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水稻耐盐响应中钾运输载体的研究进展

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摘　要：水稻是全球主要粮食作物之一，随着种植区盐渍化加剧，其产量及安全已受到严重威胁。土壤中过高的盐浓度使细胞内 Na^+ 过量累积，K/Na 失衡，造成离子毒害和渗透胁迫。为减轻盐胁迫带来的生长抑制，水稻进化出一系列适应性机制，包括钾运输载体对 K^+ 的摄取或运输以及对 Na^+ 的区隔化或外排。水稻中介导这些过程的钾运输载体家族可划分为 Shaker、TPK、KT/HAK/KUP、HKT 和 CPA 五大家族。本文总结了上述水稻钾运输载体在盐胁迫下的功能作用及调控机制的研究进展，并对未来研究前景予以展望。

关键词：水稻；盐胁迫；钾运输载体；功能；调控机理

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Advances in Potassium Carriers to Salt Stress in Rice

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Abstract: Rice is one of the world's major food crops. With increasing salinization in planting areas, grain yield and security have been seriously threatened. High salinity in the soil causes excessive accumulation of Na^+ and K/Na imbalance in cells, resulting in ion toxicity and osmotic stress. A series of adaptive mechanisms have been evolved in rice to alleviate the growth inhibition caused by salt stress, including the uptake or transport of K^+ and compartmentalization or expulsion of Na^+ by potassium carriers. The family of potassium carriers mediating these processes in rice can be divided into five families: Shaker, TPK, KT/HAK/KUP, HKT and CPA. This paper reviews recent work on the functions and regulation mechanisms of the potassium carriers in rice in response to salt stress and discusses the future perspectives of research.

Key words: rice; salt stress; potassium carriers; function; regulation

1　盐胁迫对水稻的危害及水稻耐盐机理

根据联合国粮农组织统计，全球约 20%农业用地受盐害的程度不断加重，预计到 2050 年，超过 1/2 的耕地将盐碱化[1]。不断加剧的土壤盐碱化已严重影响 13 个国家约 40.3 亿人口（占世界人口的 50%），是制约全球粮食产量和品质的主要环境因素之一[2-3]。

高盐环境对水稻各个生长阶段造成许多负面影响。萌发阶段，盐分引起水稻种子生理代谢紊乱，出苗率下降；营养生长期，Na^+、Cl^- 在叶片的过度积累会造成叶片卷曲枯黄，抑制新叶和根系的生长发育，光合作用受阻，抗氧化酶活性下降等。进入分蘖

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期和成熟期后，水稻的分蘖和伸长受到盐胁迫抑制，出现有效分蘖数降低，孕穗期缩短，抽穗延迟，穗短粒少，籽粒不饱满等情况。

水稻对盐胁迫的响应涉及许多生理过程，包括渗透调节、离子平衡、活性氧清除、激素调控等[4]。其中，维持 K^+ 和 Na^+ 的稳态对耐盐性至关重要。大量钾离子运输载体通过吸收 K^+，排出 Na^+ 或将 Na^+ 区隔化于液泡内来维持细胞质中较高的 K^+/Na^+ 值，以缓解盐胁迫引起的离子毒害[5-6]。参与这些过程的钾运输载体可归类为 Shaker、TPKs（tandem-pore K^+ channels）、KT/HAK/KUP（K^+ transporter/high-affinity K^+ transporter/K^+ uptake transporter）、HKT（high-affinity potassium transporter）和 CPAs（monovalent cation/proton antiporters）。本文就水稻钾转运载体在盐胁迫条件下发挥的功能作用以及调控机理进行了综述，并对未来研究前景予以展望，为培育耐盐高产的水稻品种提供重要的理论依据。

2 水稻钾运输载体对盐胁迫的响应及其耐盐功能

2.1 Shaker 通道

单一完整的植物 Shaker 钾离子通道由 4 个亚基组成，每个亚基上具有 6 个跨膜区和 1 个 C-末端胞内区，其中第 4 跨膜区上富含感受膜电位变化的正电荷氨基酸，负责控制通道开放与关闭，第 5、6 跨膜区间的环状结构（P-loop）包含高度保守的特异序列，使通道具有高 K^+ 选择性[7-9]。Shaker 钾离子通道具有不连续的电压门控开关，可通过电压依赖性及 K^+ 跨膜运动的方向进一步划分为内向型整流 K^+ 通道（IR）、外向型整流 K^+ 通道（OR）、弱整流型 K^+ 通道（WR）[10-11]。

研究发现，内向整流型 K^+ 通道 OsAKT1 的超极化位点在盐胁迫下被激活，促进根系 K^+ 的大量摄入[12]。OsAKT2 介导 K^+ 在韧皮部装载和再分布，有助于维持 Na^+、K^+ 的稳态并抑制根部对 Na^+ 的吸收[13]。内向整流型 K^+ 通道 OsKAT1 和 OsKAT2 也参与耐盐响应过程。OsKAT1 具有内吸 K^+ 及外排 Na^+ 的作用，能够提高酵母和水稻细胞的耐盐性[14-15]。OsKAT2 在保卫细胞 K^+ 吸收中发挥作用并通过调节气孔开放来参与水稻耐盐[16-17]。外向整流型 K^+ 通道 OsK5.2（OsGORK）在响应盐胁迫中可能也发挥重要作用，其转录水平受盐胁迫诱导上调，有利于 K^+ 在根中的保留[18-19]。另有研究发现，OsK5.2 参与调节气孔关闭，同时将 K^+ 卸载至木质部，以提高水稻的耐盐性[20]。

2.2 TPK 通道

不同于 Shaker 钾离子通道，TPK 双孔钾离子通道每个亚基仅包含 4 个跨膜区及 2 个环状结构（P-loop），虽然其对电压变化并不敏感，但是由于具备高度保守的特异序列，因此同样对 K^+ 具有高度选择性。水稻 TPK 包含 3 名成员：OsTPKa、OsTPKb、OsTPKc[21]（表 1）。

表 1 水稻钾离子通道

Table 1 Potassium channels in rice

基因名称 Gene name	基因 ID Genomic locus	表达部位 Expression position	蛋白功能 Protein Function	文献 Reference
OsAKT1	LOC_Os01g45990	根（表皮/维管组织）、茎、叶、花粉 Root (epidermis/vascular tissue), stems, leaf, pollen	质膜内向整流型 K^+ 通道，受盐胁迫诱导表达，负责根系 K^+ 吸收 The plasma membrane inward rectifying K^+ channel, which is induced by salt stress, is responsible for root K^+ absorption	[8,12]
OsAKT2	LOC_Os05g35410	叶（旗叶/叶鞘）、茎、颖壳、根 Leaf (flag leaf/sheath), stem, glume, root	质膜内向整流型 K^+ 通道，受盐胁迫诱导表达，介导 K^+ 韧皮部装载及再分配，维持 Na^+、K^+ 的平衡 The plasma membrane inward rectifying K^+ channel, induced by salt stress, mediates the loading and redistribution of K^+ phloem, and maintains the balance of Na^+ and K^+	[13]
OsKAT1	LOC_Os01g55200	茎、根中几乎不表达 Almost no expression in stem and root	内向整流型 K^+ 通道，介导吸收 K^+ 及外排 Na^+ The inward rectifying K^+ channel mediates the absorption of K^+ and the expulsion of Na^+	[14]
OsKAT2	LOC_Os01g11250	地上部均有表达（保卫细胞）Expressed in all parts of the over ground (guard cell)	内向整流型 K^+ 通道，介导保卫细胞 K^+ 吸收，调节气孔开放提高水稻耐盐性 The inward rectified K^+ channel mediates the K^+ absorption of guard cells and regulates stomatal opening to improve salt tolerance of rice	[15-17]
OsK5.2	LOC_Os06g14030	叶片、节间、叶鞘、根 Leaf, internode, leaf sheath, root	外向整流型 K^+ 通道，受盐胁迫诱导表达，保留幼苗根中的 K^+，调节气孔关闭，介导 K^+ 的木质部卸载 The outward-rectifying K^+ channel, induced by salt stress, retained K^+ in seedling roots, regulates stomatal closure and mediates xylem offloading of K^+	[18-20]
OsTPKa	LOC_Os03g54100	细胞融酶液泡（LV）Lytic vacuole	双孔钾离子通道，过表达减少 Na^+ 的积累并促进 K^+ 转运，增加盐耐受性 Two-pore potassium channels, overexpression OsTPKa reduces Na^+ accumulation and promotes K^+ transport, increasing salt tolerance	[21,24-25]
OsTPKb	LOC_Os07g01810	小的蛋白储存液泡（SV）Small protein storage vacuole (SV)	双孔钾离子通道，过表达减少 Na^+ 的积累并促进 K^+ 转运，增加盐耐受性 Two-pore potassium channels, overexpression OsTPKb reduces Na^+ accumulation and promotes K^+ transport, increasing salt tolerance	[21,24-25]

OsTPKa 和 OsTPKb 分别定位于细胞溶酶液泡(LVs)和小的蛋白储存液泡(SVs)中[22-23]，过表达 *OsTPKa* 和 *OsTPKb* 减少 Na^+ 积累并促进 K^+ 转运以维持胞内离子稳态，增强对盐胁迫的耐受性[24-25]。

2.3　KT/HAK/KUP 转运体

HAK 家族在植物 K^+ 的摄取及转运中扮演重要的角色，结构分析表明该蛋白家族具有 10～14 个跨膜区，且在第 2 和第 3 跨膜区之间包含 1 个环状结构[26]。水稻 HAK 家族包含 27 个成员，可被划分为 4 个基因进化簇：簇 Ⅰ、簇 Ⅱ、簇 Ⅲ、簇 Ⅳ[27]，其中簇 I 被认为对 K^+ 具有高亲和力，簇 II 成员的序列和功能差异较大，而簇Ⅲ、簇Ⅳ的功能特征鲜有报道[28-29]。水稻 HAK 转运体介导 K^+ 的吸收转运和 Na^+ 的外排(表 2)。大多 *OsHAK* 的表达受低钾和盐胁迫诱导，OsHAK1、OsHAK5 和 OsHAK16 通过促进 K^+ 的吸收来维持植物体内较高的 K/Na 比[29-32]，OsHAK3 和 OsHAK21 对调节胞质内 Na^+/K^+ 稳态至关重要[33-35]。OsHAK8 介导 K^+ 吸收和转运以应对低钾胁迫，耐盐性功能仍需进一步研究[36]。*OsHAK10*、*OsHAK12*、*OsHAK17* 和 *OsHAK18* 受盐胁迫诱导表达，OsHAK10 可增加老叶中 Na^+ 的积累[37]，OsHAK12 具有 Na^+ 渗透性，参与木质部 Na^+ 的回收从而降低地上部 Na^+ 含量[38]，OsHAK17 和 OsHAK18 同样受低钾诱导，但不直接参与 K^+ 吸收，而参与 K^+ 在韧皮部 K^+ 转运和再分配[39-41]。此外，某些 OsHAK 转运体对种子萌发有所调节，OsHAK9 介导盐胁迫下种子萌发中 Na^+、K^+ 的平衡[42]，OsHAK21 参与盐胁迫下 K^+ 的吸收，并在种子萌发和幼苗建立中发挥作用[43]。

表 2　水稻 KT/HAK/KUP 转运体

Table 2　KT/HAK/KUP transporters in rice

基因名称 Gene name	基因 ID Genomic locus	表达部位 Expression position	蛋白功能 Protein Function	文献 Reference
OsHAK1	LOC_Os04g32920	根(表皮/分生组织)、茎 Root (epidermis/meristem), stem	高亲和钾转运体，受低钾及高钾诱导，介导 K^+ 吸收及转运。受盐胁迫诱导表达，增加 K/Na 比 High affinity potassium transporters, induced by low and high potassium, mediate K^+ absorption and transport. Induced by salt stress, K/Na ratio was increased	[29]
OsHAK3	LOC_Os01g27170	根、花药、叶、茎、颖片 Root, anther, leaf, stem, glume	高亲和钾转运体，受低钾诱导表达，负责根系 K^+ 吸收及转运。受盐胁迫诱导，维持 Na^+/K^+ 稳态 High affinity potassium transporters, induced by low potassium, are responsible for root K^+ absorption and transport. Induced by salt stress, Na^+/K^+ homeostasis was maintained	[33]
OsHAK5	LOC_Os01g70490	根(表皮/中柱/侧根)、叶、胚、花药、种子、种壳 Root (epidermis/mesocolumn/lateral root), leaf, embryo, anther, seed, seed shell	高亲和钾转运体，受低钾和盐胁迫诱导表达，负责根系 K^+ 吸收及转运，增加 K/Na 比 High affinity potassium transporters, induced by low potassium and salt stress, are responsible for root K^+ absorption and transport, K/Na ratio was increased	[30]
OsHAK8	LOC_Os03g21890	根、茎、叶、花药、颖片 Root, stem, leaf, anther, glume	高亲和钾转运体，受低钾诱导表达，负责根系 K^+ 吸收及转运 High affinity potassium transporters, induced by low potassium, are responsible for root K^+ absorption and transport	[36]
OsHAK9	LOC_Os07g48130		高亲和钾转运体，受盐胁迫诱导表达，调控种子萌发及 Na^+、K^+ 的平衡 High affinity potassium transporter, induced by salt stress, regulates seed germination and Na^+, K^+ balance	[42]
OsHAK10	LOC_Os06g42030		高亲和钾转运体，受盐胁迫诱导表达，促进老叶中 Na^+ 的积累 High affinity potassium transporters, induced by salt stress, promote Na^+ accumulation in old leaves	[37]
OsHAK12	LOC_Os08g10550	根、茎、叶、花药、颖片 Root, stem, leaf, anther, glume	高亲和钾转运体，Na^+ 可渗透性，受盐胁迫诱导表达，介导地上部 Na^+ 的排除 High affinity potassium transporter, Na^+ permeable, induced by salt stress, mediates aboveground Na^+ exclusion	[38]
OsHAK16	LOC_Os03g37840	根(表皮)、茎(维管)、叶(叶肉/维管) Root (epidermis), stem (vascular), leaf (mesophyll/vascular)	高亲和钾转运体，受盐胁迫、低钾诱导表达，负责根系 K^+ 吸收，维持 K^+ 稳态 High affinity potassium transporters, induced by salt stress and low potassium, are responsible for K^+ absorption and maintenance of K^+ homeostasis in roots	[31-32]
OsHAK17	LOC_Os09g27580	叶(叶肉)、叶鞘、茎、根茎结合处(维管/韧皮)等 Leaf (mesophyll), leaf sheath, stem, root junction (vascular/phloem), etc	高亲和钾转运体，受低钾和盐胁迫诱导表达，参与 K^+ 在地上部转运和再分配。High affinity potassium transporters, induced by low potassium and salt stress, participate in the K^+ transport andredistribution in the shoot.	[39]
OsHAK18		根(中柱)、根茎结合处、叶、颖壳、雄蕊、雌蕊等 Root (middle column), junction of rhizome, leaf, glume, stamen, pistil, etc	高亲和钾转运体，受盐胁迫、低钾诱导表达，负责 K^+ 在韧皮部的装载及地上部 K^+ 的分配 High affinity potassium transporters, induced by salt stress and low potassium, are responsible for K^+ loading and redistribution in shoot	[40-41]
OsHAK21	LOC_Os03g37930	根等各组织器官中 Root and other tissues and organs	高亲和钾转运体，受低钾诱导表达，负责 K^+ 吸收及转运。受盐胁迫诱导，促进 K^+ 吸收，维持 Na^+/K^+ 稳态，调控种子萌发及幼苗生长 High affinity potassium transporters, induced by low potassium, are responsible for K^+ absorption and transport. Induced by salt stress, it promoted K^+ absorption, maintained Na^+/K^+ homeostasis, regulated seed germination and seedling growth	[34-35,43]

2.4 HKT 转运体

HKT 是一类 Na^+ 或 K^+ 转运体或 Na^+、K^+ 共转运体，由 4 个 MPM（membrane-pore-membrane motif）基序组成，每个基序由 2 个跨膜区和 1 个环状结构（P-loop）构成[44]。HKT 的离子选择性通常由第一环状结构的保守氨基酸性质决定[45-46]。目前已在水稻中鉴定出 9 个 *HKT* 基因，依据进化关系可划分为 2 个亚族[47]。

I 类 OsHKT 转运体主要定位于木质部薄壁细胞的质膜，具有 Na^+ 选择性[48-49]（表 3）。OsHKT1;1 和 OsHKT1;4 通过降低韧皮部或木质部汁液中 Na^+ 浓度来减轻地上部离子毒害[47-52]。OsHKT1;5 将木质部中的 Na^+ 卸载至薄壁细胞，同时促进 K^+ 向地上部的运输来维持 Na^+ 和 K^+ 平衡[53-54]。OsHKT1;3 与 OsHKT1;5 均可在盐胁迫下促进种子萌发并恢复幼苗生长[55-57]。II 类 OsHKT 转运体则对 Na^+、K^+ 均具有较强的渗透性，在维持水稻 Na^+/K^+ 稳态中发挥作用（表 3）。OsHKT2;1 介导 Na^+ 的流入以补充缺钾胁迫时 K^+ 的缺失，但其对 Na^+ 的吸收功能可被盐胁迫迅速抑制[58-60]。OsHKT2;2 在低钾条件下诱导 Na^+ 的吸收，随胞外 K^+ 浓度的增加，Na^+ 转运速率降低[61]。OsHKT2;4 具有较强的 K^+ 渗透性，高 Na^+ 浓度下 OsHKT2;4 介导的 Na^+ 转运活性受限[62-64]。

2.5 CPA 转运体

植物 CPA 家族主要包括 3 个家族：NHX（Na^+/H^+ exchanger）、CHX（cation/H^+ exchanger）和 KEA（K^+ efflux antiporter）。其中，NHX 家族在耐盐性方面的研究较为深入。NHX 一般含有 10～12 个跨膜区，跨膜区之间没有典型的环状结构。NHX 能够催化 H^+ 与 Na^+ 和/或 K^+ 的跨膜交换，对盐胁迫下维持植物细胞内 pH 平衡及离子稳态至关重要[65-66]。水稻中有 5 个基因编码 NHX 转运体，根据进化关系，可分为 2 个亚组，OsNHX1-OsNHX4 为第一亚组，定位于液泡膜，OsNHX5 为第二亚组，定位于内膜[67]。

研究表明，*OsNHX1*、*OsNHX2*、*OsNHX3* 和 *OsNHX5* 均受盐胁迫诱导表达，它们将细胞质中的 Na^+ 区隔化至液泡内或其他区室内，维持胞质内离子平衡，减少 Na^+ 的毒害[68-70]，对 OsNHX2、OsNHX3 的进一步研究发现其主要通过将 Na^+ 储存至叶鞘薄壁细胞中来提高水稻的耐盐力[70-71]。OsNHX5 的功能与家族其他成员略有不同，它介导低 Na^+ 转运，KCl 处理下其转录水平上升，推测 OsNHX5 具有 K^+/H^+ 交换的作用[72]。OsSOS1 是质膜定位的 Na^+/H^+ 反向转运体，盐胁迫下其表达上调并通过 OsCBL4-OsCIPK24-OsSOS1 途径激活，从而促进 Na^+ 外排，降低细胞内的 Na^+ 含量，调节水稻的耐盐性[72-73]。

表 3 水稻 HKT 转运体

Table 3 HKT transporters in rice

基因名称 Gene name	基因 ID Genomic locus	表达部位 Expression position	蛋白功能 Protein Function	文献 Reference
OsHKT1;1	LOC_Os04g51820	叶（维管组织）、根（中柱/薄壁细胞）Leaf (vascular tissue), root (medium column/parenchyma cell)	高亲和力钾转运体，调控 Na^+ 向地上部的运输，降低叶片 Na^+ 累积 High affinity potassium transporter regulates the transport of Na^+ to the overground part and reduces the accumulation of Na^+ in leaves	[49-50]
OsHKT1;3	LOC_Os02g07830		高亲和力钾转运体，调控种子萌发及幼苗生长 High affinity potassium transporter, regulates seed germination and seedling growth	[55-57]
OsHKT1;4	LOC_Os04g51830	根、茎、叶（叶鞘）Root, stem, leaf (leaf sheath)	高亲和力钾转运体，控制木质部汁液 Na^+ 浓度，减少幼叶中 Na^+ 积累 High affinity potassium transporter controls the concentration of Na^+ in xylem SAP and reduces the accumulation of Na^+ in young leaves	[51-52]
OsHKT1;5	LOC_Os01g20160	根（木质部上的薄壁细胞）Root (parenchyma cell on xylem)	高亲和力钾转运体，木质部 Na^+ 卸载，促进 K^+ 运输，维持钠钾平衡，缓解盐胁迫对种子萌发和幼苗生长的抑制 High affinity potassium transporter, xylem Na^+ unloading, promote K^+ transport, maintain sodium and potassium balance, relieve salt stress on seed germination and seedling growth inhibition	[53-54, 56-57]
OsHKT2;1	LOC_Os06g48810	根（皮层/内皮层）Root (cortex/endocortex)	高亲和力钾转运体，低钾诱导 Na^+ 吸收，盐胁迫抑制 Na^+ 摄取 High affinity potassium transporter, low potassium induced Na^+ uptake, salt stress inhibited Na^+ uptake	[58-60]
OsHKT2;2			高亲和力钾转运体，Na^+、K^+ 选择性，低钾诱导 Na^+ 吸收 High affinity potassium transporter, Na^+, K^+ selectivity, low potassium induced Na^+ absorption	[61]
OsHKT2;4	LOC_Os06g48800	叶、茎、初生根、侧根 Leaf, stem, primary root, lateral root	高亲和力钾转运体，高 K^+ 渗透性，介导 K^+ 吸收，降低 Na^+ 转运 High affinity potassium transporter with high K^+ permeability mediates K^+ absorption and reduces Na^+ transport	[62-64]

3　水稻钾运输载体在盐胁迫下的调控机理

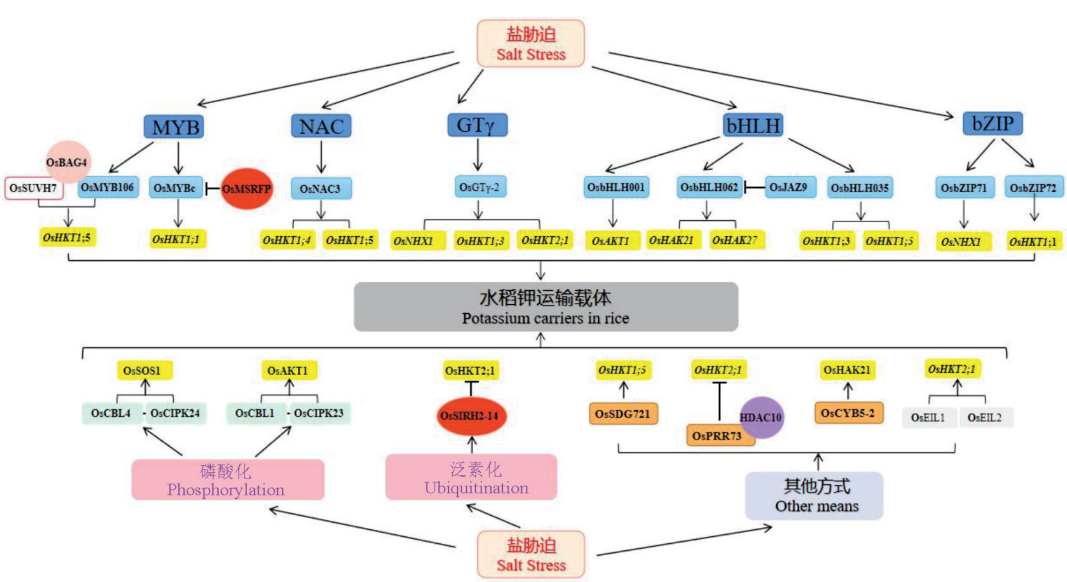
3.1　转录调控

转录调控是植物应对非生物胁迫的关键手段[74]，目前已鉴定出许多响应盐胁迫的转录因子家族，如 bHLH、WRKY、MYB、NAC 等[75]，其对钾运输载体均具有一定的调控作用（图 1）。OsMYB106（MYB 型转录因子）、OsBAG4（分子伴侣调控蛋白）和 OsSUVH7（DNA 甲基化识别酶）三者相互作用形成复合物，促进 OsMYB106 与 *OsHKT1;5* 中的顺式结合元件 MYBE 结合，激活 OsHKT1;5 的表达，减少 Na^+ 在胞内的过度累积[76]。OsGTγ-2（tri-helix transcription factor，三螺旋转录因子家族 GTγ 亚家族成员）受盐胁迫、渗透胁迫及氧化胁迫诱导表达，研究表明 OsGTγ-2 直接与 *OsNHX1*、*OsHKT1;3* 和 *OsHKT2;1* 的启动子相互作用并正向调节水稻耐盐性[77]。OsNAC3（NAC 型转录因子）通过正向调节 OsHKT1;4 和 OsHKT1;5 参与水稻耐盐响应过程[78]。OsbHLH001（bHLH 型转录因子）可通过特异性结合 *OsAKT1* 启动子区的 E-box 序列，诱导 *OsAKT1* 的表达，促进 K^+ 流入从而调节盐胁迫下水稻中的钾钠比[79]。OsbHLH035 通过激活 *OsHKT1;3* 和 *OsHKT1;5* 的表达，调控盐胁迫后的种子萌发和幼苗恢复[80]。OsJAZ9（OsTIFY11a，TIFY 型转录因子）能够与 OsbHLH062 相互作用并抑制 OsbHLH062 介导的对 *OsHAK21* 和 *OsHAK27* 转录激活[81]。转录因子 OsbZIP72 直接与 *OsHKT1;1* 启动子区域中的 ABA 反应元件结合，诱导 *OsHKT1;1* 的表达以响应盐害[82]，OsbZIP71 能够与 *OsNHX1* 的启动子结合，促进 *OsNHX1* 表达，增强水稻耐盐性[83]。

3.2　翻译后修饰

蛋白质翻译后修饰对水稻响应盐胁迫至关重要，通过磷酸化、泛素化等修饰手段可快速调节多个细胞途径中蛋白质活性、功能和定位以及不同蛋白间的相互作用，以减轻盐胁迫造成的损害[84-85]。

磷酸化是最常见修饰形式，CBL-CIPK 网络在感应盐诱导的 Ca^{2+} 信号和调节 Na^+/K^+ 稳态方面中发挥着关键作用[86-87]（图 1）。



涉及激活或调控响应盐胁迫水稻钾运输载体的途径；水稻转录因子（TF）MYB、GTγ、bHLH、bZIP 对钾运输载体的转录调控；磷酸化、泛素化等方式对钾运输载体活性的调控。

图 1　水稻钾运输载体受调控方式

Involved in the activation or regulation of rice potassium carriers in response to salt stress. Transcriptional regulation of rice transcription factors (TF) MYB, Gt-γ, bHLH and bZIP on potassium. carriers. Regulation of potassium carriers activity by phosphorylation and ubiquitination.

Fig. 1　Regulated modes of potassium carriers in rice

SOS 信号通路是植物中首个发现参与非生物逆境的信号传导途径。水稻 SOS 途径中，钙结合蛋白 OsSOS3/OsCBL4 感知盐胁迫引起的胞质钙信号，与蛋白激酶 OsSOS2/OsCIPK24 互作并磷酸化

OsSOS2，磷酸化后的 OsSOS2 蛋白迅速与质膜定位的 OsSOS1 结合并将其激活，促进 Na^+ 排出，维持细胞中离子平衡[88]。此外，盐胁迫引发的胞质内 Ca^{2+} 浓度升高，诱导 OsCBL1 和 OsCIPK23 互作并激活 OsCIPK23，形成的复合物磷酸化激活 OsAKT1 的通道活性，促进根部 K^+ 吸收[89]。

泛素化修饰在植物应激反应中也起着作用（图1）。E3 连接酶通过改变应激响应蛋白（如转录因子）的稳定性来发挥调节作用，从而改变下游反应或通过降解下游级联本身所涉及的蛋白质，其中泛素26S 蛋白酶体介导的盐相关蛋白降解在耐盐性中发挥重要功能[90-91]。据报道，RING 型 E3 连接酶 OsSIRH2-14 在高盐条件下与 OsHKT2；1 在胞质和质膜上发生强烈的物理作用，并通过泛素 26S 蛋白酶体降解 OsHKT2；1 以减少 Na^+ 的吸收[92]。OsMYBc 能够与 OsHKT1；1 启动子结合上调其活性，正向调控水稻的耐盐性[88]，RING 型 E3 连接酶 OsMSRFP 通过泛素 26S 蛋白酶体介导 OsMYBc 降解并减弱 OsMYBc 对 OsHKT1；1 的转录调控作用，降低 *OsHKT1；1* 的表达[93]。

3.3 其他调控手段

除上述提及到的调控手段，一些钾运输载体可与其他蛋白之间产生相互作用以此来完成盐胁迫环境下信号的传递、基因的表达以及对生长发育的调控等（图 1）。研究发现，在盐胁迫下，OsSDG721（SET domaing group，具有组蛋白赖氨酸甲基转移酶活性的蛋白）能够结合 *OsHKT1；5* 的启动子区域，上调 *OsHKT1；5* 的表达，维持胞内 K^+、Na^+ 稳态[94]。OsPRR73（pseudo response regulator，伪应答调控蛋白）与 HDAC10（Histone deacetylases，组蛋白去乙酰化酶）结合形成的复合物能够与 *OsHKT2；1* 的启动子区域结合，抑制 *OsHKT2；1* 的表达，从而减少细胞内 Na^+ 的流入和胞质内 ROS 的积累，增强水稻的耐盐性[59]。盐胁迫下，内质网定位的细胞色素 b_5（OsCYB5-2）能与 OsHAK21 互作，增强 OsHAK21 对 K^+ 亲和性，促进 K^+ 内吸，从而维持细胞内 K^+/Na^+ 稳态[34]。OsEIL1 和 OsEIL2（乙烯不敏感 3-LIKE1、LIKE2）能够直接激活 *OsHKT2；1* 在根中的表达，OsHKT2；1 吸收并转运过多的 Na^+，负向调控水稻幼苗的耐盐性[95]。

4 展 望

随着对水稻钾运输载体研究的不断深入，其具体结构功能也逐渐得以揭示，但目前水稻钾运输载体的分子机制研究仍处于起始阶段，在探究钾运输载体调控的方式及互作关系上仍有很大的空缺。针对这一问题，笔者认为可以从以下几个方面展开深入探究：(1)从基因和蛋白水平对耐盐及不耐盐的水稻进行分析，探究不同品种类型之间钾运输载体的差异，进一步揭示不同材料间盐胁迫反应的异质性。(2)盐胁迫下，植物感知渗透压变化和离子信号并将其转导至细胞内部，以此改变细胞特性来应对盐胁迫。通过分析寻找与钾运输载体互作的蛋白或启动子等顺式元件，来探寻钾运输载体在盐胁迫信号网络中发挥的功能作用，例如调节下游靶基因表达的转录因子或激酶等。(3)水稻钾运输载体蛋白具有不同的时间空间表达模式，进一步探究其在水稻生长的各时期阶段发挥不同的作用有重要意义。例如在盐胁迫条件下，OsHKT1；4 控制生殖生长阶段的 Na^+ 稳态，但不影响营养阶段的 Na^+ 积累；OsHKT1；5 介导的 Na^+ 调控转运，对维持盐害下水稻苗期和生殖期生长至关重要。(4)许多与水稻不同发育阶段耐盐性相关的 QTL(数量性状基因座)，可有效控制水稻茎部和根系的 K^+ 浓度、叶片光合作用和蒸腾速率、成熟期灌浆粒数和重量等性状。耐盐稻杂交所鉴定的 qSKC-1 QTL 编码 OsHKT1；5 调节盐胁迫下的钠钾稳态，中国地方品种‘九彩青’中分离出的 qSE3 QTL 具有与 OsHAK21 类似的功能，可促进盐胁迫下的种子萌发和幼苗建立。因此，进一步挖掘耐盐稻基因，为培育耐盐高产的水稻品种提供基因资源，并利用标记辅助育种(MAB)将耐盐 QTL 转移到优质水稻材料是实现水稻耐盐的一种可能途径。

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