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细胞分裂素转运蛋白在细胞分裂素平衡和信号分布中的作用

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摘 要

细胞分裂素(CK)是一类可移动的腺嘌呤衍生物，它们作为化学信号调节与植物发育和胁迫反应有关的各种生物过程。它们的合成、稳态和信号感知会引起复杂的细胞内交通、细胞间移动以及短距离和长距离转运。近二十年来，膜转运蛋白的亚群已被识别并参与CK以及相关腺苷酸的转运。本文旨在回顾参与细胞分裂素运输和易位的转运蛋白探索的主要进展，讨论它们在细胞分裂素介导的旁分泌和远距离通讯中的功能意义，并强调一些知识空白和开放性问题，以全面理解膜转运蛋白在控制细胞分裂素物种时空分布中的分子机制。

关键词

拟南芥，转运蛋白，细胞分裂素

Role of Cytokinin Transporter Proteins in Cytokinin Homeostasis and Signal Distribution

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Abstract

Cytokinins (CKs) are a group of mobile adenine derivatives that act as chemical signals regulating a variety of biological processes implicated in plant development and stress responses. Their syn-

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thesis, homeostasis, and signaling perception evoke complicated intracellular traffic, intercellular movement, and in short- and long-distance translocation. Over nearly two decades, subsets of membrane transporters have been recognized and implicated in the transport of CKs as well as the related adenylates. In this review, we aim to recapitulate the key progresses in exploration of the transporter proteins involved in cytokinin traffic and translocation, discuss their functional implications in the cytokinin-mediated paracrine and long-distance communication, and highlight some knowledge gaps and open issues toward comprehensively understanding the molecular mechanism of membrane transporters in controlling spatiotemporal distribution of cytokinin species.

Keywords

***Arabidopsis thaliana*, Transporter, Cytokinin**

1. 细胞分裂素

1.1. 细胞分裂素的种类

细胞分裂素(Cytokinin, CK)是一类能促进细胞分裂和分化的腺嘌呤衍生物[1]。在植物中，CK 通常以 N^6-(Δ^2-异戊烯基)腺嘌呤(isopentenyladenine, iP)、反式玉米素(*trans*-Zeatin, *t*Z)、玉米素(*cis*-Zeatin, *c*Z)和二氢玉米素(dihydrozeatin, DHZ)的形式存在[2]。在植物体内，细胞分裂素通常以无活性状态储存，待需要时通过代谢转化成活性形式[3]。CK 对植物生长发育至关重要，参与种子萌发与叶片发育、植物组织器官生长、离体叶片的衰老、以及幼枝和根的生长调控等生长发育过程[4] [5]。

1.2. 细胞分裂素的代谢

1.2.1. 细胞分裂素的合成

CK 主要有两种生物合成途径，分别是 tRNA 分解途径和从头合成途径[6] [7]。大部分内源 CK 通过从头合成途径合成，该途径的第一步是由异戊烯基转移酶(isopentenyl transferase, IPT)催化 5’-磷酸腺苷(AMP、ATP 或 ADP)与二甲基烯丙基二磷酸(Dimethylallyl Diphosphate, DMAPP)反应，生成 iPR 前体[8] [9]。随后在 CYP735A 催化下转化为 *t*ZR 前体，后者在异戊二烯侧链末端被羟基化[10]。对拟南芥和水稻中这些生物合成基因功能丧失突变体的表型分析表明，这些反应在从头 CK 生物合成中起核心作用[11] [12] [13] [14] [15]。

核苷酸形式的 CK 有两种转化为活性形式的途径：主要途径是通过磷酸核糖水解酶(Lonely guy，LOG)将细胞分裂素核苷酸转化为核碱基活性形式[16] [17] [18] [19]。另一种是通过两步法，细胞分裂素核苷酸如 iP 核苷 5′-单磷酸(iPRMP)可通过核苷酸酶先后转化为相应的细胞分裂素核苷如 iP 核苷(iPR)，然后通过核苷酸酶转化为细胞分裂素核碱基(如 iP) [20] [21]。最近有文章报道，*GY*3 可编码催化 iPRMP 转化为 iPR 的 LOG 样蛋白。抑制 *GY3* 等位基因表达会导致代谢库中更多的 iPRMP 转化为 *t*ZRMP，随后转化为 *t*Z 增强 *OSH*1 和 *CYCD*3；1 的表达。进一步通过维持分生活性和促进细胞分裂，最终导致穗发育出更多的二级分枝，谷物产量增加[22]。定位于细胞壁的细胞分裂素/嘌呤核苷核苷酸酶(cytokinin/purine riboside nucleosidase, CPN)也能催化细胞分裂素核苷前体和其他嘌呤核苷的去核糖基化，参与细胞分裂素代谢[23]。

*c*Z 型 CK 的合成过程是由 tRNA-IPTs 的酶催化的，它们通过异戊烯化反应将二甲基烯丙基二磷酸连接到 tRNA 分子上[24]。在调节活性 CK 浓度平衡中，*CYP*735*A*2 至关重要[10]。研究结果显示，多种活性 CK 可以诱导 *CYP*735*A*2 的表达。然而，*CYP*735*A*1 对 CK 的响应并不敏感。此外，*CYP*735*A*2 主要表达在根部，但也在花瓣、茎尖分生组织以及下胚轴中有高水平表达[10] (图 1)。

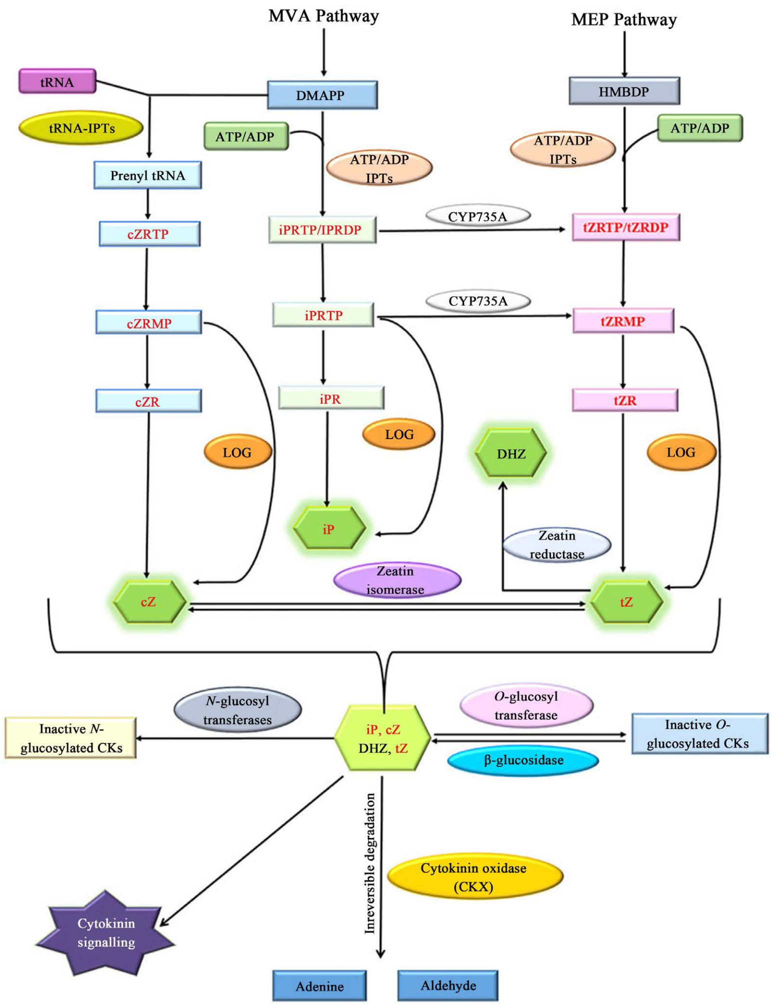

Figure 1. Cytokinin homeostasis maintenance pathway involving in situ cytokinin biosynthesis (catalyzed by ATP-ADP IPTs and tRNA-IPTs), activation (catalyzed by specific phosphoribohydrolases encoded by *LOG* genes), irreversible inactivation (catalyzed by *N*-glucosyltransferases), reversible inactivation (catalyzed by *O*-glucosyltransferases), reactivation (catalyzed by *β*-glucosidases) and irreversible degradation (catalyzed by cytokinin oxidase/dehydrogenases). Cytokininoxidase/dehydrogenases substrates are highlighted in red [25]

图 1. 细胞分裂素平衡维持途径涉及细胞分裂素的原位生物合成(由 ATP-ADPIPT 和 tRNA-IPT 催化)、激活(由 *LOG* 基因编码的特定磷酸核糖水解酶催化)、不可逆失活(由 *N*-葡糖基转移酶催化)、可逆失活(由 *O*-葡糖基转移酶催化)、再激活(由 *LOG* 基因编码的特定磷酸核糖水解酶催化)、不可逆失活(由 *N*-葡萄糖基转移酶催化)、可逆失活(由 *O*-葡萄糖基转移酶催化)、再活化(由 *β*-葡萄糖苷酶催化)和不可逆降解(由细胞分裂素氧化酶/脱氢酶催化)。细胞分裂素氧化酶/脱氢酶底物用红色标出[25]

1.2.2. 细胞分裂素的降解

细胞分裂素氧化酶(cytokinin oxidase, CKX)是植物中负责分解细胞分裂素的关键酶。*tZ* 和 iP 具有不

饱和 *N*6-侧链并被切割，而二氢玉米素和 BA 对 CKX 具有抗性[26]。最初在玉米中发现了 CKX，后续研究揭示了它在植物体中降解细胞分裂素的生物学功能[27] [28]。在拟南芥中鉴定出了 7 个 CKX，即 AtCKX1 至 AtCKX7。过表达 *AtCKX*1 至 *AtCKX*6 基因会导致植物内源性细胞分裂素含量降低，产生细胞分裂素缺乏的典型症状，如植株矮化、初生根伸长、叶原基和顶端分生组织异常发育等[4] [29]。当 *AtCKX*3、*AtCKX*5 突变时，拟南芥中的 CK 含量升高，表现出花器官增大、胚珠数量增多和种子产量提高的表型[30]。

1.3. 细胞分裂素的信号

植物对环境变化的可塑性机制是理解其行为的关键。在生长过程中，植物器官按照既定的发育程序分化，同时又能灵活地响应外部环境的变化，这有助于植物在最佳环境中发芽[31]。在生长过程中，器官对环境信号的响应，通过细胞间的信号传递进行协调。生长素和细胞分裂素的丰度以及它们之间的比率和分布对环境盐胁迫敏感[32]，这似乎是通过极性生长素转运蛋白的作用进而影响了植物根系结构[33]。冷胁迫也会导致植物生长减少，而外源性施加细胞分裂素可以提高拟南芥幼苗的抗冻性[34]。除了生长素的不对称分布外，信号传递主要依赖木质部和韧皮部运输实现[35]。在这个过程中，无机离子、信号分子、激素和肽在系统信号传递中扮演着至关重要的角色[4]。

CK 信号转导途径是一种类似细菌的双组分反应(Two-component signaling sensor, TCS)系统。其中主要包括组氨酸蛋白激酶(*Arabidopsis* histidine kinase receptor, AHK)、组氨酸磷酸转移蛋白(*Arabidopsis* histidine phosphotransfer protein, AHP)和应答调节因子(*Arabidopsis* response regulator, ARR)三个部分[36]。信号以 AHK 为媒介，经过一系列磷酸化反应传递到细胞核中的 B 型 *ARR*。B 型 *ARR* 编码转录激活因子，能直接促进下游靶基因的表达[37]。这一磷酸化系统涉及的多步反应，在 Asp 和 His 残基间进行。CK 利用此系统传递信号，参与愈伤组织形成、种子萌发、细胞分化以及叶片衰老延缓等生理过程[38]。

CK 通过三种 AHK 受体感知，进而刺激靶基因的转录，激活磷酸化信号反应[39]。这些受体结构保守，包含受体结构域、组氨酸激酶结构域和配体结合位点，且存在功能冗余[40] [41] [42] [43]。大多数受体在 ER 上被发现，并能有效结合细胞分裂素[41] [44] [45]，这暗示细胞分裂素需转运至胞内，并可能转运至 ER，从而触发依赖于细胞分裂素的信号传递[46] [47] [48]。然而，关于 CK 信号起始位点是位于质膜还是内质网膜上，目前仍存在争议[49]。

在拟南芥中，ARR 根据它们的结构和氨基酸序列被划分为 A、B、C 三类[50]。A 型 *ARR* 受到细胞分裂素的诱导，并且能够通过反馈机制调控细胞分裂素的活性[4] [51]；B 型 *ARR* 是一类编码具有 DNA 结合结构域(GARP)的转录因子，GARP 能特异性地结合并调控 A 型 *ARR* 的转录活性[4] [52]；C 类 *ARR* 不受到 CK 诱导，并且它们的结构与 AHK 类似，可能在与细胞分裂素信号传导途径有关的方面上，扮演与 A 型和 B 型 *ARR* 不同的角色[53] [54] (图 2)。

2. 细胞分裂素的转运

2.1. 细胞分裂素的分布

细胞分裂素是维持分生组织和其他生理和发育过程所必需的植物激素，涉及胚胎发育、细胞分裂、侧根形成、叶片衰老以及对热和干旱胁迫的适应性反应[56] [57] [58]。由于 CK 的生物合成由 IPT 催化，仅在特定组织中发生，因此 CK 需要通过输出和/或主动运输机制在植物体内进行转移[14] [35] [39]。CK 的合成和代谢的空间分布表明，CK 在根和芽中均有合成，并且可以通过短距离和长距离运输[60] [61]。在拟南芥中，IPT 在根、茎、叶和花等多个器官中表达[35] [59]。而 *CYP*735*A* 则在根中主要表达[10]。

新合成的细胞分裂素 N^9 位置含有一个核糖苷分子，这类细胞分裂素被称为核苷型细胞分裂素，包括 iPR 和 *t*ZR。核苷基团裂解释放出的自由碱基分别是 iP 和 *t*Z，这些是更具生物活性的形式，而核 iPR 和

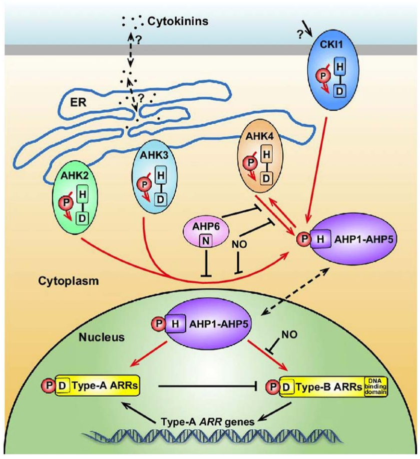

Figure 2. Core steps of the cytokinin signaling pathway [55]
图 2. 细胞分裂素信号途径的核心步骤[55]

*t*ZR 是主要的运输形式[62] [63]。因为 CK 的合成基因在空间表达模式上存在差异，导致了不同形式的 CK 在木质部和韧皮部分布不均。在木质部中，*t*Z 型 CK 为主要形式；而在韧皮部中，iP 型 CK 占主导地位[64]。根和芽中合成的 CK 类型不同，也导致了根源性 *t*Z 型 CK 主要是通过木质部向顶部运输，而茎源性 iP 型 CK 是通过韧皮部扩散或向基部运输[65] [66]。由于 CK 是可移动的信号，已知的 CK 转运蛋白家族包括 ATP 结合盒蛋白家族(ATP-binding cassette, ABC) [67]、嘌呤渗透酶蛋白家族(purine permease, PUP) [68] [69]、氮杂鸟嘌呤抗性蛋白家族(AZA-guanine resistant) [70] [71]以及平衡核苷转运蛋白家族(equilibrative nucleoside transporter, ENT) [72] (图 3)。

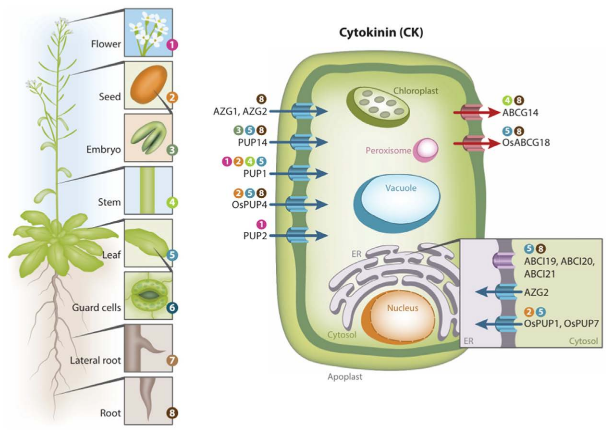

Figure 3. Overview of CK transporters in plants. (*Left*) Illustration of an *Arabidopsis* plant with magnifications emphasizing different organs. (*Right*) Overview of characterized CK transporters. Blue arrows represent importers; red arrows represent exporters. The inset is a magnification of the indicated organelles. The numbers in circles above transporter names indicate locations in the tissues in the illustration on the left (not all tissues express transporters regulating this hormone). The direction of CK transport for the three ER-localized ABCI proteins is currently not entirely clear. All transporters were characterized in *Arabidopsis* unless the transporter name is preceded by a species abbreviation. Abbreviations: CK, cytokinin; ER, endoplasmic reticulum; Os, *Oryza sativa* [73]
图 3. 植物中的 CK 转运体概览。(左图)拟南芥植株图解，不同器官的放大倍数不同。(右图)表征的 CK 转运体概览。蓝色箭头代表输入体；红色箭头代表输出体。插图为所示细胞器的放大图。转运体名称上方圆圈中的数字表示左侧插图中组织的位置(并非所有组织都表达调节这种激素的转运体)。目前还不完全清楚三种位于 ER 的 ABCI 蛋白的 CK 转运方向。除非转运体名称前有物种缩写，否则所有转运体都是在拟南芥中表征的。缩写：CK，细胞分裂素；ER，内质网；Os，水稻[73]

2.2. ABC 转运蛋白参与细胞分裂素的转运

在大多数生物体中，ABC 转运蛋白是最大的膜蛋白家族之一[74] [75]。这类蛋白负责介导多种分子跨越磷脂双分子层的转运，包括矿物质离子、肽类和脂类等。ABC 转运蛋白主要结构包含两个核酸结合结构域(nucleotide binding domain, NBD)和两个跨膜结构域(transmembrane domain, TMD) [76]，前者也常称为 ATP 结合结构域。NBD 的功能是结合及水解 ATP 以提供动力，而 TMD 则负责底物穿越膜的路径。这两个结构域协同作用，共同完成了底物的动态转运过程[77]。

ABC 蛋白家族还与嘌呤核苷酸的转运和再循环有关，这可能赋予其在转运细胞分裂素方面的调控和代谢优势。AtABCG14 是首个被报道参与 *t*Z 型 CK 长距离的转运蛋白[64] [78]，定位于质膜，具有外排 *t*Z 类 CK 的活性。*AtABCG*14 在根部的中柱和中柱鞘中主要表达，对 CK 装载到木质部和向地上运输至关重要。在 *atabcg*14 中，根部 *t*Z 型 CK 积累，而茎中降低。相比之下，iP 型 CK 水平在根和茎中均显著升高。导致根短、植株矮小且生长发育迟缓。此外，AtABCG14 也影响地上部分对 CK 的分配[64] [78]。类似地，水稻中的 OsABCG18 定位于质膜，对 CK 具有外排活性，并在茎、根和主叶脉中表达，参与 CK 从根部向地上部分的运输[79]。

2.3. PUP 转运蛋白参与细胞分裂素的转运

与 ABC 蛋白不同，PUP 主要参与细胞对激素的吸收，而不是激素从细胞中释放[80]。拟南芥的 PUP 家族有 21 个成员，其中大多数基因尚未被表征[60]。AtPUP1 和 AtPUP2 以质子偶联的方式介导游离的 iP 型 *t*Z 型 CK 向内运输[69] [81]。水稻中的 OsPUPl 和 OsPUP7 定位于内质网上，而 OsPUP4 定位于质膜[82]。在植物中，定位在质膜上的 *AtPUP*14 表达最高。其转运活性依赖于 ATP，但与质子梯度无关[68]。研究者们使用 *TCSn::GFP* 这一合成 CK 报告系统来研究拟南芥心形期胚的发育情况，并发现 *AtPUP*14 在心形期胚胎中表达量的降低与 CK 含量的升高有关。这表明 AtPUP14 可能负责将活性形式的细胞分裂素运输到胞质中，从而减少了细胞间 CK 的浓度，导致膜定位的细胞分裂素受体感知减少，进而调节植物的细胞分裂素信号传导。通过对 AtPUP14 进行激素转运实验，发现 AtPUP14 具有转运活性 CK 的能力，并且 AtPUP14 的转运活性明显强于 AtPUP1。当 AtPUP14 的功能缺失时，会影响 CK 的信号运输，导致分生组织和胚胎发育出现异常，表现出芽和叶原基的分支增多和叶序发育混乱[68]。这些综合研究表明，AtPUP14 参与了 CK 由胞外向胞内的运输。

近期研究报道了一种基因的多重敲除编辑技术，该技术是一种基因组规模的间隔短回文重复系统，用于同时针对拟南芥中多个基因家族成员的功能冗余[83]。在这项研究中，鉴定和表征了植物中 *AtPUP*7、*AtPUP*8 和 *AtPUP*21 三个基因，并通过系统发育分析确认它们属于同一单系进化枝，并且具有完整的遗传连锁。根据实验证明，质膜定位的 AtPUP8 是一个 CK 外排的转运蛋白，而液泡膜定位的 AtPUP7 和 AtPUP21 则是 CK 的内吸转运蛋白，它们都能降低细胞质和/或内质网中 CK 的水平。这两种转运蛋白的共同作用可能导致细胞质 CK 水平的下降，并显示出部分功能冗余。这种质膜和液泡膜转运蛋白网络的协调可能是决定细胞和组织内 CK 水平的关键因素，这对于在 SAM 内建立 CK 信号传导的空间模式至关重要，并在调节芽和叶序生长中发挥重要作用。

2.4. AZG 转运蛋白参与细胞分裂素的转运

研究发现，AZG 家族成员 AtAZG1、AtAZG2 均具有 CK 的转运活性[70] [71]。EnAZGA 是该家族的首个成员，在构巢曲霉中发现能转运次黄嘌呤、腺嘌呤和鸟嘌呤[84]。在拟南芥中，AZG1 和 AZG2 最初被认为是腺嘌呤和鸟嘌呤的转运蛋白[85]。AtAZG2 定位主要在内质网中，暗示其在细胞内 CK 分布和信号传递中发挥功能[71]，在质膜也有定位，但尽管 AtAZG1 和 AtAZG2 都涉及 CK 转运，但它们的转运机

制不同。AtAZG1 是依赖质子驱动力作为细胞 CK 的输入蛋白，而 AtAZG2 的转运不受电化学质子梯度或能量的影响，并且与 pH 值无关。在酵母中的研究表明，AtAZG2 能高效地双向转运不同类型的 CK，如 iP、*t*Z、6-BA 等。AZG2 在侧根原基(lateral root primordial, LRP)周围细胞中有少量表达表明它参与侧根发育过程中 CK 的调节。*azg*2 侧根密度增加，且发育迟缓，对外源性 CK 的反应降低，根部的 $TCSn_{pro}$:*GFP* 荧光信号也较弱。过表达 *AtAZG*2 的转基因株系几乎没有产生侧根。此外，生长素通过 *ARF*7 诱导 *AtAZG*2 表达，促进胞内 CK 的转运，进而抑制侧根的形成[71]。

AtAZG1 被鉴定为 CK 输入蛋白，它能与 PIN1 相互作用并稳定 PIN1 蛋白，从而影响 PIN1 蛋白的丰度。AtAZG1 定位在根尖分生组织(RAM)的形成层细胞中，通过对 CK 的再吸收，将 *t*Z 保留在分化后的维管细胞内。此外，*AtAZG1* 的表达受到 NaCl 的调控，对于调节盐胁迫下侧根密度的过程至关重要，它赋予植物对盐度的敏感性，但对干旱的敏感性没有显著影响。研究显示，AtAZG1 参与了根尖分生组织(RAM)的原生木质部中的生长素信号与原形成层中的 CK 信号的调控[70]。

2.5. ENT 参与参与细胞分裂素的转运

在真核生物中，ENT 和浓缩性核苷转运蛋白(concentrative nucleoside transporter, CNT)构成了两大主要的核苷转运体基因家族。ENT 蛋白通过促进扩散的方式工作，而 CNT 蛋白则依赖阳离子共转运机制。CNT 蛋白通常含有 13 个跨膜结构域，借助 Na+或 H+进行共转运，实现核苷的主动运输，这一过程是逆着浓度梯度的[86] [87] [88]。虽然 CNT 的运输活动在多种动物组织细胞和真细菌中已被发现[86] [87] [88]，但在拟南芥的完整基因组序列中，尚未通过生物信息学分析发现 CNT 编码基因[89]。

在酵母表达系统中进行的竞争性实验[90]表明，在表达 *AtENT*6 的酵母细胞中，iPR 显著地抑制腺苷的输入，而 *t*ZR 的影响不明显。说明 AtENT6 对 iPR 的运输具有更高的亲和力，并暗示它可能参与调控 iP 和 tZ 型细胞分裂素的分布。通过使用携带 *AtENT*6 启动子的转基因拟南芥进行 GUS 染色，发现 *AtENT*6 在根、叶和花的维管组织以及气孔中都有表达。结合酵母表达系统的竞争试验揭示了 AtENT6 参与核苷的长距离运输，特别是在维管束中对 iPR 的运输有偏好[91]。

最新研究表明，AtENT3 在植物体内负责外源或内源性细胞分裂素的分配。该蛋白主要在幼苗的根部、子叶、叶脉和叶原基的分生组织中表达[92]。在 10 日龄幼苗中，*AtENT*3 的表达在根部广泛分布，但主要局限于维管区域。对 *atent*3-1 突变体施加内源性 CK 或外源性 *t*Z 后发现，突变体根部的内源性 CK 积累减少，而向芽运输外源性 *t*ZR 的能力增强。无论在正常还是缺乏矿物营养的条件下，*atent*3-1 的根部均比野生型对照更长，这与突变体根部的 CK 水平较低有关[93]。此外，*atent*3-1 对外源性细胞分裂素核苷的敏感性也降低[94]。这表明 AtENT3 转运蛋白通过促进根部 CK 的吸收，参与 CK 在内源性环境中的分配，进而控制细胞分裂素通过木质部向地上进行运输。

在氮饥饿条件下，*AtENT*8 或 *AtENT*3 的缺失突变体表现出对 iPR 和 *t*ZR 的敏感性降低，而对 iP 和 *t*Z 的敏感性正常。相反，*AtENT*8 的过表达植株对 iPR 敏感，但对 iP 不敏感。植物体内的测定实验结果显示，在 *atent*8 和 *atent*3 突变体中，用 H 标记的 iPR 的含量减少了 40%以上[94]。表明 AtENT3 和 AtENT8 都具有 CK 的运输功能。

转基因水稻 *OsENT*2::*GUS* 揭示了 *OsENT*2 的表达模式，主要集中于发芽种子的盾片。盾片背面的组织在种子萌发期间吸收胚乳储存物质，这一过程需要大量嘌呤和嘧啶核苷酸以维持活跃的核苷酸生物合成。*OsENT*2 还在植物的维管束组织中广泛表达，尤其在叶鞘的韧皮部显著，暗示其在韧皮部的装载和卸载过程中参与核苷的远程运输。核苷类细胞分裂素的长距离转移通常涉及木质部和韧皮部[95]。水稻种子发育阶段含有最高浓度的 CK，有研究表明水稻胚乳中的细胞数量和细胞分裂活性受该组织中 CK 水平的调控[91]。此外，OsENT2 可能参与胚乳核苷的吸收，随后这些核苷在发育中的胚胎中被转化为核苷酸。

在 2 日龄幼苗的根部和成熟植物的侧根中观察到较强的 GUS 染色，这可能反映了年轻的库器官对核苷酸具有高需求。鉴于 *OsENT2* 在叶片的维管束和韧皮部组织中表达，并能介导腺苷及其他核苷的运输，包括 iPR 且其对 tZR 的亲和力更高，这表明 OsENT2 可能在核苷类 CK 的筛选性运输中扮演重要角色[90]。

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