植物学报 *Chinese Bulletin of Botany* 2017, **52** (2): 225–234, www.chinbullbotany.com
doi: 10.11983/CBB16023

·专题论坛·

植物K^+通道AKT1的研究进展

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摘要 钾(K)是植物生长发育必需的大量营养元素之一, 主要通过根细胞的K^+通道及转运蛋白介导吸收。AKT1是Shaker型K^+通道家族的重要成员, 在植物根吸收K^+和体内跨膜转运中发挥重要作用。该文综述了植物AKT1的分子结构、组织特异性表达、调控机制及生物学功能等方面的研究进展, 并对该通道今后的研究方向进行了展望。

关键词 AKT1, K^+吸收, K^+饥饿, 耐盐性

伍国强, 水清照, 冯瑞军 (2017). 植物K^+通道AKT1的研究进展. 植物学报 **52**, 225–234.

K^+是植物细胞中含量最丰富的无机阳离子之一, 主要通过根表皮细胞和皮层细胞的质膜K^+转运系统吸收并运输到植物体内(王毅和武维华, 2009; Alemán et al., 2011; Dreyer and Uozumi, 2011; Wang and Wu, 2013; Nieves-Cordones et al., 2014a)。K^+在植物生长发育、逆境胁迫响应及生理生化反应等方面起着重要作用(Alemán et al., 2011; Nieves-Cordones et al., 2014a)。一般而言, 植物细胞维持正常新陈代谢所需K^+的最佳浓度为100 mmol·L^{-1}, 但土壤中能被植物利用的K^+浓度仅为0.1–1 mmol·L^{-1}, 在一些盐碱地中甚至更低(Maathuis and Sanders, 1993; Maathuis, 2009)。因此, 土壤中的K^+远远不能满足植物正常生长需要, 使植物经常处于K^+饥饿状态, 严重影响其生长发育。鉴于复杂多变的环境及K^+的重要作用, 众多研究者对植物K^+吸收和转运机制进行了深入研究。

植物在长期进化过程中形成了一系列复杂的K^+吸收和转运系统。已知在模式植物拟南芥(*Arabidopsis thaliana*)中存在15个K^+选择性通道, 包括9个Shaker型、5个TPK (two-pore K^+ channel)型和1个Kir-like型K^+通道(Ward et al., 2009; Hedrich, 2012; Demidchik, 2014)。另外, 一些非选择性阳离子通道(non-selective cation channels, NSCC)也可以通透K^+, 主要包括20个CNGC (cyclic nucleotide gated channels)通道、20个GLR (glutamate receptor-like)通道和1个TPC (two-pore channel)通道(Shabala, 2003; Demidchik and Maathuis, 2007; Dietrich et al., 2010; Hedrich, 2012; Demidchik, 2014)。植物K^+转运蛋白主要包括KUP (K^+ uptake permease)/HAK (high-affinity K^+ transporter)/KT (K^+ transporter)、HKT (high-affinity K^+ transporter)和CPA (cation proton antiporter) (Gierth and Mäser, 2007; Kronzucker and Britto, 2011; Wang and Wu, 2013; Han et al., 2016)。近年来, 人们相继在植物中克隆到编码这些蛋白的基因, 为深入研究植物K^+吸收机制奠定了坚实的基础。

AKT1 (Arabidopsis K^+ transporter 1)是植物中广泛存在的一类内向整流K^+通道, 与动物中的Shaker型K^+通道具有高度的同源性(Pilot et al., 2003)。Sentenac等(1992)利用酵母双突变体互补法从拟南芥中克隆到第1个高等植物的Shaker型K^+通道基因*AtAKT1*。该基因位于拟南芥第2号染色体上, 含有11个外显子和10个内含子, 编码的多肽由857个氨基酸残基组成。此后, 科研人员相继在马铃薯(*Solanum tuberosum*) (Zimmermann et al., 1998)、玉米(*Zea mays*) (Philippar et al., 1999)、小麦(*Triticum aestivum*) (Buschmann et al., 2000)、番茄(*Lycopersicon esculentum*) (Hartje et al., 2000)、水稻(*Oryza*

收稿日期: 2016-02-01; 接受日期: 2016-04-26
基金项目: 国家自然科学基金(No.31460101, No.31260294)、兰州市人才创新创业专项(No.2014-2-6)和兰州理工大学“红柳杰出人才”培养计划(No.J201404)
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sativa) (Fuchs et al., 2005)、大麦(*Hordeum vulgare*) (Boscari et al., 2009)、葡萄(*Vitis vinifera*) (Cuéllar et al., 2010, 2013)和盐地碱蓬(*Suaeda salsa*) (Duan et al., 2015)等植物中分离得到*AKT1*基因。AKT1在维持植物离子稳态平衡及增强植物逆境胁迫耐受性等方面起着重要作用(Alemán et al., 2011; Wang and Wu, 2013)。本文从植物AKT1的分子结构特点、调控机制及生物学功能等方面对其主要研究进展进行了归纳总结，旨在为植物AKT1的进一步研究奠定基础。

1 AKT1的分子结构、定位及表达

植物AKT1与动物Shaker型K^+通道结构高度相似(图1)，含有6个跨膜片段(S1–S6)，其中第4个跨膜片段S4含有大量带正电荷的氨基酸残基，是电压感受器，其主要功能为响应膜电势的变化。该片段可在膜上移动，使得膜通道构象改变，从而控制通道孔的开放与关闭(Benito et al., 2014; Nieves-Cordones and Gaillard, 2014)。S5和S6之间含有1个高度保守的P环结构域，该结构域是陷入细胞膜内的一段多肽片段，构成通道孔。AKT1含有典型的TxGYG (Thr-X-Gly-Tyr-Gly)序列，为K^+选择器，这是Shaker型K^+通道的共同特点。胞质C末端从第6个跨膜片段末尾起，含有1个C-接头(约有80个氨基酸残基)，1个环核苷酸结合域(cyclic-nucleotide binding domain, CNBD)，1个锚蛋白域和1个富含疏水性、酸性残基的K_{HA}域(Nieves-Cordones et al., 2014b; Nieves-Cordones and Gaillard, 2014)。对大多数Shaker型K^+通道家族成员来说，锚蛋白域有助于通道与细胞骨架的连接、蛋白质的相互作用和细胞溶质的调节(Dreyer and Blatt, 2009; Riedelsberger et al., 2010; Nieves-Cordones et al., 2014b; Nieves-Cordones and Gaillard, 2014)。Shaker型K^+通道的重要特点之一是能够形成异源四聚体结构，可使植物调控不同细胞中的K^+转运活性。这种调控在每个器官或者组织中相对独立，并且受到环境的影响(Gambale and Uozumi, 2006)。

来源于不同植物的AKT1具有高度的同源性(图2)。不同植物的*AKT1*基因表达部位有所不同(表1)。研究表明，胡萝卜(*Daucus carota*) DcAKT1定位于

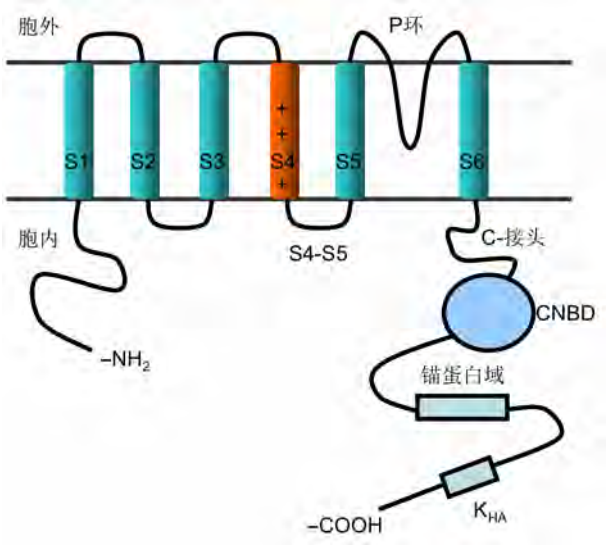

图1 植物Shaker型K^+通道拓扑结构示意图(改自Nieves-Cordones and Gaillard, 2014)

S1–S6为6个跨膜结构域; S4为电压感受器; CNBD为环核苷酸结合域。

Figure 1 Diagrammatic representation of plant Shaker type K^+ channel topological structure (Modified from Nieves-Cordones and Gaillard, 2014)

S1–S6 indicate six transmembrane domains; S4 represents voltage sensor; CNBD indicates cyclic-nucleotide binding domain.

叶原基和叶肉细胞质膜(Formentin et al., 2004)。Xu等(2014)通过绿色荧光蛋白(green fluorescent protein, GFP)研究发现，棉花(*Gossypium hirsutum*) GhAKT1定位于质膜和根尖细胞壁，而在液泡和细胞质中则没有发现。Zimmermann等(1998)利用GFP融合蛋白发现马铃薯StAKT1定位于细胞内膜(internal cellular membrane)。

在K^+饥饿状态下，小麦根*TaAKT1* (Buschmann et al., 2000)和小花碱茅(*Puccinellia tenuiflora*) *PtAKT1* (Ardie et al., 2010)的转录水平显著提高。在拟南芥中，外部K^+浓度在5 μmol·L^{-1}至5 mmol·L^{-1}范围内未影响*AtAKT1*的转录丰度(Lagarde et al., 1996)。在棉花(Xu et al., 2014)和小花碱茅(Wang et al., 2015)中也有类似报道，由此推测*AKT1*可能受转录后调控。然而，25–250 mmol·L^{-1} NaCl短期(6小时)处理能够诱导盐地碱蓬根*SsAKT1*的表达(Duan et al., 2015)。研究表明，水稻*OsAKT1*主要在根的外皮

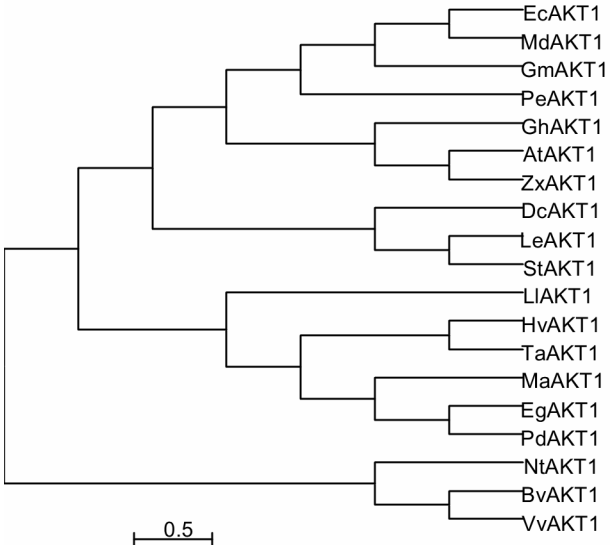

图2 植物AKT1的系统进化树

AKT1的来源及登录号为: 赤桉(*Eucalyptus camaldulensis*), EcAKT1 (AAL25648.1); 苹果(*Malus domestica*), MdAKT1 (XP_008352270); 大豆(*Glycine max*), GmAKT1 (NP_001304431); 胡杨(*Populus euphratica*), PeAKT1 (ADA79674); 棉花(*Gossypium hirsutum*), GhAKT1 (AHZ30618); 拟南芥(*Arabidopsis thaliana*), AtAKT1 (NP_180233.1); 霸王(*Zygophyllum xanthoxylon*), ZxAKT1 (ACX37089.1); 胡萝卜(*Daucus carota*), DcAKT1 (CAG27094); 番茄(*Lycopersicon esculentum*), LeAKT1 (CAA65254); 马铃薯(*Solanum tuberosum*), StAKT1 (NP_001275347); 麝香百合(*Lilium longiflorum*), LlAKT1 (ABO15470); 大麦(*Hordeum vulgare*), HvAKT1 (ABE99810.1); 小麦(*Triticum aestivum*), TaAKT1 (AAF36832.1); 小果野蕉(*Musa acuminata* subsp. *malaccensis*), MaAKT1 (XP_009386140); 油棕(*Elaeis guineensis*), EgAKT1 (XP_010925144); 海枣(*Phoenix dactylifera*), PdAKT1 (XP_008809499); 烟草(*Nicotiana tabacum*), NtAKT1 (BAD81034); 葡萄(*Vitis vinifera*), VvAKT1 (NP_001268010)。甜菜(*Beta vulgaris*) BvAKT1由本课题组克隆。通过Clustal W软件进行多重序列比对; 采用最大似然法, 用JTT (Jones-Taylor-Thornton)模型(MEGA 5.10)构建植物AKT1的系统进化树。

Figure 2 Phylogenetic tree of plant AKT1

The sources and GenBank accession numbers of AKT1 are as follows: *Eucalyptus camaldulensis*, EcAKT1 (AAL25648.1); *Malus domestica*, MdAKT1 (XP_008352270); *Glycine max*, GmAKT1 (NP_001304431); *Populus euphratica*, PeAKT1 (ADA79674); *Gossypium hirsutum*, GhAKT1 (AHZ30618); *Arabidopsis thaliana*, AtAKT1 (NP_180233.1); *Zygophyllum xanthoxylon*, ZxAKT1 (ACX37089.1); *Daucus carota*, DcAKT1 (CAG27094); *Lycopersicon esculentum*, LeAKT1 (CAA65254); *Solanum tuberosum*, StAKT1 (NP_001275347); *Lilium longiflorum*, LlAKT1 (ABO15470); *Hordeum vulgare*, HvAKT1 (ABE99810.1); *Triticum aestivum*, TaAKT1 (AAF36832.1); *Musa acuminata* subsp. *malaccensis*, MaAKT1 (XP_009386140); *Elaeis guineensis*, EgAKT1 (XP_010925144); *Phoenix dactylifera*, PdAKT1 (XP_008809499); *Nicotiana tabacum*, NtAKT1 (BAD81034); *Vitis vinifera*, VvAKT1 (NP_001268010). *Beta vulgaris* BvAKT1 was cloned by Wu's research group. Multiple alignment of AKT1 sequences was performed by the Clustal W. Phylogenetic tree of plants AKT1 was constructed by the Maximum Likelihood and JTT (Jones-Taylor-Thornton) model (MEGA 5.10).

层和内皮层细胞以及叶的木质部薄壁组织、韧皮部和叶肉细胞中表达(Golldack et al., 2003)。盐胁迫(150 mmol·L^{-1} NaCl处理48小时)下, 盐敏感型水稻品种Pokkali和BK根外皮层细胞中的*OsAKT1*转录物消失, 而耐盐型品种IR29中的则未受到影响(Golldack et al., 2003)。Su等(2001)的研究表明, 盐胁迫下盐生植物冰叶日中花(*Mesembryanthemum crystallinum*)根中与*AtAKT1*同源的K^+通道基因*McAKT1*表达水平下调。在小花碱茅中, 尽管盐处理会下调*PtAKT1*的表达, 但150 mmol·L^{-1} NaCl处理下*PtAKT1*的转录丰度显著高于25 mmol·L^{-1} (Wang et al., 2015)。然而, 也有研究报道认为, NaCl短期处理并未改变*AKT1*的表达水平(Maathuis et al., 2003; Pilot et al., 2003)。在葡萄中, *VvAKT1.1*主要在根和浆果中表达(Cuéllar et al., 2010); 而*VvAKT1.2*主要在成熟的浆果中表达, 干旱胁迫可显著提高其表达水平(Cuéllar et al., 2013)。此外, 产生活性氧(reactive oxygen species, ROS)的胁迫因子(如砷、缺氧和热胁迫等)均可下调*AKT1*的转录丰度(Ahmad et al., 2016)。由此可见, 植物*AKT1*的表达不但具有组织特异性, 而且受外界环境的影响。

2 AKT1的分子调控机制

尽管自20世纪90年代从拟南芥中克隆到第1个*AKT1*基因以来, 人们相继在其它植物中克隆得到同源基因。然而, *AKT1*基因所编码蛋白的调控机制仍不清楚。Xu等(2006)首次在植物中报道了低K^+条件下蛋白磷酸化对K^+吸收的调控机制。在爪蟾卵母细胞(*Xenopus* oocytes)中, CBL1 (calcineurin B-like protein1)/CBL9与CIPK23 (CBL-interacting protein kinases 23)互作, 通过磷酸化作用激活AKT1介导的K^+吸收(Li et al., 2006; Xu et al., 2006; Cuéllar et al., 2010, 2013)。低K^+处理下, *CIPK23*表达上调, 而*CBL1*和

表1 高等植物中的AKT1

Table 1 AKT1 in higher plants

基因	物种	表达部位	参考文献
AtAKT1	拟南芥(*Arabidopsis thaliana*)	根表皮、皮层及内皮层	Lagarde et al., 1996
LeAKT1	番茄(*Lycopersicon esculentum*)	根毛	Hartje et al., 2000
VfAKT1	蚕豆(*Vicia faba*)	叶和韧皮部	Ache et al., 2001
GhAKT1	棉花(*Gossypium hirsutum*)	叶细胞皮层、内皮层及光合细胞	Xu et al., 2014
OsAKT1	水稻(*Oryza sativa*)	根和叶	Golldack et al., 2003
McAKT1	冰叶日中花(*Mesembryanthemum crystallinum*)	茎和叶	Su et al., 2001
PtAKT1	小花碱茅(*Puccinellia tenuiflora*)	根	Wang et al., 2015
SsAKT1	盐地碱蓬(*Suaeda salsa*)	根和叶	Duan et al., 2015
StAKT1	马铃薯(*Solanum tuberosum*)	保卫细胞、叶表皮和根	Zimmermann et al., 1998
TaAKT1	小麦(*Triticum aestivum*)	根皮层细胞	Buschmann et al., 2000
ZmAKT1	玉米(*Zea mays*)	胚芽鞘细胞	Philippar et al., 1999
CaAKT1	辣椒(*Capsicum annuum*)	根	Martinez-Cordero et al., 2005
NtAKT1	烟草(*Nicotiana tabacum*)	根	Sano et al., 2007
HvAKT1	大麦(*Hordeum vulgare*)	叶	Boscari et al., 2009
DcAKT1	胡萝卜(*Daucus carota*)	茎、根毛和叶	Formentin et al., 2004
VvAKT1.1	葡萄(*Vitis vinifera*)	根和浆果	Cuéllar et al., 2010
VvAKT1.2	葡萄(*V. vinifera*)	浆果	Cuéllar et al., 2013

*CBL9*似乎是组成型表达(Xu et al., 2006; Cheong et al., 2007); 过量表达*CIPK23*可显著增强拟南芥K^+的吸收能力和低K^+耐受性(Xu et al., 2006)。CBL结构中有4个EF手型结构, 能与Ca^{2+}结合; CBL是Ca^{2+}信号感受器(Li et al., 2006, 2009)。由于CIPK与CBL互作的特异性, 在植物逆境响应中有多种不同的组合(Li et al., 2009)。AKT1-CIPK-CBL复合物能被PP2C (protein phosphatases 2C)负向调控, 参与对ABA信号的响应(Lee et al., 2007; Lan et al., 2011)。Nieves-Cordones等(2012)研究发现, AKT1在保卫细胞中受到CIPK23调节, 并参与水分胁迫响应。此外, CBL10能直接与AKT1相互作用, 通过与CIPK23竞争结合AKT1, 从而负向调控K^+通道活性(Grefen and Blatt, 2012; Ren et al., 2013)。CIPK23也可通过磷酸化作用激活HAK5介导的高亲和性K^+吸收(Ragel et al., 2015)。

*AtKC1*是Reintanz等(2002)从拟南芥中分离克隆的α-亚基Shaker通道基因, 主要在根毛、根表皮及皮层细胞中表达。AtKC1作为四聚体的组成亚基参与K^+通道四聚体的形成, 其存在对四聚体的K^+通透能力产生抑制作用(Reintanz et al., 2002; Geiger et al., 2009)。可见, AtKC1是负调控因子, 也是1个调控亚基(Wang et al., 2010)。另外, AtKC1的存在使四聚体的K^+通道活性激活电压向负电压方向偏移, 离子通道更难以被激活, 即改变了其对电压的敏感性(Duby et al., 2008)。因此, 这种负向调控阻断了由AKT1介导的吸收。短时间缺K^+处理则上调*AtKC1*的转录丰度, 随后其转录丰度下调(Shin and Schachtman, 2004), 这种现象可通过缺K^+处理几天后的*AtKC1*转录物消失而得到解释(Pilot et al., 2003)。在异源表达系统中, AtKC1不能独立形成有功能的K^+通道(Duby et al., 2008)。然而, 当AtKC1不能正常发挥功能时, 根毛中AKT1介导的内向K^+电流的生物物理特征就会发生改变(Jeanguenin et al., 2011)。Wang等(2016)进一步研究证实, 在低K^+条件下, CIPK23促进AKT1介导的K^+吸收, 而AtKC1抑制AKT1介导的K^+内流。他们认为, CIPK23和AtKC1协同调节AKT1的功能, 二者具有一定的互补性。另有研究表明, *Atkc1*与*Atakt1*突变体植株的表型相似或相反, 这主要取决于外界环境条件(Geiger et al., 2009; Wang et al., 2010)。AtKC1也是SNARE (soluble N-ethylmaleimide-sensitive factor protein attachment protein receptor)蛋白SYP121 (syntaxin protein121)的靶蛋白, SYP121参与对AKT1活性的调控(Honsbein et al., 2009)。低K^+

环境中, *syp121*突变体的根系变短, 其表型与*Atkc1*和*Atakt1*突变体相似。在爪蟾卵母细胞中共表达AtAKT1和AtKC1后, SYP121使得K^+通道被激活的膜电势负值的绝对值更大, 这种调控方式导致K^+流显著增加(Chérel et al., 2014)。最近的研究表明, 高盐胁迫下拟南芥植株体内迅速积累一氧化氮(nitric oxide, NO), 细胞K^+含量降低, 产生过量的吡哆醛5-磷酸(pyridoxal 5-phosphate, PLP) (Xia et al., 2014)。PLP作为维生素B6的一种活性形式, 显著抑制爪蟾卵母细胞表达系统和拟南芥根原生质中K^+通道AtAKT1的活性。可见, NO通过促进维生素B6 PLP的合成负向调控AKT1介导的K^+吸收(Xia et al., 2014)。

3 AKT1在植物逆境胁迫响应中的功能

3.1 AKT1与K^+饥饿耐受性

低K^+环境是影响植物正常生长发育及作物品质的主要非生物因子之一。K^+是种子萌发所需的重要渗透调节物质。在低K^+ (50–100 μmol·L^{-1})条件下, 拟南芥*Atakt1*突变体种子的胚根不能正常生长; 然而, 当在*Atakt1*突变体中超表达*AtAKT1*后, 其种子萌发活力得到恢复, 说明AKT1参与种子萌发期间K^+的吸收(Pyo et al., 2010; Xu et al., 2014)。*AKT1*功能缺失使植物根细胞膜表现出超级化, 对外界环境K^+浓度变化异常敏感(Hirsch et al., 1998)。在低K^+环境中, 拟南芥*Atakt1*突变体植株细胞内的K^+含量明显降低(Hirsch et al., 1998; Spalding et al., 1999)。电生理学实验表明, 水稻OsAKT1介导内向K^+电流, 即使在低K^+ (5 μmol·L^{-1}–1 mmol·L^{-1})条件下也是如此(Li et al., 2014)。有研究表明, 拟南芥*Atakt1*和水稻*Osakt1*突变体植株的内向K^+电流减弱, K^+吸收功能紊乱, 从而影响其生长发育(Reintanz et al., 2002; Xu et al., 2006; Li et al., 2014)。当在水稻*Osakt1*突变体中超表达*OsAKT1*后, 低K^+胁迫下转基因植株的内向K^+电流增强, K^+含量显著增加(Li et al., 2014)。这进一步证实了AKT1介导植物根吸收K^+。Xu等(2014)采用非损伤微测技术(no-invasive micro-test technology, NMT), 在棉花GhAKT1功能研究中也得到类似的结果。可见, 在低K^+环境中, AKT1介导的K^+吸收系统对维持植物正常生长发育具有重要作用。

3.2 AKT1与植物耐盐性

盐胁迫下, 植物体内积累大量的Na^+, 一方面抑制K^+的吸收, 另一方面与K^+竞争一些酶活性结合位点, 影响蛋白质合成及核糖体功能, 从而产生Na^+毒害(Horie et al., 2009; Zhang et al., 2010)。一般认为, 维持细胞质内较高的K^+/Na^+比是植物适应盐胁迫的重要策略之一(Horie et al., 2009; Shabala et al., 2010; Chérel et al., 2014)。AKT1是参与K^+吸收的重要通道蛋白, 在植物响应盐胁迫中起着重要作用。异源表达系统研究表明, 尽管AKT1对K^+具有更强的选择性, 但并不排除对Na^+的吸收(Maathuis et al., 1997)。低Na^+条件下, 内向整流K^+通道未表现出明显的Na^+进出现象; 但在高盐条件下, 其对K^+表现出明显的选择性(Amtmann and Sanders, 1999)。Golldack等(2003)研究表明, 盐处理下水稻根吸收Na^+与*OsAKT1*的表达水平有直接关系。由此证明OsAKT1参与盐胁迫下Na^+/K^+比调控, 从而增强水稻的耐盐性。Wang等(2015)研究发现, 无论是低盐(25 mmol·L^{-1} NaCl)还是高盐(150 mmol·L^{-1} NaCl)条件下, 小花碱茅*PtAKT1*选择性吸收K^+的能力显著强于Na^+ (selective absorption capacity for K^+ over Na^+, SA)。进一步研究发现, *PtAKT1*的转录水平与SA值之间呈显著正相关, 可见盐胁迫下PtAKT1是调控小花碱茅K^+选择性吸收的关键因子(Wang et al., 2015)。与野生型相比, 盐胁迫下超表达*PtAKT1*的拟南芥转基因植株K^+含量增加, 而Na^+含量降低, 表明PtAKT1增强了转基因植株对K^+的吸收能力, 从而提高其耐盐性(Ardie et al., 2010)。Duan等(2015)研究发现, 盐胁迫下盐地碱蓬SsAKT1能促进植株体内K^+积累, 进而增强植物耐盐性。在盐(100 mmol·L^{-1} NaCl)处理下, 大麦*HvAKT1*在叶伸长区的表达水平明显增加, 说明HvAKT1参与维持叶肉细胞K^+的稳态平衡(Boscari et al., 2009)。我们的研究发现, 在5–50 mmol·L^{-1} NaCl处理下, 分别添加3和6 mmol·L^{-1} Cs^+ (K^+通道AKT1特异性抑制剂)均可显著降低甜菜(*Beta vulgaris*)根的K^+净吸收速率, 可见AKT1可介导甜菜根K^+的吸收(Wu et al., 2015b)。这些研究结果表明, AKT1在K^+和Na^+选择性吸收、维持植物体内K^+含量以及增强植物耐盐性等方面具有重要作用。

3.3 AKT1与植物抗旱性

干旱是制约全球作物生长和产量的主要非生物因素之一(Chaves and Oliveira, 2004; 山仑, 2011)。植物响应干旱胁迫的重要策略之一是吸收并在体内积累大量的溶质(如K^+、Na^+和脯氨酸等) (Wang et al., 2004; Mahouachi et al., 2006; Wu et al., 2015a), 降低细胞渗透势, 从而增强植物细胞吸水能力。AKT1在植物响应干旱胁迫中的作用主要有2方面。(1) 干旱胁迫下AKT1增强植物根的K^+吸收能力。在水稻中超表达*OsAKT1*基因后, 转基因植株在干旱条件下生长良好, 且根中积累较多的K^+; 相反, *Osakt1*突变体植物表现为生长不良, 且根中K^+含量明显减少(Ahmad et al., 2016)。由此表明, 超表达*AKT1*转基因植株通过增加根部K^+的积累来改善细胞渗透调节能力, 从而增强植物的抗旱性。(2) AKT1通过调节气孔的运动影响植物体内的水分平衡。研究表明, 拟南芥*AtAKT1*在保卫细胞质膜上呈低丰度表达(Lagarde et al., 1996)。在渗透胁迫下, 拟南芥*Atakt1*突变体植株的蒸腾速率和水分消耗量明显低于野生型植株(Nieves-Cordones et al., 2012)。由此可见, AKT1功能缺失致使保卫细胞K^+跨膜转运体系受损, 气孔导度下降。Ahmad等(2016)进一步研究发现, 与野生型相比, 在干旱胁迫下水稻*Osakt1*突变体植株的气孔导度明显降低; 而超表达*OsAKT1*显著增强了转基因植株的气孔导度。这些研究结果表明, AKT1在介导保卫细胞K^+转运、调控气孔运动及维持细胞水分平衡中发挥重要作用。

4 研究展望

目前, 已从不同植物中分离到*AKT1*基因, 尽管人们对AKT1的结构、表达部位和生理功能等方面有一定程度的认识, 但对于AKT1响应逆境胁迫的作用机理及分子调控机制仍需深入研究。基于目前的研究现状, 我们认为今后的研究工作应从以下3个方面展开: (1) 利用GFP、原位杂交及免疫组化等技术手段进一步分析AKT1蛋白的组织分布特点; (2) 从具有代表性的不同类型植物中克隆*AKT1*基因, 并通过基因突变、RNA干扰及过量表达等方法对其表达特性、生理作用及其活性调控机制进行深入研究, 进一步解析AKT1在植物逆境胁迫响应中的作用机理; (3) 通过CIPK23、AtKC1与AKT1功能互作进一步阐明植物响应低K^+信号的作用机制。

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Research Advance of K^+ Channel AKT1 in Plants

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Abstract Potassium (K) is an essential macronutrient for plant growth and development. K^+ uptake was mainly mediated by K^+ channels and transporters in root cells. Arabidopsis K^+ transporter 1 (AKT1) is one of the important members of the Shaker type K^+ channel families and plays crucial roles in root K^+ uptake and transmembrane transport of plants. Here, we summarize the latest research advances for the K^+ channel AKT1, mainly its molecular structure, tissue-specific expression, regulation mechanisms, and biological function. We propose research hotspots and directions for research into the AKT1 channel.

Key words AKT1, K^+ uptake, K^+ starvation, salt tolerance

Wu GQ, Shui QZ, Feng RJ (2017). Research advance of K^+ channel AKT1 in plants. *Chin Bull Bot* **52**, 225–234.

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