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水稻盐胁迫耐受机制及氮肥营养调节效应

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摘 要:盐胁迫是限制水稻生长发育和产量形成的主要环境因素之一,植物耐盐性受多方面因素的调节,氮素作为植物生长必需的营养元素和信号分子,参与多种生理生化代谢过程,科学施用氮肥在缓解水稻盐胁迫过程中发挥着重要的作用。本文从盐胁迫对水稻生长和代谢的影响、生理与分子响应机制及氮素营养的调节机制等方面对水稻耐受盐胁迫的研究进行了综述,以期为优化盐渍地区水稻生产管理提供理论和技术支持,并为耐盐水稻分子育种提供资源。

关键词:水稻;氮肥营养;生理生化代谢;盐胁迫
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Mechanism of Rice Tolerance to Salt Stress and Regulatory Effect of Nitrogen Nutrition

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Abstract: Salt stress is one of the main environmental factors limiting the growth, development and yield formation of rice. Plant salt tolerance is regulated by multiple factors. As an essential nutrient element and signal molecule for plant growth, nitrogen is involved in various physiological and biochemical metabolic processes. Scientific application of nitrogen fertilizer plays a crucial role in alleviating salt stress-induced damage in rice. However, the main biological processes and mechanisms by which nitrogen regulates rice salt tolerance through scientific nitrogen fertilizer application remain unclear. In particular, there is a lack of molecular-level analysis on the regulation of reproductive growth (e.g., yield components). This review summarizes the research on rice tolerance to salt stress, mainly including the effects of salt stress on rice growth and metabolism, the physiological and molecular response mechanisms, and the regulatory mechanisms of nitrogen nutrition. This review provides theoretical and technical support for optimizing rice production management in saline-alkali areas, as well as target gene resources for molecular breeding of salt-tolerant rice.

Key words: Rice; Nitrogen nutrition; Physiology and biochemistry metabolism; Salt stress

盐胁迫是限制植物生长和农作物产量的主要逆境因子之一,可导致植物出现发芽率低、生长缓慢、株高降低、枝叶枯黄等症状[1-2]。盐胁迫主要通过抑制光合作用、破坏离子稳态和损伤膜系统阻碍植物生长[3]。盐胁迫大幅度增加植物叶片中Na^+和Cl^-含量、降低K^+含量引起气孔关闭,阻碍叶绿素吸收CO_2,降低细胞间CO_2浓度,从而降低光合速率[4];另外,盐胁迫对植物参与光合作用的重要组成结构造成影响,如Rubisco活性降低、叶绿素减少、叶绿体超微结构改变、叶绿体排序紊乱、类囊体腔扩大等,进而导致植物光合作用缺失[5]。离子代谢平衡是保持细胞膜稳定、促进植物生长发育的重要因素,盐胁迫加剧土壤中Na^+向植物中运输,导致植物对Cl^-的大量吸收、Ca^{2+}、

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K^+等离子的严重缺失，从而破坏细胞内离子稳态[6]。盐胁迫促进植物细胞积累大量的活性氧化物质，并破坏内质网、空泡膜等细胞器结构，从而产生氧化应激，抑制植物生长发育[7]。

水稻是盐敏感作物，盐胁迫会引发其结构(如细胞膜)损伤、代谢异常，轻则阻碍生长发育，重则导致死亡[8]。氮素是植物生长必需的营养元素，在作物耐盐机制中也发挥着重要的作用[9-10]。盐胁迫下，科学施氮可提高植物的水分传导能力、调节气孔开度、减少能量代谢、增强渗透调节、提高抗氧化能力、维持离子平衡等，从而缓解盐伤害[11-12]。水稻对盐胁迫的耐受性受供氮形态的调控，硝态氮较铵态氮更有利于提高水稻耐盐性[13-14]，相关的生理和分子机制有待进一步阐明，如硝态氮对水稻耐盐性调节的方式，尤其对水稻生殖生长阶段的耐盐调节机制尚缺乏清晰的认识。随着“海水稻”工程的推进，科学合理施用氮肥在耐盐碱水稻生产中必将发挥重要作用[15]。为此，本文从生理生化和分子水平综述水稻对盐胁迫的应答机制，分析不同形态氮素在调节水稻耐受盐胁迫中可能的作用方式及其主要生物学过程，旨在通过肥料管理措施提高水稻全生育期对盐胁迫的耐受性，为盐渍地区水稻生产提供科学依据。

1 盐胁迫对水稻生长和代谢的影响

盐胁迫严重影响水稻的生长发育和产量形成，提高耐盐性对满足日益增长的粮食需求具有重要意义[16]。盐胁迫条件下水稻营养生长受到抑制，表现为株高变矮、叶片变窄、分蘖能力降低、分蘖高峰期延迟等；生殖生长受到影响，表现为单株有效穗数减少、幼穗和颖花发育受阻、籽粒灌浆不饱满等，最终造成减产[17-18]。一般而言，盐胁迫引发的毒害包括直接的渗透胁迫、离子胁迫和间接的次级胁迫[19]。从生理层面来看，盐胁迫降低植株光合效率和矿物质营养含量，破坏无机离子平衡和渗透胁迫，减弱营养物质的摄取能力，如随着细胞中Na^+、Cl^-浓度的增加，Na^+/K^+、Cl^-/NO_3^-、Na^+/Ca^{2+}发生改变，引发离子毒害，干扰氮、磷、钾等营养元素的吸收；另外，盐胁迫通过产生次级活性氧(reactive oxygen species, ROS)损伤植株细胞膜，造成氧化胁迫伤害[20-23]。

水稻根系是摄取营养和吸收水分的器官，盐胁迫下会遭受不可逆的伤害[24]。盐胁迫主要对水稻根系形态、生理活动、氧化系统及根际微生物群落产生较大影响，具体表现为：(1)改变水稻根部木质素含量、减弱细胞壁弹性、抑制细胞伸长，进而阻碍根系生长发育、抑制根系形态构建，但一定浓度的盐胁迫可促进根系的横向发育[25-26]；(2)降低根系活力，阻碍根系对氮素的吸收和转化，降低氮肥利用率[27]；(3)抑制根系活性氧代谢，降低根际抗氧化酶活性，促进活性氧的积累，从而加速根系衰老[28]；(4)显著影响根系内源激素合成，如促进脱落酸和茉莉酸的生物合成、降低生长素含量等[29]；(5)显著改变根际微生物多样性和根际代谢产物的组成，通过添加耐盐微生物菌剂改善微生物环境，提高养分利用率和盐胁迫耐受能力[30]。

2 水稻对盐胁迫的生理与分子响应机制

水稻通过诱发渗透调节、抗氧化防卫反应、内源激素合成及耐盐相关基因应激表达、抗逆蛋白差异性表达等方式缓解盐分伤害[31]。渗透调节主要包括吸收外界无机离子(减少Na^+的吸收、增加K^+的吸收)、合成有机渗透调节物质等[32-34]。盐胁迫下，水稻体内大量积累脯氨酸[35]，富含脯氨酸的蛋白质参与植物对盐胁迫的应答，游离态脯氨酸在植物细胞质中具有渗透调节功能，在稳定生物大分子结构、降低细胞酸性、减轻氨毒害、调节细胞氧化还原等方面发挥着重要作用。内源激素在水稻应对盐胁迫伤害时发挥关键作用，脱落酸(ABA)通过调节Na^+的吸收和转运缓解离子毒害，赤霉素(GA)通过提高H^+-ATP活性，促进Na^+的排出[36]。

水稻的耐盐性受多基因控制，属于数量性状遗传[37]。越来越多的水稻耐盐相关基因被分离、鉴定，包括渗透调节基因、离子转运基因、转录因子和功能调节基因等[31]。如转录因子家族成员OsNAC1，可通过调节气孔开度提高水稻耐盐性，OsNAC5表达水平与脯氨酸和可溶性糖积累呈正相关，OsNAC106在盐胁迫诱导条件下与OsNAC5的启动子结合共同发挥应答作用[38]；TIFY家族中的转录因子OsTIFY11a可通过调控离子通道蛋白基因*OsNHX1*、*OsAKT1*和*OsSKC1*提高植株对盐胁迫的耐受性[39]。Na^+在低活性的亚细胞区域隔离也是植物对盐胁迫适应的重要机制之一，位于液泡膜中的Na^+/H^+逆向转运蛋白(NHXs)负责将Na^+转运至液泡中，从而降低其对植物的伤害[40]。在水稻中已识别出4个NHX转运体(OsNHX1、

OsNHX2、OsNHX3、OsNHX4),其中 OsNHX1 是最丰富的 Na^+/H^+转运体,介导 Na^+的液泡区划,在水稻受盐胁迫后 2~4 h 达到表达高峰[41]。Na^+由体内排至体外也是植物应答盐胁迫的主要机制之一,SOS1/SOS2/SOS3 复合体在介导植物 Na^+排出和控制根-茎运输方面起重要作用[42]。在水稻中已识别出 3 个与 SOS1、SOS2 和 SOS3 同源的基因,分别为 *OsSOS1*、*OsCIPK24* 和 *OsCBL4*,他们编码的蛋白质协同作用介导 Na^+外排,控制根-茎转运,提高水稻对盐胁迫的耐受性[43]。此外,一些盐逆境调节蛋白相继被挖掘,如水稻未知功能域(DUF)的蛋白质 OsDUF810 家族成员 OsDUF810.7 在盐胁迫下表达显著上调,增强过氧化物酶(POD)和过氧化氢酶(CAT)活性[44];盐胁迫下高表达 EhEm1 可有效降低叶绿素损失、增加脯氨酸含量、增强过氧化氢酶活性,促进水稻适应盐胁迫环境[45]。

3　氮素营养对水稻耐盐胁迫的调节作用

氮素的丰缺程度直接影响水稻的生理生化代谢,植物对盐逆境的适应受氮素吸收、分配和同化等多个过程的调节[12,46]。盐胁迫诱导植株根系大量积累硝酸盐,从而增强耐盐性[47];光呼吸过程中氨的再同化可有效缓解植株氨毒害、减轻盐伤害,该过程与氮代谢密切相关[48]。植物通过调节氮素在光合器官各组分中的分配,协调光能吸收、电子传递和 CO_2还原等过程,增强盐胁迫的耐受性[49]。科学施氮可有效改善逆境生理参数,缓解水稻遭遇盐害进而获得高产[50]。氮素营养通过提高水分传导能力、调节离子平衡、增强渗透调节和抗氧化能力等途径适应盐渍化生境[51]。此外,氮素可诱导脱落酸、吲哚乙酸等激素信号调节养分吸收和耐盐胁迫能力[52]。

氮素营养在水稻响应盐胁迫中的调节机制受到广泛关注。Liu[53]和吕丙盛[54]等研究发现,适当减氮可增强水稻生殖生长阶段对盐胁迫的耐受性,主要表现为:(1)促进脯氨酸和可溶性糖的积累,降低丙二醛含量;(2)正向调控脯氨酸生物合成基因(*OsP5CS1*、*OsP5CR*)和细胞死亡抑制基因(*OsBI1*)的表达,负向调控脯氨酸分解基因(*OsPDH1*、*OsP5CDH*)和细胞死亡相关基因(*OsNAC4*)的表达;(3)降低 Na^+/K^+,提高基因(*OsHKT1*、*OsAKT1*)的转录水平。徐晨等[55]研究发现,盐胁迫下水稻孕穗后减氮可有效减缓叶片光合作用的下降速率,提高植株抵御盐害的能力。Zhu 等[42]研究认为,分蘖肥与穗肥施氮比例 6∶4 时可减轻水稻盐害,提高籽粒产量。

铵态氮(NH_4^+)和硝态氮(NO_3^-)是植物利用的 2 种主要氮源,稻田淹水缺氧条件导致 NH_4^+为水稻主要的氮素利用形式[56-57]。但在长期进化过程中,根系形成发达的通气组织增强了泌氧能力,促进土壤微生物发生硝化作用产生大量 NO_3^-,已证实灌溉稻总氮的 40% 以 NO_3^-形式吸收[58]。因此,两种形态氮素对水稻生长发育发挥同样重要的作用[59-61]。研究表明,施加硝态氮较铵态氮更有利于水稻缓解盐胁迫带来的伤害。盐胁迫条件下供应硝态氮的木质部和韧皮部 Na^+、K^+浓度均高于供应铵态氮的植株[62]。Gao 等[13]研究发现,供应硝态氮的水稻幼苗中 Na^+贮存于质体外,保证细胞免受离子毒害,提高植株对盐胁迫的耐受性。可见,盐渍稻田施用氮肥有利于缓解过多的盐离子干扰营养元素吸收、加速铵态氮和硝态氮的同化进程,维持植株旺盛的生理生化代谢[63]。

4　展　望

有关氮素营养对水稻响应盐胁迫的调节机制研究较多集中于施氮水平、氮肥运筹比例等方面,而不同氮形态对水稻耐盐性的影响研究较少,尤其缺乏生理和分子作用机制的解析,且局限于苗期耐盐机制。水稻孕穗期和抽穗期对盐胁迫相当敏感,该阶段也是穗部发育和籽粒灌浆的关键期,探讨其调节方式及作用机制具有重要的理论意义和生产指导价值。

近年来,施氮形态对盐胁迫条件下水稻生长和发育的调节作用受到了重视,但相关的调节机制尚不清楚。未来研究需要重点关注的科学问题是:铵态氮和硝态氮在调节水稻(尤其是生殖生长阶段)对盐胁迫应答的物质基础,铵态氮和硝态氮在水稻响应盐胁迫过程中的分子调控网络,进而揭示氮素形态对水稻耐盐性的调节作用及可能的机制,并构建基因-蛋白质分子调控网络,为保障盐渍地区水稻稳产增效奠定理论基础。

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