

植物钾、磷养分吸收利用机制的研究进展

陈益芳*, 王毅, 武维华

中国农业大学生物学院, 北京 100193

* 联系人, E-mail: chenyifang@cau.edu.cn

2025-01-06 收稿, 2025-03-30 修回, 2025-04-24 接受, 2025-04-24 网络版发表

农业生物育种国家科技重大专项(2023ZD04072)资助

摘要 氮、磷、钾是植物生长发育所必需的三大矿质营养元素, 其在土壤中的有效含量直接影响作物的产量、品质以及抗逆性。然而, 全球大多数耕地土壤中的有效钾与有效磷含量较低, 难以满足农作物正常生长发育。为保障作物产量和品质, 现代农业生产中普遍依赖钾肥和磷肥的高强度投入。值得注意的是, 与大气中几乎无限的氮源不同, 作为肥料原料的钾矿与磷矿属于不可再生资源, 因此提高植物对钾、磷养分的利用效率成为实现农业绿色可持续发展的关键突破点。基于此, 系统解析植物吸收利用钾、磷元素的分子调控机制, 对于通过遗传改良提升植物钾、磷养分吸收利用效率、培育养分高效新品种具有重要科学价值。本文主要以拟南芥、水稻和玉米为例, 总结了植物在钾和磷养分感知、吸收、分配、利用等方面分子调控机制的重要研究成果, 同时探讨了氮、磷、钾养分协同吸收与利用的调控机理。

关键词 钾, 磷, 吸收, 分配, 信号转导

氮(nitrogen, N)、磷(phosphorus, P)、钾(potassium, K)是植物生长发育所必需的三大矿质营养元素。氮是蛋白质、核酸、叶绿素、植物激素、维生素等生物大分子的基本构成成分。磷是核酸、磷脂等细胞内多种功能性物质的重要成分, 参与植物的光合作用和呼吸作用, 是植物体内能量转换的重要介质元素。钾是植物细胞中含量最高的阳离子, 也是多种酶的辅因子, 参与调控植物的离子平衡、渗透平衡、电荷平衡、同化物运输等生理过程。农业生产中, 充足的氮、磷、钾肥供给是保障农作物高产和稳产的前提条件。目前, 我国氮肥生产量和施用量巨大, 而由于我国钾矿和磷矿资源匮乏, 导致钾肥和磷肥施用不足, 致使多数耕地土壤中的氮、磷、钾养分不平衡。我国农作物生产中氮、磷、钾营养元素的有效利用率普遍偏低, 加之肥料施用不平衡, 不但限制了农作物的增产, 还造成肥料的浪费和环境污染问题。因此, 提高植物/作物对氮、磷、钾养分

吸收和利用的效率, 是解决农业绿色可持续发展的重要途径。植物可以感知环境中的养分水平波动, 并调整自身对不同养分的吸收、转运、分配和利用, 因此解析这些生理过程的分子调控机制, 挖掘其中的关键调控基因, 是培育作物养分高效新品种的重要基础。本文简要介绍了植物对钾素和磷素吸收转运的关键蛋白及其调控机制, 钾信号和磷信号感受和应答的分子机制, 以及氮、磷、钾养分协同吸收与转运的调控机制。

1 钾的吸收利用与信号转导途径

植物通过根系以 K^+ 的形式从土壤中吸收钾素, 钾在植物体内以离子状态(K^+)存在。植物细胞质中的钾离子浓度通常维持在80~100 mmol/L, 而土壤中可供植物直接吸收利用的自由钾离子浓度仅为0.1~1 mmol/L。因此, 植物吸收钾离子需逆浓度梯度进行, 在自然环境中, 植物常常遭受低钾胁迫。植物从环境中吸收钾离子,

引用格式: 陈益芳, 王毅, 武维华. 植物钾、磷养分吸收利用机制的研究进展. 科学通报, 2025, 70: 4259–4271

Chen Y-F, Wang Y, Wu W-H. Progress of potassium and phosphorus transport and signaling in plants (in Chinese). Chin Sci Bull, 2025, 70: 4259–4271, doi: 10.1360/TB-2025-0028

以及钾离子在植物体内的转运和分配过程均依赖于细胞膜上的各种钾离子通道和钾离子转运体。植物中主要的钾离子通道来自Shaker钾离子通道家族和TPK (tandem-pore K^+ channel)钾离子通道家族,它们选择性地转运钾离子。植物中的钾离子转运体种类众多,包括KT/HAK/KUP(K^+ Uptake Permease)家族、HKT(high-affinity K^+ transporter)家族和CPA(cation-proton antiporter)家族,其中CPA家族又分为NHX[$Na^+(K^+)/H^+$ exchanger]、CHX(cation/ H^+ exchanger)和KEA(K^+ exchange antiporter)亚家族。这些转运体有的选择性转运钾离子,有的也可以同时转运钠离子。在拟南芥中,上述的钾离子通道和转运体共有70个左右,它们具有不同的组织表达分布、亚细胞定位、转运活性和选择性,构成了植物中的钾吸收运输系统,参与植物多种生理活动^[1]。

1.1 植物根系的钾吸收

植物根系吸收钾离子通过两类吸收系统,一类是高亲和性的钾吸收系统,在环境钾离子浓度较低(低于0.2 mmol/L)的时候发挥作用;另一类是低亲和性的钾吸收系统,在环境钾离子浓度较高(高于0.3 mmol/L)的时候发挥作用^[2]。研究表明植物中的钾离子转运体主要介导根部高亲和性钾吸收,而钾离子通道主要介导低亲和性钾吸收。拟南芥Shaker钾离子通道AtAKT1 (*Arabidopsis* K^+ transporter 1)是植物中第一个被鉴定的钾离子通道,它可以在外界钾浓度0.01~10 mmol/L范围内介导根部的钾离子吸收^[3]。AtAKT1在其他作物中的同源蛋白(如水稻中的OsAKT1和玉米中的ZMK1)也都介导根系的低亲和性钾离子吸收^[4,5]。拟南芥中的钾离子转运体AtHAK5,以及水稻和玉米中的转运体OsHAK5和ZmHAK5是介导根系高亲和性钾离子吸收的主要组分^[6~8]。水稻中还存在多个HAK转运体(如OsHAK1、OsHAK5和OsHAK21)也部分参与根系的钾离子吸收。AKT1和HAK5这两类钾转运蛋白分别参与低亲和性和高亲和性的钾离子吸收,构成了植物根系最主要的钾吸收系统。

研究发现AtAKT1和AtHAK5这两类蛋白的钾离子转运活性都受到磷酸化调控。在拟南芥中,钙离子结合蛋白AtCBL1/9(calcineurin B-like protein 1/9)与蛋白激酶AtCIPK23(CBL-interacting protein kinase 23)形成复合体,通过磷酸化作用激活细胞质膜上AtAKT1和AtHAK5的钾转运活性,从而促进根系的钾吸收^[9,10]

(图1)。在水稻和玉米中也存在类似的调控机制^[4,5]。而蛋白磷酸酶AtAIP1(AKT1-Interacting PP2C 1)则可以通过去磷酸化作用抑制AtAKT1的通道活性。此外,钾离子通道调节亚基AtKC1^[11]、钙结合蛋白AtCBL10^[12]等蛋白也可以通过与AtAKT1互作抑制其钾离子通道活性(图1)。最近的研究发现,质膜上的类受体蛋白激酶AtBAK1(BRI1-associated kinase 1)可以磷酸化激活质膜上的质子ATP酶AtAHA2(*Arabidopsis* H^+ -ATPase isoform 2),增加低钾条件下的跨膜质子电化学势梯度,进而促进AtAKT1和AtHAK5介导的根部钾离子吸收^[13]。

在低钾条件下,HAK钾转运体基因的转录水平往往受到诱导表达升高,从而促进高亲和性的钾离子吸收,这是植物应对低钾胁迫的重要调节机制之一。在拟南芥中研究发现,AtRAP2.11、AtARF2、AtMYB77等多个转录因子可以直接结合在AtHAK5启动子区,在低钾条件下调控AtHAK5转录水平升高^[14~16](图1)。以上研究表明,植物可以感受环境中的钾养分水平,在转录水平或翻译后水平调控钾离子通道和钾离子转运体的表达水平和蛋白活性,进而精准地调控根系钾离子吸收过程。

1.2 钾在植物体内的转运

钾离子被根系吸收后进入木质部导管,通过木质部集流向地上部运输,供地上部的组织器官使用。此外,在韧皮部中钾离子也可以通过筛管分子内的集流从源器官向库器官运输,或者从老叶向新叶运输。这种在维管束中的运输被称为长距离运输,这可以使钾离子在植物体内各组织器官中合理分配,并促进叶片中光合同化物的运输。

目前发现,在拟南芥根中薄壁细胞表达的外向钾离子通道AtSKOR(stelar K^+ outward rectifier)和非典型的钾离子转运体AtNRT1.5/AtNPF7.3负责将木质部薄壁细胞中的钾离子释放到木质部导管中,从而介导钾离子的根冠转运^[17,18](图1)。此外,AtKUP7和OsHAK5也参与钾离子从根到冠的转运过程^[7,19]。植物可以感受环境中钾养分水平,从而通过转录因子AtMYB59正向调节AtNRT1.5/AtNPF7.3的转录水平,进而实现钾在根和冠之间的分配平衡^[20](图1)。AtAKT2是在拟南芥韧皮部表达的双向钾离子通道,它主要负责钾离子在韧皮部中的装载和卸载,从而维持韧皮部细胞的跨膜电位,并促进蔗糖的装载和运输^[21]。AtAKT2的活性受到磷酸化调控,蛋白磷酸酶PP2CA可以调控其通道活

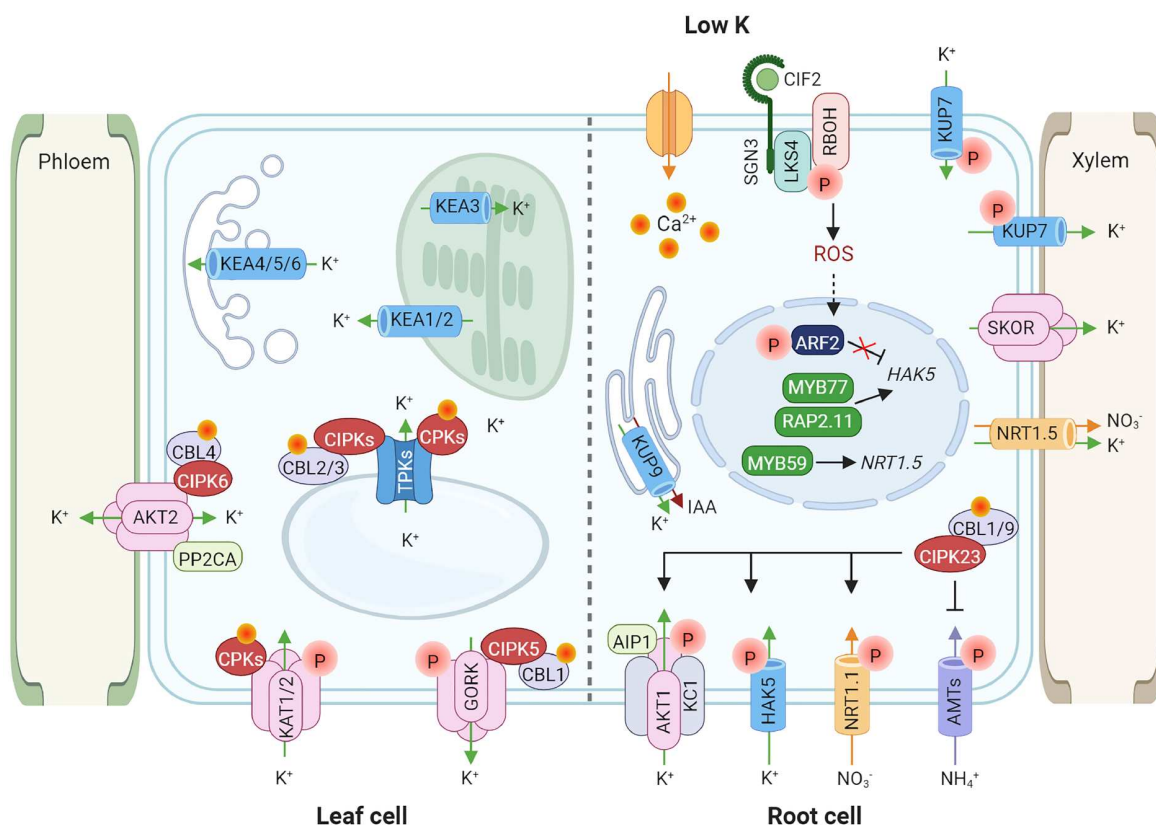


图 1 植物钾素的吸收、转运以及信号转导途径。植物体内存在多种钾转运蛋白(包括钾离子通道和钾离子转运体)参与钾离子的吸收、转运、分配等过程。例如在拟南芥中, AKT1和HAK5是负责根部钾吸收的主要组分; SKOR、KUP7和NRT1.5参与钾离子从根部向冠部运输; KAT1和KAT2参与叶肉细胞的钾吸收; AKT2介导韧皮部中钾离子的跨膜运输; TPK1可以将液泡中储存的钾离子释放到细胞质中; KEA家族成员在高尔基体和叶绿体膜上发挥钾离子转运的作用。当植物感受到环境低钾胁迫时, 会在根细胞内产生钙信号和活性氧信号, 从而激活相应的信号转导途径, 进而调控这些钾离子通道和钾离子转运体的转录水平和蛋白活性, 最终调节植物对钾的吸收、转运和分配过程。示意图使用BioRender.com绘制

Figure 1 Potassium transport and signaling in *Arabidopsis*. Potassium (K^+) uptake in plant roots and K^+ transport inside plants involve diverse K^+ channels and transporters, which move K^+ across cell membranes. In *Arabidopsis*, AKT1 and HAK5 mainly involve K^+ uptake in root cells. SKOR, KUP7, and NRT1.5 participate in K^+ loading into the xylem, facilitating the K^+ translocation from root to shoot. KAT1 and KAT2 are involved in K^+ uptake in mesophyll cells. The weakly inwardly rectifying channel AKT2 mediates K^+ loading into the phloem. TPK1 releases K^+ from the vacuole into the cytoplasm. The KEA members are located at the membrane of the Golgi apparatus and the chloroplast to transport K^+ . In root cells, after perception of external low K^+ stress, plants generate some signal molecules (Ca^{2+} , ROS, etc.) that regulate these K^+ channels and transporters at transcriptional and post-translational levels. Therefore, plants could enhance the efficiency of K^+ uptake and utilization, thereby surviving under low K^+ stress (Created with BioRender.com)

性^[22]。而AtCBL4-AtCIPK6蛋白复合体可以促进AtAKT2蛋白从内质网向细胞质膜转运, 进而调控其通道活性^[23](图1)。

很多钾离子通道和转运体在某些植物细胞类型中特异地高表达, 介导钾离子跨细胞质膜的转运, 从而调控这些细胞特有的生理活动。例如, AtKAT1/2、KZM2/3等内向钾离子通道主要在拟南芥和玉米的保卫细胞质膜上介导钾离子内流, 从而调节保卫细胞渗透势, 促进气孔开放^[24,25](图1)。外向钾离子通道AtGORK在拟

南芥保卫细胞表达, 它可以介导钾离子从保卫细胞的胞质向细胞外流动, 从而调控气孔关闭^[26](图1)。在拟南芥花粉管中特异表达的钾离子通道AtSPIK和AtTPK4介导胞外的钾离子向花粉管中流动, 从而增加细胞膨压, 推动花粉管顶端伸长生长^[27,28]。AtSPIK(shaker pollen inward K^+ channel)通道活性受钙依赖蛋白激酶AtCPK11和AtCPK24的调控^[29]。在玉米中, 发现转运蛋白ZmNPF7.9/ZmSUGCAR1(sucrose and glucose carrier 1)在籽粒胚乳基底转移层(basal endosperm transfer

layer, BETL)特异表达,介导钾离子、蔗糖、葡萄糖从母本组织向胚乳中转运,从而促进籽粒灌浆过程^[30]。

钾离子在植物细胞内也需要进行跨膜转运,从而实现钾离子在胞质和各细胞器(液泡、叶绿体、内质网、高尔基体等)之间的动态平衡。液泡是植物成熟细胞最大的细胞器,也是钾离子主要的存储库。在植物遭受低钾胁迫时,液泡内存储的钾离子会通过液泡膜定位的钾离子通道AtTPKs释放到细胞质中,从而维持细胞质中钾离子的稳态。液泡膜定位的AtCBL2/3-AtCIPK3/9/23/26蛋白复合体可以钙依赖的方式激活AtTPKs,以应对低钾胁迫^[31](图1)。

叶绿体是植物细胞中进行光合作用的重要场所。目前发现三个H⁺-K⁺反向共转运体特异在拟南芥叶绿体中表达,AtKEA1和AtKEA2定位于叶绿体的内被膜,主要参与叶绿体的发育过程^[32,33],而AtKEA3在类囊体膜上定位,通过影响跨类囊体膜的质子驱动力,进而调节不同光照条件下的光合效率^[34](图1)。该家族成员AtKEA4/5/6则主要定位在高尔基体、反式高尔基体网络(TGN)以及液泡前体区室/多囊泡体(PVC/MVB)上,调控内膜系统的pH和钾离子平衡,维持细胞器功能^[35](图1)。

内质网定位的钾离子转运体也参与调控植物多种生长发育过程。例如,H⁺-K⁺反向共转运体AtCHX21和AtCHX23主要定位在拟南芥花粉管细胞的内质网上,通过调控花粉管中的pH和钾离子平衡,影响花粉管向胚珠的定向生长和受精过程^[36]。钾离子转运体AtKUP9主要定位在拟南芥根尖静止中心(QC, Quiescent Center)细胞的内质网上,它可以同时介导钾离子和生长素从内质网向胞质中运输,从而调节低钾下根尖干细胞胞质中钾离子和生长素的稳态,进而维持干细胞活性和根生长^[37](图1)。

1.3 钾的感知与信号转导途径

已有的研究证实,植物可以感受环境中钾养分的水平,通过一系列信号转导途径调控各种生理和形态反应以适应不同的钾养分环境。在这些信号途径中,下游的各种钾离子通道和转运体的表达水平和蛋白活性会受到精确调控,从而使植物有效地吸收、转运、分配、利用钾元素。目前发现,钙离子、活性氧(reactive oxygen species, ROS)、植物激素是植物钾信号调控通路中的重要信号分子。

土壤中钾养分的匮乏首先被植物根系所感知,但

相关的感受器目前仍未被鉴定。已经发现,低钾胁迫可以在植物根中诱导产生两个时间和空间特异的钙信号。第一个瞬时钙信号在低钾胁迫后一分钟内出现在根尖分生区和伸长区交界处,而第二个持续性钙信号则在数小时后出现在伸长区和成熟区^[38]。这一钙信号可以被多种钙离子感受器(如CBL(calcineurin B-like protein)和CPK(calcium-dependent protein kinase)等)识别,进而调控多种钾离子通道和转运体的活性。

早期的研究发现,低钾可以激发植物根中产生ROS信号^[39],此信号是诱导AtHAK5转录水平升高的必要条件^[40],过氧化物酶AtRCI3(rare cold inducible gene 3)参与此ROS信号的产生^[41]。最新的研究发现,低钾诱导产生的钙信号促进AtCIF2(casparian strip integrity factor 1)小肽的生成,AtCIF2小肽结合根细胞质膜上的类受体蛋白激酶AtSGN3(schengen 3),促进其与胞质类受体激酶AtLKS4/AtSGN1的互作和磷酸化,随后AtLKS4通过磷酸化NADPH氧化酶AtRBOHC(respiratory burst oxidase homolog C)和AtRBOHD(respiratory burst oxidase homolog D)从而在根细胞内产生ROS信号(图1),进而诱导钾离子转运体基因AtHAK5转录水平升高,提高根细胞的钾吸收能力^[42]。

低钾胁迫还可以诱导根中产生乙烯信号,并促进ROS信号的产生,提高AtHAK5转录水平^[39]。同时乙烯信号还可以促进根毛的伸长生长,这样有助于根系吸收更多的钾离子^[40,41]。研究还发现,低钾胁迫可以影响根中生长素的分布,从而改变低钾下植物的根构型(如根毛长度、主根长度、侧根密度等),以适应低钾环境。钾离子通道AtAKT1可以通过影响生长素运输蛋白AtPIN1的稳定性,调控低钾下生长素的极性运输,进而影响拟南芥主根的生长^[43]。而钾离子转运体AtKUP4/AtTRH1(tiny root hair 1)和AtKUP9自身也可以转运生长素,前者通过影响AtPIN1蛋白的极性定位调控根毛发育和根向地性生长^[44],后者通过维持根尖干细胞生长素稳态调控低钾下主根的生长^[37]。

2 磷的吸收利用与信号转导途径

植物通过根系以H₂PO₄⁻和HPO₄²⁻的形式从土壤中吸收磷素。H₂PO₄⁻和HPO₄²⁻简称为Pi(phosphate)或有效磷。土壤中的H₂PO₄⁻和HPO₄²⁻容易被Fe³⁺、Al³⁺或钙固定,形成难溶化合物,或被土壤微生物转化为有机磷,或被雨水冲淋,导致土壤中的有效磷浓度极低,植物/作物经常遭受低磷胁迫。磷饥饿反应(Pi-starvation re-

sponse, PSR)是植物响应低磷胁迫的重要机制。PSR通过形态、生理、生化和分子等方面的变化来维持植物和细胞内的磷稳态,提高磷素利用效率,使植物适应或抵御低磷胁迫^[45,46]。补充无机磷或施用磷肥会减弱或抑制PSR,这可能是磷肥利用效率低下的原因之一。

2.1 植物根系的磷吸收

植物根系吸收土壤中的有效磷主要通过PHT1(phosphate transport 1)家族成员。已报道的PHT1转运体定位在细胞质膜,具有H⁺和Pi同向共转运特性。拟南芥(*Arabidopsis thaliana*)PHT1家族有9个成员,分别命名为AtPHT1;1~AtPHT1;9,其中AtPHT1;1和AtPHT1;4是负责根系磷吸收的主要磷转运体,也是最早被鉴定的高等植物磷转运体^[47]。水稻(*Oryza sativa*)中有13个PHT1成员,依序命名为OsPT1~OsPT13,其中OsPT6、OsPT8、OsPT9和OsPT10参与根系磷吸收^[46]。玉米(*Zea mays*)也有13个PHT1成员^[48],目前已知ZmPT7参与玉米根系的磷吸收^[49]。

植物和真菌的PHT1家族成员结构相似,有12个跨膜区,被一个带电的亲水环分成两组,每组6个跨膜区,并且N端和C端在胞内^[50]。真菌(*Piriformospora indica*)高亲和磷转运体PiPT蛋白晶体结构的解析,证实了预测的PHT1拓扑结构,并明确了PiPT转运体与PO₄³⁻结合位置,表明其是通过“摇杆开关”机制跨膜转运无机磷^[51]。

植物PHT1可以在多个层面响应环境磷水平变化,以维持植物体内的磷稳态。已报道的PHT1转运体属于内向磷转运体,可细分为三种类型:高亲和磷转运体、低亲和磷转运体以及双亲和磷转运体。高亲和型PHT1主要在磷浓度较低时发挥作用,低亲和型PHT1则在磷浓度高时具有功能,而双亲和型PHT1在低磷和高磷条件下都具有磷转运活性。例如,水稻OsPT2是低亲和磷转运体,OsPT6/8/9/10则是高亲和磷转运体^[46],而玉米ZmPT7是双亲和磷转运体^[49],PHT1磷转运体的这种分工有利于植物适应环境的磷水平波动。

PHT1在转录水平和蛋白水平受到精确调控(图2)。磷充足时,转录因子AtWRKY42正向调控*AtPHT1;1*的表达;低磷胁迫时,*AtPHT1;1*基因受到转录因子PHR1(phosphate starvation response 1)、NIGT1.2(nitrate-inducible, GARP-type transcriptional repressor 1.2)、WRKY45和WRKY75等的正向调控^[45,46,52,53],蛋白激酶AtMKK9(MAP kinase kinase 9)-MPK3/6(mitogen-activated protein kinase 3/6)通过AtWRKY75也参与调

控拟南芥磷吸收^[54]。拟南芥和水稻的PHF1(phosphate transporter traffic facilitator 1)调控PHT1亚细胞定位,促进PHT1蛋白从根细胞内质网运输到质膜^[55,56]。水稻OsPT8是负责根系磷吸收的主要磷转运体,蛋白激酶OsCK2(casein kinase 2)能磷酸化OsPT8的Ser-517残基,导致OsPT8滞留在内质网^[57];磷酸酶OsPP95(protein phosphatase 95)去磷酸化修饰OsPT8的Ser-517残基,使其定位到质膜,促进水稻根系磷吸收^[58]。泛素结合酶AtPHO2(Phosphate 2)调控内质网上AtPHT1的蛋白丰度,AtPHO2的功能受细胞内磷水平的调控,而细胞内的磷水平又依赖于质膜PHT1数量和活性^[59]。

2.2 植物体内的磷分配

根系吸收的无机磷,部分合成含磷有机物,其余以无机磷形式存在,参与细胞的生命活动,或储存在液泡中。磷在植物体内是可移动的,根系吸收的无机磷经木质部运输到地上部,或从衰老组织重新分配到幼叶或发育中的种子等。在细胞内,无机磷在液泡和细胞质之间的分配被精确调控。植物体以及细胞内的磷稳态维持,是植物正常生命活动的基础。

拟南芥AtPHO1(phosphate 1)和水稻的OsPHO1;2是无机磷外向转运体,负责磷素的根-冠转运,其突变体表现出根系无机磷过量积累而叶片无机磷含量降低^[60,61]。AtPHO1还参与磷素从母体组织运输至发育中的种子^[62]。在水稻中,OsPHO1;2参与了籽粒灌浆过程中的磷素分配^[63]。早期研究结果显示,拟南芥AtPHO1定位在内膜系统,例如高尔基体和反式高尔基体网络,不同于OsPHO1;2的质膜定位^[63,64]。然而,最近的研究报告显示,AtPHO1通过网格蛋白介导的内吞作用进行组成型内化,AtPHO1也能在质膜定位^[65]。AtPHO1和OsPHO1;2的质膜定位支持其将无机磷转运出细胞的功能。基于单颗粒冷冻电子显微镜技术解析了AtPHO1同源蛋白AtPHO1;H1的三维结构,发现AtPHO1;H1采用一种类似通道的机制介导Pi的外排^[66]。AtPHO1的N端具有SPX结构域,可以与磷酸肌醇结合,暗示AtPHO1还具有感知细胞内无机磷水平的功能^[67]。AtPHO1在转录水平响应环境磷水平变化(图2)。磷充足时,转录因子WRKY6和WRKY42结合到*AtPHO1*启动子,抑制*AtPHO1*的表达;低磷胁迫时,E3泛素连接酶PRU1(phosphate response ubiquitin E3 ligase 1)介导WRKY6经26S蛋白酶体途径降解,WRKY42也发生蛋白降解,但不受PRU1调控,WRKY6/42的降解解除了

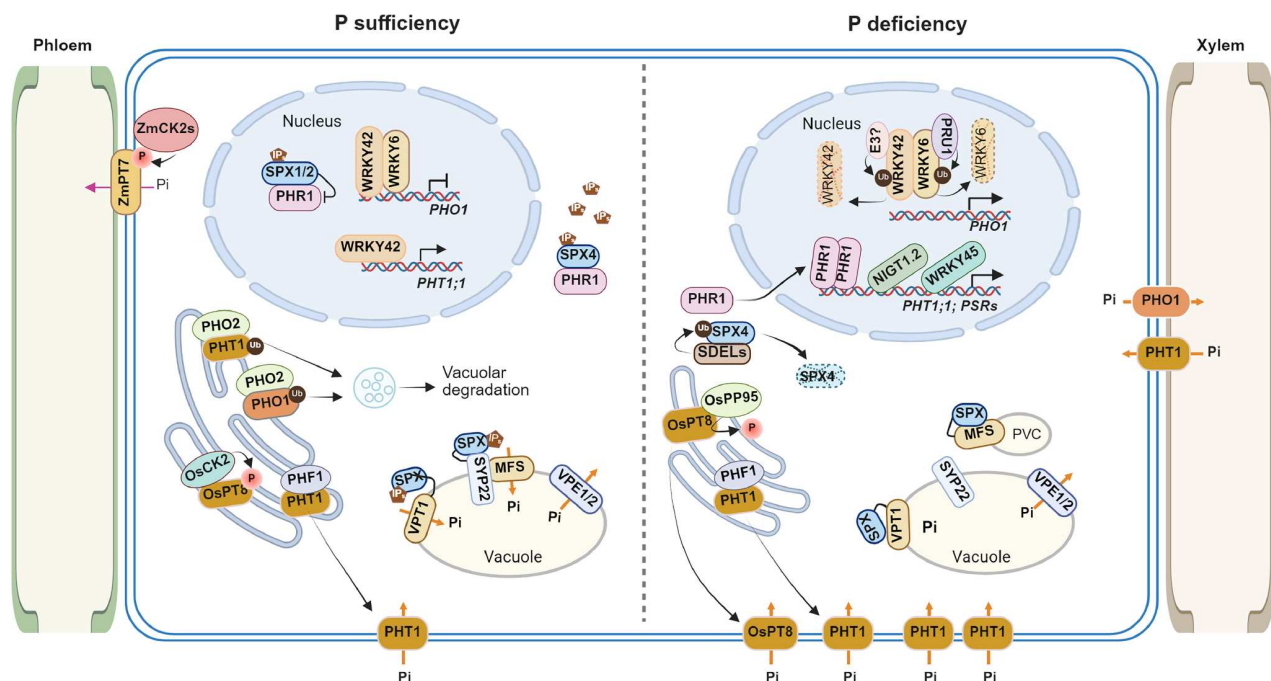


图2 植物磷素吸收、分配以及信号途径。植物体内的磷素转运系统由多个磷转运体协同调控, 共同参与磷的吸收、分配和再分配过程。具体而言, PHT1家族磷转运体负责从外界吸收无机磷, PHO1家族转运体介导磷素向木质部的装载, 促进长距离运输, ZmPT7则参与磷素向韧皮部的转运, 调控磷的再分配, 液泡膜定位的磷转运体动态调控磷的液泡储存或释放。当环境或细胞内的磷水平发生变化时, 植物通过精确调控这些磷转运体的基因表达、亚细胞定位、蛋白活性及稳定性, 维持细胞磷稳态, 从而确保正常的生理代谢活动。示意图使用BioRender.com绘制

Figure 2 Phosphate acquisition, translocation, and signaling pathway in plants. The phosphate (Pi) transport system in plants is coordinately regulated by multiple Pi transporters, which collectively mediate Pi absorption, distribution, and redistribution. Specifically, PHT1 family transporters are responsible for Pi uptake from the external environment; PHO1 family transporters mediate Pi loading into the xylem, promoting long-distance transport; ZmPT7 is involved in Pi translocation into the phloem, regulating Pi redistribution; Vacuolar membrane-localized Pi transporters dynamically modulate Pi storage or release from the vacuolar. When environmental or cellular Pi level fluctuate, plants precisely regulate the gene expression, subcellular localization, protein activity, and stability of these Pi transporters to maintain Pi homeostasis, thereby ensuring normal physiological and metabolic processes (Created with BioRender.com)

对*AtPHO1*的抑制, 有利于磷从根向地上部运输^[68-70]. *AtPHO1*也在转录后水平被调控. 泛素结合酶*AtPHO2* (phosphate 2)介导了*AtPHO1*经液泡降解途径的降解^[71].

PHT1家族成员也参与磷素的分配过程。拟南芥AtPHT1;8和AtPHT1;9参与磷的根-冠转运, 水稻OsPT2仅在中柱表达, 参与磷从根向冠的运输^[45,46]。玉米ZmPT7除了参与根系磷吸收, 还负责叶片间的磷素再分配。ZmPT7在成熟叶片的维管组织表达, 负责磷从老叶向幼叶的运输; 在玉米拔节期之后, ZmPT7在老叶/下位叶被激酶ZmCK2磷酸化, 磷转运活性提高, 有利于磷从老叶重新分配到幼叶^[49]。

磷转运蛋白SPDT(SULTR-like phosphorus distribution transporter)最先在水稻中被鉴定出功能。OsSPDT是质膜定位的磷转运体,在水稻节的木质部表达^[72]。水稻中敲除*OsSPDT*降低了籽粒的磷含量,但增加了叶片

的磷含量,说明OsSPDT在水稻节中起到磷转运开关作用,优先将磷分配到籽粒^[72]。大麦HvSPDT也参与磷装载到籽粒的过程,而拟南芥AtSPDT的主要功能是将磷优先分配到生长旺盛的组织^[46]。

细胞内的无机磷主要储存在液泡内，细胞内磷分配的研究得益于液泡膜上磷转运体的确定(图2)。拟南芥AtPHT5;1(也称为vacuolar phosphate transporter 1, AtVPT1)和水稻OsSPX-MFS1是同源蛋白，其N端具有SPX结构域，定位在液泡膜，负责将无机磷运进液泡^[73~75]。水稻OsVPE1(vacuolar phosphate efflux transporter 1)和OsVPE2也定位在液泡膜，与AtVPT1和OsSPX-MFS功能相反，OsVPE1/2负责将无机磷从液泡转运至细胞质^[76]。细胞质的磷水平影响液泡磷转运体的活性。细胞质无机磷缺乏时，AtVPT1的SPX结构域抑制自身的磷转运活性；而细胞质无机磷充足时，

AtVPT1的SPX结构域与磷酸肌醇InsPs结合,解除了对自身的抑制,AtVPT1活性增加,促进无机磷转运进液泡^[77]。细胞质磷水平还调控液泡磷转运体的液泡膜定位。细胞质无机磷充足时,InsPs结合OsSPX-MFS的SPX结构域,促使SNARE蛋白OsSYP21/22(syntaxin of plants 21/22)与OsSPX-MFS结合,有利于OsSPX-MFS定位到液泡膜;细胞质无机磷缺乏时,OsSYP21/22解除与SXP-MFS的结合,OsSPX-MFS滞留在液泡前体(pre-vacuolar compartments, PVCs),不能正确定位到液泡膜^[78]。

2.3 植物的磷信号途径

植物遭受低磷胁迫时,会通过磷饥饿反应(phosphate starvation response, PSR)来维持植物体内的磷稳态。GARP类转录因子PHR1是植物系统性磷信号途径的核心正调控因子。PHR1最初是通过拟南芥的遗传筛选被鉴定,其突变体*phr1*表现多种磷饥饿反应缺陷^[45]。PHR1与其同源蛋白PHL1(PHR1-Like 1)调控约70%的PSR上调基因和约50%的PSR下调基因^[45]。PHR是多基因家族,在水稻和玉米中,核心的PHR蛋白分别是OsPHR2和ZmPHR1^[79,80]。

SPX蛋白是PHR的负调控因子,通过与PHR蛋白互作抑制PHR的功能。磷充足条件下,拟南芥AtSPX1/2和水稻OsSXP1/2在细胞核中与AtPHR1或OsPHR2结合,抑制AtPHR1/OsPHR2结合到下游靶基因启动子的顺式作用元件P1BS,而AtSXP4和OsSPX4在细胞质中与AtPHR1或OsPHR2结合,阻止AtPHR1/OsPHR2进入细胞核,从而抑制PSR;低磷胁迫时,At/Os SPX1/2解除与AtPHR1/OsPHR2的蛋白互作,OsSPX4蛋白被降解,PHR蛋白活性增加,调控PSR基因的表达,使植物适应或抵抗低磷胁迫^[45,46](图2)。

磷酸肌醇InsPs和焦磷酸肌醇PP-InsPs能结合SPX蛋白,PP-InsPs被认为是植物磷信号传递的信号分子^[67]。细胞内磷充足时,PP-InsPs和SPX1形成二聚体,促进SPX1/2与PHR蛋白结合,阻止PHR蛋白与靶基因启动子结合;低磷胁迫时,InsPs水平降低,SPX结构域和PHR结合减弱^[81~83](图2)。这些发现加深了人们对植物体内磷信号转导机制的认识,有助于找到新的途径和方法来提高作物磷利用效率。

3 氮、磷、钾协同的调控机制

氮、磷、钾之间存在错综复杂的相互作用,植物进化出复杂的分子调控网络,可以在环境养分波动的

条件下协调氮、磷、钾的吸收和利用,以优化生长发育。近年来,在植物氮-磷协同和氮-钾协同机制方面已经取得了重要研究进展。

3.1 氮依赖的植物磷稳态调节

研究表明,在磷饥饿条件下,氮补充可激活PSR;然而,氮饥饿会强烈抑制PSR,说明PSR受到氮供应的调控^[84,85]。最早被发现参与氮依赖性PSR的重要蛋白是拟南芥AtNLA(nitrogen limitation adaptation)。AtNLA编码一个E3泛素连接酶,是植物响应低氮胁迫的正向调控因子,AtNLA和microRNA miR827以NO₃⁻依赖的方式抑制植物的磷吸收^[86]。AtNLA与AtPHO2互作,泛素化AtPHT1s,介导AtPHT1s的液泡降解^[87]。在水稻中,硝酸盐存在时,硝酸盐感受器NRT1.1B与OsSPX4互作,招募E3泛素连接酶NBIP1(NRT1.1B interaction protein 1)降解OsSPX4,进而释放OsPHR2,OsPHR2进入细胞核启动PSR^[84]。同时,OsSPX4还与氮信号关键调控因子OsNLP3(NIN-like protein 3)互作,抑制其活性^[84]。SPX蛋白可能是整合N-P信号的关键节点。

3.2 NIGT1s依赖的氮-磷调控网络

越来越多的证据表明,转录因子NIGT1s是氮-磷交互调控网络的核心调节因子。AtNIGT1s是硝酸盐响应的转录因子,在高氮条件下,抑制一系列氮饥饿响应基因的表达^[88]。除了在硝酸盐信号转导中的抑制作用外,在硝酸根存在条件下,AtNIGT1s还能抑制AtSPXs的表达,从而促进PHR1调控磷吸收和PSR^[89]。AtNIGT1s在转录水平又受到AtPHR1的调控^[90]。并且,在低磷条件下,NIGT1.2和NIGT1.1可直接正向调控AtPHT1.1和AtPHT1.4的表达,促进拟南芥磷吸收;同时抑制硝酸根转运体AtNRT1.1的表达,抑制硝态氮的吸收,维持氮磷平衡^[53]。因此,NIGT1s和PHR1协同调控了N-P信号途径,即硝酸盐激活了磷饥饿信号,而低磷胁迫下调了氮饥饿信号。

3.3 氮-钾协同运输的调控机制

早期的生理学研究表明,植物对氮(硝态氮NO₃⁻)和钾(K⁺)的吸收和转运存在显著的协同效应。硝酸根转运蛋白AtNRT1.1/AtNPF6.3/AtCHL1(chlorina 1)是拟南芥根中负责氮素吸收的重要组分,它和AtAKT1一样,自身的转运活性都受到AtCBL1/9-AtCIPK23复合体的磷酸化调控^[9,91]。此外,在高铵环境下,铵根离子转运蛋白

AtAMT1;1和AtAMT1;2也可以被AtCBL1/9-AtCIPK23复合体磷酸化调控,从而抑制铵吸收减少铵毒害^[92]。因此,植物通过AtCBL1/9-AtCIPK23复合体同时调控AtAKT1、AtNRT1.1、AtAMT1;1/1;2的转运活性,从而协同钾和氮的平衡吸收(图1)。

早期研究发现,硝酸根转运体AtNRT1.5/AtNPF7.3主要在拟南芥根部木质部薄壁细胞表达,调控硝酸根离子向木质部导管的装载^[93]。后续的研究发现,AtNRT1.5/AtNPF7.3也可以同时作为H⁺-K⁺反向共转运体介导钾离子向木质部导管装载,从而实现氮和钾从根部到冠部的协同转运^[18]。植物可以感受环境中氮和钾的供给水平,通过转录因子AtMYB59正向调节AtNPF7.3的转录水平,从而控制氮素和钾素在根与冠之间的分配平衡^[20]。最近的研究显示,AtMYB59-AtNPF7.3模块也受到光信号途径中的核心转录因子AtHY5和AtPIFs的调控。光照条件下,蒸腾拉力是推动水分和养分由根部向冠部运输的主要动力;而在黑暗中,蒸腾作用减弱,根压则成为主要的运输动力。白天AtHY5蛋白在根中积累抑制AtMYB59-AtNPF7.3的表达,减少钾和氮向木质部主动装载,从而降低能量消耗;夜晚AtPIFs在根中积累促进AtMYB59-AtNPF7.3的表达,通过耗能的方式推动钾和氮向木质部装载,维持木质部汁液渗透压和根压,从而维持夜间水分和养分的根冠运输^[94]。

4 总结与展望

自拟南芥基因组发布的20多年间,植物功能基因组学快速发展,大量磷和钾的转运蛋白被陆续鉴定,这些转运蛋白在植物磷、钾养分吸收、转运、分配、利用等方面发挥着重要作用。这些转运蛋白的分子调控机制也得到了深入的解析,其中的分子信号调控通路

也已经初步明确。然而,该领域仍有许多重要的问题尚未得到解答。首先,对植物是如何感知外界养分信号的细胞与分子机制尚不清楚。未来发掘并鉴定植物体内的钾离子感受器,是揭示钾养分信号感知的重要内容。此外,寻找膜系统上介导磷、钾特异性钙信号产生的组分(钙离子通道、钙离子泵等)也是揭示早期养分信号转导的重要一环。其次,受制于研究方法的局限,许多定位于细胞器上的磷、钾转运蛋白尚未被鉴定研究。加强对内膜系统(如液泡膜、叶绿体膜)上转运蛋白的研究,有助于阐明磷、钾养分在不同细胞器中存储、分配、利用,以及对光合作用的调控机制。再次,对多种养分协同机制的研究还处于起步阶段,氮、磷、钾养分信号的交叉互作网络有待深入探讨。寻找氮、磷、钾信号网络中的关键调控节点,阐明其分子作用机制,对于理解不同养分的协同吸收、利用和平衡有重要意义。从次,目前对于作物中磷、钾养分高效的机制研究还有待深入解析。虽然已有的研究表明作物中存在和拟南芥类似的调控机制,但是作物中养分吸收利用的遗传机制更为复杂多变,且与作物的基因型与环境因素密切相关。因此,需要进一步加强玉米、小麦、大豆等主要作物磷、钾养分高效的机制研究,并发掘其中的关键调控基因和优良变异。最后,作物磷、钾养分高效性状与重要抗逆性状的整合研究需要进一步加强。已经发现磷、钾养分高效可以增强作物的抗旱性和耐盐性,因此,解析高效性状与抗逆性状协同的遗传机制对于作物抗逆高效新品种培育具有重要的现实意义。综上所述,未来需要注重解析植物/作物感受和应答磷、钾养分信号的分子调控网络,全面鉴定解析磷、钾养分高效基因及其作用机制,发掘具有育种价值的优良等位变异等,以期为推动作物磷、钾养分高效新品种的培育提供理论基础、基因资源和技术路径。

参考文献

- 1 Wang Y, Wu W H. Potassium transport and signaling in higher plants. *Annu Rev Plant Biol*, 2013, 64: 451–476
- 2 Epstein E, Rains D W, Elzam O E. Resolution of dual mechanisms of potassium absorption by barley roots. *Proc Natl Acad Sci USA*, 1963, 49: 684–692
- 3 Hirsch R E, Lewis B D, Spalding E P, et al. A role for the AKT1 potassium channel in plant nutrition. *Science*, 1998, 280: 918–921
- 4 Li J, Long Y, Qi G N, et al. The Os-AKT1 channel is critical for K⁺ uptake in rice roots and is modulated by the rice CBL1-CIPK23 complex. *Plant Cell*, 2014, 26: 3387–3402
- 5 Han W, Ji Y, Wu W, et al. ZMK1 is involved in K⁺ uptake and regulated by protein kinase ZmCIPK23 in *Zea mays*. *Front Plant Sci*, 2021, 12: 517742
- 6 Gierth M, Mäser P, Schroeder J I. The potassium transporter AtHAK5 functions in K⁺ deprivation-induced high-affinity K⁺ uptake and AKT1 K⁺

- channel contribution to K^+ uptake kinetics in *Arabidopsis* roots. *Plant Physiol*, 2005, 137: 1105–1114
- 7 Yang T, Zhang S, Hu Y, et al. The role of a potassium transporter OsHAK5 in potassium acquisition and transport from roots to shoots in rice at low potassium supply levels. *Plant Physiol*, 2014, 166: 945–959
 - 8 Qin Y, Wu W, Wang Y. ZmHAK5 and ZmHAK1 function in K^+ uptake and distribution in maize under low K^+ conditions. *J Integr Plant Biol*, 2019, 61: 691–705
 - 9 Xu J, Li H D, Chen L Q, et al. A protein kinase, interacting with two calcineurin B-like proteins, regulates K^+ transporter AKT1 in *Arabidopsis*. *Cell*, 2006, 125: 1347–1360
 - 10 Ragel P, Ródenas R, García-Martín E, et al. CIPK23 regulates HAK5-mediated high-affinity K^+ uptake in *Arabidopsis* roots. *Plant Physiol*, 2015, 169: 2863–2873
 - 11 Wang X P, Chen L M, Liu W X, et al. AtKC1 and CIPK23 synergistically modulate AKT1-mediated low-potassium stress responses in *Arabidopsis*. *Plant Physiol*, 2016, 170: 2264–2277
 - 12 Ren X, Qi G, Feng H, et al. Calcineurin B-like protein CBL10 directly interacts with AKT1 and modulates K^+ homeostasis in *Arabidopsis*. *Plant J*, 2013, 74: 258–266
 - 13 Wang Z F, Xie Z M, Tan Y L, et al. Receptor-like protein kinase BAK1 promotes K^+ uptake by regulating H^+ -ATPase AHA2 under low potassium stress. *Plant Physiol*, 2022, 189: 2227–2243
 - 14 Kim M J, Ruzicka D, Shin R, et al. The *Arabidopsis* AP2/ERF transcription factor RAP2.11 modulates plant response to low-potassium conditions. *Mol Plant*, 2012, 5: 1042–1057
 - 15 Zhao S, Zhang M L, Ma T L, et al. Phosphorylation of ARF2 relieves its repression of transcription of the K^+ transporter gene *HAK5* in response to low potassium stress. *Plant Cell*, 2016, 28: 3005–3019
 - 16 Feng C, Luo Y, Wang P, et al. MYB77 regulates high-affinity potassium uptake by promoting expression of *HAK5*. *New Phytol*, 2021, 232: 176–189
 - 17 Gaymard F, Pilot G, Lacombe B, et al. Identification and disruption of a plant shaker-like outward channel involved in K^+ Release into the Xylem Sap. *Cell*, 1998, 94: 647–655
 - 18 Li H, Yu M, Du X Q, et al. NRT1.5/NPF7.3 functions as a proton-coupled H^+ / K^+ antiporter for K^+ loading into the xylem in *Arabidopsis*. *Plant Cell*, 2017, 29: 2016–2026
 - 19 Han M, Wu W, Wu W H, et al. Potassium transporter KUP7 is involved in K^+ acquisition and translocation in *Arabidopsis* root under K^+ -limited conditions. *Mol Plant*, 2016, 9: 437–446
 - 20 Du X Q, Wang F L, Li H, et al. The transcription factor MYB59 regulates K^+ / NO_3^- translocation in the *Arabidopsis* response to low K^+ stress. *Plant Cell*, 2019, 31: 699–714
 - 21 Gajdanowicz P, Michard E, Sandmann M, et al. Potassium (K^+) gradients serve as a mobile energy source in plant vascular tissues. *Proc Natl Acad Sci USA*, 2011, 108: 864–869
 - 22 Michard E, Dreyer I, Lacombe B, et al. Inward rectification of the AKT2 channel abolished by voltage-dependent phosphorylation. *Plant J*, 2005, 44: 783–797
 - 23 Held K, Pascaud F, Eckert C, et al. Calcium-dependent modulation and plasma membrane targeting of the AKT2 potassium channel by the CBL4/CIPK6 calcium sensor/protein kinase complex. *Cell Res*, 2011, 21: 1116–1130
 - 24 Lebaudy A, Pascaud F, Véry A A, et al. Preferential KAT1-KAT2 heteromerization determines inward K^+ current properties in *Arabidopsis* guard cells. *J Biol Chem*, 2010, 285: 6265–6274
 - 25 Gao Y, Wu W, Wang Y. The K^+ channel KZM2 is involved in stomatal movement by modulating inward K^+ currents in maize guard cells. *Plant J*, 2017, 92: 662–675
 - 26 Förster S, Schmidt L K, Kopic E, et al. Wounding-induced stomatal closure requires jasmonate-mediated activation of GORK K^+ channels by a Ca^{2+} sensor-kinase CBL1-CIPK5 complex. *Dev Cell*, 2019, 48: 87–99.e6
 - 27 Mouline K, Véry A A, Gaymard F, et al. Pollen tube development and competitive ability are impaired by disruption of a Shaker K^+ channel in *Arabidopsis*. *Genes Dev*, 2002, 16: 339–350
 - 28 Becker D, Geiger D, Dunkel M, et al. AtTPK4, an *Arabidopsis* tandem-pore K^+ channel, poised to control the pollen membrane voltage in a pH- and Ca^{2+} -dependent manner. *Proc Natl Acad Sci USA*, 2004, 101: 15621–15626
 - 29 Zhao L N, Shen L K, Zhang W Z, et al. Ca^{2+} -dependent protein kinase11 and 24 modulate the activity of the inward rectifying K^+ channels in *Arabidopsis* Pollen Tubes. *Plant Cell*, 2013, 25: 649–661
 - 30 Yang B, Wang J, Yu M, et al. The sugar transporter ZmSUGCAR1 of the nitrate transporter 1/peptide transporter family is critical for maize grain filling. *Plant Cell*, 2022, 34: 4232–4254
 - 31 Tang R J, Zhao F G, Yang Y, et al. A calcium signalling network activates vacuolar K^+ remobilization to enable plant adaptation to low-K environments. *Nat Plants*, 2020, 6: 384–393

- 32 Kunz H H, Gierth M, Herdean A, et al. Plastidial transporters KEA1, -2, and -3 are essential for chloroplast osmoregulation, integrity, and pH regulation in *Arabidopsis*. [Proc Natl Acad Sci USA](#), 2014, 111: 7480–7485
- 33 Aranda-Sicilia M N, Aboukila A, Armbruster U, et al. Envelope K^+ / H^+ antiporters AtKEA1 and AtKEA2 function in plastid development. [Plant Physiol](#), 2016, 172: 441–449
- 34 Armbruster U, Carrillo L R, Venema K, et al. Ion antiport accelerates photosynthetic acclimation in fluctuating light environments. [Nat Commun](#), 2014, 5: 5439
- 35 Zhu X, Pan T, Zhang X, et al. K^+ efflux antiporters 4, 5, and 6 mediate pH and K^+ homeostasis in endomembrane compartments. [Plant Physiol](#), 2018, 178: 1657–1678
- 36 Lu Y, Chanroj S, Zulkifli L, et al. Pollen tubes lacking a pair of K^+ transporters fail to target ovules in *Arabidopsis*. [Plant Cell](#), 2011, 23: 81–93
- 37 Zhang M, Huang P, Ji Y, et al. KUP9 maintains root meristem activity by regulating K^+ and auxin homeostasis in response to low K. [EMBO Rep](#), 2020, 21: e50164
- 38 Behera S, Long Y, Schmitz - Thom I, et al. Two spatially and temporally distinct Ca^{2+} signals convey *Arabidopsis thaliana* responses to K^+ deficiency. [New Phytol](#), 2017, 213: 739–750
- 39 Shin R, Schachtman D P. Hydrogen peroxide mediates plant root cell response to nutrient deprivation. [Proc Natl Acad Sci USA](#), 2004, 101: 8827–8832
- 40 Jung J Y, Shin R, Schachtman D P. Ethylene mediates response and tolerance to potassium deprivation in *Arabidopsis*. [Plant Cell](#), 2009, 21: 607–621
- 41 Kim M J, Ciani S, Schachtman D P. A peroxidase contributes to ros production during *Arabidopsis* root response to potassium deficiency. [Mol Plant](#), 2010, 3: 420–427
- 42 Wang F L, Tan Y L, Wallrad L, et al. A potassium-sensing niche in *Arabidopsis* roots orchestrates signaling and adaptation responses to maintain nutrient homeostasis. [Dev Cell](#), 2021, 56: 781–794.e6
- 43 Li J, Wu W, Wang Y. Potassium channel AKT1 is involved in the auxin-mediated root growth inhibition in *Arabidopsis* response to low K^+ stress. [J Integr Plant Biol](#), 2017, 59: 895–909
- 44 Rigas S, Ditengou F A, Ljung K, et al. Root gravitropism and root hair development constitute coupled developmental responses regulated by auxin homeostasis in the *Arabidopsis* root apex. [New Phytol](#), 2013, 197: 1130–1141
- 45 Paz-Ares J, Puga M I, Rojas-Triana M, et al. Plant adaptation to low phosphorus availability: core signaling, crosstalks, and applied implications. [Mol Plant](#), 2022, 15: 104–124
- 46 Yang S Y, Lin W Y, Hsiao Y M, et al. Milestones in understanding transport, sensing, and signaling of the plant nutrient phosphorus. [Plant Cell](#), 2024, 36: 1504–1523
- 47 Shin H, Shin H, Dewbre G R, et al. Phosphate transport in *Arabidopsis*: pht1;1 and Pht1;4 play a major role in phosphate acquisition from both low- and high-phosphate environments. [Plant J](#), 2004, 39: 629–642
- 48 Liu F, Xu Y, Jiang H, et al. Systematic identification, evolution and expression analysis of the *Zea mays* PHT1 gene family reveals several new members involved in root colonization by arbuscular mycorrhizal fungi. [Int J Mol Sci](#), 2016, 17: 930
- 49 Wang F, Cui P, Tian Y, et al. Maize ZmPT7 regulates Pi uptake and redistribution which is modulated by phosphorylation. [Plant Biotechnol J](#), 2020, 18: 2406–2419
- 50 Raghothama K G. Phosphate acquisition. [Annu Rev Plant Physiol Plant Mol Biol](#), 1999, 50: 665–693
- 51 Pedersen B P, Kumar H, Waight A B, et al. Crystal structure of a eukaryotic phosphate transporter. [Nature](#), 2013, 496: 533–536
- 52 Wang H, Xu Q, Kong Y H, et al. *Arabidopsis* WRKY45 transcription factor activates *PHOSPHATE TRANSPORTER1;1* expression in response to phosphate starvation. [Plant Physiol](#), 2014, 164: 2020–2029
- 53 Wang X, Wang H F, Chen Y, et al. The transcription factor NIGT1.2 modulates both phosphate uptake and nitrate influx during phosphate starvation in *Arabidopsis* and maize. [Plant Cell](#), 2020, 32: 3519–3534
- 54 Lei L, Li Y, Wang Q, et al. Activation of MKK9-MPK3/MPK6 enhances phosphate acquisition in *Arabidopsis thaliana*. [New Phytol](#), 2014, 203: 1146–1160
- 55 González E, Solano R, Rubio V, et al. PHOSPHATE TRANSPORTER TRAFFIC FACILITATOR1 is a plant-specific SEC12-related protein that enables the endoplasmic reticulum exit of a high-affinity phosphate transporter in *Arabidopsis*. [Plant Cell](#), 2005, 17: 3500–3512
- 56 Chen J, Liu Y, Ni J, et al. OsPHF1 regulates the plasma membrane localization of low- and high-affinity inorganic phosphate transporters and determines inorganic phosphate uptake and translocation in rice. [Plant Physiol](#), 2011, 157: 269–278
- 57 Chen J, Wang Y, Wang F, et al. The rice CK2 kinase regulates trafficking of phosphate transporters in response to phosphate levels. [Plant Cell](#), 2015, 27: 711–723
- 58 Yang Z, Yang J, Wang Y, et al. PROTEIN PHOSPHATASE95 regulates phosphate homeostasis by affecting phosphate transporter trafficking in rice. [Plant Cell](#), 2020, 32: 740–757

- 59 Huang T K, Han C L, Lin S I, et al. Identification of downstream components of ubiquitin-conjugating enzyme PHOSPHATE2 by quantitative membrane proteomics in *Arabidopsis* roots. *Plant Cell*, 2013, 25: 4044–4060
- 60 Poirier Y, Thoma S, Somerville C, et al. Mutant of *Arabidopsis* Deficient in Xylem Loading of Phosphate. *Plant Physiol*, 1991, 97: 1087–1093
- 61 Secco D, Baumann A, Poirier Y. Characterization of the rice *PHO1* gene family reveals a key role for *OsPHO1;2* in phosphate homeostasis and the evolution of a distinct clade in dicotyledons. *Plant Physiol*, 2010, 152: 1693–1704
- 62 Vogiatzaki E, Baroux C, Jung J Y, et al. PHO1 exports phosphate from the chalazal seed coat to the embryo in developing *Arabidopsis* seeds. *Curr Biol*, 2017, 27: 2893–2900.e3
- 63 Ma B, Zhang L, Gao Q, et al. A plasma membrane transporter coordinates phosphate reallocation and grain filling in cereals. *Nat Genet*, 2021, 53: 906–915
- 64 Arpat A B, Magliano P, Wege S, et al. Functional expression of PHO1 to the Golgi and *trans*-Golgi network and its role in export of inorganic phosphate. *Plant J*, 2012, 71: 479–491
- 65 Vetal P V, Poirier Y. The *Arabidopsis* PHOSPHATE 1 exporter undergoes constitutive internalization via clathrin-mediated endocytosis. *Plant J*, 2023, 116: 1477–1491
- 66 Fang S, Yang Y, Zhang X, et al. Structural mechanism underlying PHO1;H1-mediated phosphate transport in *Arabidopsis*. *Nat Plants*, 2025, 11: 309–320
- 67 Wild R, Gerasimaite R, Jung J Y, et al. Control of eukaryotic phosphate homeostasis by inositol polyphosphate sensor domains. *Science*, 2016, 352: 986–990
- 68 Chen Y F, Li L Q, Xu Q, et al. The WRKY6 transcription factor modulates *PHOSPHATE1* expression in response to low Pi stress in *Arabidopsis*. *Plant Cell*, 2009, 21: 3554–3566
- 69 Su T, Xu Q, Zhang F C, et al. WRKY42 modulates phosphate homeostasis through regulating phosphate translocation and acquisition in *Arabidopsis*. *Plant Physiol*, 2015, 167: 1579–1591
- 70 Ye Q, Wang H, Su T, et al. The ubiquitin E3 ligase PRU1 regulates WRKY6 degradation to modulate phosphate homeostasis in response to low-Pi stress in *Arabidopsis*. *Plant Cell*, 2018, 30: 1062–1076
- 71 Liu T Y, Huang T K, Tseng C Y, et al. PHO2-dependent degradation of PHO1 modulates phosphate homeostasis in *Arabidopsis*. *Plant Cell*, 2012, 24: 2168–2183
- 72 Yamaji N, Takemoto Y, Miyaji T, et al. Reducing phosphorus accumulation in rice grains with an impaired transporter in the node. *Nature*, 2017, 541: 92–95
- 73 Wang C, Huang W, Ying Y, et al. Functional characterization of the rice *SPX-MFS* family reveals a key role of *OsSPX-MFS1* in controlling phosphate homeostasis in leaves. *New Phytol*, 2012, 196: 139–148
- 74 Liu T Y, Huang T K, Yang S Y, et al. Identification of plant vacuolar transporters mediating phosphate storage. *Nat Commun*, 2016, 7: 11095
- 75 Liu J, Yang L, Luan M, et al. A vacuolar phosphate transporter essential for phosphate homeostasis in *Arabidopsis*. *Proc Natl Acad Sci USA*, 2015, 112: E6571
- 76 Xu L, Zhao H, Wan R, et al. Identification of vacuolar phosphate efflux transporters in land plants. *Nat Plants*, 2019, 5: 84–94
- 77 Luan M, Zhao F, Sun G, et al. A SPX domain vacuolar transporter links phosphate sensing to homeostasis in *Arabidopsis*. *Mol Plant*, 2022, 15: 1590–1601
- 78 Guo R, Zhang Q, Qian K, et al. Phosphate-dependent regulation of vacuolar trafficking of OsSPX-MFSs is critical for maintaining intracellular phosphate homeostasis in rice. *Mol Plant*, 2023, 16: 1304–1320
- 79 Zhou J, Jiao F C, Wu Z, et al. *OsPHR2* is involved in phosphate-starvation signaling and excessive phosphate accumulation in shoots of plants. *Plant Physiol*, 2008, 146: 1673–1686
- 80 Tian M, Wang H, Tian Y, et al. *ZmPHR1* contributes to drought resistance by modulating phosphate homeostasis in maize. *Plant Biotechnol J*, 2024, 22: 3085–3098
- 81 Ried M K, Wild R, Zhu J, et al. Inositol pyrophosphates promote the interaction of SPX domains with the coiled-coil motif of PHR transcription factors to regulate plant phosphate homeostasis. *Nat Commun*, 2021, 12: 384
- 82 Zhou J, Hu Q, Xiao X, et al. Mechanism of phosphate sensing and signaling revealed by rice SPX1-PHR2 complex structure. *Nat Commun*, 2021, 12: 7040
- 83 Guan Z, Zhang Q, Zhang Z, et al. Mechanistic insights into the regulation of plant phosphate homeostasis by the rice SPX – PHR2 complex. *Nat Commun*, 2022, 13: 1581
- 84 Hu B, Jiang Z, Wang W, et al. Nitrate–NRT1.1B–SPX4 cascade integrates nitrogen and phosphorus signalling networks in plants. *Nat Plants*, 2019, 5: 401–413
- 85 Medici A, Szponarski W, Dangeville P, et al. Identification of molecular integrators shows that nitrogen actively controls the phosphate starvation response in plants. *Plant Cell*, 2019, 31: 1171–1184

- 86 Kant S, Peng M, Rothstein S J, et al. Genetic regulation by NLA and microRNA827 for maintaining nitrate-dependent phosphate homeostasis in *Arabidopsis*. [PLoS Genet](#), 2011, 7: e1002021
- 87 Lin W Y, Huang T K, Chiou T J. NITROGEN LIMITATION ADAPTATION, a target of microRNA827, mediates degradation of plasma membrane-localized phosphate transporters to maintain phosphate homeostasis in *Arabidopsis*. [Plant Cell](#), 2013, 25: 4061–4074
- 88 Kiba T, Inaba J, Kudo T, et al. Repression of nitrogen starvation responses by members of the *Arabidopsis* GARP-type transcription factor NIGT1/HRS1 subfamily. [Plant Cell](#), 2018, 30: 925–945
- 89 Ueda Y, Kiba T, Yanagisawa S. Nitrate-inducible NIGT1 proteins modulate phosphate uptake and starvation signalling via transcriptional regulation of *SPX* genes. [Plant J](#), 2020, 102: 448–466
- 90 Maeda Y, Konishi M, Kiba T, et al. A NIGT1-centred transcriptional cascade regulates nitrate signalling and incorporates phosphorus starvation signals in *Arabidopsis*. [Nat Commun](#), 2018, 9: 1376
- 91 Ho C H, Lin S H, Hu H C, et al. CHL1 functions as a nitrate sensor in plants. [Cell](#), 2009, 138: 1184–1194
- 92 Straub T, Ludewig U, Neuhäuser B. The kinase CIPK23 inhibits ammonium transport in *Arabidopsis thaliana*. [Plant Cell](#), 2017, 29: 409–422
- 93 Lin S H, Kuo H F, Canivenc G, et al. Mutation of the *Arabidopsis* *NRT1.5* nitrate transporter causes defective root-to-shoot nitrate transport. [Plant Cell](#), 2008, 20: 2514–2528
- 94 Jing S, Zhang H, Yang Z, et al. Alternating inverse modulation of xylem K^+/NO_3^- loading by HY5 and PIF facilitates diurnal regulation of root-to-shoot water and nutrient transport. [New Phytol](#), 2025, 245: 2584–2599

Summary for “植物钾、磷养分吸收利用机制的研究进展”

Progress of potassium and phosphorus transport and signaling in plants

Yi-Fang Chen^{*}, Yi Wang & Wei-Hua Wu

College of Biological Sciences, China Agricultural University, Beijing 100193, China

^{*} Corresponding author, E-mail: chenyifang@cau.edu.cn

Nitrogen (N), phosphorus (P), and potassium (K) are three essential macronutrients that play fundamental roles in plant growth, development, and reproduction. As primary components of key biomolecules and critical regulators of physiological processes, their absorption, translocation, and utilization efficiencies significantly affect crop yield, quality, and stress tolerance. While plants absorb potassium in its ionic form (K^+) and phosphorus as orthophosphate (P_i , $HPO_4^{2-}/H_2PO_4^-$), these nutrients often become chemically fixed in soil particles, particularly in acidic or alkaline soils. This fixation leads to limited bioavailability, making K and P deficiencies common in both natural ecosystems and agricultural systems worldwide. Modern agriculture relies heavily on K and P fertilizers to cope with the low availability of soil K and P. However, this approach faces two major challenges: low nutrient use efficiency (NUE) and limited resource availability. Current data show that only 15%–25% of applied K or P fertilizers are actually absorbed by crops, with the remainder being lost through leaching, runoff, or soil fixation. Unlike nitrogen, which can be fixed from the abundant atmospheric N_2 through industrial or biological processes, K and P fertilizers are derived from non-renewable mineral deposits. Given current consumption rates, the crisis of K and P fertilizer scarcity may soon become a reality. Improving plant NUE provides an effective and economical way to overcome the effects of K and P deficiencies, and fulfill the demand for food security and agricultural sustainability. Achieving this goal requires a deep understanding of the molecular mechanisms underlying plant nutrient sensing, uptake, translocation, and utilization. Recent advances in plant molecular physiology have identified key transporters, sensors, and signaling pathways involved in K and P homeostasis. Furthermore, emerging evidence suggests sophisticated crosstalk and coordinated regulation among N, P, and K nutrient pathways. This review systematically examines current knowledge on K and P transport systems and signaling pathways in plants, with particular emphasis on discoveries in *Arabidopsis thaliana*, rice (*Oryza sativa*), and maize (*Zea mays*). We also explore the emerging understanding of how plants coordinate the uptake and utilization of N, P, and K nutrients, and discuss how this knowledge could be applied to improve crop NUE through molecular breeding or genetic engineering approaches. By bridging fundamental research with agricultural applications, we aim to contribute to the development of sustainable solutions for global food production challenges.

potassium, phosphorus, absorption, translocation, signaling

doi: [10.1360/TB-2025-0028](https://doi.org/10.1360/TB-2025-0028)