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植物对碱胁迫适应机制的研究进展

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摘要：碱胁迫包含离子毒害、渗透胁迫和根外高 pH 值（pH>8.5）伤害等多重胁迫，是一种主要的非生物胁迫，严重危害着植物的生长发育及作物的产量和品质。随着我国盐碱化土地不断扩增，当下生态系统平衡也遭到越来越严重的破坏，而相对于盐胁迫，目前对碱胁迫的认识还比较肤浅，对植物碱胁迫适应机制更是知之甚少。因此，了解并掌握碱胁迫以及植物对碱胁迫做出应答的适应机制，对挖掘耐碱种质资源改善生态环境，以及培育耐碱性作物品种、改良盐碱地具有重要的现实意义。基于近年来国内外研究报道，简要概述了盐、碱胁迫的定义与区别；总结了碱胁迫条件下，植物不同器官和细胞器的形态变化；阐述了植物通过细胞代谢，化学物质的合成与积累，以及活性氧的清除等途径响应于碱胁迫的生理适应机制；并从耐碱相关基因的克隆与功能鉴定、利用转录组学技术挖掘耐碱相关候选基因、Ca^{2+} 信号系统介导的植物耐碱性等 3 个方面揭示了植物应答碱胁迫的分子适应机制；指出尽管目前获得的耐碱相关候选基因较多，但真正分离克隆和功能鉴定到的基因较少。本文还对以修饰组学为主的多组学在植物耐碱机制中的研究前景做出展望，以期为挖掘植物新的耐碱相关基因并阐明其耐碱调控机制提供理论依据。

关键词：植物；碱胁迫；生理机制；分子机制

Research Advance in Plants′ adaptation to Alkali Stress

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Abstract：Alkali stress，including layers of sresses such as ion toxicity，osmotic stress and extraneous high pH（pH>8.5）injury，is a major abiotic stress that seriously endangers the growth and development of plants and the yield and quality of crops. With the continuous expansion of salinized land in China，the ecological system balance is increasingly seriously damaged. Compared with salt stress，the current understanding of alkali stress is relatively superficial，and the adaptation mechanism of plant alkali stress is even less well understood. Therefore，it is of great practical significance to understand and master the adaptive mechanism of alkali stress and plant response to alkali stress，to explore alkali-resistant germplasm resources for future improving ecological environment，and to cultivate alkali-resistant crop varieties for improving saline-alkali land. Based on the domestic and international progress recently，this paper briefly describes the definition and difference of salt and alkali stress. Morphological changes of different organs and organelles under alkali stress are summarized. The physiological adaptation mechanism of plants to alkali stress through cell metabolism，chemical synthesis and accumulation，and scavenging of reactive oxygen species is described. In addition，the molecular adaptation mechanisms of plants in response to alkali stress are indicated with three aspects：cloning and functional identification of alkali-tolerant genes，utilization of transcriptome technology to explore alkali-tolerant candidate genes，and plant alkali-tolerant mediated by Ca^{2+} signal system. It is pointed out that although many of candidate

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genes related to alkali resistance were obtained, fewer genes are actually cloned and explored with functional mechanism. Meanwhile, the research prospect of Multi-Omics which mainly focuses on modification omics in alkali tolerance mechanism of plants are prospected, in order to further provide theoretical basis for exploring new alkali resistance genes and unlocking the functional mechanism.

Key words: plants; alkali stress; physiological mechanism; molecule mechanism

据联合国教科文组织和粮农组织不完全统计，现阶段全球盐碱地面积已达到上百亿亩并且还在不断蔓延，而我国盐碱地总面积将近 14 亿亩，约占全国土地面积的 1/10，面积大、分布广、类型复杂[1-2]。近年来由于人类活动的影响，土壤盐碱化程度加剧，草地退化，耕地面积减少[3]，有些土壤的 pH 值甚至高达 10 以上，形成明显的碱斑[4-5]，使植物的生长和生产受到限制，进而使生物多样性遭到破坏[6-8]。在自然界中，土壤的盐化和碱化相伴而生，已有研究表明[9-12]，碱胁迫对植物的伤害远远大于盐胁迫的伤害。在碱胁迫下，土壤养分溶解度降低，无机离子的分布、运输和积累发生变化[13]，特别是细胞 pH 稳定遭到破坏，有机酸不平衡也相应增加，土壤渗透势下降，使离子失衡，从而抑制植物生长，降低植物的生物量，严重时会导致植物死亡[14-15]。相对于盐胁迫，人们对植物碱胁迫的适应性认识还比较肤浅，对其适应机制的研究不够深入，随着现代分子生物技术的迅猛发展，植物对碱胁迫适应性的研究越来越受到国内外研究者的关注，揭示植物对碱胁迫的适应机制，培育耐碱植物品种，提高植物的耐碱性是缓解碱胁迫对植物不良影响的有效措施，同时还可以产生较好的生态和经济效益，促进农业的可持续发展。因此本文综合前人研究成果总结了盐、碱胁迫的区别，从植物形态、生理与分子机制方面讨论植物对于碱胁迫的适应机制，并指出目前植物碱胁迫研究中存在的问题，展望了植物碱胁迫机制研究的前景，为揭示植物适应碱胁迫机制提供重要的理论基础。

1　盐、碱胁迫的定义与区别

1.1　盐、碱胁迫的定义

1954 年，美国盐应力实验室根据土壤的电导率（EC）、碱化度（ESP）和 pH 值的大小将盐碱土壤分为 3 种类型：盐土、碱土（苏打土）和盐碱土。目前世界各国已经普遍接受了将土壤电导率大于 4 ds/m（相当于 40 mmol/L NaC1 或 0.2 mPa 渗透势）定义为盐碱土的说法。19 世纪 80 年代末，中国土壤协会根据我国盐碱土的土壤特性，将其划分为盐土和盐碱土两大类[16]。学术界普遍认为，中性盐土壤的 EC>4，pH<8.5，ESP<15.0，而碱性盐土壤中 Na_2CO_3 和 $NaHCO_3$ 含量较高，土壤 EC<4，pH>8.5，ESP>15.0[17]，盐碱土壤中的盐分离子有 Na^+、Cl^-、SO_4^{2-}、CO_3^{2-} 和 HCO_3^- 等[18-19]，当这些离子过量积累后，它们会引起植物伤害，我们将这种伤害称之为盐胁迫。从广义上讲，盐胁迫包括中性盐胁迫（由 Cl^- 和 SO_4^{2-} 引起的胁迫）、碱性盐胁迫（由 CO_3^{2-} 和 HCO_3^- 引起的胁迫），以及混合盐碱胁迫（中性盐和碱性盐同时引起的胁迫）。从狭义上讲，为了研究方便，通常将中性盐胁迫称为盐胁迫。

1.2　碱胁迫与盐胁迫的区别

盐胁迫包括渗透胁迫和离子毒害，而碱胁迫不仅包括渗透胁迫和离子毒害，还包括 pH 胁迫[20]。与盐胁迫相比，碱胁迫破坏了植物细胞中已形成的各种离子的平衡状态，影响 K^+ 和 Ca^{2+} 等离子在细胞内的分布，严重影响世界范围内的作物生长和农业生产力。因此，碱胁迫离子毒性的综合作用对植物的危害更大，特别是根周围的高 pH 值环境和高渗透压，对植物在细胞、组织和器官不同层次的养分吸收，有机酸平衡，离子稳态与代谢影响更大[21-23]，从而更加严重地抑制了植物生长。但在基因表达水平上，与盐胁迫相比，碱胁迫更能强烈诱导 HKT 家族基因、NHX 家族基因、SOS 信号系统相关基因在植物根、茎和叶中的表达[24]。此外，高强度碱胁迫对光合速率的抑制程度大于盐胁迫，其原因可能更复杂，有待进一步研究[25-26]。然而，在自然环境中，碱胁迫与盐胁迫往往相互交错发生，可能对植物的生长发育造成混合效应[27-28]。

2　植物对碱胁迫的适应机制

2.1　碱胁迫下的植物形态变化

植物在不利条件下，其根、茎、叶等器官都会发生相应形态变化以适应环境变化。植物形态方面的变化是植物对于胁迫条件适应性变化最直观的体现。具体表现为，植物叶片通过增加表皮、叶肉细胞厚度，增加海绵细胞长度和直径[29-30]，以此增强耐碱性；植物根形态结构增厚阻止 Na^+ 在侧根和植物

新叶中的积累[31]；植物侧根的形成和非向地性生长也对耐碱有着非常重要的作用[32]。此外，植物通过细胞器结构和后含物的变化对碱胁迫做出了适应。例如，减少叶片细胞间隙，形成原生质膨胀和植物的大液泡，通过线粒体脊增大线粒体体积[29,33]，增加质体小球数量和体积，改变叶绿体超微结构，急剧增加细胞淀粉粒数量，有时甚至会形成巨大淀粉粒。然而，当植物受到严重的碱胁迫时，叶绿体膜膨胀甚至消失，基粒结构也会逐渐消退[34-35]。此外，不同植物在碱胁迫下的形态结构变化表现不同，在马铃薯中，叶绿体数量减少，引起细胞整齐排列[29,36]。在番茄中，叶面积减少和叶片气孔关闭[29,37]。

2.2 植物对碱胁迫的生理适应机制

2.2.1 植物细胞代谢 维持细胞内离子平衡的稳定是保障各种代谢过程正常进行的必要条件，植物细胞在碱胁迫下会发生离子区域化分布、吸收、运转等代谢过程，从而维持离子平衡，减小胁迫带来的危害。在碱胁迫条件下，离子在植物组织器官间不均匀分布[38-39]，例如 Na^+ 在植物不同组织器官中的分布表现为，新叶中 Na^+ 含量较低，老叶或老茎中含量较高[40]。在植物体内，除了离子区域化外，离子代谢还包括离子外排、离子转运等。在拟南芥中 SOS 信号系统中，盐超敏感蛋白（SOS1）负责将 Na^+ 通过根系外排到根际[41]，植物根系中 Na^+ 含量显著降低，促进水分从根部向地上部运输，从而改善地上部的水分状况[22-23]。另外植物通过水分运输，将吸收的大部分 Na^+ 分配在茎部，从而减少叶片受到伤害[42-43]。碱胁迫下植物幼嫩组织无成型的大液泡，仅有分散的小液泡，离子运输需要跨过细胞质后才能进入小液泡[44]，并且在植物幼嫩组织中，细胞远离导管，与导管中运输的离子接触较少，幼嫩组织细胞分裂、分化速度较快，代谢比较活跃[44]，无法贮存大量的离子。除了 Na^+ 吸收、运转，植物对于 NO_3^- 的吸收与运输也会发生变化。植物对硝酸盐的吸收和运输需要与质子内流同向进行，因此硝酸盐的吸收需要 H-ATP 酶等质子泵来提供电化学动力，而碱胁迫过程中离子平衡被破坏，植物细胞内硝酸还原酶（NR）活性改变，影响质子梯度分配进而影响 NO_3^- 吸收，例如，碱胁迫抑制了小麦对 NO_3^- 的吸收[45-46]，随着碱胁迫程度的增加，番茄、水稻和车前草中的硝酸盐净吸收量明显下降[47-48]。此外，玉米根中硝酸还原酶活性的下降，可能还与根中 Na^+、Cl^- 的离子毒害有关[49]。Soussi 等[50]研究结果表明，植物通过减少根瘤数量，降低固氮酶活性，从而抑制固氮过程来适应碱胁迫的伤害。而有研究证明在诸多离子的代谢中，Na^+ 和 K^+ 的代谢是植物适应碱胁迫危害的生理基础[51-52]，因此，碱胁迫条件下，植物有效的控制 Na^+-K^+ 的吸收和转运，维持 Na^+-K^+ 平衡是其适应碱胁迫的重要机制[53-54]，而 Na^+-K^+ 平衡被推测是植物抗碱的最终体现[55-58]。

植物细胞代谢的核心是光合作用和呼吸作用[59]，逆境条件下植物的光合作用会发生相应变化以适应环境伤害。许多植物在碱胁迫条件下光合作用下降，如气孔导度（Gs）和蒸腾速率（E）均随碱胁迫程度增加而下降[60-61]，而光合速率基本没有变化。但在高浓度的碱胁迫条件下，由于气孔导度的下降导致了植物净光合速率的明显降低[62-63]。Marcelis 等[64]的报道则表明，对于长期生长在天然盐碱环境下的植物而言，光合作用趋于稳定。在此环境下生长的植物主要通过改变光合面积而不是净光合速率来适应碱胁迫。Mg^{2+} 是叶绿素的重要组成部分，缺乏 Mg^{2+} 会间接影响植物的光合作用。在碱胁迫下，植物细胞中 Na^+ 增加，Ca^{2+} 降低，从而限制了 K^+ 吸收[65]，Ca^{2+} 吸收的降低和 Na^+ 的大量积累还会进一步限制 Mg^{2+} 吸收。此外，在碱胁迫下，由于 K^+ 与 Mg^{2+} 之间会发生更为严重的拮抗作用，Mg^{2+} 由根部向地上部运输受到抑制[66]，从而植物叶片中会保持较低的 Mg^{2+} 水平以便缓解碱胁迫对植物的伤害。

2.2.2 植物化学物质的合成与积累 植物通过合成积累相容性物质、抗氧化酶、还原性物质和有机酸等化学物质来适应碱胁迫，减少碱胁迫对于植物的危害。渗透调节保护剂甘氨酸甜菜碱在植物应对碱胁迫过程中起着非常重要的作用。高浓度碱胁迫下，由于花生茎叶中积累了大量甜菜碱[67]，从而使花生的耐碱性得以提高。另外，外施甜菜碱可以明显提高莴苣的生长[68]，脯氨酸作为细胞质中的另一种渗透调节物质，通常是由鸟氨酸和谷氨酸途径合成积累的，与甜菜碱一样，脯氨酸也能起到保护生物大分子和清除自由基的作用[69-70]。盐生植物如沙棘、大麦、虎尾草和星星草等，在碱胁迫条件下会积累大量的有机酸，并将其贮存在液泡中，构成主要的细胞渗透剂[71-72]。碱胁迫条件下，盐敏感作物水稻体内会合成并积累以苹果酸和柠檬酸为主的有机酸[73]，而沙棘体内主要积累草酸[74]。另外，碱胁迫下植物叶面喷施脯氨酸也可以刺激茎叶和根部的生长，增加植物干鲜重，提高光合速率[75]。

2.2.3 植物活性氧的清除 在碱胁迫过程中，植

物根会发生氧化胁迫反应，H_2O_2 和 O^{2-} 等活性氧（ROS）增加，当植物细胞受到伤害时，根系丙二醛（MDA）含量和相对电解质渗漏物（REL）含量增加，植物通过抗氧化酶系统来清除 ROS，从而减少碱胁迫对植物的伤害。对大多数清除 ROS 的抗氧化酶合成途径来说，它们可能会受到碱胁迫的抑制。Zhao 等[76]研究表明，过氧化氢酶（CAT）、AsA- 谷胱甘肽酶（AsA-GSH）合成途径受到碱胁迫抑制，这两种抗氧化酶不能有效清除 ROS，多余的 H_2O_2 可能主要通过过氧化物酶（POD）、2-Cys 过氧化物还原蛋白（PrxR）、谷胱甘肽过氧化物酶（GPX）等抗氧化酶得以清除。在活性氧清除的多种重要酶系统中，碱胁迫下，只有 POD 和 GPX 的活性增加，而超氧化物歧化酶（SOD）、CAT、抗坏血酸过氧化物酶（APX）、一脱氢抗坏血酸还原酶（MDHAR）、脱氢抗坏血酸还原酶（DHAR），谷胱甘肽还原酶（GR）、谷胱甘肽 s- 转移酶（GST）均随碱胁迫程度的增加而降低。为了减少碱胁迫带来的伤害，不同植物中的不同抗氧化酶的活性变化不同，在 50 mmol/L $NaHCO_3$ 胁迫下，番茄根中的 POD 丰度增加[70]，而在木本盐生植物猪笼草根系[77]和野生大豆根系[78]中由于几个编码 POD 的基因表达下降，导致了 POD 活性的降低。在 $NaHCO_3$ 胁迫下，柽柳细胞中的 APX 活性下降[79]，50 mmol/L $NaHCO_3$ 胁迫下野生大豆根系中的 PrxRs 活性增加，而 GSTs 的活性在该浓度碱胁迫 3~6 h 后增加，在胁迫 12 h 后下降[78]。

2.3　植物对碱胁迫的分子适应机制

2.3.1　耐碱相关基因的克隆与功能鉴定　分离耐碱相关基因，并利用基因工程技术改良植物品种，可提高植物对不良环境的抗性。近年来，几个碱胁迫相关基因 GsMIOX1a、GsSKP21 和 GsERF6 先后从野生大豆中被分离鉴定，超量表达这些基因显著提高了植物的耐碱性[80-82]；在耐盐碱植物星星草的根中，液泡 Na^+/H^+ 逆向转运蛋白基因 PutNHX 被碱胁迫特异诱导表达，PutNHX 通过调节液泡中钠离子的区室化方式参与调控根细胞内 pH 稳态，从而提高植物对碱胁迫的耐受性[83]；最近，有学者从盐生植物盐芥中分离克隆了一个可溶性无机焦磷酸酶基因 ThPP1，研究证实该基因通过上调差异表达基因调节磷酸盐和渗透调节物质的积累，进而增强了转基因水稻植株的耐碱性[84]；在番茄中，SAM 合成酶是参与 S- 腺苷酰 -L- 加硫氨酸生物合成的一个关键酶，SAM 合成酶基因 SISAM1 通过调控多胺代谢增加了转基因植株对碱胁迫的耐受性[85]。水稻是一种盐碱中度敏感的作物，目前仅有几个碱胁迫相关基因被克隆和功能鉴定。例如，Guo 等[86]和 Guan 等[87-88]先后报道了 ALT1、OsLOL5 和 OsCu/Zn-SOD 基因参与水稻对碱胁迫的应答，它们通过增强抗氧化防御系统调控水稻对碱胁迫的耐受性。综上所述，碱胁迫相关基因正被逐渐挖掘和利用，显示出它们在调控植物耐碱性中的重要性。

2.3.2　利用转录组学技术挖掘耐碱相关候选基因　利用转录组学方法从不同植物中挖掘一些耐碱相关的候选基因[89-92]，可为后期耐碱相关基因的克隆和功能鉴定提供基因资源，有助于提高植物耐盐性，培育耐碱植物品种。最近，Li 等[89]对 2 种不同水稻品种进行了转录组学分析，从差异表达基因（DEGs）中鉴定了 962 个碱胁迫响应基因（IAR），包括 28 个耐碱品种相关基因、771 个碱敏感品种相关基因和 163 个水稻品种的非特异性基因。基因本体论（GO）分析表明，大量的 IAR 基因参与了不同的胁迫反应；He 等[93]对获得的 *ThPP1* 超表达转基因水稻和野生型水稻进行了转录组测序分析，GO 结果表明碱胁迫下，参与氧化还原反应和代谢调控过程的 DEGs 数量远多于参与其他生物学过程的 DEGs 数量；Fan 等[94]通过高通量测序技术分析了盐、盐碱和干旱胁迫下大豆自交系 HJ-1 叶和根的基因表达谱，结果表明，相比于对照植株，3 种不同胁迫均上调了大豆自交系 HJ-1 叶和根中的许多 DEGs 的表达，2 种器官的基因表达谱的比较分析进一步显示，在响应于 3 种胁迫的过程中，许多与 Ca^{2+} 信号途径和核酸途径相关的基因均被上调表达，暗示了 3 种逆境信号途径发生了一定程度的交叉谈话（cross talk）。以上这些结果为深刻理解大豆抗逆分子机制提供了新的见解。Zhang 等[95]利用微阵列技术分析了星星草对盐胁迫和碱胁迫耐受性的分子特征，认为与盐胁迫相比，碱胁迫更易刺激星星草体内产生许多差异的表达基因，以及许多与 H^+ 转运和柠檬酸合成相关的上调基因，这些数据反映出星星草对盐、碱胁迫的耐受性具有不同的特征，为深入研究植物盐、碱胁迫耐受性的分子机制提供了新的视角。

2.3.3　Ca^{2+} 信号系统介导的植物耐碱性　Ca^{2+} 作为植物细胞内的第二信使，也参与了植物对碱胁迫信号的转导。DREPP 和钙网蛋白（CRTs，Calreticulin）是 2 种不同类型的 Ca^{2+} 结合蛋白，它们参与接收 Ca^{2+} 信号[76]。SvDREPP1 被证明是盐地鼠尾粟的一个碱胁迫相关蛋白，不仅可作为一个

Ca^{2+}结合蛋白，而且也能够结合钙调蛋白（CaM），可能通过Ca^{2+}/CaM信号通路，参与调控了植物对碱胁迫的响应[96]。CRTs蛋白作为Ca^{2+}结合蛋白的伴侣蛋白，通过与Ca^{2+}直接结合或是与Ca^{2+}信号通路相关蛋白直接结合发挥功能[97]。CRTs在植物响应碱胁迫中具有不同的表达模式，CRTs蛋白对碱胁迫比较敏感，其在基因和蛋白水平上都被碱胁迫所调控[76]。CaM是植物细胞中最重要的一类钙信号传感元件，主要通过与CaM结合蛋白（CaMBP）结合来调节细胞内的一些生理生化反应以适应逆境胁迫。碱胁迫下，星星草中的钙调蛋白（CaM）基因的表达被下调[76]，这一结果也在二色补血草[98]和野生大豆[99]的研究中得到印证，这表明CaM是植株根应答碱胁迫信号通路中共有的一个组分。半胱氨酸蛋白酶抑制剂（GPIs）通过抑制半胱氨酸蛋白酶来调控植物对非生物胁迫的耐受性，如野生大豆GsCPI14与Ca^{2+}/CaM结合受体类蛋白激酶GsCBRLK相互作用，协同调控植物的耐碱性[100]；类钙调蛋白激酶GRIKs是植物蛋白激酶SnRK1的上游激活因子，野生大豆GsGRIK1通过钙离子依赖途径磷酸化调控GsSnRK1.1，参与植物对碱胁迫的应答[101]。以上研究结果有助于加深对Ca^{2+}信号系统介导的植物碱胁迫应答通路的理解。

3 展望

碱土和碱化土壤改良是世界性难题。近年来，土壤碱化问题日益严峻，愈发值得关注。种植耐碱植物是改良碱（化）土的一种切实可行的方法，而培育耐碱作物品种是碱地开发利用的有效方式。因此，认识并掌握植物应对碱胁迫的适应机制可为利用分子育种技术培育耐碱作物提供坚实的理论依据。有关植物应对干旱、盐等胁迫的生理和分子机制已经得到了广泛研究，但对植物碱胁迫的适应机制研究比较肤浅，不够深入。基于目前发表的研究报道，本文详细总结了植物对碱胁迫的适应机制，但距离阐明植物应答碱胁迫的系统作用机制还存在很大的研究空白。

对植物耐碱性研究，尤其是植物耐碱分子机制的研究，主要局限在盐芥、羊草、星星草和野生大豆等盐生植物上，而对水稻、小麦等作物的研究只有零星报道。尽管借助转录组学技术筛选出大量与碱胁迫相关的候选基因，但被分离鉴定的基因为数不多。目前对植物耐碱分子机制的大部分研究报道仍停留在碱胁迫相关基因的克隆、基因表达以及生物学功能的初步分析等层面上，而对耐碱关键基因的精细定位、耐碱基因启动子关键元件的筛选鉴定、耐碱相关蛋白的功能识别、蛋白间的互作、上下游的调控关系以及与激素信号介导的关系等科学问题知之甚少。

近两年，CNS等国际著名期刊相继报道了利用修饰组学研究植物抗逆性的重要作用[102-104]，这为未来植物耐碱机制研究提供了借鉴，结合目前现有的基因编辑CRISPR/Cas9、代谢组学、表型组学及多组学联合、全基因组关联分析（GWAS）等技术，今后对植物应答碱胁迫的具体分子通路和作用机制进行多方位的深入探索，比较全面地揭示植物响应碱胁迫的精确调控机制，以便为植物耐碱性研究提供更多的理论依据，进而为利用分子育种技术培育耐碱植物品种提供技术支撑。

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