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评 述 中国知名大学及研究院所专栏 华中农业大学作物遗传改良全国重点实验室专辑

盐胁迫下作物源库关系调控机制对油菜抗逆性调控技术的启示

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摘要 源库协调是作物高效生产的重要机制, 盐胁迫严重制约作物的生长发育及产量形成. 本文系统综述了盐胁迫下作物源库器官的响应机制及调控策略, 旨在为建立盐碱地油菜配套栽培技术提供理论依据. 盐胁迫通过多种途径抑制作物源器官功能, 如诱发渗透胁迫与气孔关闭以限制CO_2同化、造成物质动态积累与能量供应矛盾、破坏光系统结构与功能, 并引发活性氧(reactive oxygen species, ROS)积累导致光损伤等. 作物通过调节源库平衡对盐胁迫做出响应, 通过形态自适应、重塑糖转运蛋白(如SWEETs, MSTs)的表达与活性、协同激素信号(如脱落酸、水杨酸、生长素)引导光合产物向根系优先分配, 以及启动渗透调节与离子稳态重建动态调控离子稳态等方式, 减轻盐胁迫毒害压力. 油菜具有较强的耐盐性, 且地上部具有较强的Na^+储存能力, 因而是改良与利用盐碱地相结合的重要作物. 本文针对作物通过源库关系调控机制, 探讨加强油菜源库平衡以提高耐盐性的栽培策略, 为高效改良与利用盐碱地提供理论与技术支撑.

关键词 油菜, 盐胁迫, 源库关系, 栽培策略

油菜(*Brassica napus* L.)作为世界第三大油料作物[1], 在全球范围内广泛种植. 联合国粮农组织最新统计结果显示, 2023年全球油菜种植面积约为43.5公顷, 总产量达9187万吨, 其中我国贡献率约占18%, 位列全球第2(FAOSTAT, https://www.fao.org/faostat/), 是我国最重要和最具潜力的油料作物. 并且油菜种子中45%以上为油脂[2], 具有较高经济价值. 菜籽油中脂肪酸组成合理, 且含有丰富的酚类化合物, 被认为是最健康的食用植物油之一[3].

盐胁迫是抑制作物生长发育的重要环境因素之一, 全球气候变化导致土壤盐碱化程度进一步恶化[4]. 我国约有1亿公顷盐碱地(约占我国国土面积的10.3%), 盐碱耕地面积约有3300万公顷[5], 而其中有至少650万公顷盐碱地具有开发利用的潜力. 种植耐盐碱作物是改良盐碱地, 增加我国耕地后备资源的重要措施[6,7], 研究表明, 油菜具有较强的耐盐碱能力, 除收

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获籽粒榨油外, 还可用作蔬菜、饲料、绿肥等, 因此油菜是改良和利用盐碱地的重要作物[8~11], 但当前仍存在耐盐油菜品种的培育不够丰富、栽培技术不配套等问题, 限制了我国盐碱地改良进程.

对于盐胁迫下作物的响应机制, 前人主要聚焦激素调控系统、渗透调节系统、抗氧化系统、离子调控系统等[12~15], 但盐胁迫下作物源库关系协调与光同化物转运研究尚不多见. 植物学中, 源器官指植物中合成、储存光合同化物(如蔗糖、淀粉等)并主动提供这些物质的器官(如成熟的叶片等); 库器官是指消耗与储存的物质远多于自身所生产的器官(如根、茎、果实和种子等), 其代谢需求主要依赖于源器官的养分供应[16,17]. 作物中韧皮部负责将光合产物等从源器官运往库器官, 而木质部则介导了相反方向的物质回流[18,19]. 值得注意的是, Fichtner等人[20]将研究聚焦于这一过程的调控核心, 即作为碳源与能量载体的糖与氮素之间的平衡(C/N平衡), 并指出该平衡所维系的源库关系对于作物生长及产量至关重要.

盐胁迫对作物的负面影响, 在胁迫早期体现在抑制光合作用上, 降低净光合速率的同时, 抑制光同化最终产物蔗糖的合成、再分配和利用, 这不利于植物体内糖在源库器官中的调配运动[21,22]. 盐胁迫造成作物减产的根源, 在于其引发源器官早衰, 从而破坏同化产物的运输与分配, 最终因库器官发育受限而减产[23]. 尽管其重要性已被认知, 但关于盐碱胁迫下油菜源库关系的协调, 尤其是光合同化产物的具体转运路径, 仍缺乏系统的综述性研究, 这一空白亟待填补. 本文旨在总结现有研究结果, 综合探讨作物在盐胁迫下的源库协调机制以及在此基础上的同化产物转运适应机制, 提出加强油菜源库平衡提高耐盐性的栽培策略, 提高盐碱地改良与利用效率.

1 盐胁迫对作物源库关系的调控机制

1.1 光合作用与源器官功能的抑制

光合作用是植物产生能量的主要途径, 通过吸收源器官周边的CO_2并合成糖运送至库器官, 为植物提供充足的能量[24,25]. 盐胁迫不仅使植物的叶绿体结构受到破坏[26], 光合色素降解[27], 还会抑制光合作用积累光同化物, 致使植物叶片加速衰老, 最终导致减产[28].

盐胁迫早期主要对植物造成渗透胁迫, 有研究发现, 盐胁迫通过诱导ABA积累, 激活其核心信号通路(PYR/PYL-PP2C-SnRK2), 促使SnRK2激酶(如OST1)激活. OST1一方面磷酸化激活SLAC1阴离子通道, 另一方面抑制KAT1钾离子通道, 共同导致保卫细胞失水、气孔关闭, 引发气孔导度(g_s)和蒸腾速率(E)骤降. 这在阻断水分流失的同时, 也严重限制CO_2的吸收, 进而阻碍CO_2的循环利用与碳固定过程, 最终因光同化物生成不足而抑制光合能力, 影响植物生物量积累[29~31]. 此外, 盐胁迫下过多的Na^+泵入影响K^+等离子的流入和代谢, 导致植物离子失衡[32], 使叶绿体的类囊体基质片层发生变化, 光合速率及相关酶活性受到影响[33], 对光合作用产生负面影响.

盐胁迫对植物的光系统反应具有严重影响. Xu等人[34]研究发现, 盐胁迫下光系统Ⅰ(Photosystem Ⅰ, PSⅠ)中的PsaD亚基的前体蛋白表达水平增加了约1.6倍, GOS5亚基的表达水平下降了约38%, 这表明PSⅠ的功能在盐胁迫下受到影响并引发了补偿机制. 盐胁迫使叶绿体中堆积大量活性氧(reactive oxygen species, ROS), ROS不仅对光系统Ⅱ(Photosystem Ⅱ, PSⅡ)造成光损伤, 还会抑制PSⅡ的损伤修复[35,36], 这致使PSⅡ过程成为光合作用中最容易受到影响的部分之一. 有研究表明, G1/S-特异性周期蛋白-D1(cyclin D1, D1蛋白)是PSⅡ系统中最核心的亚基, 负责在光照条件下衔接光合流程, 确保过程可以快速流转, 对于PSⅡ的过程发生和功能维持起关键作用[37,38], 但在盐胁迫下, 番茄叶片中D1蛋白的编码蛋白LHCB5/7和psbA的表达显著下降, 这不利于盐胁迫下PSⅡ光损伤的修复[39,40].

综上所述, 盐胁迫通过诱导渗透胁迫对植物光合系统形成多维度损伤——气孔运动异常导致CO_2吸收受限, 叶绿体结构破坏直接影响光反应场所, 电子传递链受阻抑制光能转化效率, 最终通过“源-库”互作机制抑制光合产物的合成与积累, 成为制约高盐环境下植物生长发育和生产力的关键限制因子.

1.2 渗透胁迫对源-库能量分配的影响

植物体外盐胁迫严重影响植物自身水势、渗透势及离子稳态[41]. 盐胁迫导致毒害离子(Na^+, Cl^-)浓度升高, K^+和Ca^{2+}大量流失, 造成离子失衡, 这致使植物发生离子毒害[42,43], 因此K^+/Na^+比值的升高对于降低

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Na^+至关重要[44]. 植物首先要进行的就是对盐胁迫的感知, 由MOCA1酶组成的糖基肌醇磷酸神经酰胺(glycosyl inositol phosphoryl ceramide, GIPC)鞘脂被认为是潜在的盐传感器. 高盐环境下, Na^+与GIPC结合导致细胞膜去极化, 这导致Na^+内流; 与此同时钙离子通道触发Ca^{2+}内流, 浓度瞬时升高, Ca^{2+}结合蛋白、Na^+/H^+逆向转运蛋白被激活上调, 盐胁迫信号通路就此启动[45,46]. 为应对Na^+毒性, 植物进化出高度保守的SOS (salt overly sensitive)信号通路. 盐胁迫诱导的胞质Ca^{2+}信号被钙结合蛋白SOS3(即CBL4)感知, 随即与蛋白激酶SOS2(CIPK24)相互作用, SOS2的自抑制状态被解除, 激酶活性被激活[47], 被激活的SOS2磷酸化并激活质膜上的Na^+/H^+逆向转运蛋白SOS1, 细胞内过量的Na^+被泵出细胞, 这被视为抵御盐胁迫的第一道防线[48]. Na^+/H^+逆向转运蛋白NHX在盐胁迫下, 可以将Na^+泵入液泡进行区隔化, 降低胞质Na^+浓度, 又以Na^+作为渗透调节物质降低细胞水势, 促进水分吸收, 从而提高耐盐能力[49](图1); 盐胁迫下, 马铃薯根系除减少主根伸长外, 其根内部将Na^+区隔化划分, 较多的划分在液泡及根柱区域中, 以此减少Na^+向上运输, 减轻损伤[50,51]. 高亲和K^+转运蛋白HKT在调控Na^+从根到茎的长途运输中起关键作用, 其通过介导木质部中Na^+的回收, 限制Na^+向茎部和叶片运输, 从而保护光合作用活跃的叶片免受离子毒害[52,53]. 而植物体内离子的吸收、外排及动态平衡的维持过程需要消耗大量能量, 这一机制给细胞代谢带来巨大的能量负担.

此外, 盐胁迫导致植物体内蛋白质结构改变, 导致转录后发生修饰, 以产生种类繁多的渗透调节剂帮助植物响应胁迫, 并通过减少幼嫩组织细胞的扩张, 降低气孔导度来保持水分, 最终赋予植物抵抗外界恶劣环境的潜力[54,55]. 胁迫下植物通过积累氨基酸、海藻糖、甜菜碱等渗透调节物质维持细胞膨压, 促进细胞对水分及营养物质的摄取[56]. 这些变化均建立在植物提供充足的能量基础之上.

事实上, 盐胁迫下有限的能量供应量与植物体内响应胁迫的能量所需量相矛盾. 盐胁迫导致植物生长减缓, 这可能与信号传导、光同化产物供给、光合作用产生的能量利用及供给有关[57]. 盐胁迫条件下, 植物需要为CO_2固定、水和离子转运等过程提供能量. 研究表明, 在非生物胁迫下ATP供应受阻时, 液泡焦磷酸酶(vacuolar H^+-PPase, V-PPase)这种含有高能磷酸基团的分子也可以为植物供能[58], 并且Gaxiola等人[59]和

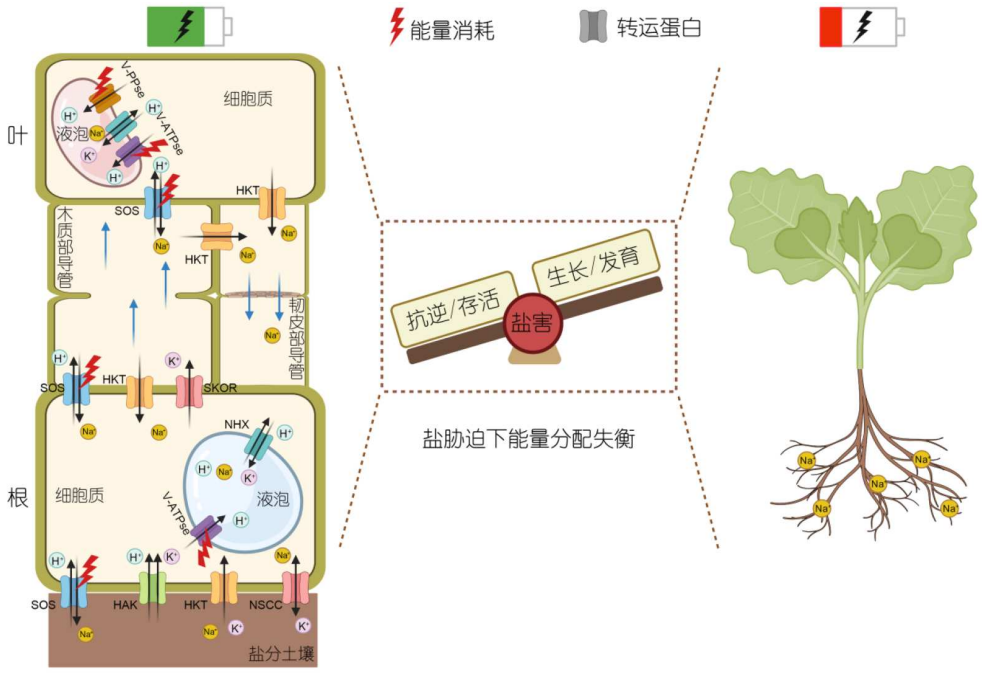


图 1 盐胁迫下能量分配失衡示意图
Figure 1 Schematic diagram of energy allocation imbalance under salt stress

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Schilling等人[60]证实V-PPase的高表达赋予植物显著的非生物胁迫耐受性. 盐胁迫下, 植物将大量的Na^+和Cl^-区隔化是其响应胁迫的手段之一, 这一过程就与V-PPase密切相关[61]. 然而K^+作为促进V-PPase发挥作用的动力[62], 与盐胁迫下K^+的匮乏情况形成冲突. 近几年有研究表明, V-PPase还与植物源-库组织间糖类及碳水化合物的转运、代谢有关[63], 进一步增加植物在盐胁迫下对能量的预算.

盐胁迫下, 作为植物光合作用场所的源器官受到严重影响. 植物为尽可能减小损伤, 需扰乱正常条件下的源库分配关系, 调动大量能量及营养物质以响应胁迫. 最终, 盐胁迫所带来的影响, 会以库器官经济性状指标损失的形式表现出来[64]. 胁迫下, 当植物器官需求增加, 而植物的碳源用尽或库器官没有及时输送时, 植物表现为生长受抑制, 表明植物的生长受到源库协作的调节[65]. 淀粉和蔗糖这两种碳水化合物主要发挥能量储存和供应的作用, 对于响应非生物胁迫至关重要[66,67]. Fang等人[68]在对耐盐水稻和敏盐水稻响应盐胁迫的机制研究中发现, 调控蔗糖合成与分解的蔗糖合成酶相关基因、β-淀粉酶相关基因等在耐盐水稻海红11(HH11)中表达上调, 这与敏盐品种IR29中的表现不同.

与敏盐油菜品种相比, 耐盐油菜品种可能具有更佳的离子调控能力和同化产物合成供应能力[69]. 这意味着耐盐品种油菜可能具备更优的能量分配机制, 将有限的能量高效分配利用, 实现能量的供需平衡. 因此, 可以对比分析不同耐盐性油菜在盐胁迫条件下, 体内基因表达和能量流动如何影响源库器官及同化产物的分配, 从而揭示不同耐盐程度的适应性机制.

1.3 作物形态及生理功能的适应机制

在植物资源分配研究中, 地下器官在生长过程中是碳库. 此外, 一些地上器官如花和叶柄也是碳库; 有的则是从库器官过渡到源器官, 如叶片; 而到成熟时期, 种子、块茎、根和茎又会从碳库过渡为源器官[70,71]. 当源库关系受到影响而波动时, 源库之间的动态平衡调节便凸显出来, 例如, 增加CO_2浓度、提高光强或延长光周期[72~74], 可以提高植物的固碳能力, 从而促进植物的生长并增加产量. 同样, 当库器官需求增加时, 则会促进源器官的光合作用[75,76]; 若库器官的需求降低时, 又会导致源器官中糖的积累, 最终导致光合作用减弱[73], 这说明库器官的需求也会影响源器官叶片的活性. 总之, 源器官(碳同化和输出)与库器官(糖的输入和使用)之间存在高度相关, 是影响作物生长与产量的关键生理过程之一.

外界胁迫导致作物叶绿体退化或衰老, 从而导致源器官的生产能力下降, 并使整株的碳氮同化和分配能力降低[77,78]. 有研究表明, 干旱胁迫下, 热带作物木薯会牺牲叶片, 待胁迫消失或者条件更有利时, 则会动员根部的碳库以产生新叶[79]. 盐胁迫导致番茄叶片扩展停滞, 光合作用降低, 而根系所受影响较小; 植物根冠比上升被视为植物的自适应现象, 以增加根系, 从而增加对水分和养分的吸收[80].

在油菜整个生育周期中, 油菜的叶片花期前被视为拦截光照进行光合作用的主要源器官. 开花后, 油菜的叶面积减小, 角果快速生长, 表面积增加, 成为吸收和利用阳光的主要源器官, 同时也作为库器官储存能量. 相关研究表明, 油菜籽粒产量的70%左右源于盛花期后角果产生的光同化产物, 角果是做出主要贡献的源器官[81~84]. 此外, 油菜地上部有较强的Na^+储存能力[85], 这不同于小麦、大豆、玉米等作物. 目前有研究表明, 盐胁迫下油菜初花期干物质更多地分配至根和叶片, 成熟期根和茎枝的干物质分配占比高于果壳和籽粒[86]; Wang等人[87]同样发现, 在油菜幼苗和开花时期, 盐胁迫影响生物量在根和叶片中的积累与分布, 成熟期果壳和籽粒的生物量分布减少, 并且更多地分布在根和茎. 油菜在不同时期的源库器官转换以及干物质在源库器官中的分配规律已经基本明确, 但至今在盐胁迫下油菜根冠协调及动态调控机制并不清晰.

1.4 光同化产物转运的分子调控机制

外界环境的干扰条件, 对碳同化过程的调节有更高要求, 植物需及时做出调整以保持该功能的正常运行[88]. 这不仅依赖于植物体内因压力差产生的动力, 还与植物内部紧密参与调节的分子网络和信号转导有关(图2).

Williams等人[89]和Chen等人[90]对*SWEETs*(sugars will eventually be exported transporters)糖转运蛋白家族基因的功能进行解析, *SWEETs*家族基因可将蔗糖从叶细胞转运到胞外体, 随后通过定位在膜上的蔗糖/H^+转运体(sucrose transporter 1, SUT1)转运到伴生细胞中. 而盐胁迫发生时, 植物在调节糖的转运及储藏

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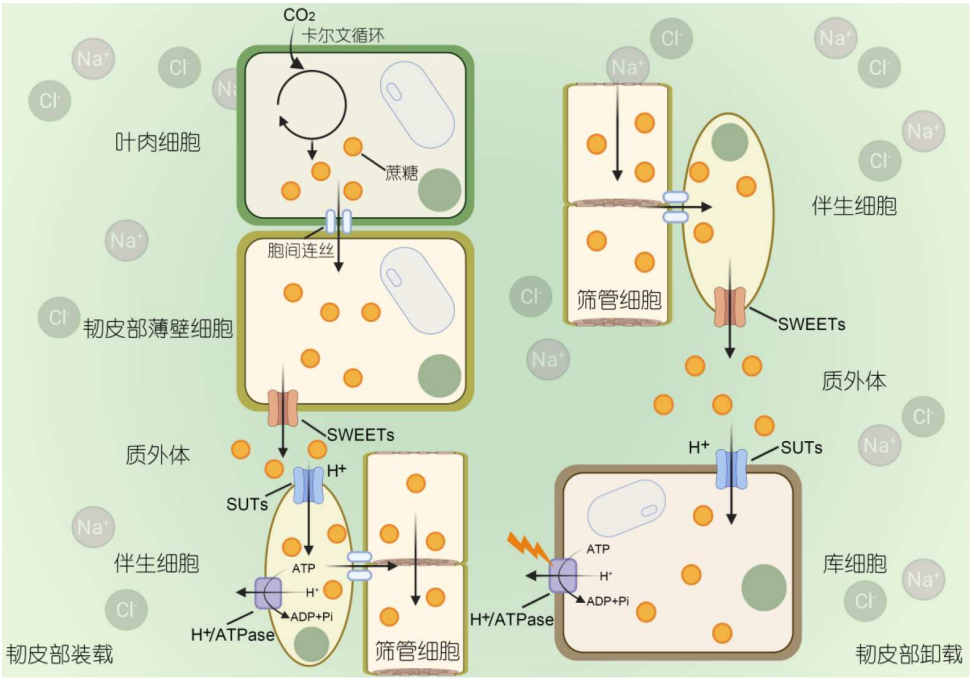


图 2 盐胁迫下蔗糖在植物韧皮部的装载与卸载
Figure 2 Loading and unloading of sucrose in the phloem of plants under salt stress

时, 部分*SWEETs*转录水平显著提升, 同时*SWEET2/16/17*在细胞质中运输蔗糖、果糖等[91]. 这些基因的表达下调和液泡中糖类储存减少的假设一致[92,93]. 单糖转运蛋白(monosaccharide transporters, MSTs)家族作为单糖转运的载体, 同样发挥碳分配的作用, 由糖转运蛋白(sugar transporter proteins, STP)、质体葡萄糖转运蛋白(plastidic glucose translocator, pGlcT)、液泡葡萄糖转运蛋白(vacuolar glucose transporter, VGT)、胞质体糖转运蛋白(tonoplast sugar transporter, TST)等7个亚群组成[94]. Zhu等人[95]研究表明*MST*家族基因对渗透胁迫和镉胁迫有响应, 并且有5个基因在盐胁迫下发挥作用. TST则通过将多余的糖转运至液泡中, 维持植物细胞的渗透压, 能有效抵御渗透胁迫[96].

糖作为光合作用的主要产物, 通过糖级联反应影响含量及分布, 对植物的生长发育有重要影响[97]. 植物激素的合成和信号传导是植物响应盐胁迫的必要信号, 与糖信号转导过程密切相关. 例如, 脱落酸(abscisic acid, ABA)通过调节气孔运动应对NaCl诱导的渗透胁迫, 其中便涉及植物内源ABA与糖协作调控调节渗透稳态的过程[98]. 渗透胁迫下, 植物体内的ABA水平提高, 激发了蔗糖相关蛋白激酶(sucrose non-fermenting1-related protein kinase, SNRK2s), 通过磷酸化AREB/ABF转录因子, 进一步调控气孔运动; 与此同时, SNRK2s通过调节β-amylase 1(BAM1)和Alpha-amylase-like 3(AMY3)将淀粉分解成糖及糖源渗透物, 共同调节渗透稳态[99,100]; 此外有研究表明, 被ABA激活的SnRK2s能够直接磷酸化位于蔗糖转运蛋白SWEET11和SWEET12羟基末端胞质区域的保守丝氨酸位点, 这显著增强了SWEET11和SWEET12的寡聚化和蔗糖转运活性, 直接促进蔗糖从叶片(源器官)向韧皮部的装载, 增加了向根部(库器官)的长距离运输. 这一变化将有限的资源优先分配给根系, 以促进根系生长并提高根冠比, 这是一种在胁迫下快速配置源库平衡的适应性策略[101]. 水杨酸(salicylic acid, SA)同样可以改善盐胁迫带来的危害, 主要通过调控K^+向茎部运输维持离子平衡来实现; 但其同样也通过提高植物体内可溶性糖含量, 降低体内ROS指标, 帮助植物应对盐胁迫[102]. Zhao等人[103]研究发现, 在水稻中存在IAA-OsARF18-OsARF2的生长素信号级联, 在盐胁迫下调节源库器官中蔗糖的分配利用.

盐胁迫下, 植物通过糖转运系统与离子稳态调控网络、激素信号等通路的协同作用对胁迫做出响应调

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整，但光合同化产物的转运绝非简单的基因表达调控所能概括，它是一个动态、多层次的网络，磷酸化反应如同“分子开关”，能根据环境信号迅速改变转运蛋白活性，寡聚化则像“拼接模块”决定转运通道能否形成以及其功能效率，这受到磷酸化的精密调控，这些快速、可逆的翻译后修饰，蛋白质的相互作用与转录调控，共同维持油菜源库器官间的物质分配平衡，提高耐盐性提供研究基础.

1.5 根际微生物介导的植物源库关系对盐碱胁迫的响应

盐碱土与正常耕作土壤的微生物群落差异显著，其成因不仅源于二者环境因子的不同，更与不同耐盐性作物根际微生物的差异密切相关[104,105]. 为应对盐胁迫，作物会依据土壤盐度及自身特性，主动招募特异的微生物群落[106,107]，从而导致其根际微生物结构与组成发生显著改变.

盐胁迫下，根际微生物不仅可以促进植物生长，而且在缓解盐胁迫毒害作用中扮演重要角色. 首先，微生物本身就是一种可利用资源，微生物的死亡体是土壤有机物的重要组成部分，在土壤有机物的周转过程中是重要的“碳泵”[108,109]. 其次，微生物与植物有着密切的共生关系，有研究表明，在盐胁迫的刺激下作物根际可通过分泌有机酸等物质招募有益的根际促生菌[110]，促进植物在盐胁迫下的生长; Zheng等人[111]研究发现，根际土壤中具有促进植物生长特性的基因显著高于整体土壤，并且Na^+转运基因和K^+/H^+逆向转运基因的丰度也显著提升. 盐胁迫下植物对养分的吸收受到严重抑制，Wael等人[112]在蚕豆的根际土壤中分离出有利于磷酸盐溶解以及氮固定的促生菌，以应对土壤盐分带来的有害影响. 不仅如此，根际有益菌还可以在盐胁迫下产生大量抗氧化酶以提高植物的耐受性[113]; 通过接种植物根际促生菌发现，植物体内生长素的含量显著增加，从而改变植株根系结构，这有利于植物根系对养分和水分的吸收[114~116]. 由此可见，根际微生物不仅可以调节离子平衡、促进养分吸收、激活抗氧化系统，还有利于次生代谢物质以及生长素、赤霉素等激素的合成，从而抵消盐胁迫的负面影响[117~120].

盐胁迫下, 微生物群落做出响应的同时, 对于植物生物量积累和营养循环也做出巨大贡献，其动态调整的过程对植物抵抗盐胁迫至关重要. 大量研究表明, 有益菌的接种有利于盐胁迫下种子的萌发，光合能力的提升, 生物量的积累, 明显改善植物的生长情况, 在耐盐方面具有巨大的潜能[121~123]; 植物根际促生菌(plant growth-promoting rhizobacteria, PGPR)和根瘤菌(arbuscular mycorrhizal fungi, AMF)则被证实可以提高CO_2的同化效率, 促进有机物的转化[124], 其中PGPR还可以固氮、从土壤中释放结合态的磷、钾离子、螯合铁等, 提高养分的吸收能力, 这有利于植物重要代谢过程的正常进行[125]; Naveen等人[126]研究发现, 一些微生物可以分泌胞外多糖, 形成稳定的生物膜, 这种生物膜在根表面形成一层保护膜, 以此来减少Na^+等有害离子向根系的迁移.

由此可见，根际微生物一方面可以在盐胁迫下通过提升光合能力、减缓氧化损伤、维持离子平衡，保护植物光合器官的功能，确保“源”的稳定输出; 另一方面，微生物通过促进养分吸收、生长激素合成、刺激地上部及地下部的生长，增加“库”的容量，与此同时，微生物通过固氮、解磷等作用将土壤中的无效养分转化为有效养分，为植物增加额外的“养分库”，在盐胁迫下系统地维持了高效的源-库动态平衡.

1.6 其他分子调控机制及复杂级联通路

在盐胁迫下, 作物源库平衡的调控, 很大程度上还依赖于相关基因或蛋白信号的间接调节作用. 相关研究表明，盐胁迫可以激活甜高粱C4固碳途径中的关键酶NADP-苹果酸脱氢酶(malic enzyme, NADP-ME)[127]，在拟南芥中过表达*NADP-ME*，可以显著提高光合效率，增强为Rubisco提供CO_2的能力[128]. 面对盐胁迫的影响，植物可以迅速做出反应，缓解Na^+对植物光合系统带来的负面影响. Kim等人[129]发现水稻中与光合作用相关的析氧蛋白表达量在盐胁迫后显著上升. 在水稻中，与介导脱落酸合成相关的蛋白OsCSLD4通过调节渗透胁迫，对增强水稻耐盐性起重要作用[130]. 在小麦中, 过表达*MYB90*(V-myb avian myeloblastosis viral oncogene homolog 90)可以减少体内ROS含量, 增强耐盐性[131]. 拟南芥中的MADS-box因子*AGL16*(Agamous-like 16)则通过下调盐相关响应基因，从而影响植物中的相关负调控因子[132].

面对盐胁迫, 植物做出相应反应, 并非单一基因或蛋白信号能实现的. 因此, 该过程存在复杂的级联信号

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通路共同协作响应完成. Abid等人[133]发现棉花首先通过利用钙结合蛋白SOS3感知细胞中急剧增加的Ca^{2+}来响应盐胁迫, 随即通过与SOS2相互作用转化下游信号级联. Zhao等人[134]研究发现一种重要的耐盐新途径, 亮氨酸重复延伸蛋白(leucine-rich repeat extensins, LRXs)-细胞因子(rapid alkalinization factors, RALFs)-受体类激酶(feronia, FER)模块通过负调控ABA、茉莉酸(Jasmonic acid, JA)、SA等激素水平, 抑制突变体的盐敏感性. 盐胁迫下, 水稻中的CAM1-1, MKK1和MKK6相互磷酸化后, 提高根中生长素含量, 促进侧根生长, 耐盐性增强[135]. 杨闯等人对油菜进行不同时长的盐胁迫处理, 以挖掘早期响应和晚期响应盐胁迫的核心基因, 在早期富集到同源锌指蛋白转录因子AtAZF2, DREB亚家族成员基因*AtDDF1*等, 这些基因可以显著增强对盐的耐受性; 在后期则富集到同源细胞分裂素信号调节因子基因*AtARR*, 同样可以由高盐条件诱导表达[136~139]. 盐胁迫下, 叶片中较高的分裂素水平可以激发光合系统中的Rubisco活性, 进而影响光合作用相关基因的表达, 延缓叶片衰老, 保护植物源器官[140].

目前, 较多研究利用群体材料、多组学等手段对多种作物进行响应基因的深度挖掘, 为作物的耐盐性改良提供关键候选基因. 针对油菜亦是如此, 通过构建群体材料、组学手段发掘响应油菜耐盐性的关键基因与通路, 并与源库调控相关联, 为遗传改良提供潜在靶点, 明确油菜盐胁迫下调控源库平衡提高耐盐性的信号通路网络. 然而, 仅仅依靠遗传改良手段尚不足以充分发挥作物的耐盐潜力. 在明确耐盐关键基因和调控网络的基础上, 还需要结合栽培调控策略, 通过优化田间管理措施协同提升油菜的耐盐性和产量表现. 其中, 基于源库调控理论的栽培管理尤为重要.

2 基于盐碱胁迫下源库调控的栽培策略

复杂的调控机制共同决定作物在盐胁迫条件下的源库平衡状态, 进而影响其耐盐性和产量的形成. 在作物栽培中, 源库调控是协调光合产物生产、运输分配与储藏利用的重要理论依据. 通过优化种植密度、水肥管理和群体结构调控等栽培措施, 可以有效打破源库失衡限制, 进一步挖掘作物产量潜力, 为盐碱地抗逆稳产提供精准调控路径.

2.1 水肥管理措施

通过优化农艺措施和外源调控手段能有效改善盐胁迫下植物的源库关系, 是调节植物生长和提高产量的重要策略之一(图3).

研究表明, 盐胁迫下钾肥影响棉花光同化相关酶活性, 并改善碳分配效率[141]. 适量氮肥可以提高稻米



图 3 优化盐碱胁迫下源库调控的栽培策略
Figure 3 Optimization of the cultivation strategies for source and reservoir regulation under saline-alkali stress

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灌浆时期叶片的光合效率, 延长灌浆时间, 从而提升水稻产量和品质[142]. 在盐碱地农业中, 科学的滴灌策略可显著减轻盐胁迫对作物生长的抑制, 稳定生物量积累和产量[143]. 盐胁迫下适度遮阴可以显著提高油葵光合效率, 有利于光合产物的积累和分配[144]. 采取补充滴灌、增施肥料的方法, 有利于增加干旱环境下玉米吐丝后干物质的积累, 延长生育期, 使籽粒稳定增产[145]. 还有研究通过早期胁迫锻炼增强作物的耐盐性, 如梅映学等人[146]使用聚乙二醇对水稻进行干旱胁迫, 这一措施提高幼苗对盐胁迫的耐受性. 为防止深层盐分向土表的转移, 高海东[147]提出通过深翻盐碱土减少表层水分的蒸发, 以减轻水分对盐分的裹挟作用. 针对盐碱地上水稻的栽培, 王洋等人[148]还提出明沟排盐、暗管排盐的栽培措施, 这是从减少土壤盐分的角度提出的相应措施. 此外, 合理调整种植密度可优化作物群体结构, 维持适宜的叶面积指数和粒叶比, 从而协调源库平衡[149].

盐碱地油菜栽培亟需通过源库调控优化光合产物分配, 以破解耐盐-高产协同提升的栽培技术瓶颈.

2.2 外源调节物质的缓解作用

外源调节物质在植物抗逆调控中发挥着关键作用, 通过改善光合效率、优化碳氮代谢及促进源库协调, 有效缓解环境胁迫对作物生长和产量的不利影响.

植物生长调节剂钙基丙烯酸酯(Pro-Ca)促进盐胁迫下水稻叶片光合效率, 降低叶片糖的分解和代谢, 减轻对光合作用的抑制效果, 与此同时, 促进糖在源库器官之间的转运, 促进种子灌浆, 提高产量. 外源施用γ-氨基丁酸(gama-aminobutyric acid, GABA)和钾肥能激活抗氧化系统, 促进氮碳同化和光合效率, 缓解盐害并提高产量[150]. Yan等人[151]研究发现, 外源褪黑素(melatonin, MT)处理提高盐胁迫下水稻净光合速率, 提高关键光合酶活性, 有利于蔗糖和淀粉的积累, 减轻产量损失. 此外, 联合施用MT和SA可以影响小麦光合机制, 显著提高光合色素含量、光合光化学反应等, 有效缓解盐胁迫对小麦生长和生产力的影响[152]. Yu等人[153]指出24-表油菜素内酯(24-epibrassinolide, 24-EBL)作为油菜素内酯生物合成的活性副产物, 能够调控盐胁迫条件下植物的氮素吸收与同化过程. 这些研究揭示外源物质调控植物抗逆性的关键机制, 为逆境条件下稳产增产提供有效干预途径.

近年来, 纳米材料因其独特的物理化学性质在提高植物抗逆性领域展现出巨大潜力. 通过精准调控植物生理代谢、增强抗氧化防御及优化营养吸收, 纳米材料能够有效缓解干旱、盐碱、重金属污染等多种环境胁迫对作物生长的不利影响. Liu等人[154]研究发现氧化铈纳米颗粒(polymer nanocomposite, PNC)可显著提高棉花的碳同化率, 有利于生物量积累, 使棉花在盐胁迫下表现更佳. 纳米硅材料(Si NPs)可调节光合基因和蛋白表达改善植物的发育和生产力[155]. 无论是在正常条件还是盐胁迫条件下施用铁纳米材料(Fe NPs), 均可显著提高小麦芽和籽粒的干重, 促进小麦生长[156]. Rizwan等人[157]发现纳米氧化锌(ZnO NPs)可以改善盐胁迫下小麦氮转运能力, 并稳定光合色素含量, 从而增强对盐胁迫的耐受能力. 纳米材料通过调控光合作用、增强抗氧化能力及优化微生物互作等多重机制, 显著提升作物对非生物胁迫的适应能力, 为现代农业抗逆栽培提供创新解决方案.

为解决土壤盐碱化这一全球性问题, 外源性微生物肥料在改善土地生产力, 提高植物耐盐性等方面被广泛应用. Wu等人[158]通过在盐碱地施用复合型微生物肥料, 大幅提升了甜高粱的产量, 不仅如此, 外源菌肥通过提高细菌和真菌群落的多样性和网络复杂性促进土壤中养分的释放, 使盐碱土地被有效治理; 此外, 通过施用增钾型细菌, 可显著增强水稻在盐胁迫下钾吸收, 提高细胞内K^+/Na^+比例, 从而促进水稻的生长和产量的提升[159]; Tu等人[160]发现盐碱地施用芽孢杆菌和生物炭后, 明显改善向日葵的生长情况, 叶绿素含量、气孔导度、抗氧化能力、蛋白质含量显著提升, 缓解盐碱胁迫对向日葵的损害. 微生物菌肥不同于种子处理与外源喷施处理, 而是从改善土壤理化性质、调节菌群组成及网络, 促进植物-土壤-微生物良性循环入手, 在盐碱胁迫下作物调节源库平衡、提高产量方面存在巨大潜力.

目前, 施用外源调节物质通过促进源库平衡提高油菜耐盐性得到验证. 刘江波等人[161]研究表明, 外源施用SA后可显著提高油菜幼苗叶片叶绿素和氮含量, 进一步提高光合能力, 进而提高油菜耐盐性; 外源施用脯氨酸(proline, Pro)可以提高盐胁迫下油菜叶片中Na^+/K^+, 提高抗氧化能力, 促进渗透物质积累, 缓解盐胁迫损伤[162]; 通过叶面喷施氧化铈纳米颗粒, 盐胁迫下油菜幼苗的生物量、叶绿素含量以及光合能力得到

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显著提升, 并通过调控Cu-Zn SOD同工酶活性缓解油菜的氧化损伤, 从而提升耐盐性[163]; Ali等人[164]研究发现纳米硒(Se NPs)可以提高α-淀粉酶活性和游离氨基酸含量, 促进盐胁迫下油菜种子萌发, 还可以维持油菜内离子稳态, 显著提高光合效率, 提高耐盐能力; Li等人[165]同样发现施用肠杆菌科菌株(HSNJ4)后可显著增加油菜幼苗的根长、茎长、侧根数量、叶绿素含量, 并且可以调节油菜幼苗中生长素和乙烯的相对含量, 从而增强其耐盐性. 尽管各类外源调节物质的靶点各异, 但均能优化油菜的源库功能, 并且验证外源调控策略对增强油菜耐盐性的有效性, 为后续开发精准高效的抗逆栽培技术奠定坚实基础.

3 未来展望

盐胁迫严重制约油菜的生长发育及产量形成, 而基于其他作物源库关系的调控研究, 为提高油菜耐盐性提供新思路.

3.1 进一步挖掘盐碱地油菜源库平衡的调控机理

基于目前的研究, 对于盐胁迫下油菜源库器官的动态协同响应机制尚不清晰, 尤其是蔗糖转运蛋白(SUTs, SWEETs等)及离子转运蛋白(NHX, SOS等)的时空表达模式需要进一步解析[166]. 如今多组学技术发展迅速, 可结合转录组、代谢组等多组学技术, 揭示盐胁迫下油菜中碳分配转运与离子转运的调控网络, 挖掘关键调控因子与机制; 结合全基因组关联分析(genome-wide association study, GWAS)、权重基因共表达网络分析(weighted gene co-expression network analysis, WGCNA)等分析手段, 挖掘“高光合-强转运”的关键基因, 开发相关分子标记并创制源库平衡的种质资源配置杂交组合, 深入解析盐胁迫下油菜源库器官的协同调控网络, 为优化油菜种质资源、阐明油菜耐盐机制、开发靶控技术及产品提供重要的理论依据和技术支撑.

盐胁迫下, 糖不仅是能量物质, 还可作为盐胁迫下的信号因子激活激素与ROS通路, 激活HXK, SnRK, TOR(target of rapamycin)等相关糖蛋白[167], 从而影响源库器官的适应性. 优化糖-激素信号网络, 解析油菜脱落酸-糖协同调控通路、生长素-蔗糖分配机制, 筛选油菜中调控源库平衡的关键基因与产物, 为开发调控盐胁迫下油菜生长的物化产品奠定基础. 在未来, 还需挖掘油菜调动体内激素响应信号用以关联体内能量转化分配的规则, 探索限制条件下的能量供需分配问题, 进一步明确动态调节盐胁迫下油菜源库器官中光同化产物的转运与分配达到源库平衡的新机制.

3.2 构建盐碱地油菜高质量群体缓解群体-个体矛盾

当前, 盐碱地油菜群体构建的研究基础仍较薄弱, 其适宜的种植密度、株行距等关键配置参数亟待明确. Tan等人[168]研究表明, 在高效油菜系统中, 产量与效益同群体密度呈显著正相关, 这印证了合理密植可通过协调个体与群体的关系, 充分挖掘群体生产潜力. 为此, 未来应致力于利用冠层管理技术, 系统优化盐胁迫下的群体结构, 以构建协同增效模式, 弥补胁迫导致的器官与营养损失, 填补高产群体优化配置的空白, 最终实现光合产物的高效分配与盐胁迫损伤的动态修复, 形成一套可推广的高产优产栽培范式.

实现上述目标, 首要任务是通过品种、播种期、密度与肥水等多因素的协同调控, 确立科学的群体配置参数. 在盐碱地品种高效选用方面, 应根据土壤盐碱化程度进行精准匹配. 针对轻度盐碱地, 可选用具有一定耐盐性且产量潜力较高的品种, 中度盐碱地应选用耐盐性中等、根系较发达的品种, 而对于重度盐碱地, 则必须选用耐盐性强、主根深扎、耐碱能力突出的专用型油菜品种, 以实现“以种适地”, 从遗传基础上增强油菜的盐适应能力. 其次, 通过播种期试验和密度试验确定最佳播期及最适基本苗, 在保障群体结构合理的基础上规避盐分胁迫高峰期. 水肥管理方面, 应优化氮钾配比, 并利用根系向肥性, 通过深施或侧深施“以肥塑根”, 引导根系下扎, 对抗盐碱地常见的浅根化趋势. Wang等人[169]研究指出, 秸秆还田可改善土壤结构, 促进细根发育与氮素吸收, 因此建议结合深耕与适度秸秆还田, 为根系拓展创造疏松的生长空间. 此外, 推广滴灌技术有助于精准控制根区水盐与养分供应, 改善源库关系, 从而减轻盐胁迫对产量和品质的不利影响.

综上所述, 通过耐盐品种的分级选用与群体构建参数的优化配置, 不仅可重塑油菜根系构型、调节源库平衡, 也是提升盐碱地油菜稳产高产能力、推动边际土地资源有效利用的关键技术路径.

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3.3 配套盐碱地油菜关键生产技术实现个体源库协调

为实现盐碱地油菜的高产稳产，未来栽培技术需形成一套从播种出苗到精准调控促进高产稳收的完整技术体系. 在播种出苗阶段，可重点研发集成种子处理、整地与播种技术，确保“一播全苗”，通过浸种等种子预处理技术增强发芽势，采用垄作方式并精准把控播种深度，为油菜萌发创造局部低盐环境. 在水分与养分管理层面，可以通过薄膜覆盖抑制返盐，并优化灌溉水量与肥料(特别是氮、钾)的用量、配比及施用位置, 利用根系向肥性引导根系下扎, 实现肥水高效利用促进苗期健壮生长. 在生理调控层面, 可在保苗基础上间接调控与耐盐性及源库平衡相关的关键基因表达, 进一步提高苗期油菜的耐盐性(如施用外源植物生长调节剂、微生物菌肥等). 这侧重于对上游调控因子(如转录因子)进行干预，进而精准影响下游一系列响应基因的表达网络，最终使调控效应靶向作用于源库器官, 缓解盐胁迫抑制, 优化光合产物分配. 未来针对技术升级，应着力推动传统调控手段与新技术的融合，一方面，可重点开发基于纳米载体的复合型植物生长调节剂，利用纳米装载技术实现活性成分在油菜源库器官的精准、可控释放，从而大幅提升传统调控措施的效率和稳定性, 进一步增强抗逆效果; 另一方面, 应着力突破当前微生物菌肥普遍存在的普适性差、依赖单菌株应用等瓶颈, 向合成菌群的设计与应用转型. 这关键在于系统解析微生物功能与油菜基因型的互作网络, 并以此为指导, 配制出具有根际定殖优势的复合菌剂. 最终实现与现有农艺措施相辅相成, 形成稳定可靠的田间增效能力.

综上所述，现有研究多聚焦于单一技术或某一生育阶段的调控，尚缺乏对多技术协同、全生育期适配的源库调控体系的系统构建. 未来突破方向应着重聚焦在两个层面: 一是在传统技术层面做好集成与优化, 将已有的水肥管理、耕作措施等进行深度整合，形成稳定可靠的栽培范式; 二是在前沿技术层面寻求创新与利用，深入解析盐碱胁迫下油菜源库互作的生理与分子网络以提供理论靶点，开发智能化的外源物质递送系统以实现精准干预，并构建以微生物-油菜-土壤为核心的生态调控新策略. 通过传统技术的优化与新技术的研发相结合，共同为实现油菜在盐碱地的高产稳产与资源高效利用提供全面理论支撑.

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Implications of the regulatory mechanism of source-sink relationship under salt stress for enhancing stress resistance in rapeseed

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Source-sink coordination is a crucial mechanism for efficient crop production. Salt stress significantly inhibits plant growth and yield formation. This review systematically examines the response mechanisms of source and sink organs under salt stress, and discusses corresponding regulatory strategies, aiming to provide a theoretical basis for developing tailored cultivation techniques for rapeseed in saline-alkali lands. Salt stress impairs the function of the source organ through multiple pathways, including the induction of osmotic stress and stomatal closure, which restricts CO_2 assimilation. This leads to imbalances between metabolic accumulation and energy supply, disrupting the structure and function of photosynthetic systems, and triggering the accumulation of ROS that leads to photodamage. In response, crops adjust their source-sink balance via morphological adaptations, remodeling of sugar transporter expression and activity (e.g., SWEETs and MSTs), hormone-mediated redirection of photoassimilates to roots (e.g., abscisic acid, salicylic acid, and auxin), and activation of osmotic adjustment and ion homeostasis mechanisms, thereby alleviating salt-induced damage. Rapeseed (*Brassica napus* L.) exhibits strong salt tolerance and a notable capacity for Na^+ accumulation in shoots, making it a promising species for simultaneous utilization and improvement of saline-alkali soils. By exploring the regulatory mechanisms of source-sink relationships under salt stress, this review proposes cultivation strategies to enhance salt tolerance in rapeseed by optimizing source-sink balance, thereby providing both theoretical and technical support for the effective utilization and reclamation of marginal lands.

rapeseed, salt stress, source-sink relationship, cultivation strategies

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