^+吸收和抗氧化活性正向调节烟草的耐盐性[79]。此外，BR 合成关键酶基因 *DWF4* 的过表达在马铃薯幼苗中可以减轻盐胁迫的负面影响[80]。

4.4. 响应盐胁迫的转录因子

转录因子通过将胁迫信号转化为基因表达的变化，将胁迫感应与许多耐受机制相联系。作为植物中最大的转录家族之一，NAC 家族的转录因子在盐胁迫下可协调关键生理生化过程[81]。*CaNAC46* 可激活 ROS 清除酶和促进辣椒根系发育[82]。*StNAC1* 过表达植株在盐胁迫下则表现出 ROS 积累减少和脯氨酸

含量增加的特性[83]。除 NAC 家族外，bZIP、WRKY、AP2/ERF 和 MYB 也是参与植物逆境响应的四类关键转录因子，它们通过调控离子平衡、渗透调节和抗氧化防御等途径减轻盐胁迫造成的损害[84] [85]。例如，番茄 *SlHDZ34* 的沉默致使植株在盐胁迫下光合速率下降和 ABA 生物合成基因表达降低[86]。AP2/ERF 和 WRKY 在茄科植物参与盐胁迫响应的研究中更加深入。*CaDREB32* 在烟草中的异源表达虽抑制生长但增强对盐和渗透胁迫的抵抗力[87]。番茄 ERF 蛋白通过 EAR 基序调控其转录活性，该基序缺失可增强胁迫响应基因表达和氧化胁迫抗性[88]。WRKY 家族成员通过激活 ERF 协同调控下游基因，维持氧化还原稳态，如 *SmWRKY11* [89]。此外，WRKY 转录因子还与植物激素信号转导途径存在密切关联。异源表达 *SmWRKY40* 能够显著调控 ABA 信号通路，而番茄 *SlWRKY42-SlMYC2* 模块则通过 JA 信号和亚精胺合成途径协同增强耐盐性[90] [91]。这些响应盐胁迫的转录因子基因均可作为未来培育耐盐番茄品种的候选基因，实现在盐度条件下生产高产优质茄科植物的目标。

5. 展望

盐碱地改良是现代农业面临的重大挑战。茄科作物作为中度盐敏感植物，其耐盐种质筛选与机制研究具有重要意义。尽管茄科植物种类丰富，但现有研究多集中于番茄、马铃薯等主要经济作物，且对野生耐盐资源的挖掘仍显不足。近年来，茄科植物耐盐机制研究在细胞内外离子转运以及植物激素信号传导等方面取得一定进展，但多局限于生理生化响应或单个耐盐基因的功能验证，而盐胁迫应答的整体调控网络仍不明确。新构建的茄科种间泛基因组为系统挖掘耐盐基因提供了革命性工具。可据此开展比较基因组学分析，强化野生近缘种耐盐资源筛选；同时可利用 CRISPR 编辑内源耐盐基因，结合合成生物学引入外源通路，协同提升耐盐性；此外，需整合基因组重测序、时空转录组、表观调控组和代谢组等多维组学数据，系统解析耐盐基因调控网络的层级响应机制。

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